Stream permanence is related to crayfish occupancy and abundance in the Ozark Highlands, USA

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Abstract: Crayfish use of intermittent streams is especially important to understand in the face of global climate change. We examined the influence of stream permanence and local habitat on crayfish occupancy and species densities in the Ozark Highlands, USA. We sampled in June and July 2014 and 2015. We used a quantitative kick–seine method to sample crayfish presence and abundance at 20 stream sites with 32 surveys/site in the Upper White River drainage, and we measured associated local environmental variables each year. We modeled site occupancy and detection probabilities with the software PRESENCE, and we used multiple linear regressions to identify relationships between crayfish species densities and environmental variables. Occupancy of all crayfish species was related to stream permanence. *Faxonius meeki* was found exclusively in intermittent streams, whereas *Faxonius neglectus* and *Faxonius luteus* had higher occupancy and detection probability in permanent than in intermittent streams, and *Faxonius williamsi* was associated with intermittent streams. Estimates of detection probability ranged from 0.56 to 1, which is high relative to values found by other investigators. With the exception of *F. williamsi*, species densities were largely related to stream permanence rather than local habitat. Species densities did not differ by year, but total crayfish densities were significantly lower in 2015 than 2014. Increased precipitation and discharge in 2015 probably led to the lower crayfish densities observed during this year. Our study demonstrates that crayfish distribution and abundance is strongly influenced by stream permanence. Some species, including those of conservation concern (i.e., *F. williamsi*, *F. meeki*), appear dependent on intermittent streams, and conservation efforts should include consideration of intermittent streams as an important component of freshwater biodiversity.

Key words: crayfish, intermittent streams, headwater streams, occupancy and detection modeling, imperiled crayfish, hydrology

Headwater streams, the sources and upper reaches of rivers (Gurugnanam 2009), are vital links in maintaining ecological integrity for most watersheds and constitute >⅔ of total stream length in a river network (Leopold et al. 1964, Meyer et al. 2003, Freeman et al. 2007). They are important to water quality, nutrient cycling, and flood mitigation, and they provide habitat and food for an array of organisms (Meyer et al. 2003). Headwater streams are the most varied of lotic habitats and often provide refuge habitats, feeding and nursery grounds, and movement corridors (Meyer et al. 2007). They can harbor a unique complement of species and are major contributors to the overall biological diversity in riverine systems. Nevertheless, they are threatened because of a combination of legal uncertainty and human land and water use. Inconsistencies in the US Clean Water Act obfuscate whether headwater streams are afforded the same legal protection as larger, perennial streams (Nadeau and Rains 2007, USEPA and USACE 2007). Urbanization, agriculture, mining, and hydrologic alteration pose threats to the integrity of running water (Malmqvist and Rundle 2002), and headwater streams are especially susceptible because of their small size and drainage area, lack of legal protection, and tendency to be intermittent, unnamed, and unmapped.

Many headwater streams are intermittent and are dry for significant periods (Meyer et al. 2003). Such streams are prevalent in both arid and semi-arid regions on every

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continent (Datry et al. 2014). Intermittent streams are vital contributors to the biological integrity and diversity of river systems. The dynamics of intermittent streams regulate the persistence of and provide spawning habitat for many aquatic species, including threatened species. The hydrologic variability inherent to intermittent streams fosters habitats that may limit use by some species, thereby creating areas with limited predation or competitive pressure. For example, Rainbow Trout (*Oncorhynchus mykiss*) spawning was greater in an intermittent stream than in several permanently flowing tributaries in California, presumably because the absence of Brook Trout (*Salvelinus fontinalis*) in the intermittent reaches allows greater survival of Rainbow Trout fry (Erman and Hawthorne 1976). Flashy flow regimes in intermittent streams help scour and maintain large pools that serve as refuges for fish during drying events, including the threatened Arkansas Darter (*Etheostoma cragini*) in southeastern Colorado (Labbe and Fausch 2000). Furthermore, hydrologic variability leads to low flows that benefit native galaxiid fish at the expense of an exotic salmonid (Leprieur et al. 2006). Benthic communities also differ between intermittent and permanent streams (e.g., Delucchi and Peckarsky 1989, Feminella 1996, Flinders and Magoulick 2003).

Crayfish fulfill a crucial role in many headwater streams by contributing to ecosystem functioning in many ways and by acting as keystone species (Momot 1995). They are major contributors to production and account for >50% of macroinvertebrate biomass in many freshwater ecosystems (Momot 1995). Crayfish act as predators (Momot 1995, Stenroth and Nyström 2003), consumers of autotrophs (Momot 1995, Dorn and Wojdak 2004), detritivores (Stenroth and Nyström 2003), and prey for fish (e.g., Smallmouth Bass: *Micropterus dolomieu*) (Rabeni 1992) and terrestrial animals (Boyle et al. 2014). They function as bioprocessors of vegetation and carrion (Taylor et al. 2007) by converting coarse particulate organic matter to fine particulate organic matter that is a food resource for other organisms (Whitledge and Rabeni 1997). Crayfish also are among the most imperiled freshwater taxa (Taylor et al. 1996, 2007) and show a high level of endemism, thus they may be especially susceptible to the consequences of habitat degradation (Taylor et al. 2007).

Intermittent streams often are neglected in research and monitoring, and despite the importance of crayfish in streams and the vulnerability of intermittent streams, few investigators have examined crayfish use of intermittent streams. DiStefano et al. (2009) found that 2 species of crayfish persist through stream drying by burrowing in the hyporheic zone, and Flinders and Magoulick (2003) observed that 2 of 4 crayfish species studied occurred in greater densities in intermittent than in permanent streams. These studies indicate that crayfish are capable of withstanding drought by burrowing and that intermittent streams may be more favorable than permanent streams to some crayfish species. In addition, recent distributional studies of Ozark crayfishes (e.g., *Faxonius meeki* and *Faxonius williamsi*) suggested that these crayfish are likely to occur in many intermittent streams (Westhoff et al. 2006, DiStefano et al. 2008, Herleth-King et al. 2015), and intermittent streams typically may not be sampled representatively in surveys for rare aquatic species (DiStefano et al. 2009).

Crayfish are ecologically important and often are imperiled, but they are frequently cryptic and difficult to detect. Imperiled or rare species may be more likely to have lower occupancy rates and lower detection probabilities than other species, and accounting for imperfect detection is crucial when estimating species occurrence for conservation purposes. Despite the importance of accounting for imperfect detection when modeling species distribution and abundance (MacKenzie et al. 2006), very few investigators have addressed detectability when examining crayfish species distributions. Pearl et al. (2013) compared detection probabilities of the introduced *Faxonius neglectus* (detection probability = 0.11) and *Procambarus clarkii* (0.44) and the native *Pacifastacus leniusculus* (0.24) in the Pacific northwestern USA. Detection probability of *Cambarus* spp. was 0.36 in the Little Tennessee River basin of the southern Appalachian Mountains (USA) and was negatively related to pebble size (Frisch et al. 2016).

Seasonal stream drying in the Ozark Highlands (USA) is a natural process in intermittent streams, but global climate change and the pressures of human water use may cause additional stress on these systems in the future. Predicted changes in climatic patterns indicate significant low-flow periods that could lead to local or total extinctions of imperiled species (Humphries and Baldwin 2003), which may include crayfish. The limited information available regarding crayfish use of intermittent streams restricts our ability to conserve imperiled crayfish and establish effective monitoring strategies. Our objectives were to: 1) estimate crayfish occupancy, detection probabilities, and species densities in intermittent vs permanent streams in the Ozark Highlands ecoregion and 2) examine the influence of stream permanence and landscape- to local-scale habitat variables on crayfish species densities.

METHODS

Study area

Sets of flow metrics that best quantified several ecologically important components of the natural flow regimes in the Ozark–Ouachita Interior Highlands of Arkansas, Missouri, and Oklahoma were used to classify these streams (Leasure et al. 2016). The Ozark Highlands ecoregion includes permanent groundwater-influenced streams with relatively low hydrologic variability and intermittent streams. Streams classified as intermittent flashy have small drainage areas (8–22 km^2) and exhibit substantial flow variability, including complete drying in late summer (i.e., drying for 1–3 mo/y). Groundwater flashy streams have a range of drainage areas from 11 to 3237 km^2. These streams have less daily flow variability than any runoff-dominated streams and never experience complete drying (Leasure et al. 2016). We used intermittent flashy streams as intermittent streams and groundwater flashy streams as permanent streams because of the contrast in their hydrologic variability and tendency to experience complete (intermittent) or no seasonal drying (permanent). Flashy refers to the rapid rates of change in the magnitude of flow in both flow classes, and both flow classes are common stream types in the Ozark Highlands ecoregion (Leasure et al. 2016).

Streams were candidates for selection if they were within a drainage area <200 km^2, at least 10 km away from one another, and had a probability ≥0.50 of being in the correct hydrologic regime, as per models published by Leasure et al. (2016). We randomly selected 10 streams of each level of permanence from the group of streams fitting these criteria (i.e., 10 intermittent and 10 permanent) (Fig. 1), and we assessed accessibility and the availability of riffle habitats in candidate streams by visiting them prior to sampling. Land use within subwatersheds (Hydrologic Unit Code [HUC] 12) of study streams was predominantly forest, pasture, hay, and livestock farming (Homer et al. 2015). Natural vegetation consisted of hickory (*Carya* spp.) and oak (*Quercus* spp.) forest. Stream beds consisted largely of boulder, cobble, pebble, and gravel substrates with occasional bedrock outcroppings. All study streams had well-defined riffle–pool sequences typical of Ozark streams.

Field sampling

We sampled the 20 streams in 2014 (10 June–23 July) and 2015 (10 June–17 July). We selected 4 distinct riffle habitats in each stream and randomly chose eight 1-m^2 areas in each riffle for sampling (n = 32 m^2/stream site). We dislodged crayfish from a 1-m^2 area (defined by a quadrat made of polyvinyl chloride (PVC) by thoroughly kicking and disturbing the substrate in the quadrat directly upstream of a seine net (3-mm mesh, 1.8-m length × 1.1-m height). Crayfish dislodged from the substrate were washed into the seine net by the water current and by pulling the seine through the sample area. We identified all crayfish collected to species based on form I (breeding) males as verification when available. We used gonopods and other morphological characteristics to identify crayfish with the aid of a taxonomic key published by Pflieger (1996). We released all crayfish at their collection sites.

We assessed how environmental variables differed among streams of varying permanence and how these variables influenced crayfish abundance. We used 4 variables

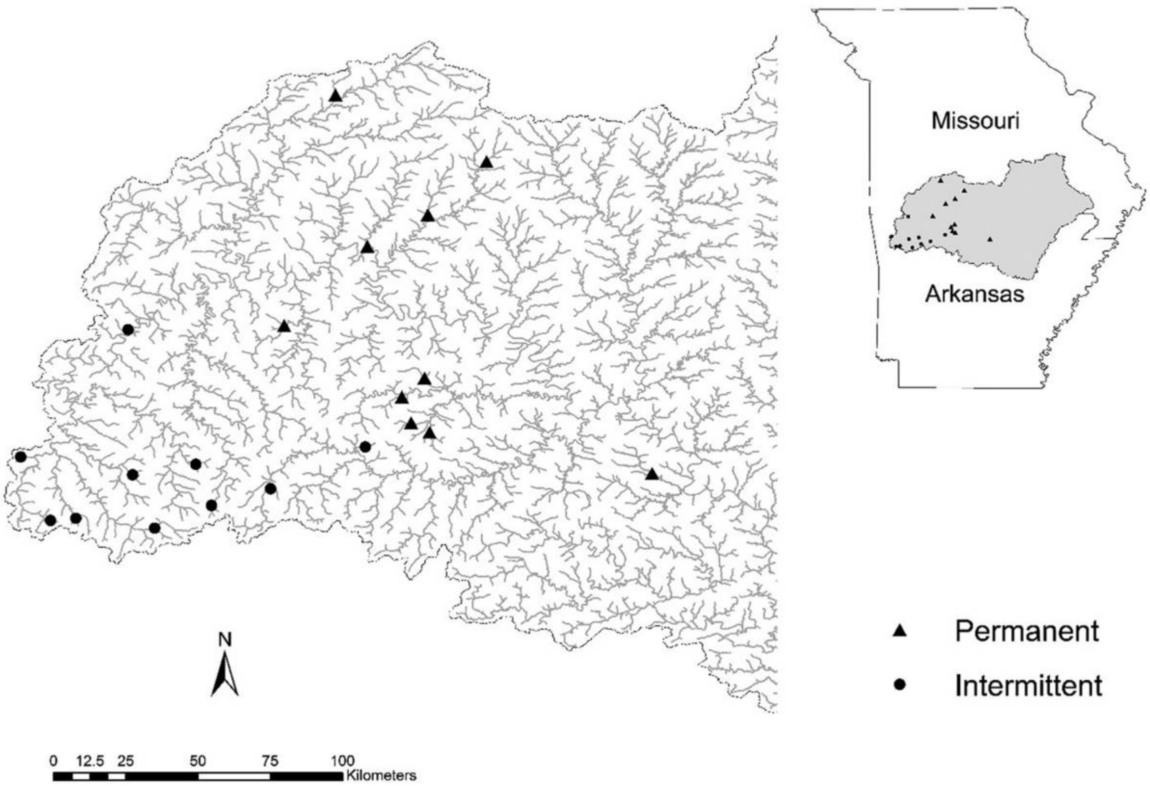

Figure 1. Study area and sample locations within the Upper White River drainage of Arkansas (AR) and Missouri (MO), USA.

(% forest cover, water depth, current velocity, and surface substrate size) selected based on previous studies that showed their importance for crayfish occupancy and abundance (e.g., Larson and Olden 2013, Pârvulescu et al. 2013, Nolen et al. 2014) in addition to stream permanence. We measured current velocity and depth directly in front of each sampling location ($n = 32$) in each stream with a Marsh–McBirney (Frederick, Maryland) model 2000 flow meter at 0.6 × depth. Within each 1-m^2 quadrat, we visually estimated % sand (0- to 0.1-cm diameter), gravel (0.1- to 3-cm diameter), pebble (3- to 6-cm diameter), cobble (6- to 12-cm diameter), and boulder (>12-cm diameter) visually as surface substrate composition (Rabalais and Magoulick 2006). We estimated % forest cover with the aid of ArcMap (version 10.3.1; Environmental Research Systems Institute, Redlands, California) and the National Land Cover Database 2011 (Homer et al. 2015). We tabulated % forested land relative to all other land-cover types within each study subwatershed at the Hydrologic Unit Code (HUC)-12 level.

Data analysis

We used principal components analyses (PCA) to reduce the number of predictor variables after $\log_{10}(x + 1)$-transformation. We used separate PCAs for 2014 and 2015. We used the first 2 principal components (PCs) as model predictor variables for both years to simplify our modeling structure and to avoid autocorrelation of predictor variables. PCA allowed us test our hypotheses with a small number of candidate models, which was important because of our small sample size ($n = 20$ streams). Large differences in the contribution of predictor variables to each PC facilitated making biological interpretations. The PCA for both years yielded 1 factor with an eigenvalue > 1. We also used the 2nd factor in both years because in both analyses it had eigenvalues close to 1 (2014: 0.94, 2015: 0.97), and we wanted to include a factor correlated with a local habitat variable.

We used the program PRESENCE (version 10.9; Proteus Research and Consulting Ltd., Dunedin, New Zealand) to estimate occupancy rates (the proportion of occupied sites) as:

$$\psi = S_D / sp^*, \qquad \text{(Eq. 1)}$$

the number of occupied sites (s_D) vs the total number of sites (s), when detection probability (p) is known. We estimated p as the probability of detecting the species at least once during a survey (given that the species is present) using MLE (maximum likelihood estimation) for the 4 most-common crayfish species (*F. luteus*, *F. meeki*, *F. neglectus*, and *F. williamsi*) of the 7 species collected as:

$$\hat{p}^*_{MLE} = 1 - (1 - \hat{p}_{MLE})^K. \qquad \text{(Eq. 2)}$$

We did not calculate detection probability and occupancy of *F. williamsi* for permanent streams because this species occupied only 1 permanent stream. We excluded 3 species (*Faxonius longidigitus*, *Faxonius punctimanus*, and *Faxonius ozarkae*) found at a small percentage of sites (<20%), not collected in both years, or with occupancy and detection models that did not converge. Occupancy and detection models used to assess the influence of stream permanence and environmental variables on crayfish occupancy and detection probability often exhibited poor fit assessed by the mean dispersion parameter ($\hat{c}$) and the parametric bootstrapping ($n = 1000$) of the Pearson's χ^2 goodness-of-fit test on the global model, presumably because of small sample size and complete separation among response variables. Therefore, we estimated occupancy and detection probability for each species based on the null (constant, no covariates used) model by year and stream permanence.

We used simple and multiple linear regression to test for relationships between crayfish species densities and environmental variables. Two candidate models included each of the PCs separately and 1 candidate model included both PCs as the global model. The 3 models were run separately for each year for each of the 4 species. Species densities were $\log_{10}(x + 1)$-transformed to meet the assumptions of normality and homogeneity of variance. We based model selection on the small-sample size-corrected Akaike Information Criterion values (ΔAICc; Akaike 1973, Burnham and Anderson 2002) and models were considered supported by the data if ΔAICc was <2.0 (Burnham and Anderson 2002). Model fit was assessed with R^2. In addition, we examined the effects of year and stream permanence on crayfish densities, diversity, and environmental variables with 2-way analysis of variance (ANOVA). We calculated Simpson's diversity based on all 7 species collected. We used a false discovery rate correction to control Type I error rates (Benjamini and Hochberg 1995).

RESULTS

We collected 3830 crayfish in 2014 and 1887 in 2015. Species densities differed significantly between stream permanence categories but not between years (Table 1, Fig. 2A, B). The pattern of differences in crayfish species occurrence between permanent and intermittent streams was the same in both years, but densities were lower in 2015 than in 2014 (Fig. 2A, B). *Faxonius luteus* and *F. neglectus* densities were greater in permanent than in intermittent streams, whereas *F. meeki* and *F. williamsi* densities were greater in intermittent than in permanent streams (Table 1, Fig. 2A, B). Total crayfish densities were significantly greater in 2014 than 2015 but did not differ between permanent and intermittent streams (Table 1, Fig. 2A, B). Simpson's diversity did not differ between stream permanence categories or year (Table 1). The year × stream permanence interaction did not affect any response variable examined (Table 1).

Table 1. Results (p-values) of a 2-way analysis of variance testing for effects of year and stream permanence on crayfish species densities, total crayfish densities, Simpson's diversity, and local habitat variables. False discovery rate correction was used to control Type I error rates.

Variable	Year	Stream permanence	Year × stream permanence
Faxonius luteus density	0.33	<0.01	0.26
Faxonius meeki density	0.32	0.02	0.19
Faxonius neglectus density	0.31	<0.01	0.08
Faxonius williamsi density	0.31	0.02	0.08
Total crayfish density	0.02	0.82	0.75
Simpson's diversity	1.00	0.76	0.75
Water depth (m)	0.09	0.01	0.72
Current velocity (m/s)	<0.01	0.16	0.92
Substrate size	0.66	0.01	0.75

Summer 2014 had slightly less than average precipitation (June: 2.24 cm, July: 2.62 cm) whereas summer 2015 was substantially wetter than average (June: 4.55 cm, July: 11.66 cm) (NOAA 2016). Current velocities were significantly greater in 2015 than 2014 and in permanent than intermittent streams (Table 1). Depths were greater in 2015 than 2014 and were significantly greater in permanent than intermittent streams (Table 1). Substrate size did not differ between years but was greater in intermittent than permanent streams (Table 1).

Detection probability and occupancy rates

Faxonius neglectus, the most commonly captured species, had the highest occupancy rate in permanent streams in both years ($\psi = 1$), and *F. luteus* had moderately high occupancy in this stream type ($\psi \geq 0.60$) (Fig. 3A, CB). *Faxonius meeki* did not occupy permanent streams, and *F. williamsi* occupied only 1 permanent stream. All species occupied intermittent streams in both years. In 2014, *F. williamsi* had the highest occupancy in intermittent streams ($\psi = 0.80$), and in 2015, *F. meeki* had the highest occupancy in this stream type ($\psi = 0.90$) (Fig. 3A, C). *Faxonius luteus* had the lowest occupancy in intermittent streams in both years ($\psi = 0.20$) (Fig. 3). Detection probabilities were moderate to high for all species in both stream types and both years (Fig. 3B, D). In intermittent streams, *F. williamsi* had the highest detection probabilities in both years ($p \geq 0.94$), whereas *F. meeki* had the lowest detection probabilities in 2014 ($p = 0.70$) and *F. neglectus* had the lowest detection in 2015 ($p = 0.58$) (Fig. 3B, D).

Faxonius neglectus and *F. luteus* had high detection probabilities in permanent streams in both years ($p \geq 0.87$) (Fig. 3B, D). *Faxonius meeki* was not detected and *F. williamsi* was detected only once in permanent streams, so detection probabilities for these species could not be estimated for this stream type. Crayfish density and detection probability were positively correlated ($r = 0.54$).

Density relationships

In 2014, the first 2 PCs explained 78.3% of the variation in the covariate data. Intermittent streams were positively correlated ($r = 0.83$) with PC1 and contributed 49.11% to the axis, and substrate size was positively correlated ($r = 0.94$) with PC2 and contributed 56.38% to the axis. In 2015, the first 2 PCs explained 68.3% of the variation in

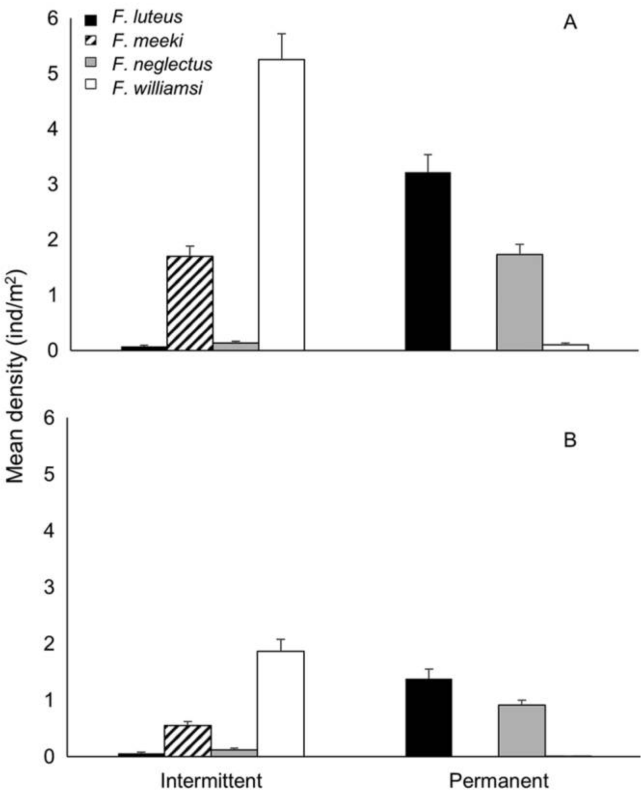

Figure 2. Mean (+SE) densities of the 4 most-common *Faxonius* crayfish species captured in 20 permanent and intermittent streams in the Upper White River drainage of Arkansas and Missouri, USA in 2014 (A) and 2015 (B). Ind = individual.

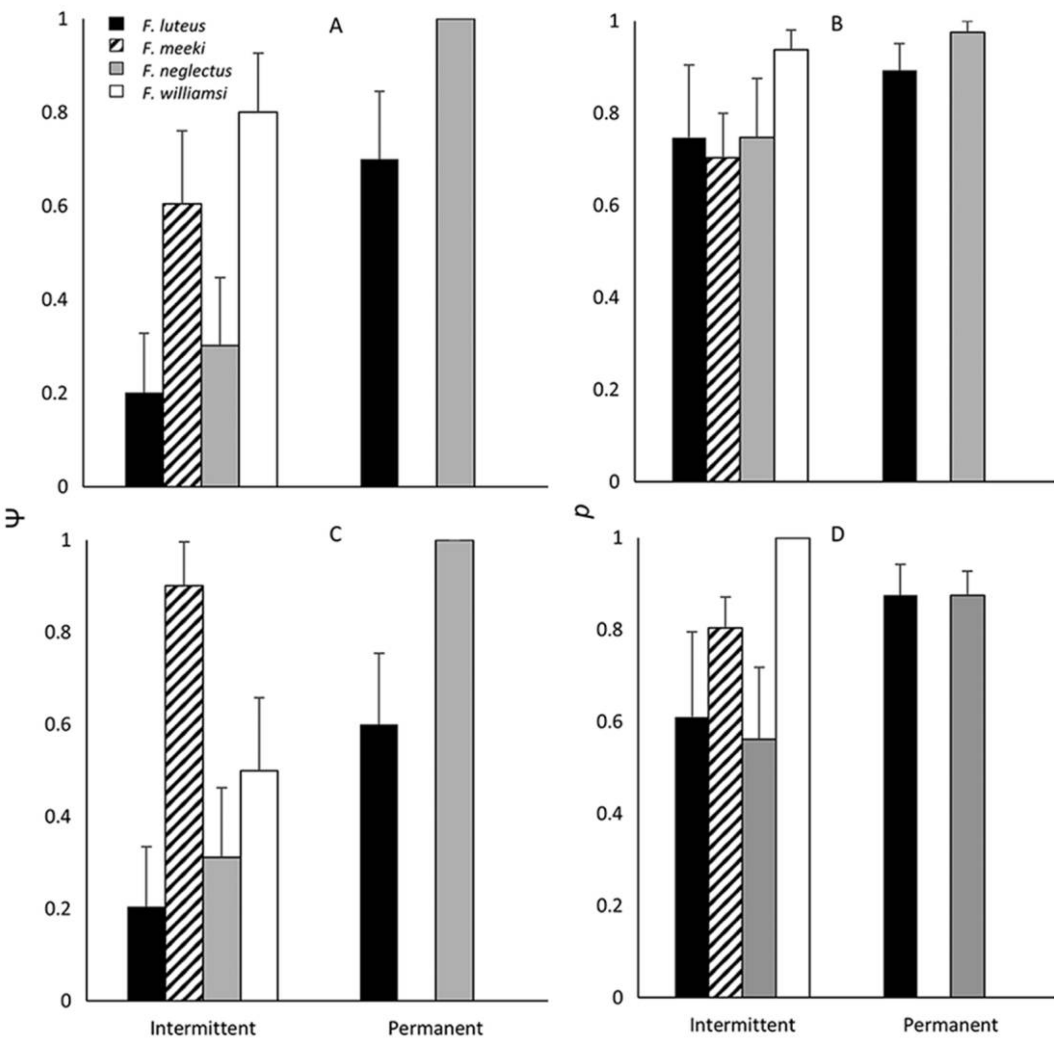

Figure 3. Site occupancy (ψ) (A, C) and detection probability (p) (B, D) of the 4 most-common *Faxonius* crayfish species captured in 20 permanent and intermittent streams in the Upper White River drainage of Arkansas and Missouri, USA in 2014 (A, B) and 2015 (C, D). Missing bars indicate species absence in stream type or model failure because of only one detection event (*Faxonius williamsi* in permanent streams).

the covariates. Intermittent streams were positively correlated ($r = 0.77$) with PC1 and contributed 53.92% to the axis, and current velocity was strongly positively correlated ($r = 0.97$) with PC2 and contributed 66.44% to the axis (Table 2).

Multiple regression modeling indicated that species densities were more strongly influenced by PC1 than PC2 (Table 3). Densities of *F. luteus* were significantly negatively related to PC1 in 2014 ($m = -0.23$, SE = 0.07, $p < 0.01$) and tended to be negatively related to PC1 in 2015 ($m = -0.12$, SE = 0.06, $p = 0.07$). Densities of *F. meeki* were significantly positively related to PC1 in 2014 ($m = 0.13$, SE = 0.06, $p = 0.05$) and 2015 ($m = 0.07$, SE = 0.02, $p = 0.01$). In the global model, *F. meeki* densities tended to be positively related to PC2 in 2015 ($m = 0.04$, SE = 0.02, $p = 0.06$). Densities of *F. neglectus* were significantly negatively related to PC1 in 2014 ($m = -0.13$, SE = 0.05, $p = 0.01$) and 2015 ($m = -0.09$, SE = 0.03, $p < 0.01$). In the global model, *F. neglectus* densities tended to be positively related to PC2 in 2014 ($m = 0.08$, SE = 0.04, $p = 0.10$). Densities of *F. williamsi* were significantly positively related to PC1 in 2014 ($m = 0.22$, SE = 0.09, $p = 0.02$) but not in 2015. PC2 and the global models were equally supported as the top-ranked model in 2015 (Table 3). Densities of *F. williamsi* were significantly negatively related to PC2 in 2015 ($m = -0.11$, SE = 0.04, $p = 0.02$) and tended to be positively related to PC1 ($m = 0.06$, SE = 0.04, $p = 0.13$).

DISCUSSION

Stream permanence significantly affects biotic communities. Stream permanence influences insect emergence (Delucchi and Peckarsky 1989), and riffle permanence can affect the structure of benthic insect assemblages (Feminella 1996).

Table 2. Principal components analyses (PCA) of 5 environmental covariates describing 20 streams in 2014 and 2015 in the Upper White River drainage of Arkansas and Missouri, USA. Correlation coefficients (r) between covariates and the first 2 principal components (PC1 and PC2) and the percent of variation explained of covariates to these components are indicated.

	PC1		PC2	
Site covariate	Contribution (%)	Correlation	Contribution (%)	Correlation
2014				
Intermittent streams	49.11	0.83	16.65	−0.28
Water depth	12.43	−0.21	16.10	0.27
Current velocity	9.47	0.16	8.09	−0.14
Average substrate size	11.83	−0.20	56.38	0.94
% forested land	17.16	0.30	2.81	−0.05
2015				
Intermittent streams	53.92	0.77	9.84	0.14
Water depth	12.92	−0.18	14.29	−0.21
Current velocity	6.16	0.09	66.44	0.97
Average substrate size	11.49	0.16	3.10	0.05
% forested land	15.52	0.22	6.35	0.09

Flinders and Magoulick (2003) found that crayfish density and crayfish–environment relationships differed between intermittent and permanent streams, and we found that site occupancy of all crayfish species differed between permanent and intermittent streams in both years. However, unlike Flinders and Magoulick (2003), who detected all crayfish species in their study in both stream types, 1 species in our study (*F. meeki*) occupied only intermittent streams and another (*F. williamsi*) occurred only once in a permanent stream. Two species in the study by Flinders and Magoulick (2003) (*Faxonius marchandi* and *Faxonius punctimanus*) occurred in significantly greater densities in intermittent than in permanent streams, whereas densities of 2 species (*Cambarus hubbsi* and *Faxonius ozarkae*) did not differ between stream types. In our study, densities of all 4 species differed significantly between permanent and intermittent streams. Overall, stream permanence appears to influence crayfish occupancy and abundance strongly. In contrast, species di-

Table 3. Multiple linear regression model output for 4 *Faxonius* crayfish species in 2014 and 2015 in the Upper White River drainage of Arkansas and Missouri, USA. Variables associated with principal components (PCs) 1 and 2 are shown in Table 2. p-values in this table correspond to statistical significance of models. p-values of coefficients are shown in Results. AICc = Akaike's Information Criterion for small sample sizes.

		2014				2015			
Species	Model	AICc	ΔAICc	r^2	p	AICc	ΔAICc	r^2	p
F. luteus	PC1	13.32	0.00	0.40	<0.01	9.20	0.00	0.17	0.07
	PC2	23.32	10.01	0.00	0.79	12.69	3.49	0.01	0.61
	Global	16.43	3.11	0.40	0.01	12.02	2.81	0.19	0.17
F. meeki	PC1	8.24	0.00	0.20	0.05	−29.58	1.26	0.31	0.01
	PC2	12.58	4.34	0.01	0.66	−24.97	5.87	0.14	0.11
	Global	11.04	2.79	0.22	0.12	−30.83	0.00	0.45	0.01
F. neglectus	PC1	−0.58	0.00	0.31	0.01	−25.55	0.00	0.42	<0.01
	PC2	4.91	5.49	0.09	0.21	−15.20	10.35	0.03	0.47
	Global	−0.54	0.04	0.41	0.01	−23.41	2.14	0.45	0.01
F. williamsi	PC1	23.31	0.00	0.26	0.02	−1.59	4.37	0.09	0.19
	PC2	29.12	5.81	0.01	0.65	−5.95	0.00	0.27	0.02
	Global	26.03	2.73	0.28	0.06	−5.55	0.40	0.37	0.02

versity did not differ between permanent and intermittent streams, a result indicating intermittence may not affect the ability of streams to support diverse and abundant crayfish populations.

Densities of individual species also were related to local habitat variables, a finding consistent with those of many other investigators (Magoulick and DiStefano 2007, DiStefano et al. 2008, Nolen et al. 2014, Herleth-King et al. 2015). Nolen et al. (2014) concluded that landscape variables have a stronger influence than local habitat variables on crayfish distributions, but local habitat variables were more important in explaining crayfish abundances.

Interannual variability in precipitation probably contributed to higher total crayfish densities in 2014 and differences in local habitat variables between years. More precipitation in 2015 elicited the faster current velocities and deeper water depths and, presumably, the increased frequency of high-flow events led to the lower crayfish densities in 2015. Moreover, the larger average substrate size in intermittent than in permanent streams may have been related to high annual maximum flow and high flood frequency in intermittent streams (Leasure et al. 2016), if smaller substrate particles were washed away during high-flow events.

Faxonius meeki is regarded as a habitat generalist relative to its species associates (e.g., *F. williamsi*; DiStefano et al. 2008), and *F. neglectus* is often observed in slow-velocity pools (Westhoff et al. 2006). One possible explanation for the differences in species–environment relationships between our study and those of others is that we focused on riffle habitats. This focus on riffles might explain why water depth was not an important habitat variable in our study and might explain the unanticipated negative association among *F. williamsi* and current velocity. Differences in annual precipitation between 2014 and 2015 also affected our finding between years and could have altered our perception of streams as intermittent or permanent.

Ours is one of the few studies of crayfish distribution in which crayfish detection probabilities were modeled to account for imperfect detection. Detection probabilities are important to consider when examining species distribution, especially when considering rare and imperiled species. An imperfect understanding of detection probabilities can lead to biased conclusions (MacKenzie et al. 2006). In our study, crayfish detection probabilities were moderate to high for all species in both years (2014: 0.70–0.98, 2015: 0.56–1.00). These detection probabilities are high compared to those reported by others. In the Pacific Northwest, detection probabilities were 0.24 for the native *P. leniusculus*, and 0.11 and 0.44 for the invasive *F. neglectus* and *P. clarkii* (Pearl et al. 2013). In the Little Tennessee River basin of the southern Appalachians, detection probability of *Cambarus* spp. was 0.36 (Frisch et al. 2016). Detection probabilities may have been higher in our study because of differences in stream size, species behavior, local habitat conditions, and sampling techniques. Pearl et al. (2013) used baited and unbaited traps, whereas Frisch et al. (2016) sampled by turning cover objects, searching leaf litter, and using leaf-litter bags. The quantitative kicknet method we used may have been responsible for the high detection probabilities in our study. We had hoped to examine whether environmental variables influenced species detection (e.g., current velocity, substrate size), but because of small sample size, our occupancy and detection models would not converge when we used covariates, and we were unable to evaluate these relationships.

We saw a moderate positive relationship between crayfish density and detection probability ($r = 0.54$). This relationship was not strong, so we think that our sampling method probably was sufficient to detect crayfish even at low densities. Furthermore, detection probabilities remained high during the wet summer of 2015 when the water was deeper and velocities were faster. Our approach appears to have been effective for sampling riffle-dwelling crayfish in small streams. Some of the species we collected also occur in other habitats, such as pools (*F. neglectus* [Westhoff et al. 2006], *F. meeki* [DiStefano et al. 2008]), which we did not sample. This sampling bias may have confounded interspecies comparisons.

Streams were spatially segregated by permanence category across our study sites. Intermittent streams were clustered in the southwestern portion of the study area, whereas permanent streams were clustered in the central part of the study area (Fig. 1). The clustering of our sites occurred at least in part because stream permanence is determined by stream size and geographic variation in groundwater discharge, topography, geology, climate, and vegetative cover (Poff et al. 1997). Stream permanence might be a surrogate for a suite of landscape variables because of the interconnected nature of hydrology and landscape-scale factors.

We documented that 2 imperiled species of crayfish (*F. meeki* and *F. williamsi*) occupy intermittent streams throughout the Upper White River drainage in Arkansas and Missouri. Because intermittent streams are important for these and other imperiled crayfish, such as *Faxonius marchandi* (Flinders and Magoulick 2003), they should be considered in surveys of imperiled biota. We detected no difference in species diversity between intermittent and permanent streams, so intermittent streams may be as capable as permanent streams of supporting diverse and abundant crayfish populations. Our study adds to the knowledge base of crayfish use of intermittent streams and highlights the importance of stream permanence for biotic assemblages, including those of conservation concern. Intermittent streams may be neglected in research and monitoring efforts, which may bias knowledge of aquatic species distributions and potentially affect conservation actions.

Our study is applicable to current discussions regarding management of intermittent streams related to the US Clean Water Act (Nadeau and Rains 2007, USEPA and USACE 2007) and the types and sizes of streams afforded protection under this policy. In addition, predicted changes in climatic patterns probably will cause significant low-flow periods that may lead to local or total extinctions of imperiled species (Humphries and Baldwin 2003), which may include *F. meeki* and *F. williamsi*. Crayfish use of intermittent streams suggests that these streams are crucial for the conservation of these species and the integrity of freshwater systems in the face of global climate change.

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