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Evolutionary history and sex are significant drivers of crayfish demography in resource-limited cave ecosystems

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Abstract

Obligate and facultative cave species both play significant functional roles in cave ecosystems. Unlike obligate cave species, facultative cave species can persist in habitats both within and outside of caves. However, no comparative demographic model explaining the sustained presence of both obligate and facultative cave species has been provided. We developed a multi-state capture–mark–recapture (CMR) analysis based on 5 years of data collected from caves in northern Alabama, USA to explore differences in survival and reproductive transition probabilities between obligate (*Orconectes australis* and *Cambarus hamulatus*) and facultative (*C. tenebrosus*) cave crayfish. Multi-state CMR analyses revealed that male obligate cave species showed significantly higher rates of transitioning to a reproductive state than male *C. tenebrosus*, while no differences among species were observed for females. Transitioning into a non-reproductive state, however, was higher for obligate cave species regardless of sex. Apparent survival rates between cave obligates and *C. tenebrosus* did not differ, suggesting that the larger population sizes of obligate cave species within our study sites may be driven by more successful male reproductive strategies. Our results suggest that obligate cave crayfishes have evolved unique sex-specific reproductive strategies not shared by *C. tenebrosus* that likely represent a specialized adaptation to the cave environment. Conversely, persistent immigration by surface populations is likely crucial for the sustained presence of facultative species within cave environments.

Keywords E-SURGE · Karst · Life history · Multi-state mark–recapture · Resource limitation

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Introduction

Ecological community structure is partly shaped by environmental filtering of the regional species pool, by which individuals possessing life-history traits adapted to local environmental conditions are able to persist (Kotliar and Wiens 1990; Poff 1997). However, local communities may also be composed of species relatively poorly adapted to local environmental conditions, but which persist through immigration (Nichols et al. 2000; Leibold et al. 2004; Chevin and Hoffmann 2017). Resource availability is a particularly strong environmental filter shaping community structure that also influences the expression of plastic life-history traits (Pianka 1970; Bronikowski and Arnold 1999; Bronikowski 2000; McBride et al. 2015). For example, reproductive activity and survival rates may both increase when a species is not limited by resources (Tessier et al. 2000; Tessier and Woodruff 2002; O'Brien et al. 2008; Tökölyi et al. 2016), but significant trade-offs between these life-history traits are commonly observed when resources are limited (Moore et al. 2016; Tökölyi et al. 2016; Engen and Sæther 2017). Consequently, plasticity in life-history trait expression may play an important role in shaping community structure within resource-limited ecosystems.

Caves provide a quintessential example of a resource-limited ecosystem with a community structure dictated by local (adaptation) and regional (immigration) ecological processes. Lack of light prevents primary production (chemoautotrophic caves are an exception; Engel 2007), which causes cave productivity to be reliant on resource subsidies (dissolved and particulate organic matter) from surface environments (Culver 1985). Low surface connectivity can limit resource subsidies to caves, which induces strong bottom-up limitation in their communities (Venarsky et al. 2014, 2018). Slow metabolism and life-history adaptions (low fecundity, long lifespan) facilitate persistence of obligate cave species (species that only complete their life cycle in caves) in resource-limited cave environments (Poulson and White 1969; Hervant et al. 2001). However, cave community biomass and biodiversity are often dominated by facultative cave species, which are species adapted to survive in relatively energy-rich surface environments ("fast" life histories; Hüppop 2000; Rétaux and Casane 2013). Thus, typical cave conditions do not universally select for obligate cave species from the regional species pool.

The apparent mismatch between the biological characteristics of facultative cave species and the resource-limited cave environment has caused facultative cave species to be commonly viewed as "transients" (e.g. entering via drift during floods, or trapped by cave pits), for which available resource levels are insufficient to support in situ population growth (Simon and Benfield 2001; Venarsky et al. 2018). Indirect evidence partially supports this hypothesis, as observational studies generally show that both biomass and species richness of facultative cave species are positively correlated with cave resource availability (Simon and Benfield 2001; Huntsman et al. 2011a; Venarsky et al. 2012a, 2014). Additionally, an experimental increase in resource availability resulted in rapid increases in facultative cave species biomass and biodiversity (Venarsky et al. 2018). However, such studies have been unable to determine whether facultative cave species are truly maladapted to the cave environment because they seldom estimate population demographic rates.

Population structure (e.g. sex, age) can explain a substantial amount of variability in demographic rates (Coulson et al. 2001), and likely interacts with resource availability and evolutionary history to influence cave community composition. Sex-specific performance may be especially relevant in this regard as most taxa tend to show divergence in energy investment during reproduction. More specifically, females usually invest more energy

into reproduction than males (Hayward and Gillooly 2011). Because unequal reproductive investment by sex can result in a significant increase in mortality in females (Veran and Beissinger 2009; Cayuela et al. 2014), the ability of obligate and facultative cave taxa to persist in the resource-limited cave environment may be tightly linked to sex-specific reproductive strategies. Furthermore, availability of reproductively active females or males can limit population growth (Fagan et al. 2010), and any reproductive asynchrony may be especially costly within the resource-limited cave environment. Consequently, intraspecific variability in reproductive strategies among individuals (e.g. sex-specific) may highlight interspecific differences in demographic contributions (local reproduction vs. immigration) to cave community structure.

In this study, we examined how evolutionary history (i.e. cave vs. surface-adapted) and population structure (e.g. sex) interact with the energy limitation of cave environments to affect crayfish demography. We incorporated 5 years of mark–recapture data from three crayfish species (two obligate and one facultative cave species) into a multi-state capture–mark–recapture framework to understand how two key demographic rates (apparent survival and transition probabilities between reproductive states) vary among crayfishes within four separate cave stream ecosystems. We hypothesized that both evolutionary history (cave vs. surface-adapted) as well as the asymmetry in sex-specific reproductive costs (e.g. eggs vs. sperm) would interact with resource availability to influence crayfish demographic rates. Specifically, we predicted that (1) apparent survival and the probability of transitioning into a reproductive state would be highest for crayfishes in caves with high amounts of organic matter because the larger communities (more species with higher abundances; see Venarsky and Huntsman 2018) encountered within high organic matter caves are presumably a result of more favorable conditions for reproduction. We also predicted that (2) differences in apparent survival and reproductive transition probabilities between obligate and facultative crayfishes would be most pronounced in caves with lower amounts of organic matter because obligate taxa have a "slow" life history that is better adapted to low-energy environments than facultative taxa with a "fast" life history (Hüppop 2000; Hervant et al. 2001). Longevity estimates for obligate cave crayfishes (*Orconectes australis* = 20+ years, no data available for *Cambarus hamulatus*; Venarsky et al. 2012b) relative to facultative cave crayfish (*Cambarus tenebrosus* = 3–4 years; Prins 1968) appear to support these opposing life-history strategies for crayfishes commonly encountered in cave environments. Lastly, we predicted that (3) apparent survival and transitioning between reproductive states would be higher for males than females and (4) sex-specific differences in these demographic rates would be most pronounced in caves with lower amounts of organic matter because crayfishes demonstrate strong differences between sexes in energetic investment for reproduction. Specifically, females expend more energy for reproduction through greater energetic costs of egg versus spermatophore production, extended parental care by females, limited courtship behavior by males, and no mate-guarding by males (Mason 1970; Pippitt 1977; Ameyaw-Akumfi 1981; Villanelli and Gherardi 1998; Aquiloni and Gherardi 2008; Jurcak et al. 2016; McLay and van den Brink 2016).

Methods

Study sites

We selected four hydrologically isolated cave streams in Jackson and Madison counties, Alabama, USA: Tony Sinks, Bluff River, Limrock, and Hering (Figure A1 in ESM). Study reaches were 327–1202 m in length and contained alternating riffle and pool habitats with sand, gravel, and bedrock substrate. Mean daily water temperatures within study reaches from 2007 to 2011 were consistently ~ 13 °C ± 1 °C (Venarsky et al. 2014). All caves contained the facultative cave crayfish *Cambarus tenebrosus* (cave-spring crayfish), a widely distributed species commonly collected from groundwater-influenced surface habitats, including springs, spring-runs, and streams flowing out of caves (Prins 1968). The obligate cave crayfish *Orconectes australis* (southern cave crayfish) occurs in Tony Sinks, Limrock and Hering caves, with the cave obligate *Cambarus hamulatus* (prickly cave crayfish) found in Bluff River Cave.

Standing crop organic matter

On each of four dates (March, July, and November 2009, as well as February 2010), 15 samples of benthic detritus (primarily decomposing wood particles) and non-crayfish macroinvertebrates were collected at random locations throughout the sampling reach from each cave using a 22.5-cm diameter corer. The core was inserted into the stream bottom, large detritus was removed, and the substrate was disturbed to a maximum depth of 4 cm. Remaining suspended detritus was sampled via ten sweeps of the water column with a 250-µm mesh net. Samples were returned to the laboratory on ice and processed within 48 h. Processing consisted of rinsing the sample through a 250-µm sieve followed by the removal of macroinvertebrates. The remaining detritus was dried at 60 °C for ~ 2 weeks, weighed, combusted at 500 °C for 6 h, and then weighed again to estimate ash-free dry mass (AFDM). We used a two-way ANOVA in R (R Core Team 2017) to test for differences in standing crop organic matter between cave streams and sampling occasions, with a Tukey's HSD multiple comparisons test to detect differences among caves and occasions. We added a small constant (0.1) to all detritus samples and used a log transformation to meet assumptions of normality and homogeneity of variance.

Crayfish sampling

Crayfish sampling began in November 2005 in Hering, January 2006 in Limrock, July 2006 in Tony Sinks, and May 2007 in Bluff River caves. We conducted crayfish surveys by foot with dip-nets semi-monthly until August 2011. We gave all crayfish without markings an internal alphanumeric tag and colored elastomer (Northwest Marine Technology, Shaw Island, WA, USA) after ocular-carapace and total carapace lengths were measured (± 0.1 mm) and reproductive state noted (see Rogowski et al. 2013). Elastomer allowed for batch-marking of crayfish and assessment of alpha-numeric tag loss (< 1% tag loss in each cave; Bluff River = 1 of 1026, Hering = 1 of 1125, Limrock = 2 of 918, and Tony Sinks = 1 of 2164). Reproductive males were easily distinguished from non-reproductive males by a more sharply pointed first pleopod. For females, apparent cement glands indicated the individual was capable of reproduction, while gravid individuals were identified by the presence of attached ova or young.

Multi-state capture–recapture model

We used a multi-state capture–recapture model for open populations (Nichols and Kendall 1995; Lebreton et al. 2009) and the program E-SURGE (Choquet et al. 2009b) to estimate apparent survival (ϕ), transition (ψ), and recapture (p) probabilities of crayfishes. We defined three true states (reproductive, non-reproductive, and dead) and three observed states (seen as reproductive, seen as non-reproductive, and not seen) to construct the multi-state model. We can express a simplified version of the multi-state model as a survival-transition matrix and an observation matrix:

True State (t)	True State ($t+1$)		
	Reproductive	Non-reproductive	Dead
Reproductive	$\phi(1-\psi)$	$\phi\psi$	$1-\phi$
Non-reproductive	$\phi\psi$	$\phi(1-\psi)$	$1-\phi$
Dead	0	0	1

True State (t)	Observed State (t)		
	Observed as reproductive	Observed as non-reproductive	Not observed
Reproductive	p	0	$1-p$
Non-reproductive	0	p	$1-p$
Dead	0	0	1

According to the above matrices, a marked reproductive individual may survive from time t to time $t+1$ and move to the non-reproductive state at $t+1$ with probability ($\phi\psi$), or it may die with probability ($1-\phi$). Here, the transitions between breeding states are modeled as a first-order Markov process (i.e. an individual reproductive/non-reproductive state at time $t+1$ depends only on its reproductive/non-reproductive state at time t given it survives). The probability of recapturing an individual is p and is conditional on survival. We compared models that included effects of time, reproductive state, sex, taxa, cave, and high-low flow periods on survival, reproductive state transitions, and recapture probabilities. We defined variation in flow as periods of high flow (December–May) and low flow (June–November) using the closest USGS stream gauging station (USGS 03574500, Paint Rock River, Woodville, Alabama, USA).

We reduced our capture–recapture data to 16 season-specific sampling intervals from summer 2007 to spring 2011 to ensure analyses among all caves occurred over the same time-period, because not all study sites were sampled on the same month. We defined winter as December-February, spring as March–May, summer as June–August, and fall as September–November; thus survival and reproductive transition probabilities (defined below) were estimated for three-month intervals. We additionally chose these reduced sampling intervals because these species are known to be long-lived (> 20 years for obligate caves species, Venarsky et al. 2012b) and were observed in a reproductive state anytime between August and February of the following year, thus three months is not a substantial amount of time in the life of the obligate cave crayfishes encountered in this study. We also defined reproductive states as either reproductive or non-reproductive, because too few gravid females were collected (Table 1). Note that crayfish regularly transition between

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Table 1 capture–mark–recapture data summary from crayfishes captured in the four study cave streams in northern Alabama, USA

Cave	Sex	Species	Evolutionary history	Total individuals captured	Total individuals recaptured	Max times an individual was recaptured	Reproductive encountered	Gravid encountered	Non-reproductive encountered	% reproductive
BR	F	C. hamulatus	Obligate	381	54	3	47	0	395	10.6
BR	M	C. hamulatus	Obligate	377	67	6	129	NA	337	27.7
BR	F	C. tenebrosus	Facultative	109	6	2	6	0	109	5.2
BR	M	C. tenebrosus	Facultative	159	18	4	20	NA	162	11.0
HR	F	O. australis	Obligate	447	127	5	53	5	557	8.7
HR	M	O. australis	Obligate	328	110	5	155	NA	315	33.0
HR	F	C. tenebrosus	Facultative	177	12	2	67	4	122	35.4
HR	M	C. tenebrosus	Facultative	173	16	3	121	NA	70	63.4
LR	F	O. australis	Obligate	480	175	7	35	2	710	4.7
LR	M	O. australis	Obligate	415	120	6	160	NA	425	27.4
LR	F	C. tenebrosus	Facultative	10	1	3	1	0	11	8.3
LR	M	C. tenebrosus	Facultative	13	1	2	3	NA	11	21.4
TS	F	O. australis	Obligate	1006	151	5	64	3	1133	5.3
TS	M	O. australis	Obligate	877	163	4	240	NA	831	22.4
TS	F	C. tenebrosus	Facultative	111	5	2	4	0	112	3.4
TS	M	C. tenebrosus	Facultative	170	10	3	44	NA	137	24.3

The cave species were *Cambarus hamulatus* and *Orconectes australis*, while the facultative cave species was *C. tenebrosus*. "Gravid encountered" is the number of times a female crayfish was observed with eggs or young crayfish attached to the abdomen over all sampling occasions (November 2005–August 2011). BR = Bluff River, HR = Herring, LR = Lim Rock, and TS = Tony Sinks caves. Total individuals captured is the number of crayfish given a unique tag. Total individuals recaptured is the number of crayfish recaptured at least once. Reproductive, Gravid, and Non-reproductive encountered are the total number of times crayfish were encountered in a reproductive, gravid or non-reproductive state. Encountered crayfish reflect the total number of crayfish in the defined state summed over all sampling occasions. Therefore, encountered crayfish can be a higher number than "Total individuals captured" because the same individual can be counted multiple times if it exists in the same state on multiple occasions. The "% reproductive" was calculated as "Reproductive encountered" divided by the total number of crayfish encountered (sum of reproductive, gravid and non-reproductive) times 100

reproductive states throughout their life span, thus reproductive state does not represent maturity.

Goodness-of-fit (GOF) tests and model selection

We performed goodness-of-fit (GOF) tests to determine whether our models violated assumptions of multi-state CMR analyses using U-CARE functions (Choquet et al. 2009a) in R with the 'R2ucare' package (Gimenez et al. 2018; R Core Team 2017). We performed a test of transience (test3Gsr), a memory test (test3Gbwa), the transience complement test (test3Gsm), and a trap happiness test (testMitec) for all data. Capture histories for GOF tests were combined for all species and sites because the memory and trap happiness tests failed to run when separately performed by species and site, likely due to too few facultative cave females encountered in a reproductive state in most caves.

We used a four-step modeling approach for model development and selection. The first step consisted of assessing recapture probability using a set of plausible models that considered different combinations of factors (time, flow status, reproductive state, sex, evolutionary history, and cave) and additive effects of those factors. We assumed that apparent survival and transition probabilities varied only by reproductive state for all models in this first modeling step. We expected stream discharge to affect the recapture probability between facultative and obligate cave species differently (i.e. a higher number of *C. tenebrosus* drifting into the cave during high flows or moving upstream when surface and cave streams were well connected), thus we constructed a single interaction model (which also included additive effects) between high-low flow and species (49 total models constructed).

We developed a second and third candidate set of models to explain variability in survival and reproductive transition probabilities, where the most parsimonious model selected from the first-step approach (see below for model selection methods) was used to define the linear constraints on recapture probability of all models in both candidate sets. Similarly, the most parsimonious model identified by the second step modeling approach (apparent survival) was used to define the linear constraints on survival of all models in the candidate set of the reproductive transition probability modeling step (step 3). We constructed all model combinations where the six predictor variables were used as additive models constraining survival and reproductive transition probabilities. We also constructed seven models with interaction effects based on biological hypotheses (Table 2), which resulted in 56 models for the survival modeling step and 56 models for the reproductive transition probability modeling step (Table A1 in ESM). We used quasi-likelihood Akaike information criterion corrected for small sample size (QAICc; Burnham and Anderson 2002) to select the best model structure in step 1 (recapture probability parameters), step 2 (survival probability parameters), and step 3 (reproductive transition probability parameters) of our model selection procedure.

We included a three-species model to test for differences among *C. tenebrosus, C. hamulatus*, and *O. australis* from the most parsimonious model identified in steps 2 (survival) and 3 (reproductive transition probability) of our model selection approach. We specifically substituted a species-specific grouping factor (all three species) for the evolutionary history grouping (obligate or facultative cave species). We then used model selection to determine whether obligate cave species should be grouped as one or separated by species to describe survival and reproductive transition probabilities.

Lastly, we used a fourth step in our model selection procedure where all combinations of models within 2 ΔQAICc units from the most parsimonious model in each
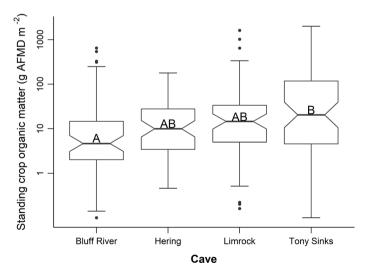
Table 2 A priori hypotheses for select interactive (*) models constructed to test effects on apparent survival (φ) and reproductive transition probabilities (ψ) in crayfishes within cave streams in northern Alabama, USA

Parameters	Model	Hypothesis
φ and ψ	rs*sex*evolution	Obligate cave species are adapted to the cave environment, where the energetic demand of reproductive conditions in both sexes should be dramatically different between obligate and facultative cave species
	rs*sex	Vital rates between sexes will strongly vary based on the reproductive state of the crayfish, no matter the species in the cave environment
	rs*evolution	Vital rates based on reproductive state will strongly vary between species due to adaptation to the cave environment
	rs*flow status	The probability of transitioning between reproductive states will depend on the only environmental variable that can vary seasonally in the cave environment, stream flow
	rs*cave*evolution	Differences in the amount of basal energy within caves will influence the strength of vital rate differences between cave species within different reproductive states. Differences between obligate and facultative cave species will be lowest in the highest energy cave, where adaptation to energy limitation is less important
	rs*cave	Vital rates are most strongly affected by the amount of energy within the cave, with differences in reproductive states on vital rates will be most pronounced when in more energy-limited caves
	rs*sex*cave*evolution	Asymmetrical energetic costs of reproduction by sex along with adaptation to the cave environment make survival and reproduction less stressful for males and obligate cave species, which will be most pronounced in resource-poor cave environments

Reproductive state is represented by "rs" and crayfish evolutionary history as "evolution"

model selection step (steps 1–3) were constructed. We did not include both the three-species and the evolutionary grouping models in this final model selection step because the species-specific model was added as a substitute for the evolutionary grouping structure in the previously described model selection step. This resulted in 4 models constructed during this fourth model selection step, which were similarly ranked using QAICc as done during steps 1–3. We used model averaging (Burnham and Anderson 2002) during this final model selection step to estimate demographic rates of crayfishes while accounting for uncertainty due to model selection and parameter estimation.

Results

Standing crop organic matter

Quantity of organic matter ash-free dry mass (presumed basal energy source) was highest in Tony Sinks (median $= 20.3$ g AFDM m^{-2}, min–max $= 0.0$–2008.0 g AFDM m^{-2}), followed by Limrock (median $= 14.5$ g AFDM m^{-2}, min–max $= 0.1$–1622.9 g AFDM m^{-2}), Hering (median $= 9.9$ g AFDM m^{-2}, min–max $= 0.4$–178.9 g AFDM m^{-2}), and lowest in Bluff River (median $= 4.6$ g AFDM m^{-2}, min–max $= 0.0$–649.7 g AFDM m^{-2}; Fig. 1). Analysis of variance indicated that organic matter significantly varied by cave ($F_{3,224} = 4.33$, $p = 0.005$), but not by date ($F_{3,224} = 1.50$, $p = 0.216$) or the interaction between cave and date ($F_{9,224} = 0.90$, $p = 0.526$). Post-hoc pair-wise comparisons indicated that the only statistically significant difference among caves in standing crop organic matter was between Tony Sinks and Bluff River caves (Tukey's HSD, $p = 0.003$, Fig. 1).

Fig. 1 Standing crop organic matter (grams ash-free dry mass per square meter) from four cave stream study sites in northern Alabama, USA. The *y*-axis is plotted on the log scale. Significant contrasts among caves identified by a Tukey's post-hoc comparison are represented by different letters

Crayfish mark–recapture

A total of 5233 crayfishes were captured from the four cave streams, with the highest in Tony Sinks ($n=2164$), followed by Hering ($n=1125$), Bluff River ($n=1026$), and Limrock ($n=918$). *Orconectes australis* was the most abundant crayfish captured ($n=3553$), followed by *C. tenebrosus* ($n=922$) and *C. hamulatus* in Bluff River ($n=758$). The majority of captured crayfishes were in the non-reproductive state (82.6%, Table 1). However, the number of crayfishes in the reproductive state varied strongly among caves and species, where the highest percentage of crayfishes in the reproductive state for all sampling occasions was found in Hering Cave (Total$=27.1$%, *O. australis*$=19.3$%, *C. tenebrosus*$=49.5$%) and the lowest in Tony Sinks Cave (Total$=13.7$%, *O. australis*$=13.4$%, *C. tenebrosus*$=16.2$%, Table 1).

Mark–recapture analysis

Few facultative cave crayfish were observed in a reproductive state within each cave, resulting in failed GOF tests when performed on caves and species separately (test3Gbwa and testMitec tests for facultative species, Table 3). Thus we performed GOF tests on all crayfish capture histories as one group. Our GOF results for all crayfish collectively indicated that the test for transience was significant (i.e. crayfish leaving the sampling area, test3Gsr; Pearsons test statistic$=63.21$, $df=28$, $p<0.01$, Table 3), although the overdispersion parameter for the transience test ($\hat{c}=\frac{63.21}{28}=2.26$) was less than a critical value of

Table 3 Goodness-of-fit results for capture–mark–recapture analysis performed on crayfishes within cave streams in northern Alabama, USA

Group	Test	Pearson's Statistic	DF	p value	$\hat{c}$
All Crayfish	test3Gsr	63.21	28	0.00	2.26
	test3Gbwa	11.81	16	0.76	0.74
	test3Gsm	77.23	113	1.00	0.68
	testMitec	42.06	34	0.16	1.24
	Overall				1.02
Obligate Cave	test3Gsr	40.22	28	0.06	1.44
	test3Gbwa	11.89	16	0.75	0.74
	test3Gsm	70.18	111	1.00	0.63
	testMitec	28.99	30	0.52	0.97
	Overall				0.82
Facultative Cave	test3Gsr	12.41	28	1.00	0.44
	test3Gbwa	0.00	0	1.00	NA
	test3Gsm	2.26	10	0.99	0.23
	testMitec	NA	NA	NA	NA
	Overall				0.39

Estimates of the overdispersion parameter ($\hat{c}$) was calculated as the ratio of the Pearson's Statistic and degrees of freedom (DF). The "All Crayfish" group represents the collective GOF analysis for all crayfish, while "Obligate Cave" and "Facultative Cave" are GOF analyses performed on evolutionary histories separately. Test statistics are reported for the transience (test3Gsr), memory (test3Gbwa), transience complement (test3Gsm), and trap happiness (testMitec) tests

3 (Burnham and Anderson 2002; Choquet et al. 2009a). Additionally, overdispersion of all tests collectively indicated no issue of overdispersion ($ĉ = \frac{63.21+11.81+77.23+42.06}{28+16+113+34} = 1.02$).

The most parsimonious model structure for the recapture probability parameter (step 1 model selection) was an additive model in which recapture probability varied by cave, evolutionary history, and time, with 43% of the QAICc model weight (Table 4). The second most parsimonious model had 30% of the QAICc model weight and differed from the top model by including an additive sex effect (time + cave + sex + evolution, Table 4). All other models within the recapture probability candidate set were at least 2 QAICc units away from the most parsimonious model (Table 4). A fully interactive model among reproductive state, sex, evolutionary history, and cave was the most parsimonious model structure for survival identified by model selection (step 2 model selection, Table 1 in ESM); however, multiple parameters in that model were not identifiable as indicated by confidence limits of parameter estimates at the extreme ends of parameter space (e.g. survival confidence intervals from 0 to 1). Consequently, we excluded this model from model selection and the next three highest ranked models within the survival candidate set were within 2 QAICc units (Table 4). Each of these models included reproductive state, and were differentiated by the inclusion of either evolutionary history, species, or sex (Table 4). The top two models within the reproductive transition probability candidate set had nearly all model weight and were within 2 ΔQAICc units (step 3). Both models had a three-way interaction with reproductive state and sex shared between the models, and only differed by the inclusion of both obligate cave taxa as a single evolutionary group (rs*cave*evolution, QAICc Weight = 0.49) or maintaining species-specific structure (rs*cave*species, QAICc Weight = 0.51, Table 4).

The final modeling step (step 4) included the construction of four models, with the top two models containing greater than 99.6% of the total model weight (Table 4). All four models had an additive time, cave, and evolutionary history effect on the recapture probability parameter, with two of those models also containing an additive sex effect (Table 4). An interactive model that included reproductive state, cave, and evolutionary history (rs*cave*evolution), and a similar interactive model with sex substituted for cave (rs*sex*evolution) were the two constraints identified for the apparent survival parameter in each of the four constructed models (Table 4). Lastly, the transition probability parameter was found to be constrained by an interaction that included reproductive state, cave, and species in all four constructed models (rs*cave*species, Table 4).

Recapture probability (*p*) identified from step 4 model averaging was relatively low among all sites, evolutionary history, sex, and sampling occasions (mean recapture probability < 0.39, Fig. 2). Recapture rates were consistently higher for obligate cave species compared to the facultative cave species (Fig. 2). Mean recapture probability was as high as 0.39 for obligate cave crayfishes in Limrock during the early sampling periods and as low as 0.02 in multiple cave streams for obligate cave crayfishes near the end of sampling. Recapture rates were also highest at the start of the study for facultative cave crayfish in all caves, and similarly decreased with time (Fig. 2).

Apparent survival (φ) was relatively high regardless of evolutionary history, cave, or reproductive state (Fig. 3). Survival was less precise for *C. tenebrosus* (the facultative cave species) than the obligate cave species and was likely influenced by differences in sample size between species captured within caves (Table 1). Non-reproductive facultative cave crayfish from Hering cave had significantly lower survival (model average = 0.42, 95% confidence interval = 0.23–0.63) than nearly all obligate cave crayfish, with the exception of slight overlap in 95% confidence intervals with obligate cave crayfish in the non-reproductive state from Bluff River (model average = 0.71, 95% confidence interval = 0.63–0.77)

Table 4 Four-step model selection of recapture probability (p, step 1), apparent survival probability (ϕ, step 2), transition probability (ψ, step 3), and the top models from all 3 steps (Full Set, step 4) for crayfish multi-state capture–mark–recapture models in each of the four study cave streams in northern Alabama, USA

Step	Model	# Parameters	Deviance	QAICc	QAICc	ΔQAICc	QAICc Weight
1 (p)	p(time+cave+evolution)	24	15,988.32	16,036.32	16,036.50	0.00	0.43
	p(time+cave+sex+evolution)	25	15,987.00	16,037.00	16,037.20	0.70	0.30
	p(rs+time+cave+evolution)	25	15,988.30	16,038.30	16,038.50	2.00	0.16
	p(rs+time+cave+sex+evolution)	26	15,986.92	16,038.92	16,039.13	2.63	0.11
2 (ϕ)	φ(rs*cave*evolution)	54	15,906.42	16,014.42	16,015.33	NA	NA
	φ(rs*sex*evolution)	30	15,960.41	16,020.41	16,020.69	0.00	0.40
	φ(rs*cave*evolution)	38	15,944.79	16,020.79	16,021.24	0.55	0.31
	φ(rs*sex*species)	34	15,953.09	16,021.09	16,021.45	0.76	0.28
3 (ψ)	ψ(rs*sex*species)	40	15,791.0383	15,871.04	15,871.54	0.00	0.51
	ψ(rs*sex*evolution)	36	15,799.1752	15,871.18	15,871.58	0.04	0.49
4 (Full Set)	p(time+cave+evolution), φ(rs*cave*evolution), ψ(rs*sex*species)	48	15,762.845	15,858.845	15,859.56	0.00	0.65
	p(time+cave+sex+evolution), φ(rs*cave*evolution), ψ(rs*sex*species)	49	15,762.0327	15,860.0327	15,860.78	1.22	0.35
	p(time+cave+sex+evolution), φ(rs*sex*evolution), ψ(rs*sex*species)	41	15,788.8856	15,870.8856	15,871.41	11.85	0.00
	p(time+cave+evolution), φ(rs*sex*evolution), ψ(rs*sex*species)	40	15,791.0383	15,871.0383	15,871.54	11.97	0.00

Apparent survival and transition probabilities to and from each reproductive state (rs) are presented. Additive models are represented by "+" and interactions with "*". Grouping factors are represented by time, reproductive state (rs), sex, evolutionary history (evolution, obligate cave species grouped together), species (obligate cave species separated into two species), and flow status (either wet or dry part of the year). The same model structure was used for ϕ and ψ during model development. Model selection was assessed by Quasi-Akaike's information criterion (QAIC) corrected for small sample sizes (QAICc), the difference in the focal QAICc and QAICc from the most parsimonious model (ΔQAICc), and QAICc model weight (QAICc Weight)
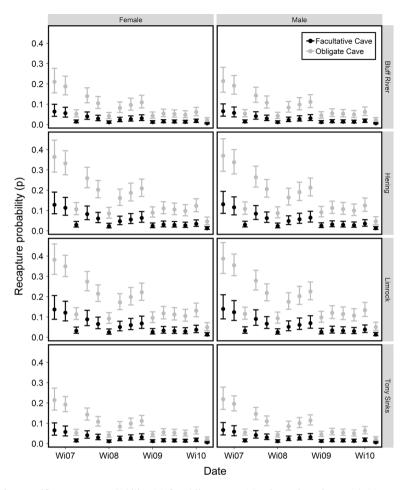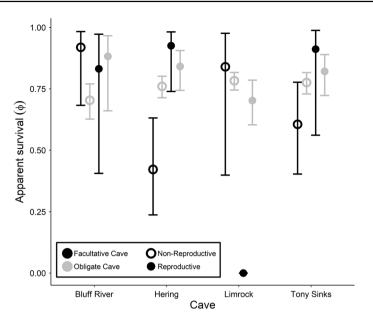
Fig. 2 Sex-specific recapture probability (*p*) for obligate cave (*Cambarus hamulatus* and *Orconectes australis*) and facultative cave (*Cambarus tenebrosus*) crayfishes on each sampling occasion within four cave streams in northern Alabama, USA. Error bars represent 95% confidence intervals. Labels on the *x*-axis are for winter (Wi) of each year in which recapture was estimated

and obligate cave crayfish in the reproductive state from Limrock (model average = 0.70, 95% confidence interval = 0.61–0.79; Fig. 3). Survival was not estimable for facultative cave crayfish in a reproductive state from Limrock cave due to too few facultative crayfish encountered in this state (*n* = 4, Table 1).

Reproductive transition probabilities (ψ) showed much greater separation among species, sexes, and reproductive states than did apparent survival (Figs. 3, 4). Most transitions between reproductive and non-reproductive states were higher for both obligate cave species (*C. hamulatus* and *O. australis*) than for *C. tenebrosus* (Fig. 4). Females transitioning from non-reproductive to reproductive states were no different regardless of among-species comparisons (*C. hamulatus*: mean = 0.10, 95% confidence interval = 0.04–0.22; *O. australis*: mean = 0.06, 95% confidence interval = 0.04–0.08; *C. tenebrosus*: mean = 0.10, 95% confidence interval = 0.03–0.31). Females transitioning from reproductive to non-reproductive states were higher for both obligate cave species than the facultative cave species,

Fig. 3 Apparent survival (ϕ) for obligate cave (*Cambarus hamulatus* and *Orconectes australis*) and facultative cave (*Cambarus tenebrosus*) crayfishes in reproductive and non-reproductive states from four cave streams in northern Alabama, USA. Error bars represent 95% confidence intervals
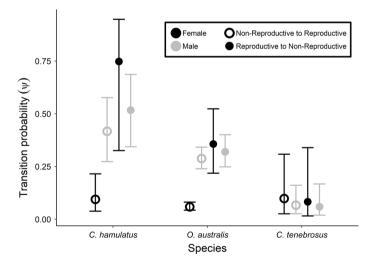

Fig. 4 Reproductive transition rates (ψ) for obligate cave (*Cambarus hamulatus* and *Orconectes australis*) and facultative cave (*Cambarus tenebrosus*) crayfishes in four cave streams in northern Alabama, USA. Error bars represent 95% confidence intervals

although this difference was not significant based on overlapping 95% confidence intervals (Fig. 4). However, transition rates into and out of a reproductive state were significantly higher for male obligate cave species when compared to male facultative cave species (Fig. 4). Within both obligate cave species (*O. australis* and *C. hamulatus*), transition from

a non-reproductive to reproductive state was significantly higher for males than females, but was not different between sexes from reproductive to non-reproductive states (Fig. 4). No transition between sexes or reproductive states significantly differed for *C. tenebrosus*, and all transitions for *C. tenebrosus* (besides females going from non-reproductive to reproductive) were relatively low compared to transitions for obligate cave species (Fig. 4).

Discussion

Our study was designed to determine whether the presence of obligate and facultative crayfishes within the cave environment was the result of comparable demographic performance, or whether obligate cave species possess adapted life-history characteristics suited to persistence in the low-energy cave environment. We found similar survival rates between cave and surface species among cave streams with different levels of organic matter, which contradicted part of our first and second predictions that crayfish survival rates would be highest for obligate cave species, particularly when in the most resource-depleted cave environments. Crayfish survival was similar among cave streams, indicating that resource availability (standing crop organic matter) and seasonal patterns in discharge played relatively minor roles within the time-scale of this study. Apparent survival in particular was similarly high for obligate and facultative crayfishes, indicating that occupancy of the cave environment is not directly detrimental to facultative cave crayfish. Furthermore, the similarity in demographic rates between the two obligate cave crayfishes indicated that the suite of biological and physiological adaptations commonly associated with obligate cave species resulted in the convergence of population demographic rates among our populations (confidence intervals between obligate species in reproductive transition probabilities overlapped for all comparisons).

Had we not explored sex-specific patterns within species, we would have missed the key demographic factors that are likely driving differences in population demographics between obligate and facultative cave crayfishes. The interaction among reproductive state, sex, and crayfish evolutionary history indicated that the probability of a female crayfish transitioning into a reproductive state was similar among obligate and facultative cave crayfishes, while large differences between species were observed in the probability of males transitioning between reproductive states. We suggest these patterns indicate that reproductive activity differs by sex and that the availability of reproductive crayfishes— both of females and, surprisingly, of males—is a key factor limiting population growth of facultative cave crayfish. Population biologists acknowledge the presence of sex-specific variability in demography but for the sake of simplicity often ignore this variability when constructing population models (Caswell 2001; Rankin and Kokko 2007). Our study illustrates how accounting for sex-specific demographic rates can be important for describing the mechanistic underpinnings of community structure (Gerber and White 2014).

The cave environment is not favorable for the reproductive efforts of either obligate or facultative female crayfish

The similarity among crayfish taxa in female non-reproductive to reproductive transition probabilities indicates that the cave environment is a difficult landscape for obligate and facultative females to reproduce. There was a less than 35% probability that a female crayfish would become reproductive between intervals, which is low given that greater than

50% of individuals in these crayfish populations are of reproductive size (Venarsky et al. 2012b). In fact, the highest number of reproductive female crayfishes encountered, regardless of evolutionary history was 11% (obligate cave species from Bluff River Cave), much lower than the number of reproductive female crayfishes reported in surface environments from other studies (number of reproductive *Austropotamobius pallipes*: mean = 41% from Brewis and Bowler 1985; number of reproductive *Faxonius virilis*: mean = 50% from Rogowski et al. 2013). This number was equally low when broken down by season where the number of reproductive females encountered was less than 20% regardless of season, species, or cave (facultative females from Hering Cave were the exception, see below). Furthermore, the probability of females transitioning into a non-reproductive state was either similar or higher than that of females transitioning into a reproductive state, which along with the low number of females observed in a reproductive state during surveys, indicates that the number of reproductive females is consistently low. Consequently, maintaining a higher number of reproductive females without a steady source of reproductive immigrants would require a higher rate of crayfish transitioning into a reproductive than non-reproductive state, a likely mechanism explaining the high number of reproductive *C. tenebrosus* in Hering Cave (77% in spring) but low estimate of reproductive transition probability. Hering Cave in particular was well connected to an ephemeral surface stream in spring, which likely explains the high number of reproductive facultative cave crayfishes (males and females) encountered in this cave as opposed to other caves in this study.

We suggest that the similarity in females transitioning into a reproductive state among species is the result of the interaction between the environment and life-history evolution. While variation in resource availability among caves did not influence demographic rates, the general resource limitation within cave environments compared to the surface likely influences a female's ability to become reproductive and then maintain a reproductive state. Standing crop organic matter at our study sites is relatively constant on intra- and inter-annual timescales and quantitative food web analyses indicate that these cave streams are running at or near the carrying capacity for community productivity given resource availability (Venarsky et al. 2014, 2018). Constant resource limitation presents female crayfish with a challenging landscape for reproduction, because female crayfish not only invest a large amount of energy into ova production, but the physical attachment of eggs and young to female crayfish represents a significant energy expenditure (Covich and Thorp 1991; Gutiérrez-Yurrita and Montes 1999). Furthermore, significant differences in organic matter were only observed between the caves with the highest and lowest organic matter. Thus, greater variability in organic matter among caves may be needed to detect differences in female (and male) crayfish demography among caves.

The higher probability of obligate females transitioning into a non-reproductive state than facultative females suggests that female obligate cave crayfishes may be employing the "skipped-spawning" concept documented for many fishes (McBride et al. 2015) and other taxonomic classes (amphibians, reptiles, and birds; Jenouvrier et al. 2005; Boretto et al. 2014; Cayuela et al. 2014). Fishes delay or skip spawning in certain years when reproductive conditions are not favorable (Trippel and Harvey 1989; Henderson et al. 2000; McBride et al. 2015). This behavioral response is typically followed by physiological responses such as oocyte and follicle resorption (i.e. atresia; Jegla 1966; Hunter et al. 1986; Rideout et al. 2000). Atresia has also been observed in obligate cave and surface crayfishes (Jegla 1966; Sarojini et al. 1995) and may be an especially important physiological response for female crayfishes coping with the energetic stress of the cave environment.

The lack of seasonal environmental cues along with relative resource limitation of the cave environment likely compounds the difficulties of reproduction for facultative cave

crayfish. Seasonal cues in temperature and photoperiod drive crayfish reproductive phenology and are typically absent in cave streams (Aiken 1969; Vlaming 1972; Rogowski et al. 2013). Even though seasonal reproductive timing in other cave crayfish species has been documented (Jegla 1966) and patterns in cave stream temperatures may track seasonal variations in cave stream flow, we found no evidence of temporal patterns in demographic rates of obligate or facultative cave crayfishes. Given the lack of a cyclical photoperiod in caves, it seems probable that seasonal cues are likely factors influencing transition probabilities of facultative cave crayfish, the relative weakness of which may make facultative species less adapted to cave conditions.

Importance of male crayfish reproductive strategies within cave environments

The ability of male obligate cave crayfishes to reproduce in the cave environment strongly differed from male facultative cave crayfish. Male obligate cave crayfishes were ~ 4 times more likely to transition into a reproductive state than facultative male crayfish. Resource dynamics and environmental cues, discussed above, likely contribute to male facultative cave crayfish having lower transition probabilities than male obligate cave crayfishes. These differences indicate that male obligate cave crayfishes within caves are more likely to reproduce than facultative cave crayfish of either sex or female obligate cave crayfishes. We suggest that these differences highlight an important and unique reproductive strategy employed by obligate cave crayfishes to maximize reproductive success within cave stream ecosystems.

Males invest much less energy into reproduction than females, because of the comparably low amount of energy required to produce and maintain sperm, as well as the lack of time and energy provided for the caring of eggs and young (Hayward and Gillooly 2011). However, transitioning into or out of a reproductive state requires molting in crayfishes, which is both highly stressful and carries an increased probability of mortality (Covich and Thorp 1991). Thus, if a reproductive state is achieved, maintaining the reproductive state carries a small energetic cost with a potentially large reproductive award for males. Population densities are low in caves and the high probability that a reproductive female will transition into a non-reproductive state indicates a male has a low probability of encountering a reproductive female. Thus, the longer a male cave crayfish can maintain a reproductive state, the higher probability of successful reproduction.

The striking difference in male obligate cave crayfishes transitioning between reproductive states compared to females and male facultative cave crayfish suggests that males play a critical role in crayfish population dynamics in cave streams. This runs counter to the common approach to population modeling, which generally focuses on the female perspective (Caswell 2001). While the lack of females transitioning into a reproductive state certainly limits population growth, the difference in male transition probabilities among species suggests that the availability of reproductive males is an important limiting factor to facultative cave species. For example, a female facultative crayfish in a reproductive state would likely find it difficult to locate a male in a reproductive state, thus limiting the probability of reproduction (i.e. reproductive asynchrony between sexes; Robinet et al. 2008). This contrasts with female obligate crayfishes, which are much more likely to encounter reproductive males. Thus, given the similarity in survival among facultative and obligate cave crayfishes and the low probability of successful reproduction by facultative cave crayfish, we suggest that facultative populations are likely sustained via regular immigration because of limited availability of reproductive individuals. However, further analyses

investigating the movement of facultative crayfishes into the cave environment is needed for greater support of this hypothesis.

Conclusions

Our research used a robust mark–recapture data set to show that obligate and facultative cave crayfishes use different reproductive strategies to cope with the resource-limited cave environment. Previous studies have used caves as an extreme endpoint of heterotrophic energetic pathways to describe the impacts of resource limitation on life-history evolution (Venarsky et al. 2012b; Soares and Niemiller 2013), food web theory (Simon et al. 2003; Huntsman et al. 2011a; Venarsky et al. 2014; 2018) and ecosystem function (Schneider et al. 2011; Huntsman et al. 2011b; Venarsky et al. 2012a). We showed that resource limitation may also shape community structure by influencing sex-specific reproductive behavior, hinting that the evolution of reproductive strategies allows obligate cave taxa to persist in energy-limited cave environments.

Author's contributions BMH, MPV, FA and CLC conceived the ideas; MPV, ADH, BRK, and JPB designed methodology;BMH, MPV, ADH, BRK, and JPB collected data; BMH and FA analyzed the data; BMH led writing ofthe manuscript; all authors contributed critically to the drafts and gave final approval for publication.

Data availability The datasets analyzed during the current study are available from the corresponding author on reasonable request.

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