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Habitat Associations Of Stream-Dwelling Salamanders At Multiple Spatial Scales In Central Kentucky Headwaters.

John Mark Yeiser
Eastern Kentucky University

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By

John M. Yeiser

Thesis Approved:

Chair, Advisory Committee

David Brown

Member, Advisory Committee

Member, Advisory Committee

Dean, Graduate School

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HABITAT ASSOCIATIONS OF STREAM-DWELLING SALAMANDERS AT MULTIPLE SPATIAL SCALES IN CENTRAL KENTUCKY HEADWATERS.

By

John M. Yeiser

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Richmond, Kentucky
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in partial fulfillment of the requirements
for the degree of
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DEDICATION

This thesis is dedicated to my parents, David and Elizabeth Yeiser, and my wife-to-be Carrie Lee Fay, who have sacrificed much to support my pursuit of a master's degree.

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ABSTRACT

Headwater stream systems are productive habitats that are often at risk of human perturbation, and it is crucial that ecologists understand natural patterns and processes within these ecosystems. Using a multi-scale approach, I investigated factors influencing habitat associations of *Ambystoma barbouri* (streamside salamander) and *Eurycea cirrigera* (southern two-lined salamander) in a relatively undisturbed stream network in central Kentucky. I used likelihood ratio G-tests to identify associations between species and mesohabitat types (i.e., runs, riffles, and pools). I used second order Akaike's Information Criterion (AIC_c) model selection to predict patterns of presence and abundance throughout headwater reaches. Fine-scale abiotic habitat conditions influenced habitat associations and distribution patterns at larger spatial scales. Individual *A. barbouri* displayed strong negative associations to riffle habitat at both micro- and stream-reach scales shortly after hatching, likely as a result of passive in-stream dispersal in response to increased water velocity and turbulence. *Ambystoma barbouri*, in later stages of development, displayed evidence of active dispersal, resulting in stronger positive associations to run habitat and stronger negative associations to riffles. Habitat associations in late spring suggested interspecific interactions between *A. barbouri* and *E. cirrigera*, and further research is needed on the potential reversal of predatory roles between the two species as *A. barbouri* larvae develop. My results demonstrated the effectiveness of a multi-scale approach to investigating complex ecological processes of aquatic organisms and the utility of AIC_c in selecting biologically relevant predictive models of salamander presence and abundance in aquatic habitats.

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CHAPTER I

INTRODUCTION

Understanding processes within relatively undisturbed stream ecosystems allows ecologists to predict and quantify the responses of species to both natural and anthropogenic disturbances (Power *et al*., 1988). The distribution of organisms influences ecosystem functions and processes, and understanding the factors that govern distribution patterns is a central goal of stream ecology (Barr & Babbit, 2002; Smith & Grossman, 2003; Lowe, 2005; Teresa & Romero, 2010). Headwater streams, which can constitute up to 70–80% of a total catchment area, are productive ecosystems that are connected to upland and downstream habitats (Gomi, Sidle & Richardson, 2002). Headwaters provide habitat to a variety of organisms and link uplands and wetlands to downstream fluvial systems by processing and transporting nutrients and organic matter (Vannote *et al*., 1980; Peterson *et al*., 2001; Gomi, Sidle & Richardson, 2002; Meyer *et al*., 2007). Aquatic species are intricately related to the type of habitat within the stream channel (Huryn & Wallace, 1987; Power *et al*., 1988; Frothingham, Rhoads & Herricks, 2002). In headwater stream ecosystems the most abundant vertebrates are typically salamanders (Burton & Likens, 1975a), and they provide many functions to ecosystem processes (Wells, 2007). Salamanders can function as mid-level predators that contribute to species diversity by preventing other predators from dominating food resources (Davic & Welsh, 2004). Salamanders prey on many different taxa including nematodes, crayfish, spiders, worms, beetles, and centipedes (Davic, 1991; Maerz *et al*., 2005). Populations can consume up to 5.80 kcal/m^2 of prey annually (Hairston, 1987) and are relatively efficient at converting energy into new tissue (Burton & Likens, 1975b). Salamanders are prey to many taxa as well, including mammals, birds, fishes, amphibians, and invertebrates (Davic & Welsh, 2004; Wells, 2007).

Although research on the response of salamanders to anthropogenic habitat alterations and perturbations is extensive (Corn & Bury, 1989; Welsh & Ollivier, 1998; Willson & Dorcas, 2003; Lowe & Bolger, 2002; Means & Travis, 2007; Peterman & Semlitsch, 2009; Grant, Green & Lowe, 2009; Price *et al*., 2010; Keitzer & Goforth, 2012), the ecology and behavior of larval stream salamanders in natural systems is less studied (but see Gustafson, 1993; Gustafson, 1994; Barr & Babbitt, 2002; Smith & Grossman, 2003; Lowe, 2005; Martin *et al*., 2012). In headwater streams lacking fishes, aquatic salamander larvae can be the dominant vertebrate predator (reviewed in Davic & Welsh, 2004) and are vital components of headwater ecosystems. Distribution patterns of larval salamanders are the result of complex interactions that are subject to seasonal shifts. For example, larval *Eurycea* (Plethodontidae) can display shifts in distribution based on availability of microhabitat conditions (Smith & Grossman, 2003) or a combination of biotic and abiotic factors such as presence of fish predators and variation in landscape characteristics (Barr & Babbitt, 2002). Body size is an important factor governing distribution and presence of larval salamanders. For example, larger *Gryonophilus porphyriticus* (spring salamander) salamanders have greater predatory influence on *Eurycea cirrigera* (southern two-lined salamander) (Gustafson, 1994). Body size is also a factor in abiotic interactions, for example, adult *G. porphyriticus* in the northeastern U.S.A. are negatively associated with mesohabitats containing smaller substrate (runs), and larvae are negatively associated with mesohabitats with larger substrate (cascades) (Lowe, 2005). Interstitial space can restrict distribution of larval salamanders via physical exclusion from spaces too small for their body size or by negative interactions with predators that may inhabit larger interspatial spaces (Martin *et al*., 2012).

My objectives were to investigate abiotic factors driving distribution patterns of larval *Ambystoma barbouri* (streamside salamander) and *E. cirrigera* within a relatively undisturbed headwater stream network in central Kentucky. I studied distribution patterns within three headwater streams and assessed two spatial scales in an attempt to uncover the primary factors driving headwater distribution patterns. I addressed reach-scale patterns by determining associations of larvae to mesohabitat (i.e. pool, run, or riffle), and I investigated fine-scale patterns by using microhabitat variables to predict presence and abundance of salamanders.

Study Organisms

Ambystoma barbouri are in the Ambystomatidae and are sister species to pond breeding *A. texanum* (smallmouth salamanders; Kraus & Petranka, 1989). Populations are restricted to central Kentucky, southeastern Indiana, southwestern Ohio and a few isolated locations in Tennessee. *Ambystoma barbouri* is listed as a Near Threatened species on the IUCN Red List (IUCN, 2011) and was recently petitioned to be listed under the U.S. Endangered Species Act (USFWS, 2011). Adults have been found up to 400-m from the nearest stream and rarely inhabit areas without extensive surrounding forest (Petranka, 1998). Unlike most other ambystomatid salamanders, *A. barbouri* only occasionally breed in ponds (Petranka, 1984a). Typical breeding habitats are fishless, ephemeral headwater streams containing pools and large, flat limestone rocks for oviposition. Breeding occurs from October to March in Kentucky and sometimes extends into April (Petranka, 1998). Larvae are strictly aquatic and are usually found within fishless regions of streams where they feed mainly on isopods (*Lirceus fontinalis*) (Smith & Petranka, 1987).

Eurycea cirrigera are in the Plethidontidae and are sister species to *E. bislineata* (northern two-lined salamanders). Individuals are common in streams east of the Mississippi River extending to the Atlantic Coast and range from central Indiana and Ohio to eastern Louisiana and northern Florida (Petranka, 1998). Adults breed in headwater streams from September to May and spend most of the year in the surrounding uplands (Petranka, 1998). Larvae are strictly aquatic and forage on a variety of macroinvertebrates; older larvae have been reported to prey on young *A. barbouri* larvae (Petranka, 1984b).

In Kentucky, *A. barbouri* hatch in mid to late April and metamorphose within 6–10 weeks (Petranka, 1984c; Petranka & Sih, 1986). *Eurycea cirrigera* hatch in late May and early June and usually transform after approximately one year of development (Petranka, 1984b; McDowell, 1995), resulting in a mix of first-year and second-year larvae within the stream. In early spring, newly hatched *A. barbouri* and second-year *E. cirrigera* share aquatic habitat. Second-year *E. cirrigera* larvae prey on *A. barbouri* as they hatch, but as *A. barbouri* larvae grow larger they are no longer suitable prey for *E. cirrigera* (Petranka, 1984b). In late spring, newly hatched *E. cirrigera* share the stream with second-year *E. cirrigera* and *A. barbouri*, some of which are possibly approaching metamorphosis. Although it has not been documented, research on the role of body size in predation in other species (Gustafson, 1994) suggests *A. barbouri* could potentially predate on *E. cirrigera* hatchlings. This would effectively reverse predator-prey roles and influence distribution patterns of both species. The brevity of aquatic development of *A. barbouri* allows for the unique opportunity to investigate the shifts in habitat associations and patterns of abundance as 1) a response to individual growth and development, and 2) a response to the introduction of a new cohort of sympatric salamanders, without having to account for large shifts in habitat availability. While biotic interactions between the two species were not directly measured, shifts in patterns of habitat use and mechanisms of distribution may suggest possible interspecific interactions.

CHAPTER II

MATERIALS AND METHODS

Study Site

I studied natural distributions of *E. cirrigera* and *A. barbouri* in three fishless, headwater reaches of Raven Run at the Raven Run Nature Sanctuary in Fayette County, Kentucky. Raven Run is located within the Inner Bluegrass Ecoregion (Woods *et al*., 2002) and is a network of first and second order streams that converge into a main channel that empties into the Kentucky River. While some of the headwaters are exposed to residential and pastureland areas, much of the stream area is surrounded by an extended forest buffer that is wide enough to support the core habitat requirements of amphibian species in the area (Semlitsch & Bodie, 2003), and likely remediate most negative effects of these landscape disturbances (Naiman & Décamps, 1997). The stream gradient, velocity, width, and depth; slope of the bank; and substrate composition are variable throughout the stream channel, producing a heterogeneous habitat that supports populations of *A. barbouri* (Storfer, 1999) and *E. cirrigera* (Petranka, 1984b).

I sampled three watersheds with similar characteristics as independent replicates. Within each of the three study watersheds, I randomly selected a 100-m reach within the longest stretch of suitable stream habitat. I defined suitable habitat as areas of stream length that had substantial forest buffer, presence of multiple mesohabitat types, and no evidence of fish. I measured physical microhabitat and mesohabitat composition at each site for both sampling sessions to compare natural characteristics among sites and to determine if any temporal shifts in habitat composition occurred. I sampled each 100-m reach twice in spring of 2012 (April 13th–15th and May 18th–20th; hereafter referred to as early spring and late spring sampling events, respectively). Every 3-m, I established a 1-m wide transect across the stream and arranged three 0.25-m^2 sampling plots within the transect with a plot bordering the left shoreline, a plot in the midpoint of the stream channel, and a plot bordering the right shoreline. To search for salamanders, I overturned each substrate item within the 0.25-m^2 sampling plot, including items that were in contact with the border of the sampling plot. To reveal population distributions and species coexistence within the stream, I documented the location of each observation as an x,y coordinate along the stream channel. I measured individuals after each capture to the nearest millimeter of total body length (TL), and I only attempted capture when it would not displace nearby larvae.

Mesohabitat Associations

In each study stream, I mapped the 100-m reach according to mesohabitat type: run, riffle or pool. The following description of mesohabitat is specific to headwaters primarily composed of bedrock (modified from Montgomery & Buffington, 1997). Runs generally have laminar flow and low gradients and are either dominated by limestone bedrock or are composed of a variety of substrate. Riffles are characterized by relatively turbulent flow, moderate to low gradients, and a variety of substrate that causes non-laminar flow, including undulating bedrock or multiple vertical incisions in bedrock. Pools have laminar flow and low gradients but can be differentiated from runs based on slower water velocity caused by an obstruction in the stream channel or an abrupt incision in the stream bed. I represented natural availability of mesohabitat types by percentage of total sampling reach area, and I used this to calculate the expected frequencies of captures within each mesohabitat type. To uncover mesohabitat associations of *A. barbouri* and *E. cirrigera*, I compared observed frequencies of captures within each mesohabitat type to expected frequencies using likelihood ratio G-tests (Sokal & Rohlf, 1995; Lowe, 2005). I calculated likelihood G-values for each site from each sampling event, and graphically represented overall habitat associations by combining sites as independent replicates. This allowed me to compare patterns between sites during a single sampling event and to compare patterns at each site between sampling events.

Microhabitat Sampling

Within each sampling transect, I randomly designated a 0.25-m^2 sampling plot for microhabitat sampling. I measured the following microhabitat variables within the sampling plots: percent embeddedness, percent debris coverage, percent vegetative coverage, percent coverage of each substrate class (see below), size class of substrate item under which an individual was captured (or reported as exposed if under no cover), water depth, and micro-condition. Micro-condition (micro-pool, micro-run, or micro-riffle) is analogous to mesohabitat type but at a finer scale. It is a comprehensive, qualitative metric that incorporates variables difficult to quantify in first order streams (i.e. water velocity). This method also allowed me to empirically evaluate distinct microhabitats within a dominant mesohabitat. Within each 0.25-m^2 plot, I visually estimated a) embeddedness as a percentage of total substrate area covered in fine sediment, b) debris and vegetative coverage as the percent coverage of the total surface area in the sampling plot, and c) percent coverage of substrate for the following categories: pebble (< 64 mm), cobble (64–256 mm), boulder (>256 mm with visible edges), and bedrock (> 256 mm with no visible edges) (Bain, 1999).

I used multiple regression analyses to predict presence and abundance of individuals in the 0.25-m^2 sampling plots. I excluded dry sampling plots from analyses because larval stages of *A. barbouri* and *E. cirrigera* are strictly aquatic. I initially used negative binomial distribution models in multiple regression analyses to predict abundance. If the variance term was not significant, I used a Poisson distribution. I used logistic distribution models to predict presence. For all analyses, I performed model selection using second order Akaike's Information Criterion (AIC_c) or quasi AIC_c ($QAIC_c$) for models with Poisson distributions in R version 2.15.1 (R Development Core Team, Vienna, Austria) using the 'AICcmodavg' package (Mazerolle, 2013). Akaike's Information Criterion model selection is an information theoretic approach that determines a top predictive model from a list of candidate models produced *a priori* to data analyses (Burnham & Anderson, 2002). This model selection process ranks every candidate model based on parsimony (number of parameters, K) and goodness of fit (log-likelihood), with the best model having the lowest AIC_c value (Mazerolle, 2006). Model weights (w_i) represent the probability a given model is the best model and are used in direct comparison of two candidate models. Some variables in top models could confound results, especially in the case of more than one model having $AIC_c < 2$ and only differing by one variable. Arnold (2010) argues that this is quite common in wildlife literature, and that statistically competitive models are often erroneously considered biologically relevant. As a solution for potential uncertainty in making inferences from top models, I used model averaging to conduct multi-model inference. Model averaging consists of combining the estimates of important parameters across candidate models and allows for biological inferences to be based on all models containing the variable, and not just a singular top model that may have insufficient statistical support or biological meaning. I used regression coefficients (β) and confidence intervals to represent effect sizes of continuous independent variables for both logistic and multiple regression analyses and I interpreted values as the relative contribution of each variable to the response. I determined the effect sizes of categorical variables via dummy coding and interpreted values relative to a reference category (i.e. effect of micro-riffles on abundance compared to effect of micro-pool on abundance). I computed odds ratios of a parameter from logistic regression by exponentiating the estimated β value. Odds ratios allowed for comparison between the odds of a model predicting presence versus the odds of a model predicting absence. In the case of categorical variables such as micro-condition, I compared the odds between an individual occurring in one microhabitat type versus another. I used confidence intervals of 85% for parameter estimates to promote compatibility between the information-theoretic approach and statistical inference (Arnold, 2010). If 85% confidence intervals included zero, I interpreted the variable as having no effect on the response.

CHAPTER III

RESULTS

I observed a total of 672 *A. barbouri* larvae (pools = 137, runs = 369, riffles = 166) and 160 *E. cirrigera* larvae (pools = 11, runs = 75, riffles = 75) across all sites during this study. In early spring I observed 453 *A. barbouri* (pools = 120, runs = 214, riffles = 119), with densities reaching 90 individuals/m^2 ($\bar{x}$ = 8.11 ± 0.94 SE). I captured and measured a total of 274 individuals in early spring ($\bar{x}$ = 17.96 mm TL ± 0.21 mm SE). I observed seventeen *E. cirrigera* (pools = 6, runs = 5, riffles = 6) and captured and measured 12 individuals ($\bar{x}$ = 48.17 mm ± 1.93 mm SE). Due to low sample size, interpretations of *E. cirrigera* results for this sampling period were limited, but *A. barbouri* displayed clumped distribution throughout each sampling reach (Figure 1)[1]. In late spring I detected 219 *A. barbouri* (pools = 17, runs = 155, riffles = 47) and 144 *E. cirrigera* (pools = 5, runs = 70, riffles = 69). Densities of *A. barbouri* reached 60 individuals/m^2 ($\bar{x}$ = 3.91 ± 0.54 SE), and density of *E. cirrigera* reached 40 individuals/m^2 ($\bar{x}$ = 2.52 ± 0.38 SE). I captured and measured 70 *A. barbouri* ($\bar{x}$ = 30.34 mm ± 1.05 mm SE) and 27 *E. cirrigera* (first year larvae, $\bar{x}$ = 17.33 mm ± 0.63 SE; second year larvae, $\bar{x}$ = 44.67 mm ± 4.03 mm SE). Both species displayed aggregated spatial distribution and often shared the same habitat space (Figure 2). Mean length of individuals in did not differ between mesohabitats in early or late spring.

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[1] All figures and tables are listed in the appendix

Multicolinearity of Predictive Microhabitat Variables

I used Pearson's correlations to determine multicolinearity among predictive variables of presence and abundance. If variables were correlated in either sampling session I removed them from all analyses. Because of the low number of *E. cirrigera* individuals found in early spring, presence of *E. cirrigera* was not included in early spring models predicting *A. barbouri* abundance and presence. Models used to predict response of *A. barbouri* in early spring were used in late spring as well. The similarity in candidate models promoted comparability between seasons. The following variables were removed from analyses: percent cobble coverage, percent pebble coverage, and transect location. Models for both species were constructed based on review of literature and patterns I observed during data collection.

Habitat Associations: Early Spring

Ambystoma barbouri displayed positive associations to runs and pools, and a strong negative association to riffles (Figure 3). Observed frequencies of individuals within each mesohabitat type were not equal to expected frequencies based on natural availability (Site 1: G = 9.91, df = 2, $p = 0.007$; Site 2: G = 135.00, df = 2, $p < 0.0001$; Site 3: G = 73.73, df = 2, $p < 0.0001$). *Eurycea cirrigera* displayed similar patterns (Figure 3) but low sample size precluded statistical analysis. Percent bedrock coverage, percent boulder coverage, and micro-condition best predicted presence of *A. barbouri* (Table 1). The weight of the top model was less than 0.90; therefore, I performed model averaging on top predictive variables. Percent bedrock coverage was the only predictive variable that had an effect on *A. barbouri* presence statistically different from zero (Table

2). Percent bedrock coverage, percent boulder coverage, and micro-condition also best predicted abundance of *A. barbouri* in early spring (Table 3), and had sufficient support to warrant no multi-model inference. Micro-condition is categorical, so I averaged parameter estimates across all models in order to understand the effects of one microhabitat type versus the others. Effect of micro-runs compared to micro-pools was not different from zero and micro-riffles had negative effects compared to micro-pools ($\beta = -1.670$, 85% CI [-2.413, -0.927]).

Habitat Associations: Late Spring

In late spring *A. barbouri* displayed strong positive association with runs and strong negative associations with riffles, and held no associations to pools (Figure 4). Observed frequencies of individual *A. barbouri* within each mesohabitat type did not equal the expected frequencies (Site 1: G = 33.85, df = 2, $p < 0.0001$; Site 2: G = 105.42, df = 2, $p < 0.0001$; Site 3: G = 11.72, df = 2, $p = 0.004$). Multiple predictive models of *A. barbouri* presence held similar weight including: percent bedrock coverage and depth, depth, depth and micro-conditions, and percent embedded (Table 4). I averaged several parameter estimates across all models (Table 5). Depth and percent embedded had positive effects on *A. barbouri* presence. The best model predicting abundance of *A. barbouri* was depth and micro-conditions (Table 6). Depth, percent embedded, and micro-runs compared to micro-pools had positive effects on *A. barbouri* abundance. Micro-riffles had negative effects on abundance compared to effects of micro-pools (Table 7).

Eurycea cirrigera was negatively associated with pools and riffles and positively associated with runs in late spring (Figure 4). The difference between observed and expected frequencies within each mesohabitat type was significant at two sites, but were not as pronounced as in *A. barbouri* (Site 1: $G = 16.64$, $df = 2$, $p < 0.001$; Site 2: $G = 3.08$, $df = 2$, $p = 0.214$; Site 3: $G = 8.13$, $df = 2$, $p = 0.017$) The model best predicting presence of *E. cirrigera* in late spring was bedrock and depth, however multiple candidate models had relatively substantial weights (Table 8). Depth and *A. barbouri* presence had positive influence on *E. cirrigera* presence (Table 9). The variance term for the global model of abundance for *E. cirrigera* in late spring was non-significant, so I used Poisson distribution instead. The data for this test was overdispersed ($\hat{c} = 3.16$) so I used quasi Akaike's Information Criterion ($QAIC_c$) to rank models. The best model predicting *E. cirrigera* abundance in late spring was percent embedded and depth (Table 10). Model averaging revealed depth had positive effects on *E. cirrigera* abundance, and percent boulder coverage and percent embedded had negative effects on abundance (Table 11).

CHAPTER IV

DISCUSSION

The multi-scale approach of my study allowed for comprehensive understanding of the distribution of larval *A. barbouri* and *E. cirrigera* in natural headwater systems in central Kentucky. Strong mesohabitat associations dictated locations of aggregated individuals within the headwater reaches. Fine-scale environmental conditions effectively predicted presence and abundance of individuals and were driving factors behind mesohabitat associations. Pockets of distinct, slow-moving, laminar areas of stream habitat (i.e. micro-pools and micro-runs) with increased bedrock coverage and decreased boulder coverage were determinants of *A. barbouri* distribution patterns during early stages of larval development. This type of habitat was abundant in runs and pools. Individuals were negatively associated with the fast-moving, turbulent conditions (riffles) at fine and mesohabitat scales, and this indicates that in-stream dispersal of recently hatched *A. barbouri* is a passive result of stream flow. The strong negative association to riffle habitat was likely driving statistical deviations from expected frequencies of individuals. A negative relationship between *A. barbouri* and riffles has been previously reported (Petranka, 1984a; Holomuzki, 1991), and this association is likely due to the lack of mobility in newly hatched larvae (Petranka, 1984a). Proportion of overall observations in riffles was low, but the frequency of individuals observed in riffles contrasted what has previously been reported in the literature. Holomuzki (1991) only found one egg clutch in riffle habitat and Petranka (1984a) found that *A. barbouri* larvae generally avoided riffles. I observed 166 individuals (24.7%) in riffle habitat throughout this study. This could be due to the overall predominance of limestone bedrock in Raven Run, a top predictive variable of presence and abundance, or it could be the result of small pockets of distinct microhabitats within larger riffle habitats. A total of 40 transects in this study were in riffle habitat, and of the 146 sampling plots that held water across both sampling events, 61 plots (41.8%) of riffle area consisted of slow moving, laminar flow. This highlights the importance of fine-scale heterogeneity to *A. barbouri* residing in generally unsuitable mesohabitat. The absence of depositional microhabitats within riffles would likely result in exclusion of *A. barbouri* from these areas throughout their aquatic stage. Riffle habitats are at high risk of drying, however, and this likely played a role in the negative associations of both species to riffle habitat.

The majority of *A. barbouri* were observed exposed in the water column shortly after hatching (83.2% ± 5.9% SE), and would have little resistance to downstream displacement from high velocity areas to low velocity areas. The lack of substrate use indicates that the relationship between body size and interstitial space was not an important factor compared to species in other systems (Gustafson, 1994; Lowe, 2005; Martin *et al*., 2012). Passive response to stream flow promotes susceptibility to downstream displacement, and individuals that drift downstream to fish habitat would likely not survive (Petranka & Sih, 1986). In addition to passive downstream displacement, the evolutionary history of the species may influence habitat associations. Female *A. barbouri* lay eggs on the undersides of large limestone substrate and prefer to oviposit in slow moving areas (Holomuzki, 1991), which is logical considering *A. barbouri* also breed in ponds and that most members of Ambystomatidae are strictly pond breeders (Petranka, 1998).

In late spring, associations to habitat at both fine- and reach-scales shifted. In fact, the top predictive model of abundance and presence of *A. barbouri* in early spring held no weight in late spring. There was no clear top model predicting presence of *A. barbouri* in late spring so I relied on multi-model inference to determine main factors driving presence. *Ambystoma barbouri* presence and abundance were positively influenced by increasing depth and embeddedness in late spring. Embeddedness had relatively small influence on presence and abundance (Table 5, Table 7) and was likely not an important factor driving distribution patterns. Depth had stronger influence on *A. barbouri*, as every increase in approximately 4 cm resulted in the increase of one individual ($\beta = 0.236 \pm 0.063$ SE). Areas of turbulent, relatively fast moving waters negatively influenced *A. barbouri* abundance, but passive in-stream dispersal is unlikely in late spring. Older *A. barbouri* larvae have better developed limbs and increased mobility compared to recently hatched larvae, and larger individuals are less susceptible to downstream displacement (Petranka *et al*., 1987). If in-stream dispersal was passive at this time, individuals likely would have been equally associated with micro-runs and micro-pools because the average depth of each microhabitat was similar (micro-pools = 4.46 cm ± 0.72 cm SE, micro-runs = 4.16 ± 0.72 cm SE, $t = 0.296$, df = 35, p = 0.796). However, micro-runs had positive influence compared to micro-pools, indicating that areas of low velocity, laminar flow were no longer important factors driving distribution of *A. barbouri*. This change in relationship between individuals and fine-scale abiotic characteristics caused a shift in mesohabitat associations. Percentage of individuals observed in pools dropped from 26.8% ± 2.5% SE in early spring to 9.4% ± 4.5% SE in late spring. This strengthened both the positive association to runs and the negative association to riffles (Figure 4).

The changes in associations to micro-condition and mesohabitat could be caused by 1) individuals actively seeking runs because of increased density of some prey items (Holomuzki, 1991), 2) individuals being stranded in run habitat because of partial stream intermittence, or 3) *A. barbouri* residing in pools early in development metamorphosing earlier than individuals in other habitats. Although Holomuzki (1991) reported one prey species having higher density in runs, overall prey density was not different between runs and pools in his study stream. Stream drying, while more prevalent in late spring (dry sampling plots in early spring = 20; late spring = 31), was likely not a factor in habitat association shifts. Mean depth in pools did not differ between sampling sessions (early = 2.76 cm ± 0.70 cm SE, late = 2.78 cm ± 0.68 cm SE), and only transects in riffle habitat became completely dry in late spring (Figure 2). Holomuzki (1991) found no differences in growth of *A. barbouri* between pools and runs but did observe different survivorships to metamorphosis between the two mesohabitats (15.9% ± 4.1% SE for pools, 3.5% ± 1.4% SE for runs), and recorded time to metamorphosis in pools as approximately 30 days (days between my sampling events were 33). The overall number of observations decreased in late spring across all sampling reaches, and other studies have reported overall survival of *A. barbouri* to metamorphosis as very low (Petranka, 1984a; Petranka & Sih, 1986). While the lower number of individuals in my study streams in late spring is likely the result of many factors, the number of individuals in pools decreased disproportionately more than in other habitats. While I cannot say for certain why associations of *A. barbouri* to pools at fine- and reach-scales shifted, the most likely explanation is that individuals in pools metamorphose and leave the stream earlier than individuals in other mesohabitats. Further study on rates and proportions of individuals metamorphosing from different habitats is required to truly understand these patterns.

The introduction of the new cohort of *E. cirrigera* may have caused interspecific interactions between the two salamander species in late spring. Mesohabitat associations of *E. cirrigera* were not as strong as those of *A. barbouri* but both species displayed similar patterns. Presence of *E. cirrigera* was greatly influenced by presence of *A. barbouri*, as individual *E. cirrigera* were approximately 5*x* more likely to occur in an area where *A. barbouri* were present than not (odds ratio = 4.92). The relative predictive strength of this variable compared to abiotic variables measured suggests an interaction between *A. barbouri* and *E. cirrigera* in late spring could be driving distribution patterns of both species (Table 9). Competition or mutual avoidance of predators could cause both species to use the same habitat, and mean body length of both species suggests that *A. barbouri* were not able to predate heavily on all *E. cirrigera* larvae (*A. barbouri*: $\bar{x}$ = 30.34 mm ± 1.05 mm SE; *E. cirrigera*: $\bar{x}$ = 23.26 mm ± 2.39 mm SE). However, it is possible that larger *A. barbouri* individuals were actively seeking and preying on smaller *E. cirrigera* before the late spring sampling event. The mean body length of *E. cirrigera* in presence of *A. barbouri* was greater than mean body length of individuals in absence of *A. barbouri* (present: $\bar{x}$ = 29.10 mm ± 4.85 mm SE ; absent: $\bar{x}$ = 19.76 mm ± 2.22 mm), but this difference was not statistically significant (Mann-Whitney U test: n = 27, Z = -1.09, p = 0.14). Although these results are not statistically significant, there may be a biological pattern, and predation of smaller *E. cirrigera* by *A. barbouri* could possibly be contributing to distribution patterns in late spring. However, my data does not directly address interspecific interactions and further research on the interactions between the two species is needed.

The high density of individuals in Raven Run is likely the result of heterogeneous microhabitat within larger reach-scale habitat, and its relatively low disturbance, especially compared to other streams in the Inner Bluegrass Ecoregion of Kentucky. Stream flow within headwaters of Raven Run greatly increases after heavy rains and the presence of depositional habit may decrease the downstream displacement of individuals during storm events. Disturbances can homogenize habitat across large scales, and this is likely the reason *A. barbouri* are rarely found in streams without extensive forest buffer (Petranka, 1998). Headwater streams are susceptible to human disturbance (Corn & Bury, 1989; Pond *et al.*, 2008). Therefore, in response to the threat of anthropogenic disturbance, it is necessary to understand both the natural processes behind aquatic community characteristics (Wilkins & Peterson, 2000), and how anthropogenic disturbance is affecting stream biota (Pond, 2012). Significant disturbance events (i.e. increased sedimentation) have negative effects on stream organisms (Corn & Bury, 1989; Keitzer & Goforth, 2012), and would likely be devastating to populations of *A. barbouri* if distinct pockets of preferred microhabitat were eradicated. The physical habitat quality of Raven Run is near best-available condition in central Kentucky, and future research on the habitat associations and distribution patterns of *A. barbouri* across large portions of its range would add insight into the effects of both natural habitat variation and human disturbance on habitat associations of aquatic organisms.

My study elucidated factors driving distribution patterns of *A. barbouri* and *E. cirrigera* in relatively undisturbed headwaters and demonstrated that multi-scale research is vital to understanding complex relationships between aquatic organisms and their surrounding environment. In early stages of *A. barbouri* larval development habitat use is a passive response to stream flow. Individuals are influenced by fine-scale conditions differently in late stages of development. Active dispersal, metamorphosis of individuals from pool habitat, and the increase in abundance of larval *E. cirrigera* into the stream are likely driving distribution of *A. barbouri* nearing metamorphosis. My study highlights the complexity of interactions between aquatic organisms and their abiotic and biotic surroundings, and demonstrates the importance of heterogeneous habitat to prevalence of stream dwelling larval salamanders in central Kentucky headwater streams.

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APPENDIX

Table 1. Top candidate models predicting presence of *Ambystoma barbouri* in early spring.

Model[a]	K[b]	Log-likelihood	AIC$_c$	Δ_i	w_i
bedrock + boulder + microcondition	5	-19.16	49.55	0	0.73
microcondition	3	-23.31	53.09	3.54	0.13
depth + microcondition	4	-22.56	53.92	4.37	0.08
microcondition + embedded	4	-23.31	55.41	5.86	0.04
bedrock + depth	3	-26.26	58.99	9.44	0.01

[a] Global model: microcondition (micro-run, micro-riffle, micro-pool), stream, mesohabitat (run, riffle or pool), bedrock (%bedrock cover within 0.25m^2 plot), boulder (%boulder cover within 0.25m^2 plot), embedded (% of substrate embedded within 0.25m^2 plot), debris (%debris coverage within 0.25m^2 plot), veg (%vegetative coverage within 0.25m^2 plot), depth (depth at midpoint of sampling plot)

[b] Includes intercept

Table 2. Results of averaging across all models that include top predictive parameters of *Ambystoma barbouri* presence in early spring.

Parameter	β	85% CI Lower	85% CI Upper	Odds Ratio
micro-run v micro-pool	0.057	-1.951	2.065	1.059
micro-riffle v micro-pool	-3.420	-262.5	255.7	0.033
bedrock	0.029	0.010	0.047	1.029
boulder	-0.050	-0.117	0.018	0.951
depth	0.132	-0.039	0.302	1.141
embedded	$-0.6\text{x}10^{-4}$	-0.020	0.019	0.999

Table 3. Top candidate models predicting abundance of *Ambystoma barbouri* in early spring.

Model	K^b	Log-likelihood	AIC_c	Δi	w_i
bedrock + boulder + microcondition	6	-112.01	237.76	0	0.94
Global[a]	14	-103.59	245.69	7.93	0.02
bedrock + boulder + debris + veg	6	-116.03	245.81	8.04	0.02
bedrock + boulder + debris + depth + embedded + veg	8	-114.11	247.35	9.58	0.01
bedrock + boulder	4	-119.00	247.50	9.74	0.01
bedrock + boulder + embed + debris + veg	7	-115.82	248.02	10.26	0.01

[a] Global model: microcondition (micro-run, micro-riffle, micro-pool), stream, mesohabitat (run, riffle or pool), bedrock (%bedrock cover within 0.25m^2 plot), boulder (%boulder cover within 0.25m^2 plot), embedded (% of substrate embedded within 0.25m^2 plot), debris (%debris coverage within 0.25m^2 plot), veg (%vegetative coverage within 0.25m^2 plot), depth (depth at midpoint of sampling plot)

[b] Includes intercept

Table 4. Top candidate models predicting presence of *Ambystoma barbouri* in late spring.

Model	K[b]	Log-likelihood	AIC_c	Δi	w_i
bedrock + depth	3	-23.80	54.17	0	0.28
depth	2	-25.05	54.37	0.20	0.25
depth + microcondition	4	-22.87	54.71	0.54	0.21
embedd	2	-25.91	56.10	1.93	0.11
bedrock+ depth + debris + veg	5	-23.17	57.83	3.66	0.04
bedrock + embedded	3	-25.88	58.33	4.16	0.04
bedrock + boulder + debris + depth + embedded + veg	7	-20.81	58.56	4.39	0.03
microcondition + embedd	4	-24.88	58.73	4.56	0.03

[a] Global model: microcondition (micro-run, micro-riffle, micro-pool), stream (site 1, site 2, site 3), mesohabitat (run, riffle or pool), bedrock (%bedrock cover within $0.25m^2$ plot), boulder (%boulder cover within $0.25m^2$ plot), embedd (% of substrate embedded within $0.25m^2$ plot), debris (%debris coverage within $0.25m^2$ plot), veg (%vegetative coverage within $0.25m^2$ plot), depth (depth at midpoint of sampling plot)

[b] Includes intercept and variance

Table 5. Results of averaging across all models that include top predictive parameters of *Ambystoma barbouri* in late spring.

Parameter	β	85% CI Lower	85% CI Upper	Odds Ratio
micro-run v micro-pool	-0.623	-0.549	1.794	0.536
micro-riffle v micro-pool	-1.847	-4.070	0.376	0.158
bedrock	0.013	-0.003	0.029	1.013
depth	0.433	0.212	0.655	1.542
embedded	0.036	0.016	0.056	1.037

Table 6. Top candidate models predicting abundance of *Ambystoma barbouri* in late spring

Model	K	Log-likelihood	AIC$_c$	Δ_i	w_i
depth + microcondition	5	-66.29	144.09	0	0.63
microcondition + embedd	5	-67.13	145.77	1.68	0.27
embedd	3	-71.76	150.10	6.01	0.03
bedrock + depth	4	-70.75	150.47	6.38	0.03
bedrock + embedded	4	-71.45	151.87	7.78	0.01
bedrock + boulder + debris + depth + embedded	7	-67.47	151.89	7.80	0.01
bedrock + depth + debris	6	-70.88	153.26	9.17	0.01
depth	3	-73.39	153.35	9.26	0.01
microcondition	4	-72.30	153.57	9.48	0.01

[a] Global model: microcondition (micro-run, micro-riffle, micro-pool), stream (site 1, site 2, site 3), mesohabitat (run, riffle or pool), bedrock (%bedrock cover within 0.25m^2 plot), boulder (%boulder cover within 0.25m^2 plot), embedd (% of substrate embedded within 0.25m^2 plot), debris (%debris coverage within 0.25m^2 plot), veg (%vegetative coverage within 0.25m^2 plot), depth (depth at midpoint of sampling plot)

Table 7. Results of averaging across all models that include top predictive parameters of *Ambystoma barbouri* abundance in late spring.

Parameter	β	85% CI Lower	85% CI Upper
micro-run v micro-pool	0.946	0.294	1.598
micro-riffle v micro-pool	-1.810	-3.565	-0.056
depth	0.236	0.145	0.328
embedded	0.027	0.014	0.039
bedrock	0.008	-0.001	0.017
boulder	0.004	-0.021	0.030
debris	-0.010	-0.070	0.049

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Table 8. Top candidate models predicting presence of *Eurycea cirrigera* in late spring.

Model[a]	K	Log-likelihood	AIC_c	Δi	w_i
bedrock + depth	3	-23.46	53.49	0	0.19
depth	2	-24.67	53.62	0.13	0.18
A. barbouri presence	2	-24.93	54.13	0.64	0.14
depth + bedrock + boulder	4	-22.74	54.46	0.96	0.12
embedd + depth	3	-24.13	54.83	1.34	0.10
debris + depth	3	-24.63	55.84	2.34	0.06
microcondition + depth	4	-23.94	56.86	3.37	0.04
Intercept	1	-27.39	56.87	3.37	0.04
A. barbouri presence + microcondition	4	-23.98	56.94	3.45	0.03
stream	3	-25.35	57.26	3.77	0.03
boulder + bedrock	3	-25.66	57.88	4.39	0.02
bedrock	2	-27.09	58.45	4.96	0.02
embedd	2	-27.35	58.98	5.48	0.01
mesohabitat	3	-26.57	59.72	6.23	0.01
boulder + bedrock + embedd	4	-22.30	60.03	6.54	0.01

[a] Global model: microcondition (micro-run, micro-riffle, micro-pool) + stream (site 1, site 2, site 3) + mesohabitat (run, riffle, pool) + bedrock (%bedrock cover within sampling plot) + boulder (%boulder cover within sampling plot)+ embedd (%substrate embedded within sampling plot) + debris (%debris coverage within sampling plot) + depth (depth at midpoint of sampling plot) + *A. barbouri* presence (presence of *Ambystoma barbouri* within sampling plot)

Table 9. Results of averaging across all models that include top predictive parameters of *Eurycea cirrigera* presence in late spring.

Parameter	β	85% CI Lower	85% CI Upper	Odds Ratio
depth	0.261	0.095	0.427	1.30
boulder	-0.059	-0.140	0.023	0.94
bedrock	0.010	-0.006	0.027	1.01
embedded	-0.011	-0.028	0.007	0.99
A. barbouri presence	1.593	0.500	2.689	4.92
micro-riffle v micro-pool	1.176	-0.330	2.681	3.24
micro-run v micro-pool	0.515	-0.719	1.750	1.67

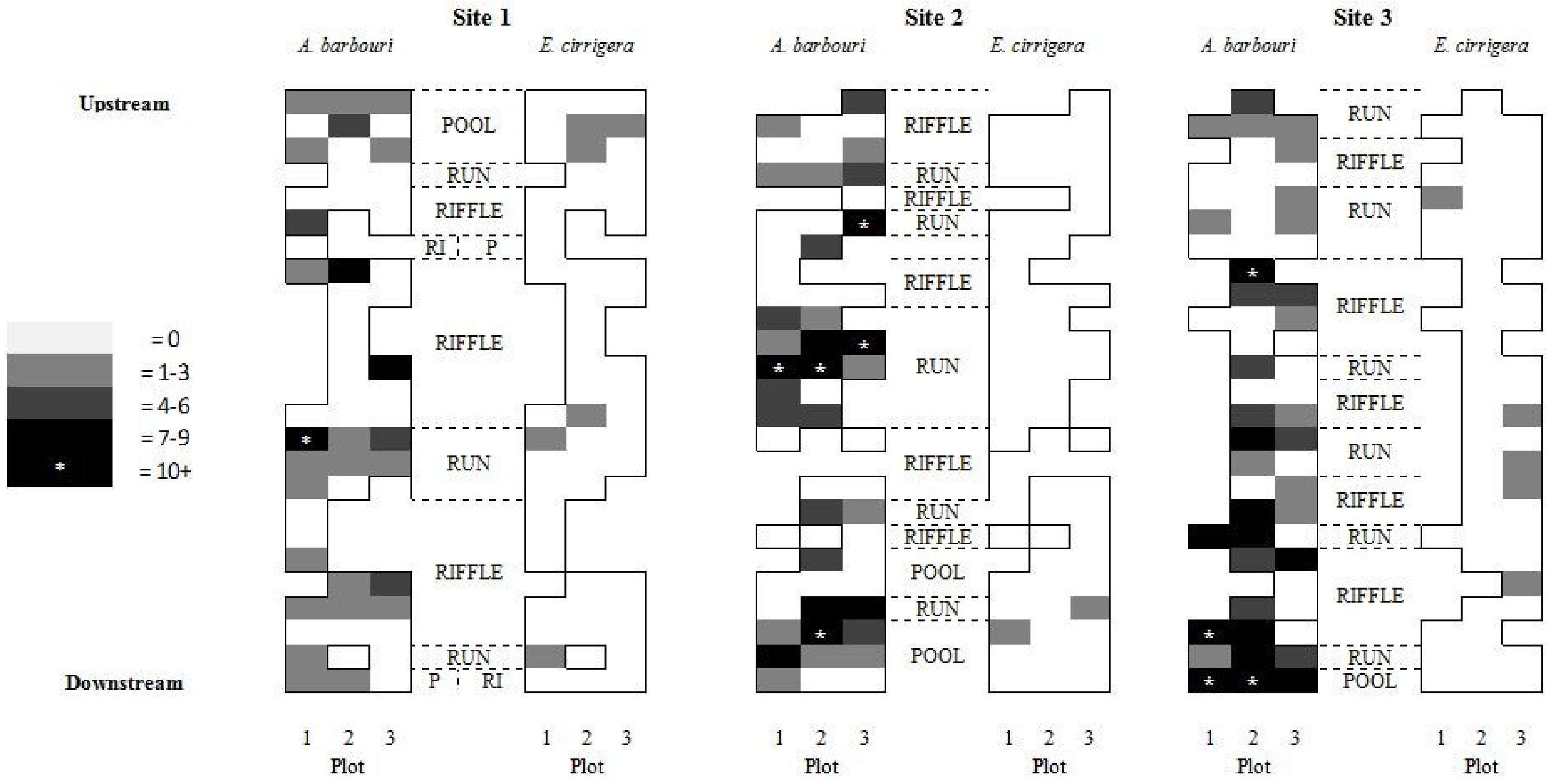
Table 10. Top candidate models predicting abundance of *Eurycea cirrigera* in late spring.

Model	K	Quasi Log-likelihood	$QAIC_c$	Δi	w_i
depth + embedded	4	-22.67	54.31	0	0.48
boulder + bedrock + embedded	5	-22.94	57.38	3.07	0.10
depth + microcondition	5	-23.38	58.25	3.94	0.07
embedded	3	-26.01	58.60	4.29	0.06
boulder + bedrock	4	-24.88	58.74	4.43	0.05
depth	3	-26.19	58.96	4.65	0.05
stream	4	-25.21	59.39	5.08	0.04
depth + bedrock + boulder	5	-23.96	59.43	5.12	0.04
mesohabitat	4	-25.63	60.24	5.93	0.02
intercept	2	-28.34	60.96	6.65	0.02
debris + depth	4	-26.04	61.05	6.74	0.02
bedrock + depth	4	-26.17	61.31	7.00	0.01
microcondition	4	-26.46	61.89	7.58	0.01
bedrock	3	-27.98	62.54	8.23	0.01
A. barbouri presence + microcondition	5	-25.69	62.87	8.56	0.01
A. barbouri presence	3	-28.17	62.91	8.60	0.01
microcondition + embedded	5	-25.75	62.99	8.68	0.01

[a] Global model: microcondition (micro-run, micro-riffle, micro-pool) + stream (site 1, site 2, site 3) + mesohabitat (run, riffle, pool) + bedrock (%bedrock cover within sampling plot) + boulder (%boulder cover within sampling plot)+ embedd (%substrate embedded within sampling plot) + debris (%debris coverage within sampling plot) + depth (depth at midpoint of sampling plot) + *A. barbouri* presence (presence of *Ambystoma barbouri* within sampling plot)

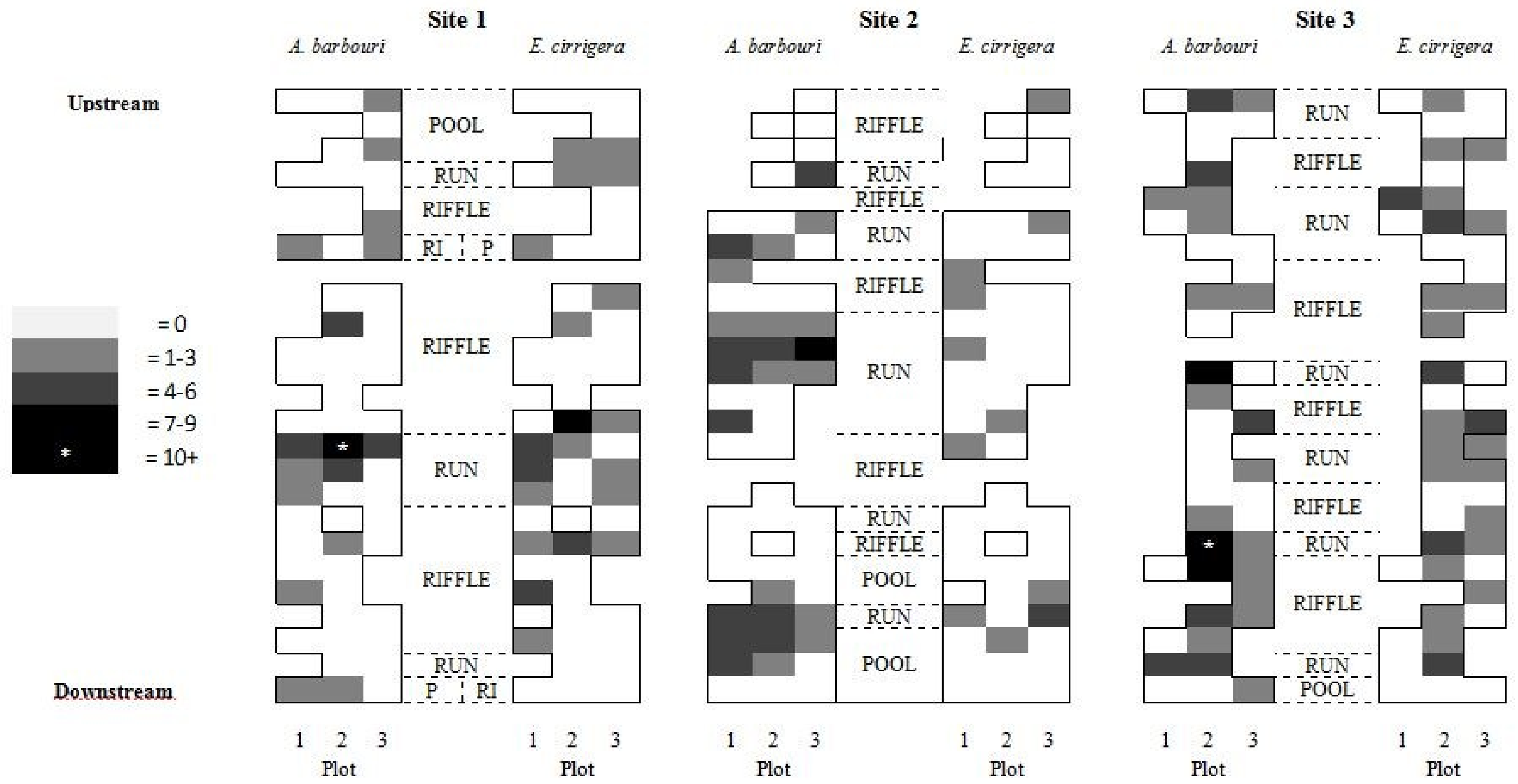
Table 11. Results of averaging across all models that include top predictive parameters of *Eurycea cirrigera* abundance in late spring.

Parameter	β	85% CI Lower	85% CI Upper
depth	0.179	0.090	0.273
boulder	-0.067	-0.108	-0.026
bedrock	-0.004	-0.018	0.009
debris	0.034	-0.008	0.075
embedded	-0.015	-0.028	-0.002
micro-run v micro-pool	-0.274	-1.134	0.587
micro-riffle v micro-pool	-0.4722	-1.458	0.514



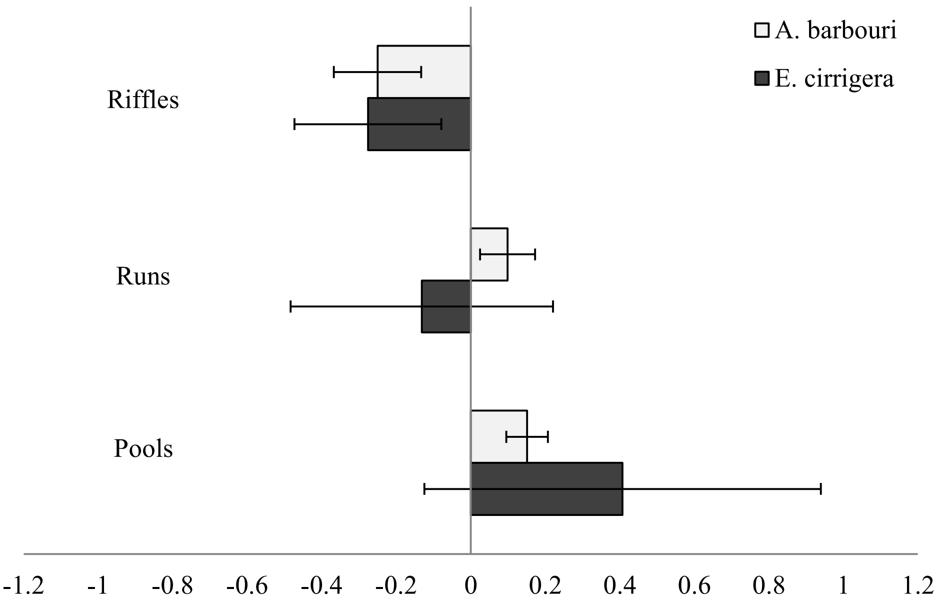
Notes: Solid outlines represent areas of the stream that held water. Shaded areas represent number of observations in a sampling plot. Dotted lines represent boundaries between mesohabitat types within streams.

Figure 1. Graphical representation of distribution patterns of *A. barbouri* and *E. cirrigera* during early spring



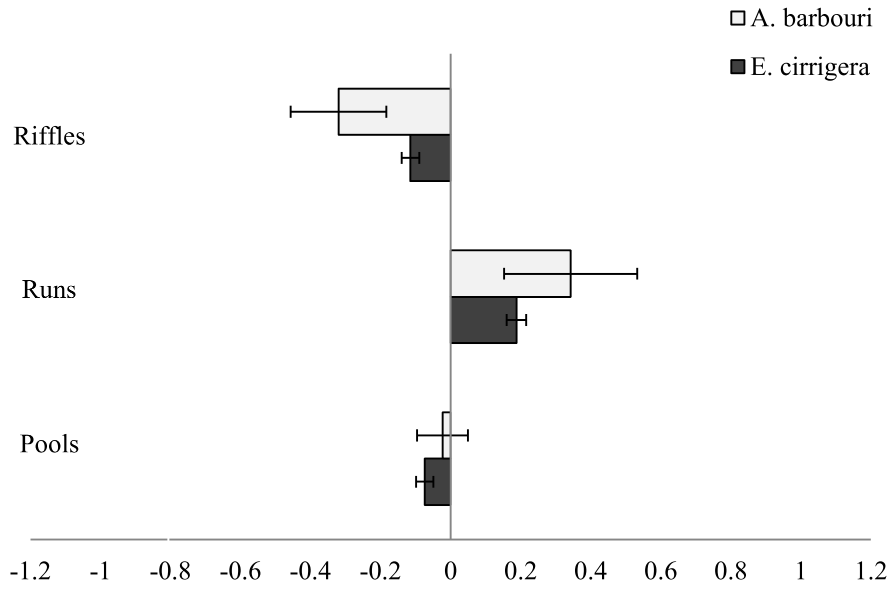
Notes: Solid outlines represent areas of the stream that held water. Shaded areas represent number of observations in a sampling plot. Dotted lines represent boundaries between mesohabitat types within streams.

Figure 2. Graphical representation of distribution patterns of *A. barbouri* and *E. cirrigera* during late spring



Notes: Bars represent difference between observed proportions of captures compared to natural availability represented by the zero line. Error bars represent 95% CI

Figure 3. Mesohabitat associations of larval salamanders in early spring averaged across all sites.



Notes: Bars represent difference between observed proportions of captures compared to natural availability represented by the zero line. Error bars represent 95% CI

Figure 4. Mesohabitat associations of larval salamanders in late spring averaged across all sites.