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AMPHIBIAN LARVAE DISTRIBUTION AMONGST INTERMITTENT STREAM POOLS
IN THE FLINT HILLS COVARIES WITH VEGETATION AND FISH COLONIZATION

A Thesis by

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Bachelor of Science, Pittsburg State University, 2019

Submitted to the Department of Biological Sciences
and the faculty of the Graduate School of
Wichita State University
in partial fulfillment of
the requirements for the degree of
Master of Science

May 2021

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IN THE FLINT HILLS COVARIES WITH VEGETATION AND FISH COLONIZATION

The following faculty members have examined the final copy of this thesis for form and content, and recommend that it be accepted in partial fulfillment of the requirement for the degree of Master of Science, with a major in Biological Sciences.

Thomas Luhring, Committee Chair

Leland Russell, Committee Member

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DEDICATION

To my family, friends, and my wife, Sarah, for their everlasting support.

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ABSTRACT

Climate change is expected to increase the frequency and severity of droughts and precipitation events. The connectivity and hydroperiod among stream pools are expected to change due to these climatic events, therefore influencing what organisms occupy them. Intermittent stream pools in the Great Plains present an idealized replicated system to study the impacts of variable climatic conditions on the distribution of aquatic species, including amphibians. In the Great Plains, intermittent stream pools are the most abundant spawning habitat for amphibians. We sampled 117 stream pools to investigate the effects of fish presence, stream vegetation, hydroperiod, connectivity, and pool volume on larval amphibian distribution, biomass, and density in the Flint Hills of Kansas. Larval amphibians preferred fishless, isolated pools and the effect of volume depended on the connectivity and fish occupancy of that pool ($p < 0.05$). In small pools where amphibian larvae occurred ($n=31$), density(g/m^3) was higher in pools dominated by macrophyte vegetation and decreased as pool volume increased ($p < 0.01$). We sampled during a wet year (12.24 inches above the 10-year average) which implies that fish distribution is at a maximum across the streams on this landscape and are having a large effect on the spatial distribution of amphibian larvae. Although more precipitation has the potential to increase the likelihood of larval amphibian presence by filling up more pools, this also increases connectivity among stream pools allowing for increased predatory fish colonization. Understanding how fish and amphibian larvae currently utilize intermittent streams in the Flint Hills will allow us to detect distribution shifts due to climate change.

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CHAPTER 1

INTRODUCTION

1.1 Climate Change

Shifts in precipitation and thermal regimes are particularly important to the aquatic landscape of the Great Plains, which exists in a balance of interspersed droughts and floods (Dodds et al. 2004). Effects of climate change are becoming more prevalent, including increasing temperatures, increasing precipitation intensity, and more severe droughts (Overpeck and Udall 2010; Woldeamlak et al. 2007; Walther et al. 2002). Shifts such as these will likely influence fish and amphibian distribution (Comte & Olden, 2017) and how they interact with each other (Blois et al., 2013). Understanding how fish and amphibian larvae currently utilize intermittent streams in the Flint Hills will allow us to detect distribution shifts due to climate change.

The Great Plains is an imperiled landscape (Samson et al. 2004) where few studies have focused on the intermittent stream ecosystems within it and the distribution of fishes and amphibians among them. Wetlands that are temporary but colonized by fish and wetlands that are permanent but fishless represent understudied categories of freshwater ecosystems that may influence herpetofaunal diversity (Holbrook & Dorn, 2016). This is concerning because the Great Plains intermittent stream system (GPISS) is the most abundant habitat for amphibians and fishes. Additionally, small streams constitute more than 50% of the total channel length in most watersheds (Hansen, 2001). Intermittent streams in particular can be highly susceptible to climatic disturbances (Poff & Ward, 1989). Depending on habitat location and connectivity to water sources, such as off-stream wetlands and isolated ephemeral stream pools, flooding could introduce fishes into an aquatic habitat that previously lacked them.

It is hypothesized that hydroperiod, or the length of time an area holds water (Brooks and Hayashi 2002; Babbitt and Tanner 2000), and connectivity, or the water flow between stream pools, shapes the composition of aquatic communities. Increased connectivity may enhance the presence of fish which are known to negatively impact the occupancy of amphibian larvae in other systems (Hecnar & M'Closkey, 1997; Pilliod et al., 2010). Many commonly dispersing fishes are opportunistic predators that feed on larval amphibians (Heyer et al. 1975) and amphibians actively avoid ovipositing in wetlands with fish present (Hopey & Petranka, 1994; Kats & Sih, 1992; Petranka & Holbrook, 2006; Resetarits & Wilbur, 1989). This increased fish predation would lead to a top-down change in the trophic structure of the aquatic ecosystem (Wilkins et al., 2019).

1.2 Great Plains Fish Ecology

Population dynamics of fishes are affected by seasonal and interannual variations in climatic, hydrological, and geographical processes (Nakagawa, 2019). Fishes are a mobile component of stream ecosystems and their abundance is regulated by both hydrology and spatial position of aquatic resources in the landscape (Fausch et al., 2002). Many fishes of the Great Plains have adapted to the unpredictable, harsh conditions and can migrate to permanent bodies of water, reproduce fast, and can endure poor water quality in isolated pools (Labbe and Fausch 2000; Matthews 1987).

Most adult fishes in prairie ecosystems avoid areas with excessive currents produced from flooding or pools that dry frequently (Dodds et al. 2004). An example would be headwater species that move downstream to avoid harsh conditions from drought (Alford & Richards, 1999; Deacon, 1961). Effects of disturbance on prairie stream fishes can vary depending on connectivity to refugia habitat (Larimore et al. 2011) and the fishes ability to reproduce after the disturbance (Fausch & Bestgen, 1997). Fish assemblage is influenced by species identity and life stage because swimming

strength is proportional to body size and smaller individuals may not be able to resist displacement and will be washed downstream (Dodds et al., 2004; Harvey, 1987).

Timing of droughts and floods effect fish communities. Floods that occur early in the year during spawning season will flush fish eggs and larvae from the stream whereas floods in late summer will have a lower impact since most fish have spawned and their young have grown large enough to be more effective swimmers (Dodds et al., 2004). Flooding usually happens during the spring in the Great Plains, but many stream fishes can initiate spawning immediately after a disturbance (Dodds et al., 2004). Floods also increase connectivity to upper stream reaches that have valuable resources and allow fishes to move past upstream barriers to reach ephemeral pools (Dodds et al., 2004). Precipitation tends to occur less frequently as summer advances, which may lead to fishes being stranded in ephemeral pools, becoming easy prey (Dodds et al., 2004).

Droughts may have little effect on fish assemblage and recovery happens rapidly (Matthews and Marsh–Matthews 2003). Fish diversity within the Flint Hills is typically higher in permanent, downstream pools (Tripe & Guy, 1999). The fish that colonize the upper reaches have to move back downstream when drying occurs (Deacon 1961; Ross et al. 1985) or they would desiccate. Consecutive years of drought, however, may cause severe impacts on fish assemblage. The potential impacts of consecutive droughts on fish have not been documented in the Great Plains (Deacon 1961; Matthews and Marsh–Matthews 2003).

1.3 Effects of Abiotic and Biotic Factors on Amphibians

Interactions among organisms within their ecosystem depend on abiotic factors such as temperature, droughts, and floods. (Luhring et al. 2019; Thurman & Garcia, 2019), which are all expected to increase in severity due to climate change. Organisms may adapt to climate change through rapid evolution and/or by changes in behavior, physiology, and life history (Charmantier

et al. 2008; Charmantier and Gienapp 2014; Anderson et al. 2012; Schaum et al. 2017; Angilletta et al. 2010; Seebacher et al. 2015; Réale et al. 2003; Padfield et al. 2016; Knies et al. 2009; Knies et al. 2006; Tseng and O'Connor 2015). Species specific responses to climate change suggest that favorable conditions should be different among species for resisting population decline and competitive exclusion (Thurman & Garcia, 2019). Moreover, biotic factors such as predator cues can strongly influence amphibian evolution, development, behavior, physiology, and life history (Flowers and Graves 1997; Mushet et al. 2012; McCollum and Van Buskirk 1996; Szuroczki and Richardson 2011).

By understanding natural stressors on larval amphibian distribution, we can accurately monitor shifts caused by climate change. In the Great Plains, amphibians prefer to breed in seasonal and semipermanent wetlands but will also use permanent wetlands if fish are absent (Petranka 1989; Sexton and Phillips. 1986; Bradford 1989; 1991; Bradford et al. 1993; Fellers and Drost 1993; Bronmark and Edenhamn 1994; Lannoo 1998). However, some amphibians can coexist well with fish, as observed with *Lithobates catesbeianus* (American bullfrog). During drought events, amphibians are excluded from seasonal and permanent wetlands since they are dried up, therefore relying on fishless, permanent wetlands for breeding (Pechmann et al. 1989; Wissinger and Whiteman 1992; Dodd 1994; Semlitsch et al. 1996; Lannoo 1998). Amphibians must adjust their breeding strategy based on shifts in the landscape to increase survival of their physiologically limited larvae. Species with longer larval stages usually are heavily dependent on water sources not drying, but some species have been documented to be more tolerant these stresses (Crump, 2005).

Larval amphibian distribution in the Flint Hills is not as thoroughly analyzed compared to other systems. Based on studies in other systems, larval amphibians are successful in habitats with

large surface areas and shallow depths (Wheeler et al., 2015), but they have also been observed to be more abundant in intermediate sized ponds since they have a long enough hydroperiod for larval development and have a lower probability to contain fish (Semlitsch et al., 2015). However, fish also persist in areas with long hydroperiods, and most amphibians cannot coexist with fish. If more rainfall increases the rate in which intermittent streams connect to water sources occupied by fishes, the chance of colonization by fishes increases. By considering the connectivity of aquatic ecosystems, we can determine which areas are more likely to have fish and thus predict the effects on the amphibian community.

1.4 Importance of Amphibians

Amphibians serve important roles in ecosystems through nutrient cycling, burrowing, and controlling insect populations (Hocking & Babbitt, 2014). Additionally, these ectotherms serve as indicators of environmental degradation (Halliday 2000) and are one of the most imperiled groups of vertebrates, with populations declining faster than birds or mammals (Stuart et al., 2004). These declines have been accelerating due to the impacts of climate change on their physiology and life history strategies (Ceballos et al., 2015; Wake & Vredenburg, 2008). Secondary productivity is the rate of growth organisms acquire through consumption across time and space. Secondary production estimates have been conducted on a variety of organism in nature such as macroinvertebrates (Whiting et al. 2011) and fishes (Meyer & Poepperl, 2004), but can be applied to almost any taxa. Few studies have examined larval amphibian production in nature, especially in the Great Plains. While presence/absence data may provide information on species richness, measuring secondary production is more informative for quantifying and characterizing assemblages in lotic ecosystems (Whiting et al. 2011). Further, secondary production accounts for

multiple factors, such as abundance, biomass, growth, reproduction, and survivorship (Benke & Huryn, 1996).

1.5 Amphibian Landscape Use in the Great Plains

Climate variability is likely to alter hydrology of wetlands and streams, causing connectivity among populations to decrease during drought or increase during periods of deluge (Pilliod et al., 2015). Amphibian distribution in the Great Plains is strongly influenced by climatic events and distribution of adequate habitats. Depending on the species, amphibians utilize a variety of aquatic habitats, including wetlands, streams, ponds, lakes, ditches, and rivers. Wetlands are critical ecosystems that provide services, such as suitable habitat and breeding sites that promote amphibian populations (de Groot et al. 2012; Junk et al. 2013). How wetlands obtain their water will influence their hydroperiod, physio-chemical characteristics, vegetation composition and structure. This in turn influences the amphibians and fishes that use these wetlands (Burt and Haycock 1996; Semlitsch and Bodie 1998; Hayashi et al. 1998; Moore and Richardson 2003).

Larval amphibian response to connectivity and hydroperiod is expected to be strong in the Great Plains due to changes in suitable habitat resulting from climatic variation. Amphibians utilize isolated, ephemeral wetlands or streams that obtain their water source by rainfall compared to wetlands that are flooded into by other bodies of water that introduce fish (Greenberg et al. 2017). Water deposition in wetlands depends on the topography of the landscape, the proximity of water sources (connectivity), and the severity of climatic events.

Fishes and amphibians in the Flint Hills region of the Great Plains inhabit the intermittent (seasonal) streams, which are more abundant than wetlands and perennial streams (Dodds et al., 2004). Streams and their riparian zones promote dispersion and migration of amphibians between habitats (Dupuis et al. 1995; Rosenberg et al. 1997; Johnson 2004; Mazerolle 2005; Perkins and

Hunter 2006; Semlitsch 2008). While small streams can support amphibians (Rosenberg et al. 1997; Moore and Richardson 2003), their connectivity and fish occupancy determine the suitability of habitat for larval amphibians.

1.6 Hypotheses

Here, we investigate the effects of hydroperiod, water connectivity, total pool volume, dominant stream vegetation, and fish occupancy (presence/absence) on larval amphibian occupancy, biomass, and density in the GPISS. Across the landscape we sampled, we test the following hypotheses: the likelihood of larval amphibian presence will decrease in the presence of fish, the likelihood larval amphibian presence will increase as hydroperiod increases, and the likelihood of larval amphibian presence will increase in isolated pools. For stream pools where amphibian larvae were present, we test the following hypotheses: larval amphibian secondary production (biomass/density) will decrease in the presence of fish, larval amphibian secondary production will increase as hydroperiod increases, and larval amphibian secondary production will increase in isolated pools.

CHAPTER 2

MATERIALS AND METHODS

2.1 Study Site

Most aquatic habitats of the Great Plains have been negatively impacted by agriculture or urbanization, resulting in pollution, hydrologic disturbance, and physical modification of these ecosystems (Dodds et al. 2004). The Flint Hills of Kansas are unique because the landscape is too rugged for agriculture and most of the region is utilized for cattle grazing instead (Hickey & Webb, 1987). We used Youngmeyer Ranch (YMR), a Wichita State University field station that is 4,700 acres located in the Flint Hills of Elk County, Kansas (Figure 1). Elevation is highly variable with the west side of YMR being relatively flat at approximately 460 m in elevation, whereas the middle and east sides feature steep to gradual slopes that give way to sloped hillsides with elevations between 370-400 m (Houseman et al., 2016). The study site area is about 17.98 km² with about 39.40 km of first, second, and third order streams that flow along the elevational gradient of the site from either west to east or north to south. It has been shown that the number of fish species increases from headwaters to higher-order streams (Rahel & Hubert, 1991; Schlosser, 1987; Sheldon, 1968).

Several cattle ponds and wetlands are found throughout YMR. 12 out of the 13 cattle ponds currently have predatory game fish occupying them (Ward K., unpublished data). The station is predominantly grassland with scattered black oaks (*Quercus velutina*) along creeks (Houseman et al., 2016). YMR has been historically known for cattle grazing and prescribed fires that routinely occur every 1-3 year (Houseman et al., 2016). There are potentially 65 species of fish, 12 species of anurans, and 2 species of caudates within Elk County based on current range maps (Collins et al. 2010; Kansas Fishes Committee, 2014).

2.2 Mapping and Hydroperiod Indices

Initial hydroperiod indices were calculated using Google Earth Pro©(Gorelick et al., 2017). Streams were mapped by creating paths in approximately 100 m increments until the stream lengths were fully mapped. Of the total 31,400 m of streams mapped, we picked a subset of 19 streams that were representative of the site to select pools for hydroperiod score collection. A limitation of our stream pool selection was trying to distinguish pools from runs and riffles. Pools are typically characterized by larger depths and low velocity stream flow, whereas runs and riffles have shallower depths and faster water flow. These two stream characteristics cannot be accurately determined by using satellite imagery. For each 100 m segment of stream, we chose two pools at random to calculate initial hydroperiod scores, for a total of 318 stream pools. Scores were calculated by recording the presence of water at each of the four most recent historical time periods (10/17/2010, 2/28/2012, 2/16/2013, 11/5/2014) that were available through Google Earth Pro© (Figure 2). We made sure to select two years where the image was taken during the early, wet season and two years representing the later, dryer season. We added an additional hydroperiod score if pools had water during the day of sampling, so pool scores could be 1-5, in which 1 is ephemeral and 5 is permanent.

2.3 Sampling Design

We used a variety of sampling techniques as they have been shown to be generally more effective at collecting a wider array of species (Luhring, 2007) due to the sequence of events leading up to a successful capture being susceptible to an individual's behavior or physiology biases (Luhring et al. 2016). Aquatic surveys were completed using active sampling techniques: dip netting and seining. To be successful, the mesh size needed to be small enough to prevent larval amphibians from escaping (Luhring et al. 2016).

Surveys took place from 5/19/2020 to 6/30/2020. We sampled a total of 117 stream pools out of 151 (34 were dry). Before pool sampling, we recorded the type of bank vegetation (grasses, shrubs, trees, bare ground), in-stream vegetation (macrophytes, grasses, bare), algae type (filamentous, mat, none), and the inflow/outflow status. We also recorded the percent cover (0%, 25%, 50%, 75%, 100%) of canopy, vegetation litter, algae, and biofilm present. To measure stream pool connectivity, if it had inflow or outflow, the pool was considered connected, however if it lacked flow, it was considered isolated. We used seines, hand capture, and enclosures with dip nets for active capture of fishes and larval amphibians. Additionally, visual observations would help determine presence and absence of amphibians.

We used constrained volume sampling with an enclosure to subsample each pool. We used a cylindrical rubber trash can (51 X 51 X 65 cm) with the bottom cut off as our enclosure trap and it was placed throughout the open water habitat. These were randomly placed (random number generator) on either the left (1), middle (2), or (3) right side on the downstream end. If the pool was less than 14 m long, enclosure placements progressed upstream in 1 m increments. If a pool was between 14-24 m long, enclosures progressed upstream in 2 m increments. If a pool was between 24-34 m long, enclosures progressed upstream in 3 m increments. We chose to increase increment distance as pool length increased so that large pools were not oversampled relative to smaller pools. Using a 10 m long pool with an initial placement at the middle for example, the next placements would follow a subsequent systematic design going from middle (0 m) to right (1 m), right to left (2 m), left to middle (3 m), and so on. Depth readings were taken in the center of every enclosure placement, which is how we calculated sampled volume (length and width held constant). For each placement, a round dip net with 0.3 cm mesh was swept through the water column within the enclosure until 3 consecutive dip net sweeps returned no larval amphibians,

fishes, or invertebrates (this project was nested in a larger project). Captured organisms were kept in separate buckets filled with water from the habitat. Amphibian larvae were identified using *A Guide to Larval Amphibian Identification in the Field and Laboratory* (Hoverman et al., 2015). Following identification, larval amphibian mass was measured via volumetric displacement in graduated cylinders, whereby volume in milliliters was converted to grams in a 1:1 ratio based on the assumption that measured larvae had the same density as water. Organisms were released back into their habitat after the data collection.

After enclosure sampling, we completed two seine passes through the pool. The size of the pool and the amount of aquatic vegetation determined which seine size we would use. Three different sized seines were used: a 3' width x 3' height, small seine with fine mesh (<0.1 cm), a 10' width x 3' height, medium size seine with 0.5 cm mesh, and a 15' width x 6' height bag seine with a 6'x6'x6' bag in the center with 1.3 cm mesh. The data recorded and the containment and release of organisms was the same as enclosure sampling.

2.4 Estimating Total Pool Volume, Total Biomass, and Density

We estimated total pool volume (TV) by collecting cross sectional width and depth measurements every 2 m along the length of the stream pools, see Appendix C to view the protocol for measuring pool volume. We did this to extrapolate our sampled larval biomass (SB) within our sampled volume (SV) retrieved from enclosure sampling to estimate the total larval biomass (TB) within the entire stream pool which is calculated using equation (1). The total larval amphibian biomass is the measurement we used for analysis. Density was the concentration of sampled larval biomass (SB) per sampled volume (SV).

$$\frac{TV}{Pool} * \frac{SB}{SV} = \frac{TB}{Pool} \quad (1)$$

2.5 Statistical Analysis

2.5.1 Presence/Absence

Presence/absence analysis was limited to pools that held water (n=117, out of 151; 34 were dry) across all trap types used (enclosure, seine, dip net, visual, or hand capture). We encountered five species of larval amphibians: *Anaxyrus americanus* (American toad), *Pseudacris maculata* (boreal chorus frog), *Lithobates blairi* (plains leopard frog), *Lithobates catesbeianus* (American bullfrog), *Ambystoma texanum* (small-mouthed salamander). We further analyzed all larval amphibians combined, *L. blairi* tadpoles, and *A. americanus* tadpoles since they had sufficient sample sizes (detected at 15+ stream pools).

To investigate which factors affected larval amphibian occupancy (probability of presence), we constructed candidate models including 1-3 factor generalized linear models (GLMs) with every possible combination, including interactions, between fish presence, total pool volume, and connectivity as explanatory variables. GLMs were fitted for a binomial regression using the logit function. Models were ranked using Akaike Information Criterion values corrected for small sample size (AICc). AICc weights and comparisons were calculated using ‘AICctab’ in the ‘bbmle’ package (Bolker, 2013). The strongest models (AICc values < 2.0) (Burnham & Anderson, 2002) were further analyzed using an analysis of variance (‘Anova’ in the ‘car’ package; Fox and Weisberg 2019). Type II sum of squares (SS) were used on models with no interaction effects and Type III SS for models with interactions. All statistical analyses were conducted using RStudio 3.6.1 (RStudio Team 2020).

2.5.2 Biomass and Density

Biomass and density analyses included enclosure captured larvae and only pools where larval amphibians occurred (n=31). We focused on enclosure sampling since this technique was

how we estimated total biomass and density. Rather than focusing on the distribution of larval biomass and density across the landscape (which occupancy essentially explains), we wanted to observe what influences their production and concentration where they occur. We further analyzed all larval amphibians combined, *L. blairi* tadpoles (n=21), and *A. americanus* tadpoles (n=18).

We excluded models that contained a two-way interaction between fish occupancy and stream vegetation and a two-way interaction between connectivity and vegetation due to us sampling a relatively small number of pools and not having a particular fish (present or absent) or connectivity (connected or isolated) observation across all three stream vegetation categorical observations (macrophytes, grasses, and bare). Similarly for *L. blairi* biomass, we had to avoid interactions between stream vegetation and hydroperiod. For *A. americanus* density we avoided models with interactions between fish occupancy and connectivity, fish occupancy and hydroperiod, and stream vegetation and hydroperiod. We used AICc model comparison and ANOVA similarly as the presence/absence analysis. Models that had dominant stream vegetation as the best predictor variable with no interaction, were further analyzed using a Tukey's HSD post hoc test to determine if macrophytes, grasses, or bare differed from each other (using 'glht' in the 'multcomp' package; Hothorn et al. 2008).

For total larval biomass, we constructed candidate models, including 1-4 factor GLMs with every possible combination, including interactions, with fish occupancy, connectivity, hydroperiod, and dominant stream vegetation as explanatory variables and log transformed larval amphibian biomass as the response variable. Amphibian biomass was log transformed due to raw data having a right skewed distribution. We excluded total pool volume from the biomass models since total pool volume was used to estimate total amphibian biomass. The only difference for the larval amphibian density analysis is that we included log total pool volume as an explanatory

variable. Larval density and pool volume were log transformed because the data had a right skewed distribution. We used fish occupancy instead of fish abundances because there were no differences in detecting significant effects on larval amphibian abundances, especially since few pools had fish (n=7) and the use of either main effect did not alter our results.

CHAPTER 3

RESULTS

3.1 Factors Influencing Larval Amphibian Occupancy

Out of the 151 pre-selected pools, 117 held water and were sampled. We detected five different species of larval amphibians across YMR and recorded occupancy, biomass, and density data (Table 1). There was little overlap between larval amphibian and fish occupancy across the property, with larval amphibians present in 40 pools, fishes in 68, and only 13 pools had both. 30 pools were macrophyte dominated, 34 grass, and 53 bare.

Amphibian larvae occupancy was best explained by a model with fish occupancy, connectivity, and total pool volume as main effects, with every possible two-way interaction between them, and a three-way interaction between them ($\chi^2_1 = 5.60$, $p = 0.02$; Table 2). As predicted, amphibian presence was higher when fish were absent and increased with pool volume (Figure 3). In isolated pools where fish were present, the likelihood of amphibian larvae being present decreased as volume increased. This contrasts with connected pools where amphibian occupancy increased as volume increased even with fish present. Hydroperiod was not a significant predictor of amphibian presence, potentially because our sampling occurred following a wet year when fish were widespread across pools that normally dry between years.

Predictors for presence of larval amphibians were species specific. Fish had a negative effect on *L. blairi*, but where fish were present, the likelihood of larvae being present increased as pool volume increased ($\chi^2_1 = 10.41$, $p = 0.001$; Figure 4). *Lithobates blairi* preferred isolated habitats where fish were present but where fish were absent, they did not have a preference on connectivity ($\chi^2_1 = 4.11$, $p = 0.04$; Figure 5). The top model that best explained *L. blairi* occupancy had fish occupancy, connectivity, and pool volume as main effects, with every possible two-way

interaction between them, and a three-way interaction between them (Table 3), however, the three-way interaction at best was only marginally significant ($\chi^2_1 = 3.12$, $p = 0.08$). The second-best model has two, two-way interactions from the same three variables and has a low AICc score of 0.8. A two-way interaction between fish and pool volume was significant in both models, but the two-way interaction between fish and connectivity was only significant in the top model, so including the three-way interaction provides more explanatory power but we only further analyzed the two significant two-way interactions.

Regardless of the connectivity status, fish presence negatively affected *A. americanus* tadpoles and vice versa ($\chi^2_4 = 4.07$, $p = 0.04$; Figure 6). When fish were absent, *A. americanus* was more likely to occupy connected habitats, which may be due to a large sample in a highly connected stream that had a physical barrier downstream, therefore preventing fish colonization to upper reaches. This would imply that fish presence is the mechanism that determines amphibian occupancy. Although there were other strong models (fish, and fish + connectivity), having the interaction between fish and connectivity better explained the occupancy of *A. americanus* (Table 4). Fish was significant in all three models but connectivity was only significant if the interaction with fish was included.

3.2 Factors Influencing Larval Amphibian Biomass

For the 20 connected and 11 isolated stream pools where larval amphibians occurred, the average estimated total amphibian biomass was $256\text{g} \pm 541$ ($\bar{X} \pm \text{SD}$). For the east side ($n = 16$), the average biomass was $41\text{g} \pm 40$ per pool whereas the west side ($n = 15$) had an average of $485\text{g} \pm 718$. All 16 pools were connected on the east side and the west side had 11 isolated and 4 connected stream pools. Out of the 31 stream pools where larval amphibians occurred, only 7 of the pools had fish present. 10 pools were macrophyte dominated, 18 grass, and 3 bare.

Macrophyte dominated pools had higher larval amphibian biomass ($\chi^2_2 = 38.86$, $p < 0.001$; Figure 7) compared to grass ($t_2 = 5.87$, $p < 0.001$) and bare pools ($t_2 = 4.20$, $p < 0.001$). In addition to the top model, the other model with support only had significant vegetation effects (Table 5). *Lithobates blairi* larval biomass was higher in macrophyte dominated pools ($\chi^2_2 = 23.33$, $p < 0.001$) compared to grass pools ($t_2 = 5.3$, $p < 0.001$; Figure 8). The second strongest model for *L. blairi* included an additional significant effect from hydroperiod but after further analysis, there were no significant differences among categories (Table 6). The third strongest model only had significant vegetation effects. Similarly, *A. americanus* larval biomass was higher in macrophyte dominated pools ($\chi^2_2 = 14.34$, $p < 0.001$; Figure 9; Table 7) compared to grass ($t_2 = 3.54$, $p = 0.007$) and bare pools ($t_2 = 3.12$, $p = 0.02$). Our small sample size of barren pools could not be used for meaningful conclusions. Conversely, since we only found 3 barren pools out of the 31 with larvae present, this could be due to their preference for pools with vegetation. Regardless, our sample size for both grasses and macrophytes were large enough to report that larvae preferred pools with macrophytes over grasses.

3.3 Factors Influencing Larval Amphibian Density

The average amphibian density across YMR was $28\text{g/m}^3 \pm 102$. On the east side of the property the average density was $8\text{g/m}^3 \pm 20$, while the west side had an average of $60\text{g/m}^3 \pm 156$. For the 31 stream pools where larval amphibians occurred, the average amphibian density was $63\text{g/m}^3 \pm 139$. For the east side, the average density was $37\text{g/m}^3 \pm 106$ whereas the west side had an average of $186\text{g/m}^3 \pm 718$.

Larval amphibian density was higher in isolated pools ($\chi^2_1 = 11.46$, $p < 0.001$; Figure 10) and pools that were dominated by macrophytes ($\chi^2_2 = 22.98$, $p < 0.001$) compared to grass ($t_2 = 4.74$, $p < 0.001$) and bare pools ($t_2 = 3.24$, $p = 0.009$). Larval amphibian density was highest in

small pools where macrophytes dominated ($\chi^2_3 = 11.31$, $p = 0.01$), but as pool volume increased, amphibian density decreased (Figure 11). All pool sizes above 10 m³ were macrophyte dominated. Grass dominated and bare pools tended to be smaller and amphibian density was lower than macrophyte dominated pools of similar size. The two top models shared significant connectivity and vegetation main effects (Table 8). Here, we presented results from the top model which included an interaction between log pool volume and vegetation.

Lithobates blairi density was higher in macrophyte dominated pools ($\chi^2_2 = 6.79$, $p = 0.03$) compared to grass pools ($t_2 = 2.49$, $p = 0.05$; Figure 12). Larval *L. blairi* density was higher in isolated pools compared to connected pools ($\chi^2_1 = 16.15$, $p < 0.001$; Figure 13). The two top models are similar in that connectivity seems to be the main driver for *L. blairi* density (Table 9). Macrophyte dominated pools had higher *A. americanus* densities ($\chi^2_2 = 39.14$, $p < 0.001$; Figure 14; Table 10) compared to grass ($t_2 = 6.15$, $p < 0.001$) and bare pools ($t_2 = 4.89$, $p < 0.001$).

CHAPTER 4

DISCUSSION

Larval amphibian occupancy was most influenced by fish occupancy, connectivity, and pool volume. It was no surprise that fish were a strong predictor for explaining amphibian occupancy (Heyer et al. 1975; Bradford 1989; Hecnar and M'Closkey 1997). Larval amphibian occupancy was higher in isolated pools to an extent, but other factors such as fish occupancy and pool volume, affected amphibian occupancy differently in isolated and connected pools. Sensitivity to volume and connectivity were species specific, but both factors played a role in whether amphibians and/or fish were present in stream pools. Where larval amphibians occurred, the vegetation community showed strong effects on both biomass and density.

Although few studies have looked at larval stream amphibian distribution in the Flint Hills, there are studies in other systems that have shown similar results. *Rana sierrae* (Sierra Nevada yellow-legged frog) tadpole abundance in lakes showed negative responses to fish presence, although the model had high uncertainty (Wilkins et al., 2019). *Hyla versicolor* (gray treefrog) tadpoles were nine times less abundant when *Lepomis macrochirus* (bluegill sunfish) were present in experimental ponds (Smith et al., 1999). Conversely, *L. catesbeianus* tadpole abundance increased in the presence of bluegill (Smith et al., 1999). Many studies provide evidence that fishes have a negative impact on most amphibian species across all life stages (Heyer et al. 1975; Bradford 1989; Hecnar and M'Closkey 1997). Our study extends this pattern to larval amphibian species in the Flint Hills.

Habitat size has been found to be both positively and negatively correlated with amphibian richness and abundance (Asad et al., 2020; Eterovick, 2003; Strauß et al., 2010; Wilkins et al., 2019). Pool size is important, but the effect is context specific. Pool volume alone may not predict

larval amphibian presence, biomass, and density, due to other factors having strong influences (e.g. fish presence, vegetation). However, pool volume is a crucial abiotic component in this system since it influences how the biota interact and should be considered in further studies to understand its relationship with predator-prey interactions.

Few studies have specifically investigated the relationship between larval or adult amphibians and stream connectivity. If connectivity from a water source that has fish increases, observing a positive response from amphibians is unlikely. Supporting this hypothesis, amphibian occupancy and density was generally higher in isolated pools. In isolated pools with fish present, amphibian occupancy decreased as pool volume increased, most likely because larger isolated pools allow for more fish to be present. Where connected pools had fish present, pool volume had the opposite effect; amphibian occupancy slightly increased as pool volume increased. This suggests that connected pools allow fish to distribute elsewhere rather than being trapped in one pool preying on available amphibian larvae. Intermittent stream connectivity should be further evaluated since larval amphibian presence depends on how connected a stream is, especially since the flow of the stream will determine 1) distribution of amphibian eggs and larvae, and 2) colonization capability of fishes (Dodds et al., 2004; Mims et al., 2015).

Having sufficient amounts of aquatic vegetation benefit amphibians in many ways, such as cover from predators, oviposition sites, shade, oxygen production, and periphyton substrate for grazing (Babbitt & Tarr, 2002; Sredl & Collins, 1992; Stebbins & Cohen, 1995) and abundance of vegetation is positively correlated with amphibian abundance (Egan & Paton, 2004; Hamer & Parris, 2013; Hartel et al., 2007; Holzer, 2014; Shulse et al., 2010). Amphibians may have higher production in macrophytes instead of grasses due to the relatively complex structure of macrophytes. Macrophytes may benefit larvae by providing cover from predators as a fish's ability

to capture prey decreases in structurally complex habitats formed by macrophytes (Crowder & Cooper, 1982; Diehl & Kornijów, 1998; Savino & Stein, 1982). Additionally, *L. blairi* and *P. maculata* tadpoles have been observed to use aquatic vegetation as cover (Crawford et al. 2005, E.C.M., personal observation). Further, it has been shown that metaphyton (i.e. filamentous algae) are associated with habitats containing macrophytes (Iacarella et al., 2018), which also serve as an important food source for most tadpoles (Ruibal and Läufer 2012; Beiswenger 1975; Schiesari et al. 2009; Whitaker 1971). Thus, larval amphibian biomass and density in the Flint Hills likely increases in macrophyte dominated pools since they provide cover, food, and oviposition sites.

Hydroperiod length is frequently a dominant factor in other aquatic habitats (Snodgrass et al. 2000; 2001; Babbitt 2003; Rubbo and Kiesecker 2005; Mathwin et al. 2020), but it appeared to be less important among intermittent stream pools in explaining occupancy, biomass, and density trends at YMR. This is possibly due to us sampling during a wet year (12.24 inches above the 10-year average) which implies that fish distribution is at a maximum across the streams on this landscape and are having a large effect on the spatial distribution of amphibian larvae. In this system, ephemeral wetlands are colonized by fish during wet years. Therefore, high connectivity of intermittent streams may override the impacts of drying and refilling on aquatic predators seen in more isolated systems.

Larval amphibians should respond across a temporal scale. This was a natural snapshot experiment where we sampled from 5/19/2020 to 6/30/2020, when there is high climatic variation in Kansas. Kansas typically has a wetter climate in May and a dryer climate towards the end of June. We would expect larval amphibian presence to decrease as the summer season progresses either due to dryer conditions or from larvae metamorphosing into adults. The relationship between

pool volume, hydroperiod, connectivity, and the distance of pools from the mainstream could be beneficial for predicting where amphibians occur along a longitudinal gradient.

The Flint Hills is primarily used for cattle grazing therefore impoundments have been constructed to provide water for them. It would be interesting to explore how the impoundments on cattle pastures effect amphibians, by either disrupting the natural flow regime (pool volume, hydroperiod, connectivity) or by promoting predatory fishes through stocking or serving as refugia during droughts. Research indicates that tadpole density downstream of impoundments is much lower than upstream due to impoundments acting as barriers for downstream movement and that 50% of the larval population are found within the first 20% of the area upstream of the pond (Dare et al., 2020), which is likely due to impoundments causing discontinuity in the stream (Hall et al. 2011). For ponds at our field site, we may see a similar or more extreme results since they have been previously stocked with game fish that may wash out to pools downstream of ponds.

Overall, larval amphibians preferred isolated, macrophyte dominated pools where fish were absent. Although more precipitation has the potential to increase the likelihood of larval amphibian presence, it also makes pools more susceptible to fish colonization due to increased connectivity. These results are expected to vary seasonally and annually due to the highly variable climatic nature of the Great Plains which makes it an ideal system to study the effects of climate change. With both prairies (Samson et al. 2004) and amphibians (Stuart et al., 2004) imperiled and understudied, interpreting the complex landscape use of this community should be a priority to manage the Great Plains intermittent stream system effectively.

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APPENDICES

APPENDIX A

Figures

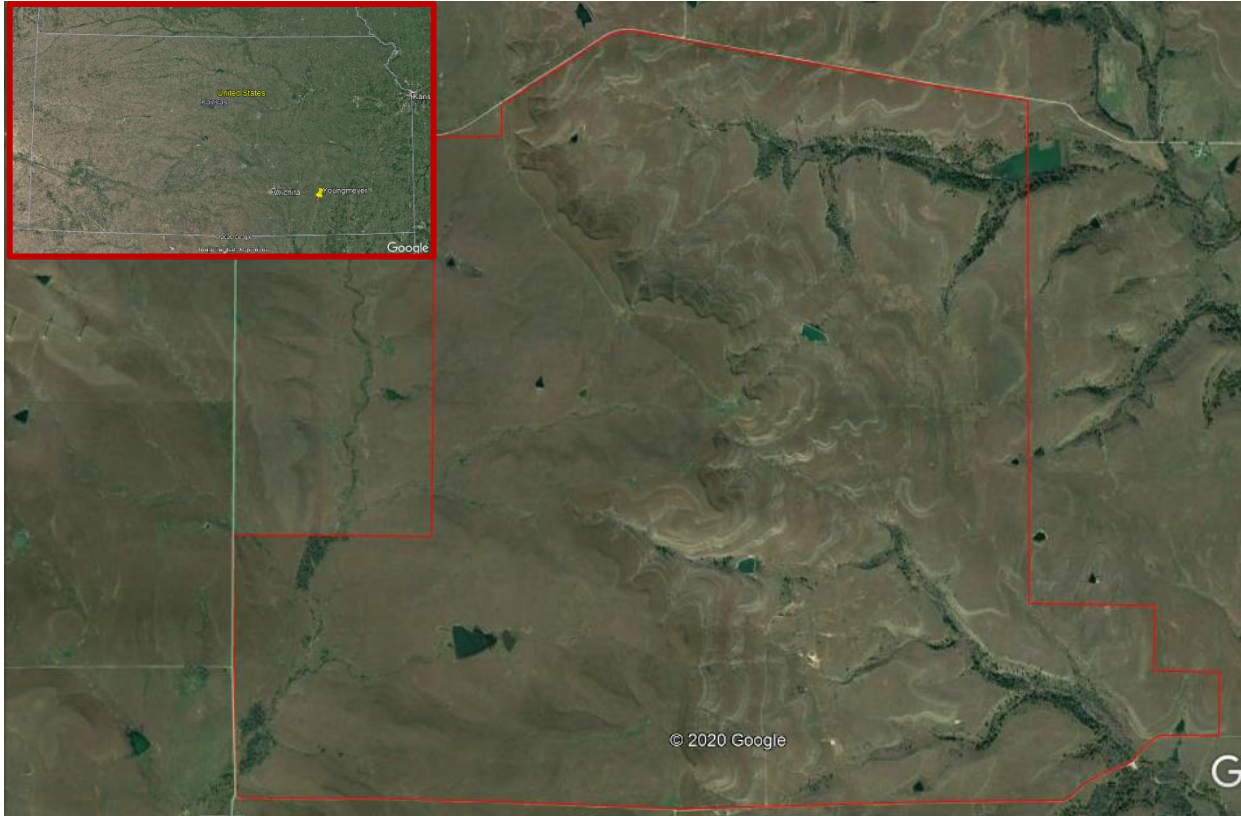


Figure 1. Location of Youngmeyer Ranch (yellow pin) in Southeast Kansas, United States (inset) with property line highlighted in red (image from Google Earth Pro©).

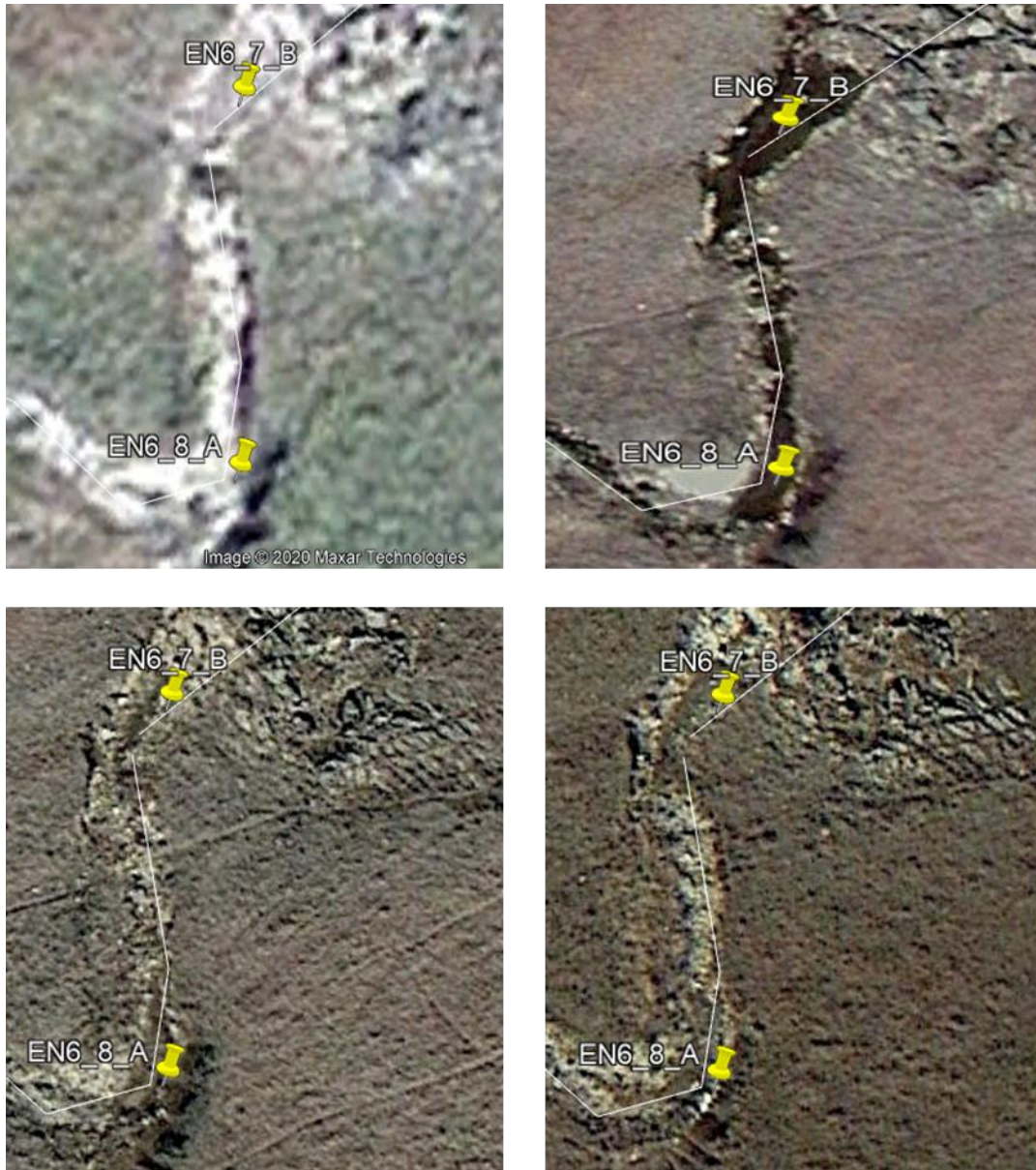


Figure 2. Example of two stream pools (yellow placemarks) where hydroperiod scores were collected using satellite imagery across four years: Oct. 17, 2010 (top left), Feb. 28, 2012 (top right), Feb. 16, 2013 (bottom left), and Nov. 5, 2014 (bottom left) (images from Google Earth Pro©). The only year when water was present for these two pools was 2012.

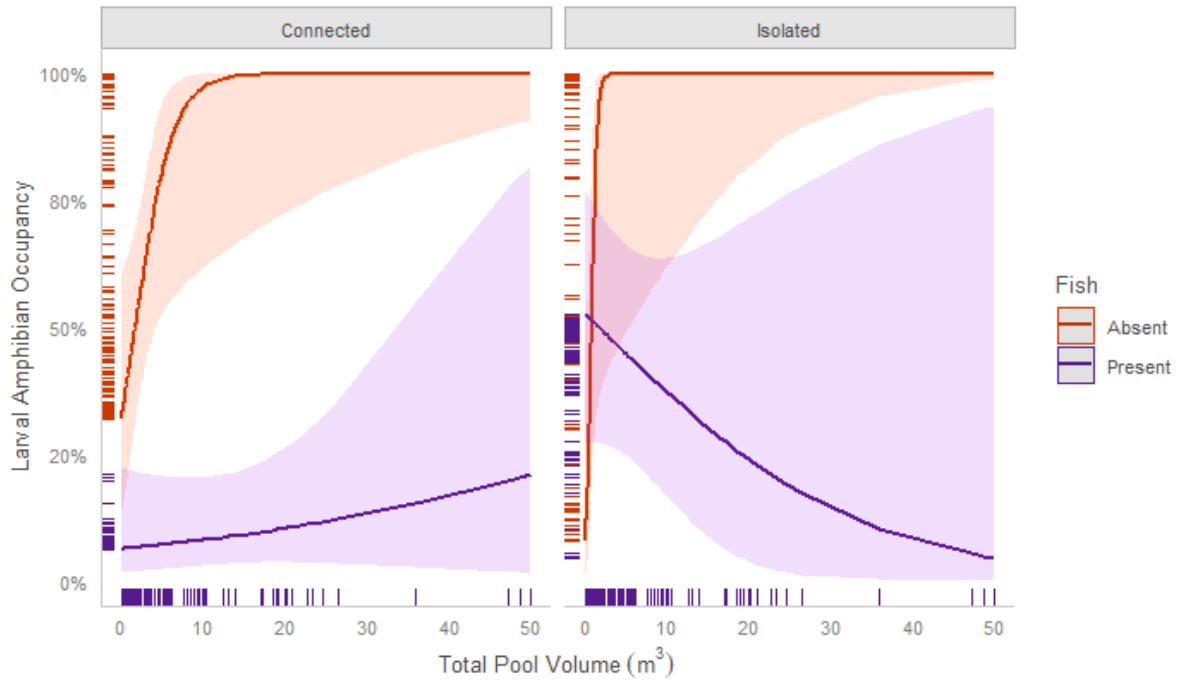


Figure 3. Probabilities of larval amphibians being present as total pool volume increases, when stream pools are connected (left graph) or isolated (right graph), and when fish are absent (orange) or present (purple).

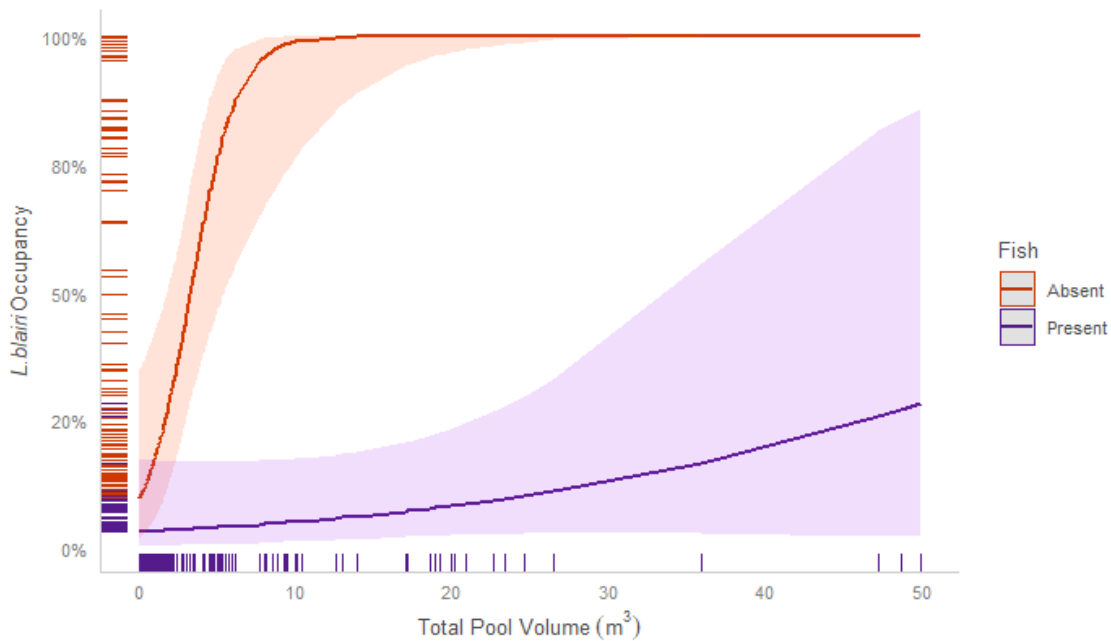


Figure 4. Probabilities of larval *L. blairi* being present when fish are absent (orange) or present (purple) as total pool volume increases.

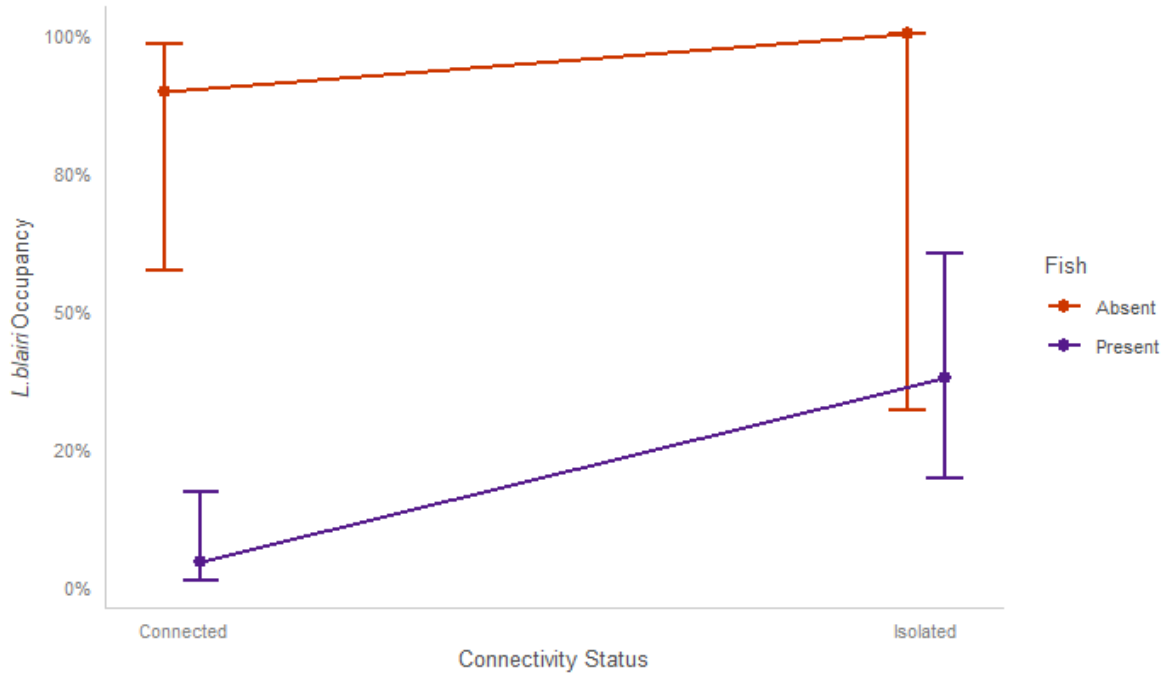


Figure 5. Probabilities of larval *L. blairi* being present when fish are absent (orange) or present (purple) and when a pool is connected (left) or isolated (right).

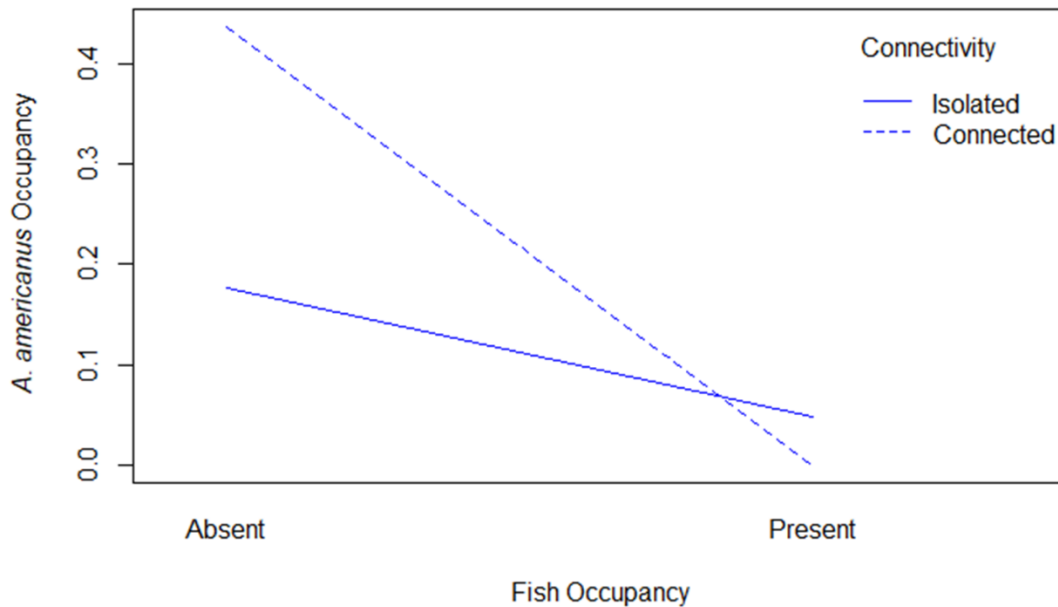


Figure 6. Probabilities of larval *A. americanus* being present when fish are absent (left) or present (right) and when pools are connected (dashed line) or isolated (dotted line).

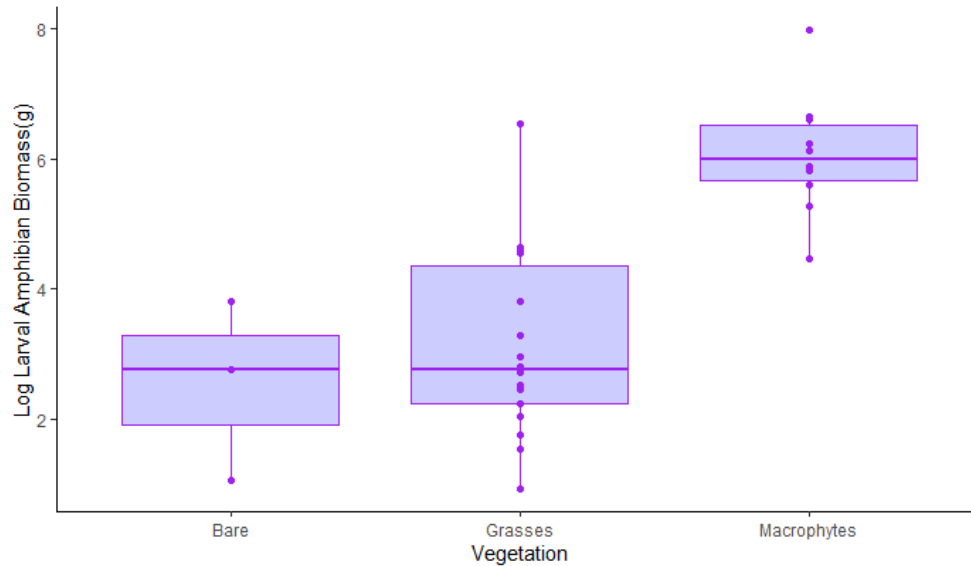


Figure 7. Boxplots of log larval amphibian biomass across bare, grass, and macrophyte dominated stream pools. Only three observation for bare pools, therefore the relationship with bare is inconclusive. The middle bar in each boxplot represents the median. The middle 50% density measurements fall within the inter-quartile range, which is the box. The values that stretch over a wider range of density than the inter-quartile range are represented by the lower and upper quartiles (outer 50%).

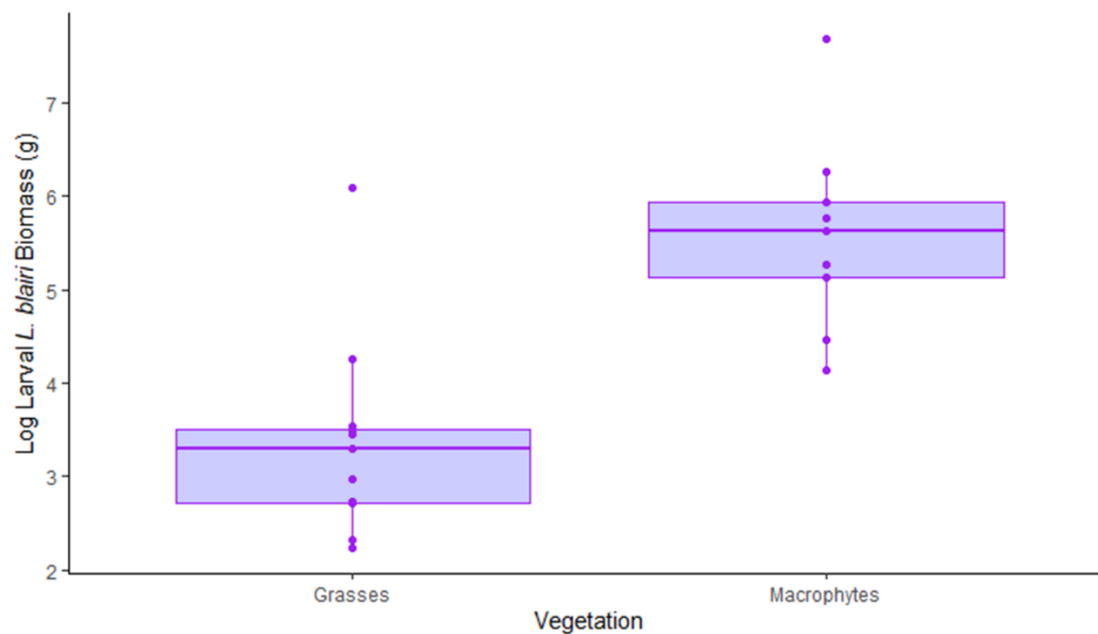


Figure 8. Boxplots of log larval *L. blairi* biomass across grass and macrophyte dominated stream pools. Only one observation for bare pools, therefore it is not included in the figure. See Figure 7 for interpretation of boxplots.

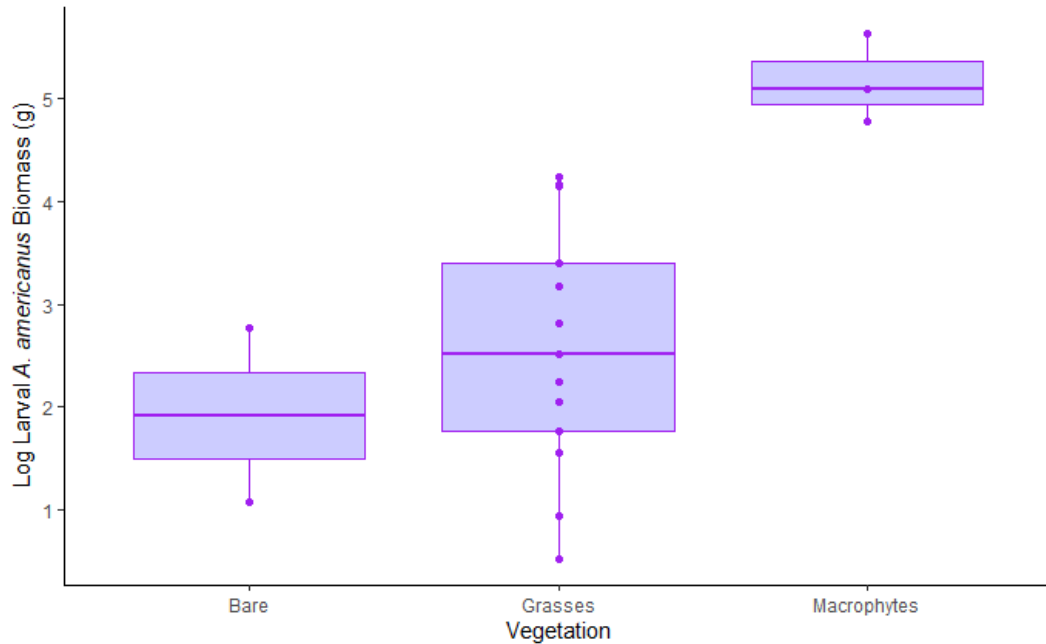


Figure 9. Boxplots of log larval *A. americanus* biomass across bare, grass, and macrophyte dominated stream pools. Only two observations for bare pools, therefore the relationship with bare is inconclusive. See Figure 7 for interpretation of boxplots.

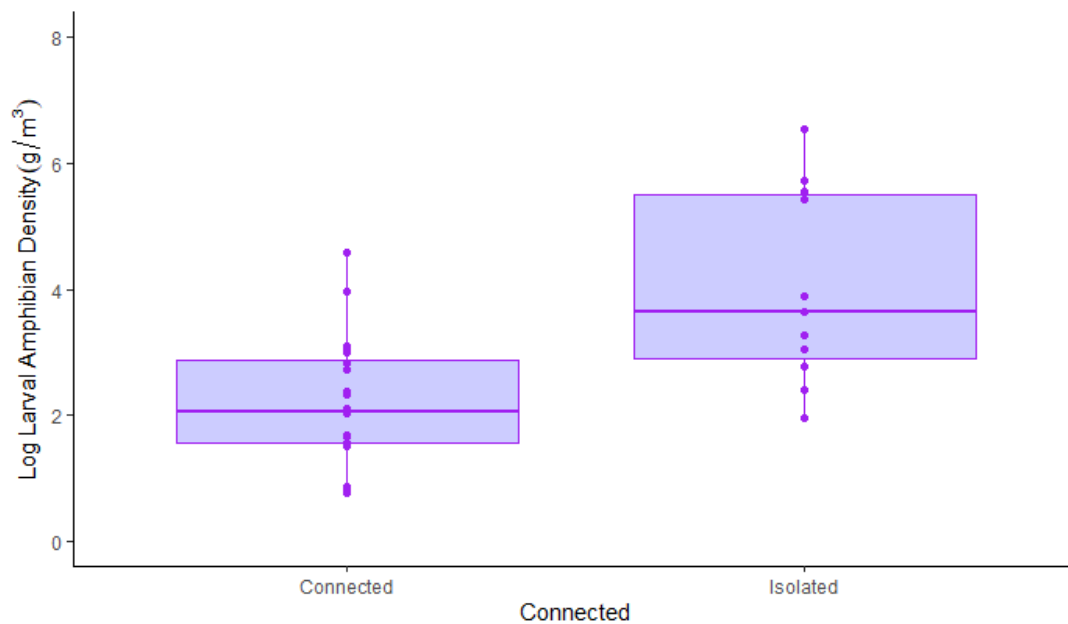


Figure 10. Boxplots comparing log larval amphibian density between connected and isolated stream pools. See Figure 7 for interpretation of boxplots.

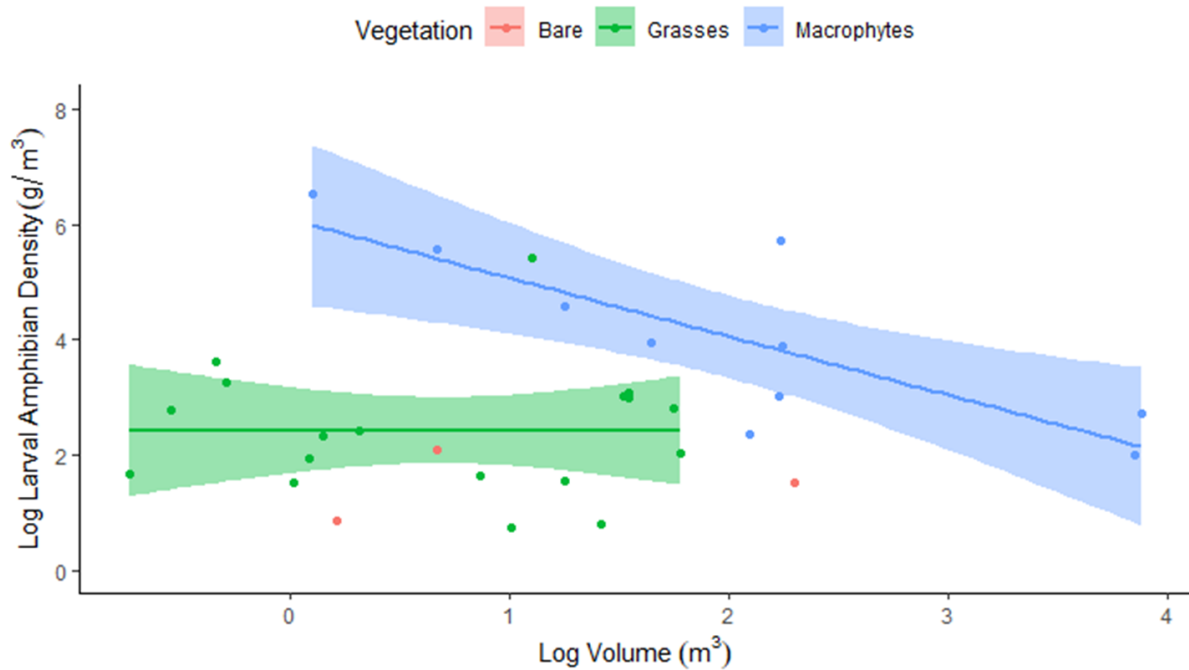


Figure 11. Interaction plot between log total pool volume and dominant stream vegetation, and their effects on log larval amphibian density. Bare pools are depicted as red, grasses are green, and macrophytes are blue. The bare pool line and error bars are not included due to only three observation for bare pools, therefore the relationship with bare is inconclusive.

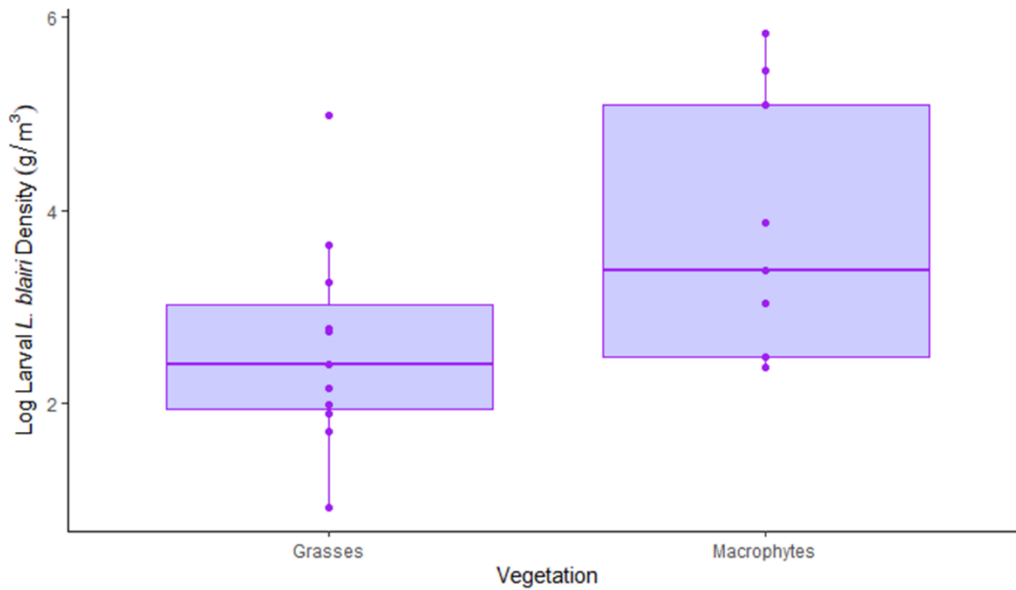


Figure 12. Boxplots comparing log larval *L. blairi* density between grass and macrophyte dominated pools. Only one observation for bare pools, therefore it is not included in the figure. See Figure 7 for interpretation of boxplots.

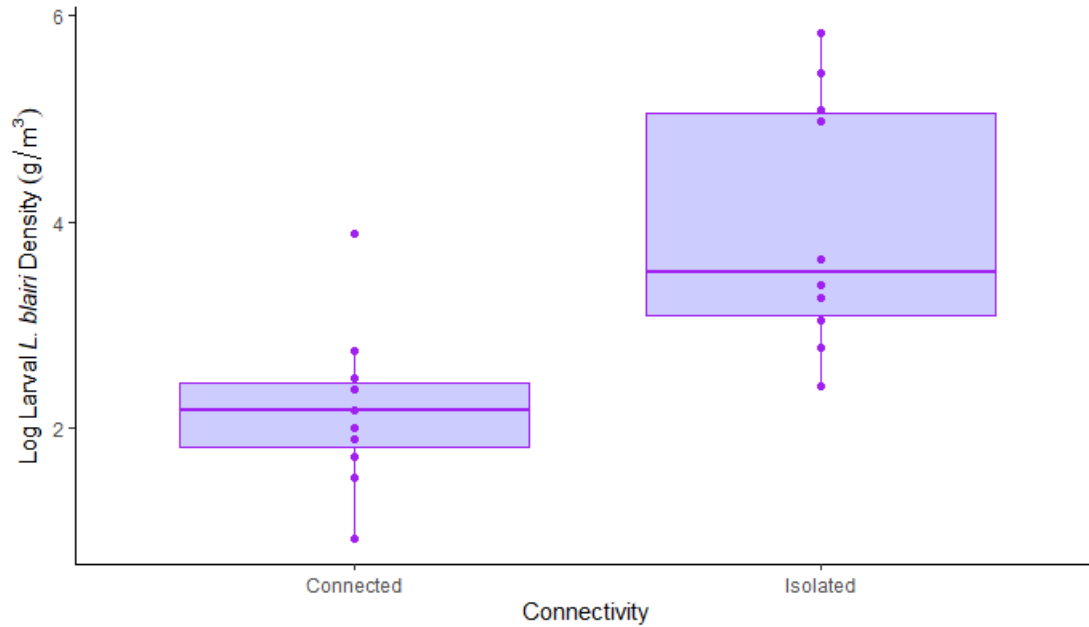


Figure 13. Boxplots comparing log larval *L. blairi* density between connected and isolated stream pools. See Figure 7 for interpretation of boxplots.

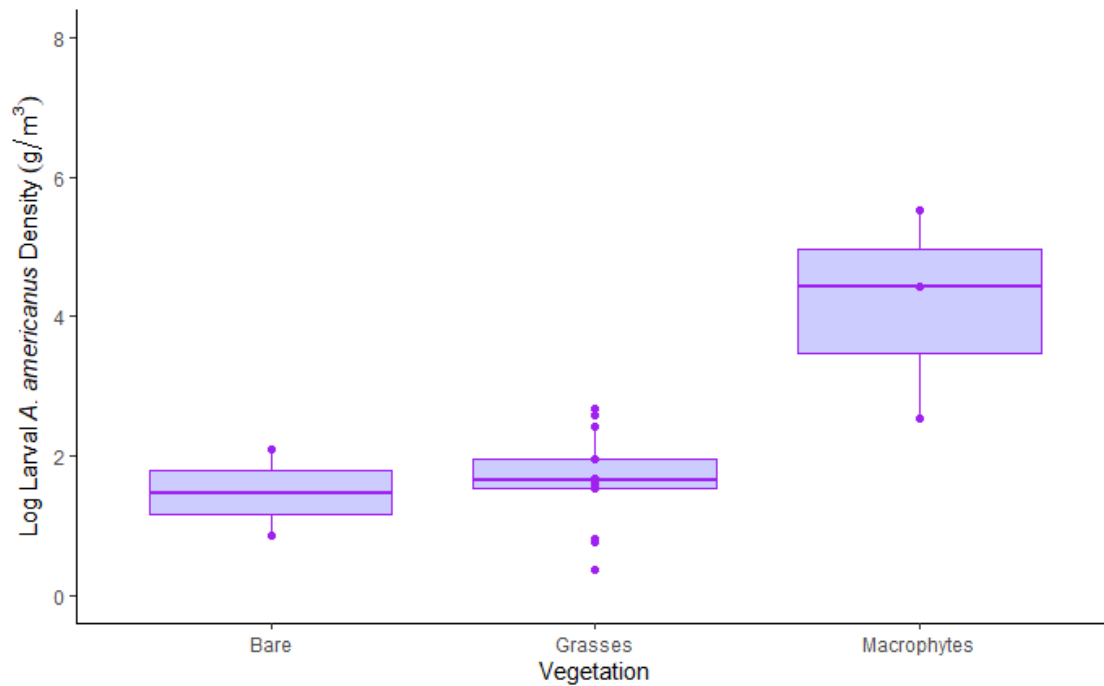


Figure 14. Boxplots comparing log larval *A. americanus* density between bare, grass, and macrophyte dominated pools. Only two observations for bare pools, therefore the relationship with bare is inconclusive. See Figure 7 for interpretation of boxplots.

APPENDIX B

Tables

Table 1. Number of total larval amphibians sampled and the sampled biomass from enclosure samples across all pools.

Common Name	Scientific Name	Number of Individuals	Biomass (g)
Small-mouthed Salamander	<i>Ambystoma texanum</i>	64	44
American Toad	<i>Anaxyrus americanus</i>	1,471	113
Plains Leopard Frog	<i>Lithobates blairi</i>	233	456
American Bullfrog	<i>Lithobates catesbeianus</i>	4	35
Boreal Chorus Frog	<i>Pseudacris maculata</i>	48	14
Frogs & Toads	Anura	1,756	618
Amphibians	Amphibia	1,820	662

Table 2. Results of AICc model comparisons for larval amphibian occupancy. Explanatory variables are fish occupancy (Fish), connectivity status (Connectivity), and total pool volume (Pool Volume). Models with “^” tests for each main effect and each two-way (^2) or three-way (^3) interaction in the model and “:” specifies an interaction between two variables. For each model, a dAICc score is provided which was used for model comparison, models were considered strong if dAICc scores were below 2.0 and were bolded. df represents degrees of freedom and w_i represents weight of the model.

Model	AICc	df	w_i
(Fish + Connectivity + Pool Volume)^3	0.0	8	0.82
(Fish + Connectivity + Pool Volume)^2	3.3	7	0.16
Fish * Pool Volume	8.1	4	0.01
Fish * Connectivity	9.4	4	0.01
Fish + Connectivity	15.7	4	<0.001
Fish	16.2	2	<0.001
Fish + Connectivity + Pool Volume	17.8	4	<0.001
Fish + Pool Volume	18.3	3	<0.001
Connectivity	29.9	2	<0.001
Pool Volume + Connectivity	30.3	3	<0.001
Pool Volume	30.3	2	<0.001

Intercept	30.6	1	<0.001
Pool Volume * Connectivity	32.4	4	<0.001

Table 3. Results of AICc model comparisons for larval *L. blairi* occupancy. View Table 2 for description of explanatory variables and components of the table.

Model	AICc	df	w_i
(Fish + Connectivity + Pool Volume)^3	0	8	0.5958
(Fish + Connectivity + Pool Volume)^2	0.8	7	0.3967
Fish * Pool Volume	8.8	4	0.0072
Fish * Connectivity	15.5	4	<0.001
Fish + Connectivity	19.5	3	<0.001
Fish + Connectivity + Pool Volume	20.9	4	<0.001
Fish	21.3	2	<0.001
Fish + Pool Volume	23.1	3	<0.001
Connectivity	27.4	2	<0.001
Pool Volume + Connectivity	29.3	3	<0.001
Intercept	29.4	1	<0.001
Pool Volume	31	2	<0.001
Pool Volume * Connectivity	31.3	4	<0.001

Table 4. Results of AICc model comparisons for larval *A. americanus* occupancy. View Table 2 for description of explanatory variables and components of the table.

Model	AICc	df	w_i
Fish * Connectivity	0.0	4	0.44
Fish	1.7	2	0.19
Fish + Connectivity	1.9	3	0.16
Fish + Pool Volume	3.5	3	0.07
Fish + Connectivity + Pool Volume	4.0	4	0.06
Fish * Pool Volume	5.1	4	0.03
(Fish + Connectivity + Pool Volume)^2	6.4	7	0.01
(Fish + Connectivity + Pool Volume)^3	8.8	8	0.01
Pool Volume	24.8	2	<0.001
Pool Volume + Connectivity	25.0	3	<0.001
Intercept	26.4	1	<0.001
Pool Volume * Connectivity	26.4	4	<0.001
Connectivity	27.4	2	<0.001

Table 5. Results of AICc model comparisons for log larval amphibian biomass. Explanatory variables are fish occupancy (Fish), connectivity status (Connectivity), hydroperiod score (Hydroperiod), and dominant stream vegetation (Vegetation). Models with “^” tests for each main effect and each two-way (^2) or three-way (^3) interaction in the model and “:” specifies an interaction between two variables. For each model, a dAICc score is provided which was used for model comparison, models were considered strong if dAICc scores were below 2.0 and were bolded. df represents degrees of freedom and w_i represents weight of the model.

Model	dAICc	df	w_i
Vegetation	0	4	0.5288
Connectivity + Vegetation	1.9	5	0.2048
Fish + Vegetation	2.7	5	0.1372
Hydroperiod + Vegetation	4.7	6	0.0507
Fish + Connectivity + Vegetation	4.9	6	0.0461
Fish + Connectivity + Hydroperiod	7.3	7	0.0137
Fish + Connectivity + Vegetation + Fish:Connectivity	7.7	7	0.0112
Hydroperiod * Vegetation	9.7	9	0.0041
Global	11	8	0.0022
Fish + Connectivity + Vegetation + Connectivity:Hydroperiod	14.1	10	<0.001
Fish + Connectivity + Vegetation + Fish:Hydroperiod	15	9	<0.001
Fish * Connectivity	17	5	<0.001
(Fish + Connectivity + Hydroperiod)^2	17.2	10	<0.001
Fish + Connectivity + Vegetation + Vegetation:Hydroperiod	17.3	11	<0.001
Fish	17.9	3	<0.001
Fish + Connectivity	18	4	<0.001
Connectivity * Hydroperiod	19.4	7	<0.001
Connectivity	21.7	3	<0.001
Intercept	21.9	2	<0.001
Fish + Hydroperiod	23	5	<0.001
Fish + Hydroperiod + Connectivity	23.8	6	<0.001
Fish * Hydroperiod	24.3	6	<0.001
Hydroperiod	24.5	4	<0.001
Connectivity + Hydroperiod	25.1	5	<0.001

Table 6. Results of AICc model comparisons for log larval *L. blairi* biomass. View Table 5. for description of explanatory variables and components of the table.

Model	dAICc	df	w_i
Vegetation	0	4	0.3792
Hydroperiod + Vegetation	0.6	6	0.288
Connectivity + Vegetation	1.8	5	0.1556
Fish + Vegetation	2.7	5	0.1001
Connectivity + Vegetation + Hydroperiod	4.7	7	0.036
Connectivity + Vegetation + Fish	5	6	0.0308
Fish + Connectivity + Vegetation + Fish:Connectivity	9.5	7	0.0032
Global	10.1	8	0.0025
Intercept	10.9	2	0.0017
Connectivity	12	3	<0.001
Fish	12.1	3	<0.001
Fish + Connectivity	13.5	4	<0.001
Fish * Connectivity	15.2	5	<0.001
Hydroperiod	16	4	<0.001
Fish + Connectivity + Vegetation + Fish:Hydroperiod	16.4	9	<0.001
Fish + Hydroperiod	16.8	5	<0.001
Fish * Hydroperiod	17.5	6	<0.001
Connectivity + Hydroperiod	18.3	5	<0.001
Fish + Connectivity + Hydroperiod	19.9	6	<0.001
Fish + Connectivity + Vegetation + Connectivity:Hydroperiod	23.2	10	<0.001
Connectivity * Hydroperiod	24.5	7	<0.001
(Fish + Connectivity + Hydroperiod)^2	32.9	10	<0.001

Table 7. Results of AICc model comparisons for log larval *A. americanus* biomass. View Table 5. for description of explanatory variables and components of the table.

Model	dAICc	df	w_i
Vegetation	0	4	0.5389
Connectivity	2.7	3	0.1385
Connectivity + Vegetation	3.6	5	0.0874
Fish + Vegetation	3.7	5	0.0841
Intercept	5.8	2	0.0297
Fish * Connectivity	5.9	4	0.0276
Fish + Connectivity	5.9	4	0.0276

Fish	6.9	3	0.0169
Hydroperiod + Vegetation	7	6	0.0166
Fish + Connectivity + Vegetation	8.1	6	0.0096
Connectivity * Hydroperiod	8.4	6	0.0082
Connectivity + Hydroperiod	9.9	5	0.0038
(Fish + Connectivity + Hydroperiod)^2	10.1	7	0.0035
Hydroperiod	10.7	4	0.0025
Hydroperiod * Vegetation	11.1	7	0.0021
Hydroperiod + Connectivity + Vegetation	11.4	7	0.0018
Fish + Hydroperiod	13.7	5	<0.001
Fish + Hydroperiod + Connectivity	14.5	6	<0.001
Global	15.5	8	<0.001

Table 8. Results of AICc model comparisons for log larval amphibian density. Explanatory variables are fish occupancy (Fish), connectivity status (Connectivity), hydroperiod score (Hydroperiod), dominant stream vegetation (Vegetation), and log total pool volume (Log Volume). Models with “^” tests for each main effect and each two-way (^2) or three-way (^3) interaction in the model and “:” specifies an interaction between two variables. For each model, a dAICc score is provided which was used for model comparison, models were considered strong if dAICc scores were below 2.0 and were bolded. df represents degrees of freedom and w_i represents weight of the model.

Model	dAICc	df	w_i
Connectivity + Vegetation + Log Volume:Vegetation	0	8	0.5123
Connectivity + Vegetation	1.8	5	0.2055
Connectivity * Hydroperiod	3.2	7	0.1058
Fish + Connectivity + Vegetation + Fish:Connectivity	5.3	7	0.0362
(Connectivity + Log Volume + Hydroperiod)^2	5.5	11	0.0324
(Connectivity + Log Volume + Fish)^2	5.9	8	0.0269
(Connectivity + Hydroperiod + Fish)^2	6.7	10	0.018
Fish * Connectivity	8	5	0.0094
Connectivity	8	3	0.0092
Log Volume * Vegetation	8.4	7	0.0076
Connectivity + Log Volume	8.6	4	0.0068
Log Volume + Vegetation	9	5	0.0058
Fish + Connectivity	9.6	4	0.0043
(Connectivity + Log Volume + Fish)^3	9.9	9	0.0036
Global	10.7	9	0.0024

Vegetation	10.8	4	0.0023
Vegetation + Log Volume + Fish	11.1	6	0.002
Connectivity + Log Volume + Fish	11.3	5	0.0018
Connectivity * Log Volume	11.3	5	0.0018
Fish + Vegetation	11.9	5	0.0013
Vegetation + Log Volume + Hydroperiod	12.7	7	<0.001
Hydroperiod * Vegetation	12.9	9	<0.001
Hydroperiod + Vegetation	13.1	6	<0.001
Hydroperiod + Connectivity	13.4	5	<0.001
Log Volume + Hydroperiod + Connectivity	13.4	6	<0.001
Connectivity + Hydroperiod + Vegetation + Connectivity:Hydroperiod + Hydroperiod:Vegetation	14.9	12	<0.001
(Connectivity + Log Volume + Hydroperiod)^3	15.2	13	<0.001
Fish + Log Volume + Vegetation + Fish:Log Volume + Log Volume:Vegetation	15.5	9	<0.001
Fish + Hydroperiod + Vegetation + Fish:Hydroperiod + Hydroperiod:Vegetation	18.2	11	<0.001
Intercept	18.9	2	<0.001
Fish	20	3	<0.001
Log Volume	21.3	3	<0.001
Fish + Log Volume	22.5	4	<0.001
Hydroperiod	23.9	4	<0.001
Fish * Log Volume	24.3	5	<0.001
Fish + Hydroperiod	25.4	5	<0.001
Log Volume + Hydroperiod	26.8	5	<0.001
Fish + Log Volume + Hydroperiod	28.3	6	<0.001
Fish * Hydroperiod	28.5	6	<0.001
Log Volume * Hydroperiod	29.4	7	<0.001
(Log Volume + Hydroperiod + Vegetation)^2	35.3	14	<0.001
(Fish + Log Volume + Hydroperiod)^2	38.1	10	<0.001

Table 9. Results of AICc model comparisons for log larval *L. blairi* density. View Table 8. for description of explanatory variables and components of the table.

Model	dAICc	df	w_i
Connectivity + Vegetation	0	5	0.2942
Connectivity	0.5	3	0.2331
Connectivity + Log Volume + Vegetation	2.2	6	0.0985
Fish * Connectivity	2.3	5	0.0919

Connectivity + Log Volume	3.4	4	0.0532
Fish + Connectivity	3.5	4	0.0503
Fish + Connectivity + Vegetation + Fish: Connectivity	3.8	7	0.0438
Hydroperiod + Log Volume + Vegetation	4.7	7	0.0284
Hydroperiod + Connectivity	5.1	5	0.0227
Log Volume + Vegetation	6.2	5	0.0134
Log Volume * Connectivity	6.4	5	0.0118
Hydroperiod * Connectivity	6.6	7	0.011
Fish + Connectivity + Log Volume	6.9	5	0.0092
Global	7.4	9	0.0073
Hydroperiod + Vegetation	7.4	6	0.0071
Connectivity + Log Volume + Vegetation + Connectivity:Log Volume + Log Volume:Vegetation	8.3	8	0.0046
Connectivity + Log Volume + Hydroperiod	8.3	6	0.0045
Fish + Log Volume + Vegetation	8.8	6	0.0037
(Fish + Connectivity + Log Volume)^2	9.6	8	0.0025
Log Volume * Vegetation	9.6	6	0.0024
Vegetation	10.5	4	0.0015
Intercept	10.9	2	0.0013
Hydroperiod * Vegetation	11.3	8	0.0011
Log Volume	12.2	3	<0.001
Fish + Vegetation	12.2	5	<0.001
Fish	13.6	3	<0.001
Hydroperiod	14.1	4	<0.001
(Fish + Connectivity + Log Volume)^3	14.4	9	<0.001
Fish + Log Volume	14.9	4	<0.001
Fish + Hydroperiod	16.4	5	<0.001
Log Volume + Hydroperiod	16.8	5	<0.001
(Fish + Connectivity + Hydroperiod)^2	17	10	<0.001
Fish * Log Volume	18.3	5	<0.001
Fish + Log Volume + Vegetation + Fish:Log Volume + Log Volume:Vegetation	18.4	8	<0.001
Fish + Log Volume + Hydroperiod	19	6	<0.001
Hydroperiod * Log Volume	19.8	7	<0.001
Fish * Hydroperiod	20.3	6	<0.001
Connectivity + Hydroperiod + Vegetation + Connectivity:Hydroperiod + Hydroperiod:Vegetation	21	11	<0.001
Fish + Hydroperiod + Vegetation +	21.7	10	<0.001

Fish:Hydroperiod + Hydroperiod:Vegetation			
(Log Volume + Connectivity + Hydroperiod)^2	26.2	11	<0.001
(Fish + Log Volume + Hydroperiod)^2	34.2	10	<0.001
(Fish + Log Volume + Hydroperiod)^3	36.2	12	<0.001
(Vegetation + Log Volume + Hydroperiod)^2	38.3	12	<0.001

Table 10. Results of AICc model comparisons for log larval *A. americanus* density. View Table 8. for description of explanatory variables and components of the table.

Model	dAICc	df	w_i
Fish + Vegetation	0	5	0.5388
Connectivity * Hydroperiod	2.8	6	0.1331
Fish + Log Volume + Vegetation	3.2	6	0.1083
Vegetation	4	4	0.0724
Log Volume * Vegetation	4.7	7	0.0524
Connectivity	5.7	3	0.0314
Fish + Connectivity	7.1	4	0.0158
Connectivity + Vegetation	7.8	5	0.0111
Log Volume + Vegetation	7.8	5	0.0109
Log Volume + Connectivity	8.9	4	0.0062
Fish + Log Volume + Connectivity	9.2	5	0.0054
Connectivity + Log Volume + Vegetation + Connectivity:Log Volume + Log Volume:Vegetation	10.2	8	0.0033
Log Volume * Connectivity	10.2	5	0.0033
Fish + Log Volume + Vegetation + Fish:Log Volume + Log Volume:Vegetation	11.3	8	0.0019
Connectivity + Hydroperiod	11.7	5	0.0016
Connectivity + Log Volume + Vegetation	12.3	6	0.0011
Hydroperiod + Vegetation	12.5	6	0.001
(Fish + Connectivity + Log Volume)^3	13.6	6	<0.001
Intercept	14	2	<0.001
Connectivity + Log Volume + Hydroperiod	15.4	6	<0.001
Fish	16.7	3	<0.001
Log Volume	16.9	3	<0.001
Vegetation + Log Volume + Hydroperiod	18	7	<0.001
Hydroperiod	19.2	4	<0.001
Fish * Log Volume	20.1	4	<0.001
Fish + Log Volume	20.1	4	<0.001
Global	22.2	9	<0.001

Fish + Hydroperiod	23	5	<0.001
Log Volume + Hydroperiod	23.1	5	<0.001
Fish + Log Volume + Hydroperiod	27.7	6	<0.001
(Connectivity + Log Volume + Hydroperiod)^2	30.8	10	<0.001
Log Volume * Hydroperiod	32.6	7	<0.001
(Fish + Log Volume + Hydroperiod)^3	39.3	8	<0.001
(Connectivity + Log Volume + Hydroperiod)^3	41	11	<0.001

APPENDIX C

Estimating Pool Volume Protocol

Materials

Wetland Volume Estimation Sheet, 2-4 Measuring Tapes (metric), rebar, hammer, leather gloves
Clipboard, Pen/pencil, Metal Meterstick

Terminology

Flow = Direction of flow for overall drainage

DT = Downstream Terminus of Pool

UT = Upstream Terminus of Pool

DFDT = Distance from downstream Terminus

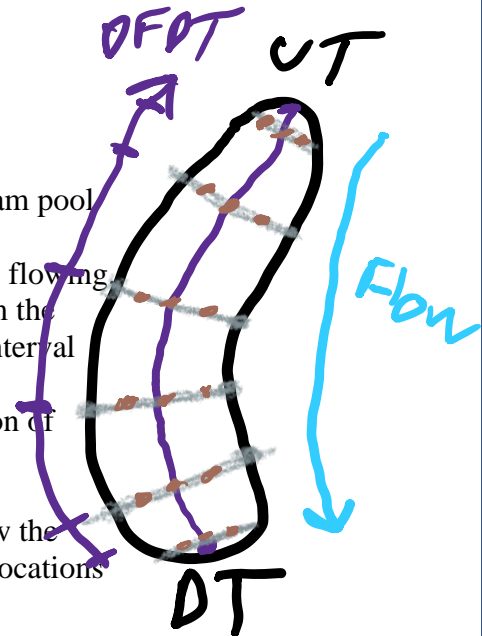
Example to the right shows the boundaries of an oblong stream pool in black.

The blue line indicates the direction of flow when the pool is flowing.

The purple line outside indicates the increasing distance from the downstream terminus with hashmarks indicating a 2 meter interval where measurements are taken.

The purple line in the middle of the pool indicates the location of the measuring tape centered in the middle or deepest part of the pool (default to deepest part).

The silver lines running perpendicular to the purple line show the locations where the second measuring tap is laid to identify locations to take depth measurements (brown dots).



Procedure (collected after all biotic samples)

Laying out the main line

1. Attach measuring tape to a piece of rebar or other object at the DT.
2. Unwind the tape along the center of the pool (or follow the deepest part of the pool if obvious).
 - a. Anchor tape at bends with binder clips to rebar
 - b. Anchor tape at UT with binder clip to rebar (or tie to rebar)
3. **Record the Pool Total Length** on the Wetland Volume Estimation Sheet

Measuring Widths and Depths

1. Take the first width measurement at 0.25m from the DT with a second measuring tape and **record TW & DFDT** on the datasheet. DFDT and TW can be recorded once and a line drawn down for the next two boxes on the datasheet (it will always be the same). **Record "1" for sample** on datasheet.
2. The first depth reading will always be at the main line whether that is in the middle or closer to a bank. Take this with a metal meterstick. **Record the depth and DFLS** on the datasheet.
3. The second depth reading will always be halfway between the mainline and the left bank (facing upstream). **Record depth and DFLS**.

4. The second depth reading will always be halfway between the mainline and the right bank (facing upstream). ***Record depth and DFLS***
5. After the first width measurement, all subsequent measurements will be taken at a regular 2m intervals starting with 2m, 4m and so on (rather than at 2.25m). These will be **samples 2, 3, etc.**
6. The last width measurement will be taken 0.25m from the UT.