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Influence of Multi-scale Drivers on Stream Salamander Occupancy, Abundance, and Reproduction in an Exurban Landscape

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Influence of Multi-scale Drivers on Stream Salamander Occupancy, Abundance,
and Reproduction in an Exurban Landscape

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Influence of Multi-scale Drivers on Stream Salamander Occupancy, Abundance,
and Reproduction in an Exurban Landscape

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Introduction

The number of city-dwelling humans currently exceeds half of the world's population and is expected to increase in the future (Meyer et al. 2005; Barrett and Price 2014); however, urban development significantly alters the surrounding ecological community. Urbanization increases the amount of impervious surfaces on the landscape, fragments or destroys habitats, produces pollutants and nutrient contaminants, promotes the introduction and invasion of non-native species, increases disease transmission, and alters biotic communities (Allan 2004; Bar-Massada et al. 2014). The manifestation of urbanization in stream ecosystems is a number of consistent symptoms collectively known as urban stream syndrome (Walsh et al. 2005; Hamer and McDonnell 2008). Urban streams typically have flashier hydrographs, increased sediment and pollutant loads, and altered channel morphology and stability (Walsh et al. 2005; Hamer and McDonnell 2008). These ecosystem changes reduce biotic richness, leaving a predominance of tolerant, generalist species in urban streams (Walsh et al. 2005; Hamer and McDonnell 2008).

Urbanization currently threatens more than one-third of the world's known amphibian species (Hamer and McDonnell 2008). Urban development has been linked to reduced amphibian species richness, declines in individual species occurrence and abundance, loss of genetic diversity and population isolation, and altered biotic communities and interactions (Hamer and McDonnell 2008; Barrett and Price 2014). Moreover, salamanders make up a considerable portion of the vertebrate biomass in forest and wetland ecosystems (Burton and Liken 1975; Hamer and McDonnell 2008; Barrett and Price 2014). Thus, severe declines or extirpation of salamander populations will have a substantial influence on nutrient cycling and trophic interactions in the riparian ecosystem (Barrett and Price 2014).

In southern New England, reforestation has occurred since the 1850's along with the establishment of low-density residential communities beginning in the 1920's (Foster 1992). Reforestation plateaued by the mid-1970's with forest conversion to residential land use resulting in forest loss during the last 20-30 years in southern New England (Jeon et al. 2014). Today, exurban development, defined as human housing density of 6-25 houses per square kilometer (Hansen et al. 2015), dominates the landscape (Foster 1992; Jeon et al. 2014). Despite exurban development being the fastest growing form of land use in the United States since the 1950's (Hansen et al. 2005), the range of ecological effects that occur within exurban development are not well understood (Bar-Massada et al. 2014). In southern New England, we are just now beginning to understand how wildlife populations persist over multiple decades in this landscape of second growth forest intermixed with exurban development.

Addressing the challenges of urban stream syndrome and amphibian declines will require a basic understanding of species-specific amphibian ecology, identification of multi-scale and interactive drivers of population declines, and a multi-scale approach to management (Hamer and McDonnell 2008; Barrett and Price 2014; Semlitsch et al. 2017). Preventing salamander population declines within exurban development requires identifying what features of an exurban landscape influence population dynamics. Thus, I examined the influence of multi-scale drivers on stream salamander occupancy, abundance, and reproduction in the exurban landscape of eastern Connecticut. Moreover, my thesis addresses a recent call for research that examines species-specific responses to urbanization, focuses on gradients of housing development, and highlights the potential legacy effects associated with housing development (Hamer and McDonnell 2008; Barrett and Price 2014). Connecticut is home to three species of stream-dwelling salamander species. The northern spring salamander, *Gyrinophilus porphyriticus*, is

restricted to a few known locations and thus not included here. I focused on the responses of the other two stream salamander species, *Eurycea bislineata* and *Desmognathus fuscus*, to a range of exurban housing development densities and ages.

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**Interaction between exurban development and housing age influences persistence of stream
salamanders**

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ABSTRACT.—Exurban development is the fastest growing form of land use in the United States and is already the predominant land use in southern New England, where mature forest is intermixed with low-density residential housing. Runoff produced by housing developments affects stream ecosystems by altering hydrological processes, increasing levels of pollutants and sedimentation, and altering the biotic community. When these changes persist or become cumulative through time, amphibian populations are reduced or extirpated. Despite this, many stream salamanders are considered to be ubiquitous in the region. To determine what stream and watershed features enhance long-term population persistence in an exurban landscape, I compared the occupancy and abundance of two stream salamanders, *Eurycea bislineata* and *Desmognathus fuscus*, in watersheds that differed in housing density and time since construction. I estimated *E. bislineata* occupancy at 100% and found strong support for an interaction between the quadratic of average housing development age and the amount of development in a watershed influencing abundance. *Eurycea bislineata* abundance was sensitive to new and high-density housing developments and increased in watersheds that were more than 20 years post-construction when housing density was low. In comparison, *D. fuscus* occupancy was estimated at 18% and best explained by fine-scale stream features including soil temperature, water conductivity, dissolved oxygen, discharge, and sediment distribution. Notably, estimates of *D. fuscus* relative abundance within all watersheds, including watersheds with little housing, were much lower than comparable estimates in the literature. This result is suggestive that populations in the region may be experiencing an extinction debt. I suggest using an adaptive management approach to monitor and manage remaining *D. fuscus* populations in the region. Future decisions about wildlife management in exurban landscapes should consider interactions between housing age and development as well as legacy effects from development.

Key Words: abundance, amphibian; conservation; exurban development; occupancy; salamander; urban stream syndrome, urbanization

INTRODUCTION

Housing developments affect forest ecosystems through habitat fragmentation, the creation of interior edge habitat, increased impervious surfaces, and altered hydrological processes (Allan 2004; Lindenmayer and Fischer 2006; Wilson and Chester 2009). These changes to the system can affect larval and adult amphibians across multiple ecological scales and gradients of development (Willson and Dorcas 2003; Hamer and McDonnell 2008; Barrett et al. 2010; Gagné and Fahrig 2010; Canessa and Parris 2013). Exurban development, defined as human housing density of 6-25 houses/km², has been the fastest growing form of land use in the United States since the 1950's (Hansen et al. 2005). In southern New England, reforestation has occurred since the 1850's along with the establishment of low-density residential communities beginning in the 1920's (Foster 1992; Jeon et al. 2014). Reforestation plateaued by the mid-1970's and conversion to residential land use has contributed to the loss of forests during the last 20-30 years (Foster 1992; Jeon et al. 2014; Wilson and Chester 2009). Thus, we are just now beginning to understand how wildlife populations persist over multiple decades in this landscape of second growth forest intermixed with exurban development. While most ecological research quantifies changes in wildlife along rural-urban gradients, the range of ecological effects that occur within exurban development are much less clear (Bar-Massada et al. 2014).

The ecological effects of development on amphibian populations can be swift and acute. Development across just 15% of a watershed alters ecosystem function and reduces organismal abundance and diversity (Limburg and Schmidt 1990; Booth and Jackson 1997; Bledsoe and Watson 2001; Paul and Meyer 2001; Barrett et al. 2010; Canessa and Parris 2013). This amount

of urbanization creates dispersal barriers, isolates populations, and reduces amphibian densities (Fahrig et al. 1995; Gibbs 1998; Noël et al. 2007; Gravel et al. 2012; Munshi-South et al. 2013). In addition to the direct loss of habitat (Hamer and McDonnell 2008), conductivity, sedimentation, and stream scour can cause stream-dwelling amphibian populations to decline precipitously within the first five years of urban construction (Price et al. 2011; Price et al. 2012). For example, stream-associated southern two-lined salamanders, *Eurycea cirrigera*, showed declines in abundance just one year after urban development and a reduction in occupancy by 30-40% four years following urbanization in North Carolina (Price et al. 2011; Price et al. 2012). Ultimately, substantial land use changes within the watershed have measureable and immediate effects to ecosystem structure and function, leaving amphibian populations vulnerable to population declines, genetic isolation, and loss of suitable microhabitats (Semlitsch and Bodie 2003; Price et al. 2006; Noël et al. 2007; Hamer and McDonnell 2008; Munshi-South et al. 2013).

In addition to the acute effects of development, cumulative and prolonged environmental stressors associated with exurban development may also affect the long-term persistence of amphibian populations. As housing developments and the associated road networks increase, so do impervious surfaces that produce runoff. Runoff into headwater streams causes flashier hydrographs, altered sedimentation processes, increased concentrations of nutrients and contaminants, modified channel morphology and stability, and leads to a loss of biotic richness and predominance of tolerant generalist species (Allan 2004; Freeman and Schorr 2004; Meyer et al. 2005; Walsh et al. 2005; Roy et al. 2007; Halstead et al. 2014). The enduring nature of these hydrological changes can significantly influence amphibian populations long after the initial construction disturbance (Price et al. 2006; Hamer and McDonnell 2008; Karraker et al.

2008; Barrett et al. 2010; Gagné and Fahrig 2010; Canessa and Parris 2013; Barrett and Price 2014). Altered stream hydrology from urbanization can reduce larval salamander retention (Barrett et al. 2010), while increased sedimentation and pollutants from urban areas disrupt osmoregulatory processes, alter animal behavior, and reduce amphibian survivorship, growth, and development (Price et al. 2006; Hamer and McDonnell 2008; Karraker et al. 2008; Barrett et al. 2010; Denoël et al. 2010; Karraker and Gibbs 2011; Canessa and Parris 2013). One study found that anuran abundances generally decline with increasing residential development age and could lead to extirpation from the area over time (Gagné and Fahrig 2010). The results from this study suggest that the cumulative and prolonged hydrological changes associated with urbanization may preclude opportunities for populations to regain pre-construction disturbance abundances (Walsh et al. 2005; Gagné and Fahrig 2010). However, despite increasing residential land use and adverse effects from urban stream syndrome, many stream salamanders are considered to be ubiquitous throughout New England.

My goal was to understand what watershed and stream features affect the persistence of salamanders in an exurban landscape by comparing the occupancy and abundance patterns of *Eurycea bislineata* (Northern Two-lined Salamander) and *Desmognathus fuscus* (Northern Dusky Salamander) in watersheds that differed in housing density and time since construction. My first objective was to quantify the importance of watershed-scale features such as several metrics of development age, the percentage of development within the watershed, and interactions between age and development to salamander occupancy and abundance. Previous studies examining amphibian responses to development have used the amount of impervious surfaces in the watershed as a proxy (Willson and Dorcas 2003; Barrett et al. 2010; Rizzo et al. 2016), lumped development with other land use types such as agriculture and turf (Willson and

Dorcas 2003), or examined a gradient of disturbance, but not a gradient of housing development specifically (Orser and Shure 1972; Willson and Dorcas 2003; Brannon and Purvis 2008; Barrett et al. 2010). Here, I sought to examine the influence of exurban housing developments specifically. I hypothesized that occupancy and abundance would be highest for both species in watersheds with no development and would decline as the percentage of development within the watershed increased. I also anticipated that salamander abundance would decline linearly in response to development age due to prolonged exposure to the habitat alterations associated with increasing development (Gagné and Fahrig (2010). Alternatively, I expected abundance would show a quadratic response to development age with abundance declining following the initial construction disturbance then increasing after a period of time similar to the observations of Gagné and Fahrig (2010). I predicted that occupancy and abundance would be greater for *E. bislineata* than *D. fuscus*, as found by others (Barr and Babbitt 2002; Ward et al. 2008; Campbell Grant et al. 2014), and that *D. fuscus* would be absent from the more highly developed watersheds due to its relatively low tolerance for development (Orser and Shure 1972; Willson and Dorcas 2003; Price et al. 2011; Price et al. 2012).

My second objective was to quantify the importance of stream-scale features associated with increasing urbanization and salamander occupancy and abundance. While many habitat features have been related to amphibian occupancy and abundance (Orser and Shure 1972; Willson and Dorcas 2003; Barret et al. 2010; Brannon and Purvis 2008; Campbell Grant et al. 2014), few studies have focused exclusively on these features within the context of exurban development. Based on these previous association studies, I predicted that high temperatures, a dominance of small sediments, increased turbidity, high conductivity, elevated stream discharge, and low dissolved oxygen concentrations could reduce occupancy and abundance for both *E.*

bislineata and *D. fuscus*. As before, I anticipated that *D. fuscus* occupancy and abundance would be reduced relative to *E. bislineata* due to its sensitivity to development disturbance (Orser and Shure 1972; Willson and Dorcas 2003; Price et al. 2011; Price et al. 2012).

My third objective was to identify the scale at which management actions would be most effective by determining whether watershed or stream features best predict salamander occupancy and abundance. Conservation and management resources are often limited, and the effort and resources required to reach a conservation goal vary based on the scale and scope of the project. By identifying whether management for these salamander species should target the watershed or stream reach, I hope to reduce inefficiencies, promote effective use of resources, target future research needs, and reduce the time necessary to take action.

METHODS

Study Species.—*Eurycea bislineata* is a semi-aquatic salamander with a range that extends from southeastern Canada, throughout New England, to Ohio, West Virginia, and Virginia (Conant and Collins 1998). *Eurycea bislineata* typically inhabit first- through third-order streams, although the adults frequently use the terrestrial forest adjacent to streams (Conant and Collins 1998). Eggs are laid, sometimes communally, under rocks within the stream, and females regularly brood these egg clutches (Ferguson et al. 2014). Larvae are fully aquatic with external gills and undergo metamorphosis after two to three years in New England (MacCulloch and Bider 1975). Species in this genus tend to be tolerant of urbanization, frequently occurring in urban streams (Willson and Dorcas 2003; Barrett and Guyer 2008; Ward et al. 2008; Price et al. 2011; Price et al. 2012).

Desmognathus fuscus is a semi-aquatic salamander species, exclusively occurring in or near running water (Conant and Collins, 1998). However, the species is rarely found in fast-

flowing water, preferring stream banks and seepages (Wilder 1913). *Desmognathus fuscus* can be found throughout the mid-Atlantic and northeastern states and ranges as far west as Indiana and Kentucky (Conant and Collins, 1998). Adults inhabit natural cover objects in streams and along streambeds. Eggs are similarly deposited under natural cover objects in or near water. Larvae are fully aquatic.

Study Sites.—I selected 15 first-order streams in the towns of Mansfield and Coventry, Connecticut, USA with similar percent landcovers as quantified by the Connecticut CLEAR 2010 landcover layers (CLEAR 2010; Table 1). I chose sites near road crossings that had a minimum forest buffer width of 25-meters to accommodate my sampling methods. I selected sites based on the first private landowner who provided access to the stream, and thus sampling segments fit within the property boundaries. The goal was to examine forested watersheds across a gradient of housing development age and development densities. Therefore, all selected sites had watersheds that were primarily composed of mixed deciduous and coniferous forest with forest totals ranging from 42.2% to 99.4% (Table 1). Development made up between 0% and 35.9% of each watershed and included roads, roofs, and other impervious surfaces associated with residential development (Table 1). I attempted to eliminate streams with watersheds containing other non-forest cover types, but agriculture (i.e. crops or pasture) and grass associated with large residential lawns made up a small proportion of the stream watersheds (Table 1). Next, I overlaid the delineated watersheds with a parcel layer, recorded the age of every home in each watershed, and calculated an average housing age (referred to as development age) for each watershed, which ranged from 1934 to 1992 across all watersheds (Table 1). I also used this parcel layer to ensure that the watersheds I selected across the development gradient were composed almost exclusively of residential, rather than commercial

or industrial, development. Lastly, I used a forest vegetation layer developed for the Connecticut Department of Energy and Environmental Protection (Rittenhouse 2014) to calculate the percent of each watershed consisting of regenerating forest (0% to 14%) and persistent forest (55% to 99%) as an alternative metric to average development age (Table 1).

Field Sampling.—I conducted area-constrained stream surveys once a month at each site from May 2014 to August 2014, April 2015 to September 2015, and April 2016 to September 2016. I designated a 30-meter stream segment starting at the base of each watershed. I marked sampling segments using wire flags and completed all surveys within these segments. To perform surveys, two observers simultaneously sampled on opposite sides of the stream bank, starting downstream at 0 meters and working upstream to 30 meters. Observers lifted any natural cover objects (rocks, logs, leaf litter) while holding an aquarium dipnet (6 in) directly downstream to increase successful capture. We replaced all disturbed cover objects to the original position. Captured salamanders were held in containers until the survey was complete, prohibiting double-capture. We identified each salamander to species, measured snout-to-vent length, and recorded stage of development. After processing, I returned all animals to their original location along the stream using the distance referenced on the containers.

I also used transects of artificial cover-boards to capture *E. bislineata* use of the terrestrial habitat in a consistent and minimally invasive manner at every study site for each of the 2014, 2015, and 2016 sampling periods (Hesed 2012). White oak trees were harvested from the University of Connecticut Forest to create a total of 60 artificial cover-boards, which were weathered for more than six months before sampling at the study sites. All artificial cover-boards measured 60.96 cm X 30.48 cm X 3.81 cm, a size sufficient to retain moisture and a stable thermal environment (Hesed 2012). I placed four artificial cover-boards perpendicular to the

streambed at each of the 15 sites. I positioned a cover-board at distances of 5, 10, and 20 meters from the streambed and the fourth cover-board at a distance of 5 meters on the opposing side of the streambed. I placed the transect of three cover-boards on the side of the stream with the largest forest buffer. I checked all of the boards at a site on the same days that I performed area-constrained surveys of the stream. I marked and measured any salamanders under the cover-boards using the same methodology as the salamanders captured during the stream surveys.

Habitat data.—I identified sediment distribution, turbidity, specific conductivity, dissolved oxygen (DO), temperature, and stream discharge as stream-scale habitat variables important to salamander occupancy. I recorded water, soil, and air temperatures from the 30-meter mark at each stream during each sampling period using a Taylor Instant Read Digital Thermometer (model 9840N). I wanted to capture the upper threshold of DO, discharge, and conductivity experienced by the stream. Thus, I recorded conditions during April 2015 to capture a “snapshot” of each stream after a period of spring rain, snowmelt, and runoff containing high concentrations of road salt. I measured specific conductivity and DO concentrations in the streams using a handheld sonde (Yellow Springs Instruments, YSI 556 MPS). I calculated stream discharge by measuring wetted channel width and using a SonTek FlowTracker Handheld Acoustic Doppler Velocimeter to measure mean water-column velocity and depth at regular intervals across the stream width according to USGS guidelines (Fitzpatrick et al. 1998). In May 2015, I also collected water samples from each stream in acid washed and field rinsed bottles, which I transported to the lab on ice and kept frozen until analysis. I measured the turbidity in each of these samples using a DRT 100B Turbidimeter (HF Instruments, Inc.). Finally, I measured sediment distribution in June 2015 at each stream. I walked the length of each stream segment, randomly collecting as many particles as possible. I measured particles along the

intermediate axis and recorded in the corresponding size class according to Dunne and Leopold (1978). I used the mode particle size class for each stream as a quantifiable habitat covariate.

Data Analysis.—I used an information theoretic approach to determine how coarse-scale watershed features and fine-scale stream features influence *E. bislineata* and *D. fuscus* (Akaike 1973; Burnham and Anderson 2002). I used the same candidate model sets for both occupancy and abundance and also for both species. Candidate models were expressed as occupancy models based on detection/non-detection data or N-mixture models based on count data. Both model types use repeated measures to account for imperfect detection (MacKenzie et al. 2002; MacKenzie et al. 2003; Royle and Nichols 2003; MacKenzie 2006; Costa et al. 2014; Petitot et al. 2014; Denes et al. 2015). These types of models are particularly effective for cryptic and/or low-density animals such as salamanders for which data may be difficult to acquire (MacKenzie et al. 2002; MacKenzie 2006; Costa et al. 2014; Petitot et al. 2014). I performed a Pearson's correlation matrix of all coarse- and fine-scale variables to ensure that none of the variables within a candidate model were correlated ($\rho > 0.7$).

Occupancy Analyses.—I expressed occupancy models according to the original formulation of MacKenzie et al. (2002) with detection/non-detection records for each respective species. I recorded observations, $x_{i,j,t}$, as a detection ($x = 1$) or non-detection ($x = 0$) at site i (1, 2, ..., 15) during sampling period j (1, 2, ..., 6) in year t (2014, 2015, 2016). I modeled occupancy, $z_{i,t}$, as a Bernoulli distribution with probability $\psi_{i,j,t}$, where $z_{i,j,t} = 1$ when a salamander is present at site i , during sampling year t and zero otherwise. Occupancy probability, $\psi_{i,j,t}$, was modeled as a logit link function of selected occupancy covariates. Similarly, I modeled detection probability, $p_{i,j,t}$, as a logit link function of detectability covariates for survey j . In this situation, repeated sampling events within a period where changes in occurrence status are assumed to be closed (here, one

survey season) allows for the estimation of detection probabilities and the probabilistic differentiation of non-detections from true absences (MacKenzie et al. 2002, MacKenzie et al. 2003; MacKenzie 2005; Zipkin et al. 2012). Given that sites were surveyed repeatedly over several years where closure could not be assumed, I accounted for potential temporal dependence in occupancy by including an auto-logistical term in my specifications of occupancy (Royle and Dorazio 2008). The auto-logistical parameter, ϕ , specifies the correlation between $z_{i,j,t}$ and $z_{i,j,t+1}$ (Royle and Dorazio 2008; Zipkin et al. 2012).

Abundance Analyses.— I expressed N-mixture models according to the formulation of Royle (2004) and Royle et al. (2005) with further elaboration by Wenger and Freeman (2008). I recorded observations, $x_{i,j,t}$, as a specific abundance count at site i (1, 2, ... , 15) during sampling period j (1, 2, ... , 6) in year t (2014, 2015, 2016). Abundance $N_{i,t}$ was modeled as a Poisson distribution of $\lambda_{i,t}$, which was calculated as the log function of the abundance covariates. I modeled detection probability, $p_{i,j,t}$, as a logit link function of the detectability covariates where $p_{i,j,t} = 1$ when a salamander is detected at site i , during sampling period j in year t . In this situation, multiple sampling periods allows for the estimation of detection probabilities by differentiating non-detections from true absences (MacKenzie et al. 2002, MacKenzie et al. 2003; MacKenzie 2005; Zipkin et al. 2012). Expected abundance, $y_{i,t}$, was calculated as a binomial distribution of $N_{i,t}$ and $p_{i,j,t}$. Similarly to the occupancy analyses, I accounted for potential temporal dependence by incorporating an auto-logistical parameter that made the abundance at one time period dependent on abundance from the previous time period (Royle and Dorazio 2008; Zipkin et al. 2012).

I created and ran all models in a Bayesian framework using the package R2jags in R version 3.1.2 through the interface RStudio version 0.98.1091 (R Core Team 2014; RStudio, Inc.

2014; Su and Yajima 2015). I used vague prior distributions that would not influence the posterior probability distributions. I inferred posterior probability distributions from the Monte Carlo-Markov chain (MCMC) output produced by R2jags (Su and Yajima 2015). I ran a total of three MCMC chains with 30,000 iterations, a burn-in of 10,000, and a thinning rate of 10 for a total of 6,000 posterior draws.

Coarse-Scale Model Sets.—Prior to creating my coarse-scale candidate model set, I ranked four model formulations that tested separate hypothetical drivers of salamander occupancy and abundance related to development age. The first driver, age, was the average of the year a residence was built for all parcels falling within a watershed boundary. Inherently, the three stream sites with 0% development did not have an associated housing age. Thus, I assigned the mean housing age of the remaining sites to these three locations. The age metric tests the hypothesis that occupancy and abundance decline with increasing average housing age due to cumulative and persistent alterations to the watershed. The second driver, age², is the quadratic of average house ages within a watershed and tests the hypothesis that occupancy and abundance decline following the initial construction disturbance but that abundance begins to increase after a period of time. As salamanders depend on the surrounding forests for nutrients, water filtration, and regulation of temperature and moisture (Vannote et al. 1980; Allan 2004), I also included two forest features that quantify relative forest age in the watershed. The third driver, regeneration, is the percentage of regenerating forest (up to 20 years) within a watershed and tests the hypothesis that the forest regeneration that occurs following construction contributes to increasing abundance after the initial construction disturbance. The last driver, persistent, is the percentage of persistent forest within a watershed and represents the antithesis to my previous hypotheses—if a watershed contains a high percentage of persistent forest, then there has not

been housing development or any other form of canopy cover disturbance within the watershed recently; therefore, salamander occupancy and abundance should be high.

My coarse-scale candidate model set aimed to clarify the importance of development and development age on occupancy and abundance at the watershed scale (i.e. coarse-scale). Thus, I incorporated the development age driver from the previous step that best predicted salamander occupancy or abundance into the candidate model set. Development was quantified as the percent of the watershed that is developed. I also added total watershed area into the candidate model set to account for the variability in watershed area across the sites. In addition to an intercept only model, three models tested the main effects of age, development, and total watershed area independently. An additional four models tested combinations with two or three of these main effects. The final two models included an interaction between development age and the percentage of development and were only included if the development age driver from the previous step was age or age². The interaction models tested the hypothesis that occupancy probability and abundance will be lower at new, low development sites than older, low development sites but lower at old, high development sites than newer, high development sites. Support for this hypothesis would indicate that the acute effects of exurbanization drive occupancy and abundance in low development watersheds with the potential for increases in occupancy and abundance over time but that the cumulative, persistent effects of exurbanization drive occupancy and abundance in high development watersheds by causing steeper declines for high development watersheds. The detectability process models for all candidate models included observer as a random effect, Julian date, and an intercept. None of the coarse-scale occupancy process models contained more than five parameters.

Fine-Scale Model Sets.—I also created an a priori fine-scale candidate model set to examine the importance of fine-scale stream features associated with increasing urbanization and salamander occupancy and abundance (Paul and Meyer 2001; Wenger et al. 2009). Barrett and Price (2014) identified hydrological, geomorphological, and water chemistry features as primary in-stream stressors to amphibians. Similarly, I sought to compare how hydrogeomorphology features and water chemistry features associated with osmoregulation affect *E. bislineata* and *D. fuscus* occupancy and abundance. Thus, the first hypothesis I tested was that stream features affecting salamander osmoregulation are the best determinants of occupancy and abundance. The models I created to test this hypothesis included the main effects and combinations of DO and conductivity, both of which are important determinants of salamander occupancy and abundance (Orser and Shure 1972; Willson and Dorcas 2003; Komínková 2012; Price et al. 2012; Campbell Grant et al. 2014; Bourne 2015; Epstein et al. 2016). I assigned the conductivity of all sites to one site because the field-collected value was an extreme outlier (1.6 mS/cm² compared to the mean of 0.12 mS/cm² across all other sites), suggesting there was a measurement error. I removed water temperature as a potential covariate because many of the streams were ephemeral, drying out before the end of summer, which resulted in uninformative average temperatures due to differences between permanent and ephemeral streams.

The second hypothesis I tested was that stream features affecting hydrogeomorphology are the best determinants of occupancy and abundance. The hydrogeomorphology models included the main effects and combinations of discharge (Orser and Shure 1972; Barrett et al. 2010), the mode of sediment distribution size categories (Orser and Shure 1972; Smith 2002; 2008; Rizzo et al. 2016), and soil temperature (Orser and Shure 1972; Willson and Dorcas 2003; Barrett et al. 2010; Campbell Grant et al. 2014). I included soil temperature rather than air

temperature because both salamander species are ground dwelling and often have a barrier of water or cover objects between their body and ambient air temperatures; thus, I assumed that soil temperature would be a more accurate representation of the temperature conditions experienced by the salamanders. Equipment failure in the field at some sites caused me to remove all temperature measurements from the sixth sampling period in 2015 and the fourth sampling period in 2016. Finally, I removed turbidity from the candidate models. I found that turbidity was significantly correlated with sediment distribution ($R = -0.54$, $p = 0.04$), and a number of studies suggest that turbidity either does not deleteriously affect salamander populations (Keitzer and Goforth 2012) or that turbidity alone is not sufficient to lead to extirpation (Barrett and Price 2014).

I also tested the hypothesis that a combination of osmoregulatory and hydrogeomorphology parameters predicts salamander occupancy and abundance best (Orser and Shure 1972; Willson and Dorcas 2003; Campbell Grant et al. 2014). I tested this by creating a model combining parameters from the top-ranking osmoregulation and hydrogeomorphology models and comparing the combined model to those top-ranking models. The detectability process models for all candidate models included observer as a random effect, Julian date, and an intercept. I did not include any interaction terms, and all process models contained six or fewer parameters.

Management-Scale Model Set.—Finally, I identified the scale at which management actions would be most effective by creating a model set that included the top-ranking coarse- and fine-scale models and an intercept-only model. As before, the detectability process models for all candidate models included observer as a random effect, Julian date, and an intercept.

Model Selection.—I used the Watanabe-Akaike information criterion (also known as Widely Applicable Information Criterion; WAIC) to rank occupancy and abundance models that best supported the data (Watanabe 2010; Gelman et al. 2014; Watanabe 2013; Vehtari and Gelman 2014). WAIC is a fully Bayesian approach to model selection that approximates cross-validation calculations (Gelman et al. 2014; Vehtari and Gelman 2014). For this reason, WAIC is often considered an improvement over DIC and traditional, non-Bayesian AIC methods for evaluating predictive accuracy of models (Gelman et al. 2014; Vehtari and Gelman 2014). I selected top models on the basis of having the lowest WAIC score and being at least two Δ WAIC smaller than the next top model (Burnham and Anderson 2002). Due to the nested nature of my candidate model sets, I discarded models from consideration if a nested model, containing a subset of parameters from the model, had a lower WAIC score (Burnham and Anderson 2002; Arnold 2010). Moreover, I focused inference on only the top-ranking models, although I acknowledged parameters of importance if nested models were competing (i.e., within two WAIC scores of the top model). For staged model selections such as identifying the age metric and combining parameters from the top-ranking osmoregulation and microhabitat suitability candidate model sets, I only allowed top-ranking models to propagate in subsequent model selections (Arnold 2010).

Goodness of Fit.—While model selection and parameterization was conducted using comparisons of WAIC, I independently assessed whether highly-ranked occupancy models had suitable fit. To assess the goodness-of-fit for top-ranking occupancy models, I calculated the posterior distribution of the area under the receiver operating characteristic curve (AUC) using the ROCR package in R (Sing et al. 2005; Fawcett 2006; Zipkin et al. 2012). AUC scores are calculated based on the probability of false positives relative to true positives when comparing

posterior distributions to observed data (Fawcett 2006; Zipkin et al. 2012). This approach allowed me to calculate confidence intervals around the mean AUC value and, thus, to quantify uncertainty in my posterior distributions while accounting for detection biases (Rota et al. 2011; Zipkin et al. 2012). Mean AUC values > 0.6 suggest that models provide acceptable fit to the data (Zipkin et al. 2012).

I performed posterior predictive checks and calculated a Bayesian p-value to assess the goodness-of-fit of top-ranking N-mixture models (Kéry 2010). I compared the average observed abundances for each site and sampling year to the corresponding average of the predicted abundance distributions. Then, I calculated the Bayesian p-value as the probability that the average observed abundance would be less than the average predicted abundance. Bayesian p-values near 0.5 suggest that models provide acceptable fit to the data (Kéry 2010). Finally, I examined the posterior distributions of each variable in the top-ranking models and determined the credible intervals of each variable and the direction and magnitude of each variable's effect on occupancy, abundance, and detection probabilities for each species.

RESULTS

I counted a total of 1,285 unique individuals, including 1,208 *E. bislineata* and 77 *D. fuscus* (Table 2). A total of 15, 16, and 27 *E. bislineata* individuals and 2, 8, and 6 *D. fuscus* individuals were recaptured in 2014, 2015, and 2016, respectively. *Eurycea bislineata* was present at 13 of 15 sites throughout the study. *Desmognathus fuscus* was present at 8 of 15 sites.

Occupancy of E. bislineata.—The top coarse-scale occupancy model for *E. bislineata* included the quadratic of average housing age, the percentage of development, and total watershed area (Table 3; Table 4). This model had adequate fit with a mean AUC of 0.76 (95% CI: 0.74, 0.79). Occupancy was positively related to total watershed area and negatively related

to average housing age, with the lowest occupancy probability in watersheds with predominantly new developments (Figure 1). Sampling date was not a significant predictor of detectability (0.041 95% CI: -0.369, 0.454). Average occupancy probability across all sites was estimated at 1 (95% CI: 1, 1) with a detection probability of 0.89 (95% CI: 0.83, 0.94).

The best supported fine-scale model for *E. bislineata* occupancy was a combination of stream features including conductivity, DO, discharge and sediment distribution and had a mean AUC of 0.72 (95% CI: 0.70, 0.77) (Table 4; Table 5). Dissolved oxygen was negatively related to occupancy. Conversely, sediment distribution was positively related to occupancy, with increased occupancy in watersheds where large pebbles, cobbles, and boulders dominated. Detection probability was not influenced by sampling date (0.045, 95% CI: -0.339, 0.432). Average occupancy probability across all sites was estimated at 1 (95% CI: 1, 1) with a detection probability of 0.87 (95% CI: 0.81, 0.92). The auto-logistic parameter overlapped zero for all of the top-ranking occupancy models for both species, suggesting that occupancy during one time period was not related to occupancy during the previous time period. Moreover, the variance associated with the random effect of observer was minimal for all top-ranking occupancy and abundance models, suggesting that observers were similarly able to detect salamanders when they were present.

Abundance of E. bislineata.—The best model for predicting abundance of *E. bislineata* was separated by more than 5 WAIC units and contained total watershed area, the quadratic of average housing age, the percent of development, and an interaction between age and development (Bayesian p-value: 0.58; Table 3; Table 4). Abundance was inversely related to development and the average year of construction and positively related to total watershed area (Figure 2). Detectability improved as the sampling season progressed (0.286, 95% CI: 0.203,

0.372), and the auto-logistic parameter was estimated at -0.382 (95% CI: -0.669, -0.102), suggesting that abundance during one time period was negatively related to abundance during the previous time period. Average abundance across all sites was estimated at 53.2 salamanders per 30-meter stream segment (95% CI: 38.4, 80.4) with a per-individual detection probability of 0.89 (95% CI: 0.83, 0.94).

The top-ranking fine-scale abundance model for *E. bislineata* included average soil temperature (Bayesian p-value: 0.39; Table 4; Table 5), which was inversely related to abundance. Detectability improved as the sampling season progressed (0.356, 95% CI: 0.258, 0.456), and the auto-logistic parameter was estimated at -0.523 (95% CI: -0.763, -0.284). Average abundance across all sites was estimated to be 24.7 salamanders per sample (95% CI: 20.2, 30.8) with a per individual detection probability of 0.28 (95% CI: 0.21, 0.36).

Occupancy of D. fuscus.—The top-ranked coarse-scale model for *D. fuscus* occupancy included the quadratic of average housing age, the percentage of development, the total watershed area, and an interaction between the quadratic of average housing age and the percentage of development (Table 3; Table 4), and had a mean AUC of 0.60 (95% CI: 0.57, 0.66), indicating poor fit. Occupancy was negatively related to the quadratic of housing age, with the lowest probability of occupancy in watersheds with recent development. Occupancy was not significantly related to total watershed area (-5.81, 95% CI: -27.58, 42.91) or watershed development (0.950, 95% CI: -31.73, 15.67). The interaction between housing age and development indicates that occupancy is lowest at recently developed watersheds with little to no previous development. Sampling date was a strong predictor of detection probability (0.487, 95% CI: 0.118, 0.873), with increasing detectability as the sampling season progressed. Average

occupancy probability across all sites was estimated to be 1 (95% CI: 0.50, 1.00) with a detection probability of 0.30 (95% CI: 0.21, 0.42).

The top-ranked, fine-scale occupancy model for *D. fuscus* was the full model, which included features of the stream affecting osmoregulation such as conductivity and DO as well as microhabitat features such as soil temperature, discharge, and sediment distribution. The model had a mean AUC of 0.65 (95% CI: 0.62, 0.72) (Table 4, Table 5). Occupancy probability was positively related to sediment distribution, and inversely related to soil temperature, conductivity, and DO (Figure 3). Sampling date was positively correlated to detection probability (0.544, 95% CI: 0.161, 0.952). Average occupancy probability across all sites was estimated to be 0.18 (95% CI: 0.00, 1.00) with a detection probability of 0.37 (95% CI: 0.27, 0.48).

Abundance of D. fuscus.—The top-ranking coarse-scale abundance model for *D. fuscus* included average housing age (Bayesian p-value: 0.54; Table 3; Table 4); however, this model was within 2 Δ WAIC of the null model. Thus, I present the results of this top-ranking model while acknowledging that there is mixed support for the model. Abundance was positively related to housing age, with the highest abundance in watersheds with new developments. Relative abundance across all sites was estimated to be 0.80 (95% CI: 0.50, 1.27), with an estimated per-individual detection probability of 0.21 (95% CI: 0.10, 0.37). Sampling date was positively correlated to detection probability (0.929, 95% CI: 0.551, 1.363). The auto-logistic parameter did not overlap zero (0.850, 95% CI: 0.140, 1.495), suggesting that occupancy during one time period was positively related to occupancy during the previous time period.

The fine-scale abundance model with the most support included average soil temperature, which was positively related to abundance, and discharge, which was negatively related to abundance (Bayesian p-value: 0.52; Table 4; Table 5; Figure 4). Detectability increased as the

sampling season progressed (0.946, 95% CI: 0.564, 1.379), and the auto-logistic parameter was estimated at 1.027 (95% CI: 0.293, 1.682), suggesting that occupancy at one time period was positively related to occupancy in the previous time period. Average abundance across sites was estimated to be 0.70 (95% CI: 0.41, 1.14) with a per-individual detection probability of 0.21 (95% CI: 0.09, 0.37).

Comparison among spatial scales.—Coarse-scale models best predicted both occupancy and abundance of *E. bislineata* (Table 6). In fact, the top-ranking, fine-scale abundance model was more than 120 Δ WAIC greater than the top-ranking, coarse-scale abundance model. In contrast, fine-scale models best predicted *D. fuscus* occupancy and abundance (Table 6).

DISCUSSION

I found that the persistence of salamanders in a landscape composed of mature, second growth forest perforated by houses is influenced by the amount of development and time since the houses were constructed as well as specific combinations of habitat features within the stream reach. Although salamander responses to development may not become fully apparent for many more decades, my results from a landscape that began its transition to residential land uses in the 1920's may inform places currently undergoing rapid development. Here, I found that *E. bislineata* abundance was best explained by an interaction between the quadratic of average housing age and the amount of development in a watershed, suggesting that *E. bislineata* abundance is sensitive to new and high-density housing developments but that abundances can increase more than 20 years post-construction. In contrast, *D. fuscus* abundance and occupancy were best predicted by a combination of fine-scale features of the stream as opposed to coarse-scale features of the watershed. Surprisingly, my estimates of relative *D. fuscus* abundance in this study were much lower than previous studies using comparable sampling efforts. This may

indicate that populations in Connecticut's increasingly exurban watersheds have experienced or are experiencing an extinction debt, where susceptible populations have already disappeared or are composed of a few remaining adults (Semlitsch et al. 2017). Ultimately, forests perforated with exurban development contain many areas where salamanders could potentially persist, yet the details as to when and how populations persist within an intermixed ecosystem have yet to be fully articulated.

Eurycea bislineata was ubiquitous, with occupancy estimated at 100%, but abundance was quite variable and best explained by an interaction between the quadratic of average house age and the percent of development within the watershed. A previous study also found that *E. bislineata* is fairly resilient to development, occurring at most sites albeit at reduced abundances (Barrett and Guyer 2008); however, my study provides evidence of an interaction between housing age and percent development influencing salamander abundance. In contrast to my original hypothesis, I found that age was the strongest determinant of abundance with increasing development dampening the magnitude of the response. *Eurycea bislineata* abundance was diminished most in watersheds with new and high-density housing developments, but I also found that abundances increased more than 20 years post-construction. The most recently built housing development in this study had an average construction year of 1992, more than 24 years old at the time of sampling. Abundance was lowest during this period post-construction. I do not have pre-construction abundance estimates to compare to my current estimates; however, abundance was higher within control watersheds with no development, indicating that the low abundance was likely a decline from pre-construction abundance levels. While initial population declines following disturbance can be substantial (Gagné and Fahrig 2010; Price et al. 2012), *Hyla versicolor* frogs showed increases in relative abundance approximately 35 years after

development (Gagné and Fahrig 2010). My results suggest that *E. bislineata* abundance declines for more than 20 years but then abundance increases if housing density in the watershed is low. Further, high levels of development impede increases in salamander abundance as housing ages.

Although reduced *E. bislineata* abundance was expected in highly developed watersheds (Willson and Dorcas 2003; Barrett and Guyer 2008), the reduction documented here was more severe than I anticipated. I found that relative abundance dropped with any amount of development in the watershed. Further, I estimated a 50% reduction in relative abundance at 15% watershed development and approximately 20 individuals per 30-meter stream segment remaining at 35% watershed development. Other studies with *E. cirrigera* in North Carolina and Georgia have found higher relative abundances at low levels of watershed disturbance (Willson and Dorcas 2003) or lower magnitude declines at similar levels of urbanization (Barrett and Guyer 2008).

In contrast to *E. bislineata*, I found strong support for fine-scale habitat features influencing patterns of *D. fuscus* occupancy and abundance. This result highlights the importance of osmoregulatory, hydrological, and geomorphological to the persistence of this species. In accordance with previous findings, I observed a reduction in *D. fuscus* occupancy as conductivity increased and detected a significant positive correlation between conductivity and the amount of development in the watershed (Willson and Dorcas 2003; Price et al. 2012; Campbell Grant et al. 2014; Bourne 2015). I also found increased *D. fuscus* occupancy probabilities at streams with a majority of larger sediment sizes such as cobble and boulders, which could indicate that large sediments provide crucial protective cover or microhabitat. Correspondingly, *D. fuscus* densities are generally reduced with increased deposition of fine sediments in urban streams (Orser and Shure 1972; Willson and Dorcas 2003) and salamander

observations increase in streams with a high percentage of gravel, pebble, and cobble strata and increased rock density (Smith 2002; Brannon and Pruvis 2008). *Desmognathus fuscus* also exhibited reduced abundance in watersheds with high discharge rates. Previous research has found that increased discharge from urbanization runoff reduces *E. cirrigera* larval salamander densities and that finer substrates in urban streams can further lower the water velocity threshold necessary to flush salamander larva downstream (Barrett et al. 2010).

Desmognathus fuscus occupancy and abundance did not respond to temperature or dissolved oxygen as predicted. While *D. fuscus* occupancy diminished with increasing soil temperatures as anticipated (Orser and Shure 1972; Campbell Grant et al. 2014), *D. fuscus* abundance increased with increasing soil temperature. However, the average temperature range measured in this study (approximately 13 to 15.5 °C) was near the low end of all temperatures measured in other studies (14 to 24 °C) (Orser and Shure 1972; Campbell Grant et al. 2014) and well below the thermal preference and limit for the species (Layne and Claussen 1982, Moore and Sievert 2001). At this thermal range, warmer temperatures can promote surface activity such as foraging (Hutchinson and Spriesterbach 1986; Bakkegard 2002; Anderson et al. 2014; Marvin et al. 2016), which could influence the number of salamanders observed at the surface. I also found a reduction in *D. fuscus* occupancy probability beyond 90% DO saturation, which contrasts with previous research showing increased densities of *D. fuscus* and *E. cirrigera* with elevated DO (Orser and Shure 1972; Willson and Dorcas 2003). One study observed increasing *D. fuscus* densities up to 7.4 ppm (Orser and Shure 1972). Converting this result is difficult without additional information about temperature, barometric pressure, and elevation at the collection site; however, the 90% saturation point I measured under average temperature and elevation conditions during that sampling period corresponds to approximately 10.5 ppm

(Mortimer 1956; Mortimer 1981). I expect that the reduction in occupancy in sites with elevated DO is due to a positive relationship between discharge and DO. This species rarely inhabits streams with fast-flowing water (Conant and Collins 1998), and I observed reduced abundance at sites with high discharge.

My estimate of *D. fuscus* relative abundance and capture rates were consistently much lower than expected when compared to previous studies with similar sampling efforts. I anticipated relatively low occupancy and abundance estimates for *D. fuscus* because numerous studies have found that *D. fuscus* is sensitive to urbanization (Orser and Shure 1972; Willson and Dorcas 2003; Price et al. 2011; Price et al. 2012), but I found just 77 *D. fuscus* individuals across 15 sampling sites, including undeveloped controls, throughout 16 sampling periods. The estimated density, which accounts for detection probability, was less than one individual for a given 30-meter stream segment. Previous studies examining *D. fuscus* response to urbanization produced drastically different estimates. Researchers in Georgia estimated densities as high as 70 individuals per 10-meter stream segment (Orser and Shure 1972). In North Carolina, 10-meter surveys at streams that roughly correspond to the highest degree of exurbanization in this study produced an estimated 20 individuals (Willson and Dorcas 2003) while sampling efforts across a gradient of watershed urbanization (1%-78%) produced 2,669 individuals over five years and 100% occupancy for adults (Price et al. 2012). In contrast, the highest density of unique *D. fuscus* individuals I observed in a given stream for a year was 12 individuals. Moreover, in three years of sampling, the highest number of unique individuals observed at a given site was 26 individuals. Even when extrapolating across the length of a headwater stream, these abundances are incredibly low given that most estimates for minimum viable population sizes suggest a minimum of 500 individuals with many species requiring many thousands of individuals

(Lehmkuhl 1984; Thomas 1990; Reed et al. 2003; Lannoo 2005). Further, when combined with a limited home range of less than 50 m², exceedingly short dispersal movements, and the propensity to stay within 20-30 meters of the aquatic habitat (Barbour et al. 1969; Semlitsch and Bodie 2003; Perkins and Hunter 2006; Campbell Grant et al. 2010), low abundance can pose a threat to the long-term persistence of a species. Particularly in an exurban landscape, where mature forest is intermixed by an often impermeable matrix of development that is unlikely to provide the area or connectivity needed for sensitive species with low abundance and limited dispersal (Semlitsch and Bodie 2003; Hansen et al. 2005; Noël et al. 2007; Prugh et al. 2008; Campbell Grant et al. 2010; Munshi-South et al. 2013).

While I lack pre-development abundance estimates for both *E. bislineata* and *D. fuscus*, I expect that extinction debt has played a role in the reduced occupancy and abundance of *D. fuscus* relative to *E. bislineata* (Semlitsch et al. 2017). I assume that both species were ubiquitous decades ago as forests continued to regenerate and residential housing was sparse on the southern New England landscape (Foster 1992; Jeon et al. 2014). However, with continued residential development, I expect that suitable habitats were destroyed, populations were isolated, abundance declined, and susceptible populations disappeared (Price et al. 2011; Price et al. 2012; Munshi-South et al. 2013; Semlitsch et al. 2017). In the case of *E. bislineata*, I presume that vulnerable individuals were not reproductively successful or did not survive the disturbance, reducing population abundances for more than two decades after construction. However, *E. bislineata* populations were resilient enough to persist and eventually increase in abundance. *Desmognathus fuscus* likely faced similar declines in abundance as well as the loss of inadequately resilient populations, reducing occupancy in this region of the state. However, the remaining populations I observed appear to be experiencing an extinction debt. Relative

abundance estimates were less than one individual per stream, and of the 77 individuals captured throughout the study, 69 were adults. Just eight captures were larva, and I never observed a *D. fuscus* egg clutch during my three years of sampling.

I suggest using an adaptive management approach to monitor and manage *E. bislineata* and *D. fuscus* populations in the region (Holling 1978). Monitoring the remaining *E. bislineata* and *D. fuscus* populations will improve our understanding of population dynamics, identify stochastic events that could threaten population persistence, and provide a baseline to assess the effectiveness of management practices. Given the results of this study, I suggest initially managing for the fine-scale stream features associated with *D. fuscus* occupancy and abundance in this region. For example, managers can enforce more conscientious deposition of road salts to reduce conductivity in freshwater ecosystems and encourage the use of low-impact-development technologies to reduce and filter runoff from highly developed communities. For *E. bislineata*, I recommend trying to reduce the acute impacts of development to minimize the declines in abundance we suspect occurred in the 20 years post-construction as well as reducing the amount of impervious surfaces in watersheds with a high percentage of development such that increases in abundance are not dampened. Future research can further elucidate when and how populations persist within an intermixed ecosystem.

My results demonstrate the importance of considering interactions between multiple local stressors as well as the scale at which environmental conditions influence population persistence (Rohr and Palmer 2013; Barrett and Price 2014). I demonstrated that *E. bislineata* abundance is influenced by an interaction between housing age and development and that *E. bislineata* abundance can increase more than 20 years after the initial construction disturbance. This finding highlights the importance of considering both the synergistic and legacy effects of urbanization

during planning and zoning processes and subsequent decisions about wildlife management. Further, this study demonstrates the vulnerability of *D. fuscus* salamanders in Connecticut's exurban landscape. I suggest using an adaptive management approach to monitor and manage *D. fuscus* populations in the region (Holling 1978), focusing first on the fine-scale stream features associated with *D. fuscus* occupancy and abundance. First-order streams and associated wildlife have become a model system for understanding the ecological effects of urbanization because alterations within the watershed manifest themselves in the stream through altered hydrology, water quality, and community assemblages in a process known as urban stream syndrome (Allan 2004; Freeman and Schorr 2004; Meyer et al. 2005; Walsh et al. 2005; Alexander et al. 2007; Matzen and Berge 2008; Barrett et al. 2010; Canessa and Parris 2013; Johnson 2013; Halstead et al. 2014). Ultimately, my results here contribute to this body of research by highlighting the range of outcomes that can occur within low to moderate amounts of development.

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Tables

Table 1. Watershed features and the range, mean, and standard deviation values of these features across the 15 sampling sites.

Feature	Range	Mean	SD
Average Year Built	1934-1992	1967	17
% Developed	0.0-35.9	11.6	11.3
% Deciduous	40.1-99.4	72.5	18.8
% Coniferous	0.0-14.0	2.8	5.3
% Total Forest	42.2-99.4	75.3	18.3
% Regenerating Forest	0.0-14.3	5.3	4.8
% Persistent Forest	53.6-98.5	83.2	13.2
% Grass and Turf	0.0-29.8	6.9	8.2
% Agriculture	0.0-14.6	3.0	4.2
Total Area km²	0.08-0.78	0.35	0.20

Table 2. Cumulative *E. bislineata* and *D. fuscus* counts for the 2014, 2015, and 2016 sampling years. Counts were measured as the number of unique larval and adult individuals. Also included is how many of the 15 sampling sites were occupied by *E. bislineata* and *D. fuscus* during the 2014, 2015, and 2016 sampling years.

		2014	2015	2016
<i>Eurycea bislineata</i>	Adult Count	85	123	141
	Larvae Count	339	295	225
	Total Count	424	418	366
	Number of sites present	13	13	12
<i>Desmognathus fuscus</i>	Adult Count	27	25	17
	Larvae Count	2	4	2
	Total Count	29	29	19
	Number of sites present	8	5	6

Table 3. Exploratory WAIC ranking of potential development age metrics for occupancy and abundance models for both *E. bislineata* and *D. fuscus*. The top-ranking age parameter (denoted *X*) was then incorporated into the coarse-scale occupancy and abundance candidate model sets for each species. The resulting occupancy and abundance model sets were ranked using WAIC and weighted with respect to the top-ranking model (Δ WAIC), which is bolded. The number of parameters, *K*, for each model is also included.

		<i>Eurycea bislineata</i>		<i>Desmognathus fuscus</i>	
Coarse-Scale Models	K	WAIC	Δ WAIC	WAIC	Δ WAIC
Occupancy-Age					
Intercept + Age	3	193.03	1.97	221.19	23.91
Intercept + Age ²	3	191.06	0	197.28	0
Intercept + Regeneration	3	270.62	79.56	225.99	28.71
Intercept + Persistent	3	272.69	81.63	212.32	15.04
Occupancy-Candidate Model Set					
Intercept + <i>X</i> + Developed + TotalArea + <i>X</i> *Developed	6	159.85	0.90	190.48	0
Intercept + <i>X</i> + Developed + <i>X</i> *Developed	5	186.45	27.50	201.66	11.17
Intercept + <i>X</i> + Developed + TotalArea	5	158.95	0	217.79	27.31
Intercept + Developed + TotalArea	4	239.99	81.03	219.25	28.76
Intercept + <i>X</i> + Developed	4	193.61	34.66	218.16	27.68
Intercept + <i>X</i> + Total Area	4	160.37	1.42	221.89	31.41
Intercept + Developed	3	269.24	110.29	215.99	25.50
Intercept + TotalArea	3	245.79	86.84	220.90	30.42
Intercept + <i>X</i>	3	193.03	34.08	197.28	6.80
Intercept	2	264.11	105.15	220.05	29.57
Abundance-Age					
Intercept + Age	3	1402.38	45.77	245.62	0
Intercept + Age ²	3	1356.61	0	246.89	1.28
Intercept + Regeneration	3	1425.81	69.21	245.98	0.36
Intercept + Persistent	3	1431.74	5.93	251.12	5.51
Abundance-Candidate Model Set					
Intercept + <i>X</i> + Developed + TotalArea + <i>X</i> *Developed	6	1241.56	0	265.46	19.84
Intercept + <i>X</i> + Developed + <i>X</i> *Developed	5	1345.57	104.01	262.66	17.04
Intercept + <i>X</i> + Developed + TotalArea	5	1247.10	5.54	265.46	19.84
Intercept + Developed + TotalArea	4	1372.82	131.26	264.75	19.14
Intercept + <i>X</i> + Developed	4	1356.60	115.04	259.683	14.07
Intercept + <i>X</i> + Total Area	4	1387.97	146.41	250.022	4.41
Intercept + Developed	3	1423.41	181.85	260.698	15.08
Intercept + TotalArea	3	1404.26	162.70	248.390	2.78
Intercept + <i>X</i>	3	1356.61	115.05	245.615	0
Intercept	2	1428.95	187.39	246.934	1.32

Table 4. Predictor estimates and 95% credible intervals for top-ranking occupancy and abundance models for *E. bislineata* and *D. fuscus*. Significant predictors are bolded.

Predictor	Estimate	Lower 95% CI	Upper 95% CI
<i>Eurycea bislineata</i>: Coarse-Scale Occupancy			
Age ²	-19.914	-34.549	-7.503
Developed	-0.825	-13.427	14.550
TotalArea	19.837	7.557	34.886
<i>Eurycea bislineata</i>: Fine-Scale Occupancy			
Conductivity	15.195	-0.916	41.000
DO	-22.822	-56.869	-3.886
SedimentDis	21.704	5.646	52.819
Discharge	8.890	-20.413	48.132
<i>Eurycea bislineata</i>: Coarse-Scale Abundance			
Age ²	-0.846	-0.965	-0.730
Developed	-0.524	-0.639	-0.414
TotalArea	0.810	0.704	0.921
Age ² *Developed	0.263	0.148	0.381
<i>Eurycea bislineata</i>: Fine-Scale Abundance			
SoilTemp	-0.477	-0.566	-0.394
<i>Desmognathus fuscus</i>: Coarse-Scale Occupancy			
Age ²	-17.286	-29.581	-5.060
Developed	0.949	-31.733	15.673
TotalArea	-5.806	-27.580	42.913
Age ² *Developed	-48.296	-93.407	-15.639
<i>Desmognathus fuscus</i>: Fine-Scale Occupancy			
SoilTemp	-21.234	-40.861	-6.129
Conductivity	-16.672	-26.841	-7.212
DO	-48.008	-76.745	-21.031
SedimentDist	21.219	7.595	35.610
Discharge	-7.819	-27.487	18.265
<i>Desmognathus fuscus</i>: Coarse-Scale Abundance			
Age	0.539	0.211	0.894
<i>Desmognathus fuscus</i>: Fine-Scale Abundance			
Discharge	-0.836	-1.788	-0.178
SoilTemp	0.640	0.300	1.006

Table 5. WAIC ranking of fine-scale, hydrogeomorphology and osmoregulation models for occupancy and abundance of both *E. bislineata* and *D. fuscus*. Parameters from top-ranking hydrogeomorphology and osmoregulation models were combined and compared to the top-ranking models using WAIC and weighted against the top-ranking model using Δ WAIC. The top-ranking model from the combined model set is bolded. The number of parameters, K, for each model is also included.

		<i>Eurycea bislineata</i>		<i>Desmognathus fuscus</i>	
	K	WAIC	Δ WAIC	WAIC	Δ WAIC
Fine-Scale Models					
Occupancy-Hydrogeomorphology					
Intercept + SoilTemp + Discharge + SedimentDist	5	214.36	9.98	199.78	0
Intercept + SoilTemp + SedimentDist	4	207.42	3.03	228.50	28.72
Intercept + SoilTemp + Discharge	4	227.68	23.29	229.17	29.39
Intercept + Discharge + SedimentDist	4	204.39	0	214.61	14.83
Intercept + SoilTemp	3	267.60	63.22	226.62	26.84
Intercept + SedimentDist	3	206.14	1.76	220.45	20.67
Intercept + Discharge	3	258.05	53.67	221.85	22.07
Intercept	2	264.90	60.51	219.73	19.95
Occupancy-Osmoregulation					
Intercept + Conductivity + DO	4	182.52	0	197.60	0
Intercept + Conductivity	3	266.41	83.88	217.97	20.38
Intercept + DO	3	259.18	76.66	198.94	1.34
Intercept	2	264.90	82.38	219.73	22.14
Occupancy-Combined					
<i>Eurycea Bislineata</i>					
Intercept + Discharge + SedimentDist + Conductivity + DO	6	181.91	0	-	-
Intercept + Discharge + SedimentDist	4	204.39	22.47	-	-
Intercept + Conductivity + DO	4	182.52	0.61	-	-
Intercept	2	264.90	82.99	-	-
<i>Desmognathus fuscus</i>					
Intercept + SoilTemp + Discharge + SedimentDist + Conductivity + DO	7	-	-	163.33	0
Intercept + SoilTemp + Discharge + SedimentDist	5	-	-	199.78	36.45
Intercept + Conductivity + DO	4	-	-	197.60	34.26
Intercept	2	-	-	219.73	56.40
Abundance-Hydrogeomorphology					
Intercept + SoilTemp + Discharge + SedimentDist	5	1369.11	6.48	248.35	4.61
Intercept + SoilTemp + SedimentDist	4	1366.09	3.46	246.96	3.21
Intercept + SoilTemp + Discharge	4	1364.47	1.84	243.75	0
Intercept + Discharge + SedimentDist	4	1413.62	50.98	247.07	3.33
Intercept + SoilTemp	3	1362.63	0	245.01	1.26
Intercept + SedimentDist	3	1417.79	55.15	246.82	3.07
Intercept + Discharge	3	1425.26	62.62	247.65	3.91
Intercept	2	1429.42	66.78	246.49	2.75
Abundance-Osmoregulation					
Intercept + Conductivity + DO	4	1439.21	9.80	261.26	14.77
Intercept + Conductivity	3	1432.09	2.67	259.37	12.87
Intercept + DO	3	1434.58	5.16	251.29	4.80
Intercept	2	1429.42	0	246.49	0
Abundance-Combined					
<i>Eurycea Bislineata</i>					
Intercept + SoilTemp	3	1362.63	0	-	-
Intercept	2	1429.42	66.78	-	-
<i>Desmognathus fuscus</i>					
Intercept + SoilTemp + Discharge	4	-	-	243.75	0
Intercept	2	-	-	246.49	2.75

Table 6. WAIC model selection of top-ranking, coarse- and fine-scale models of occupancy and abundance for both *E. bislineata* and *D. fuscus*. The top-ranking model from the combined model sets is bolded and weighted against the other models (Δ WAIC). The number of parameters, K, for each model is also included.

Management-Scale Models	K	WAIC	ΔWAIC
<i>Eurycea bislineata</i>			
Occupancy			
<i>Top Coarse-Scale Model</i>			
Intercept + Age ² + Developed + TotalArea	5	158.95	0
<i>Top Fine-Scale Model</i>			
Intercept + Discharge + SedimentDist + Conductivity + DO	6	181.91	22.96
<i>Intercept Model</i>			
Intercept	2	264.11	105.15
Abundance			
<i>Top Coarse-Scale Model</i>			
Intercept + Age ² + Developed + TotalArea + Age ² *Developed	6	1241.56	0
<i>Top Fine-Scale Model</i>			
Intercept + SoilTemp	3	1362.63	121.08
<i>Intercept Model</i>			
Intercept	2	1428.95	187.39
<i>Desmognathus fuscus</i>			
Occupancy			
<i>Top Coarse-Scale Model</i>			
Intercept + Age ² + Developed + TotalArea + Age ² *Developed	5	190.48	27.15
<i>Top Fine-Scale Model</i>			
Intercept + SoilTemp + Discharge + SedimentDist + Conductivity + DO	7	163.33	0
<i>Intercept Model</i>			
Intercept	2	220.05	56.72
Abundance			
<i>Top Coarse-Scale Model</i>			
Intercept + Age	3	245.62	1.87
<i>Top Fine-Scale Model</i>			
Intercept + SoilTemp + Discharge	4	243.75	0
<i>Intercept Model</i>			
Intercept	2	246.93	3.19

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Figure 4. Significant fine-scale predictors—average soil temperature and discharge—of *Desmognathus fuscus* abundance and 95% credible intervals.

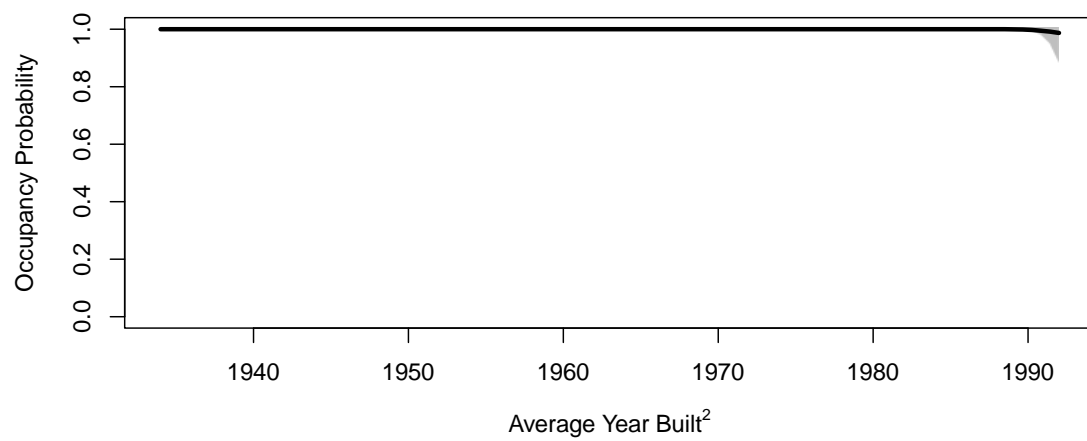


Figure 1.

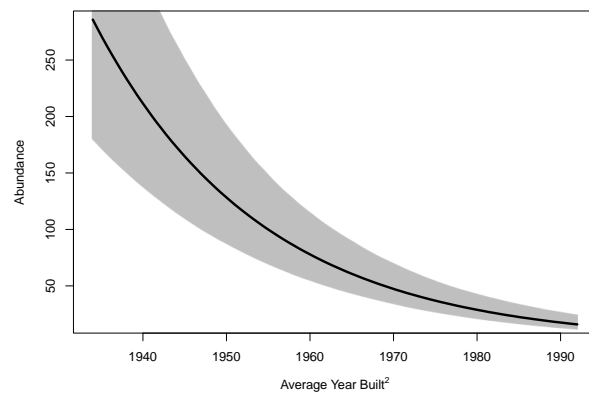
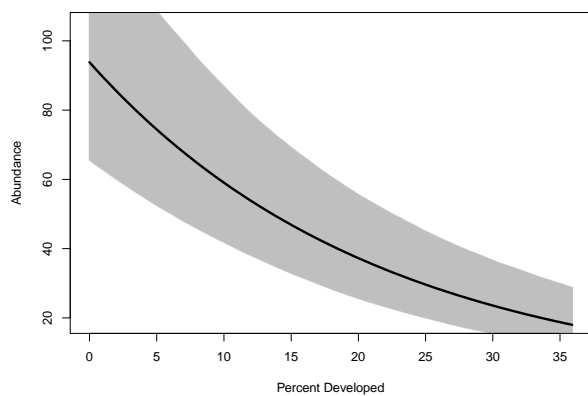
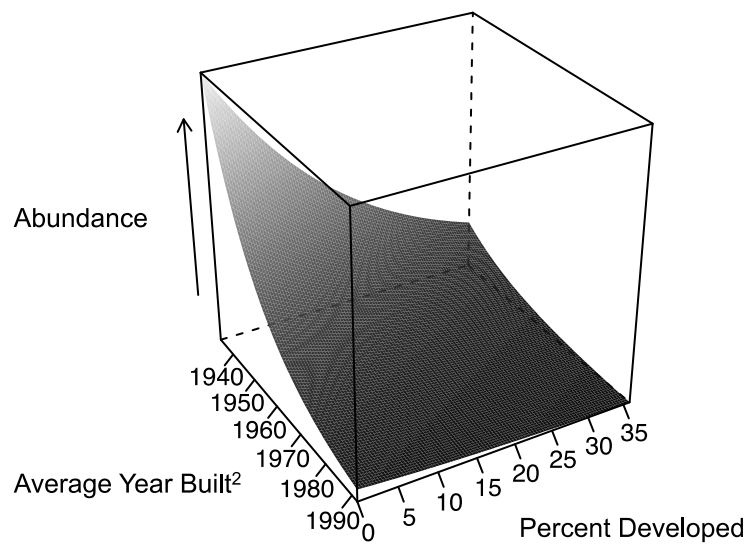
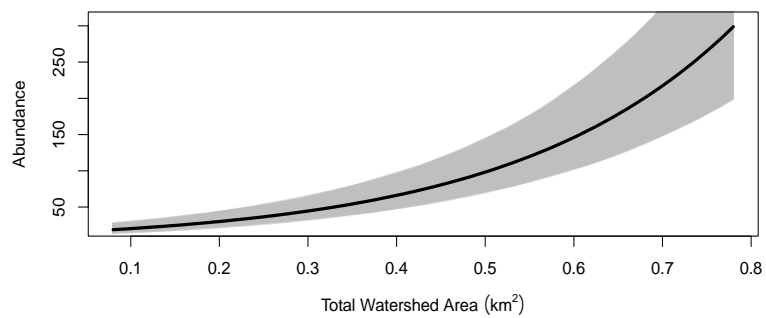


Figure 2.

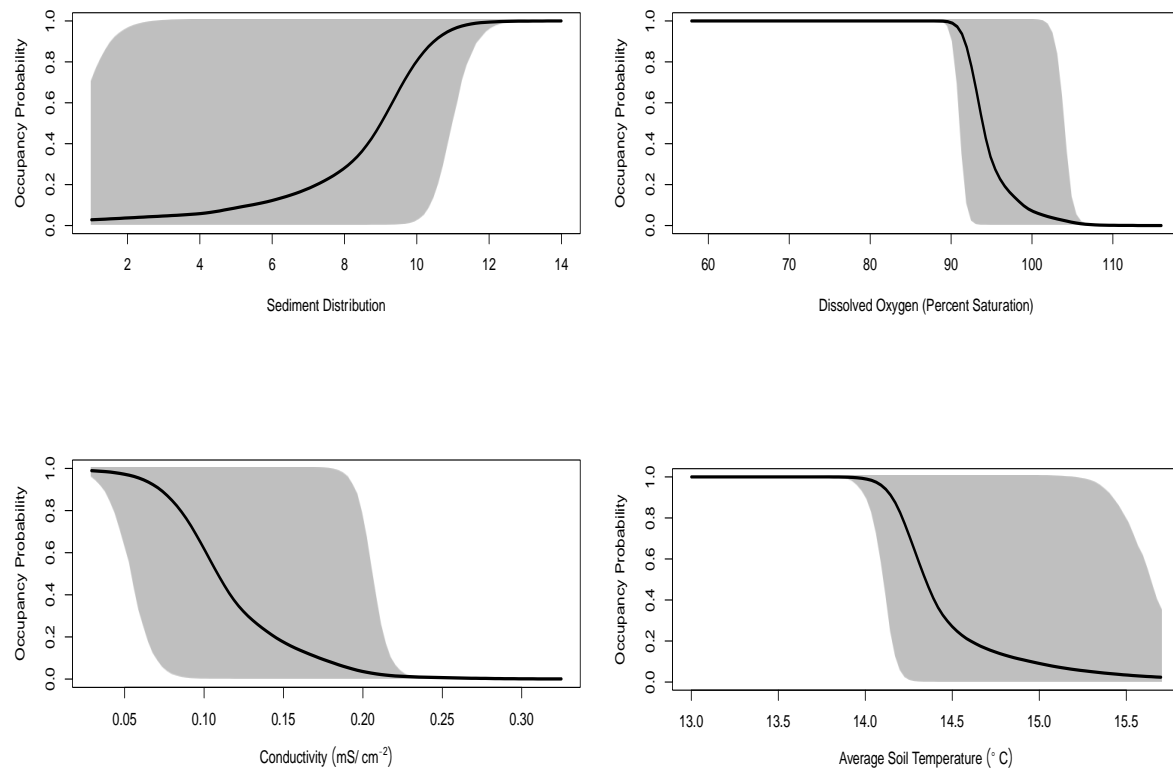


Figure 3.

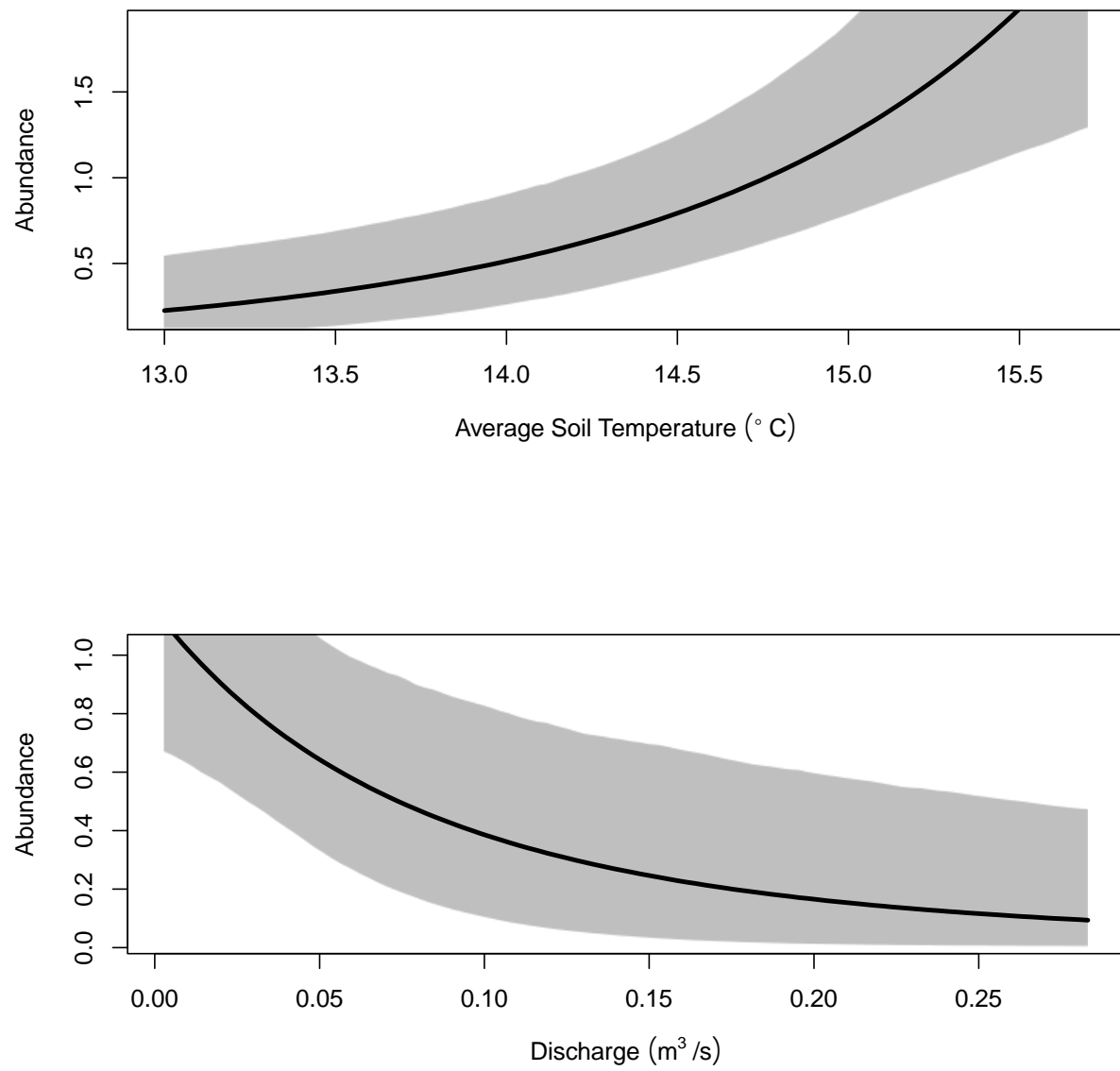


Figure 4.

Exurban housing development age influences stream salamander reproductive patterns

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ABSTRACT.— Amphibians exhibit many reproductive and parental care strategies that are based on the trade-off between reproductive success and enhanced growth and survival. Furthermore, reproduction is a plastic response that allows amphibian populations to persist in volatile environmental conditions. However, anthropogenic influences like climate change, pollution, selective harvesting of wildlife, and habitat fragmentation are now altering animal reproduction strategies, and these shifts may profoundly influence population dynamics. Thus, I chose to examine how exurban housing development might influence the reproductive strategies of a stream-dwelling salamander, *Eurycea bislineata*. I sought to quantify how coarse- and fine-scale covariates associated with exurban housing development as well as adult salamander counts influenced the reproductive output, communal ovipositing, and brooding behavior of *E. bislineata*. Contrary to expectation, the percent of the development in the watershed did not influence any of our responses. Adult count was highest in newly developed watersheds, declining in watersheds with older housing developments. Reproductive output, communal ovipositing, and brooding behavior at the stream level were most strongly influenced by fine-scale features such as average soil temperature and sediment distribution. Further, I found that all three reproductive responses were highest in watersheds with low adult counts or old housing developments. One explanation for these responses is that females are clustering around limited resources in a disturbed habitat. A second explanation is that urbanization altered the biological community in such a way as to reduce or eliminate predators. Ultimately, this research highlights the reproductive variability of *E. bislineata* and provides the first evidence of housing development age influencing the reproductive strategies of an amphibian. We expect that the variation documented may be a plastic response to housing development that could serve to improve embryo and/or adult survival and fitness in disturbed environments.

Key Words: amphibian; conservation; egg clutch; exurban development; oviposit; parental care; reproductive strategy

INTRODUCTION

Amphibians exhibit reproductive and parental care strategies that are based on the trade-off between reproductive success or enhanced growth and survival (Salthe 1969; Duellman and Trueb 1986; Crump 1996; Townsend et al. 1984; Townsend 1986). For example, predation, desiccation, and competitive pressures strongly influence reproductive success and, thus various egg-deposition strategies have evolved (Duellman and Trueb 1986; Lima and Dill 1990; Magnusson and Hero 1991). Terrestrial oviposition is evolutionarily favored when predation pressure in wetlands reduces embryonic survival more than terrestrial desiccation (Duellman and Trueb 1986; Magnusson and Hero 1991). Similarly, parental care is expected to evolve when care increases offspring survival enough to offset the costs incurred by the parent (Clutton-Brock 1991). Parental care increases offspring survival by protecting against predators and desiccation (Townsend et al. 1984; Poo and Bickford 2013). However, care-providing parents have reduced foraging and reproduction opportunities (Townsend 1986, Stearns 1992; Delia et al. 2013) and reduced survival due to high energetic costs and increased vulnerability to predators and environmental stress (Stearns 1992; Church et al. 2007; Harshman and Zera 2007). Parental care can even reduce future reproductive success with care-giving females producing fewer or small clutches in subsequent reproductive periods (Salthe and Duellman 1973; Church et al. 2007).

Amphibians exhibit phenotypic plasticity in many reproduction responses (e.g. timing or location of oviposition, egg number), and this plasticity often enhances reproductive success in variable environments (Kaplan 1987; Touchon and Warkentin 2008; Takahashi and McPhee 2016). Iteroparous amphibians defer breeding in years when the risk of adult mortality is high

(Church et al. 2007). Facultative oviposition was found in *Notophthalmus viridescens* salamanders, which avoided ovipositing during water reduction simulations (Takahashi and McPhee 2016). Similarly, *Dendropsophus ebraccatus* frogs exhibit plasticity in oviposition site, selecting aquatic oviposition in disturbed, unshaded environments and terrestrial oviposition sites under shaded conditions (Touchon and Warkentin 2008). The characteristics of amphibian egg clutches are also plastic. In general, the number and size of ova are inversely related and predominantly limited by the size of the female, her reproductive capacity, and the mode of reproduction (Crump 1996). Egg size for most amphibian species is fixed (Salthe and Duellman 1973), but the number of eggs per clutch is highly variable and influenced by environmental factors (Kaplan 1987; Mitchell and Pague 2014). One study found that temperature and food availability influenced both egg size and number produced by female *Bombina orientalis* frogs (Kaplan 1987). These highly plastic reproductive responses in the egg and larval life stages are important due to their subsequent influence on hatchling and larval size (Kaplan 1989).

Parental care behaviors are also plastic responses in amphibians with transport, feeding, nest care, and temporal commitments to nest attendance being strongly influenced by environmental variation (Ringler et al. 2013; Delia et al. 2014; Ferguson et al. 2014). For example, *Hyalinobatrachium fleischmanni* glassfrogs in Mexico adjust the frequency of parental care based on weather conditions and egg dehydration (Delia et al. 2013). Dendrobatid frogs, which provide a diversity of parental behaviors to offspring such as transport, nest attendance, and supplemental feeding, exhibit adaptive plasticity in these behaviors and between the sexes (Ringler et al. 2013). Amphibians have evolved complex reproductive strategies for their environments and exhibit reproductive plasticity that guards against environmental volatility.

Anthropogenic influences like climate change, pollution, selective harvesting of wildlife, and habitat fragmentation are now altering reproductive strategies (Miner et al. 2005; Lane et al. 2011). For example, a study on *Trichosurus cunninghami* possum populations found that resource clumping in disturbed roadside habitats favored smaller female distributions and polygyny while uniform resource distribution in forested habitat favored females with larger distributions and more monogamous pairings (Martin and Martin 2007). Similarly, researchers found that populations of *Rana latastei* frogs with larger census sizes had greater rates of polygyny, increased variance in male mating success, and reduced N_e/N relative to populations with weaker levels of polygyny (Ficetola et al. 2010). Such shifts in reproduction can lead to increased variance in mating success and have the potential to reduce the effective number of breeding adults (N_e or N_b) in the population (N) (Bateman 1948; Emlen and Oring 1977; Wade and Arnold 1980). Substantial population declines and reductions in N_b , which are likely to occur as a result of urbanization (Hitchings and Beebee 1997; Hitchings and Beebee 1998; Price et al. 2006; Hamer and McDonnell 2008; Price et al. 2012), can make populations more susceptible to stochastic events, inbreeding depression, and genetic drift (Hitchings and Beebee 1997; Hitchings and Beebee 1998; Jehle et al. 2001; Noël and Lapointe 2010; Ficetola et al. 2010; Palstra and Fraser 2012; Munshi-South et al. 2013). Ultimately, altered reproductive strategies can influence population dynamics, reduce population resilience, and make populations vulnerable to extirpation (Miner et al. 2005; Lane et al. 2011).

My goal was to examine how exurban housing development influences the reproductive strategies of stream-dwelling salamanders. Thus, I sought to quantify how reproductive output, communal ovipositing, and brooding behaviors were influenced by coarse- and fine-scale covariates associated with exurban housing development. I also tested whether the abundance of

adult salamanders is important to reproduction because abundance varies greatly with housing development (Price et al. 2006; Gagné and Fahrig 2010). The focal species for the study was *Eurycea bislineata*, a plethodontid salamander species that exhibits reproductive variability in ovipositing and parental care (Ferguson et al. 2014). I anticipated that the number of adults in the population, a proxy for abundance and availability of receptive females, would be a strong predictor of *E. bislineata* reproductive strategies. I expected that adult counts would be inversely correlated with housing development density (Hamer and McDonnell 2008) and that counts would decline with increasing age of development due to the cumulative and persistent effects of urbanization (Price et al. 2006; Gagné and Fahrig 2010). As a species that exhibits explosive breeding, primarily ovipositing during the month of May in Connecticut, I expected *E. bislineata* populations would respond similar to the *Rana latastei* frog populations studied by Ficetola et al. (2010). I predicted that populations with high adult counts would exhibit high reproductive output due to increased N_e and that populations with large census sizes would produce more polygynous matings, potentially increasing the frequency of communal ovipositing and brooding behaviors. By extension, I assumed that these reproductive responses would be similarly influenced by exurban development and the environmental factors that affect adult abundance. Thus, I predicted that increased reproductive output, communal oviposition, and brooding would be more likely in undisturbed streams with newer housing developments that support high adult salamander abundances.

METHODS

Study Species.—*Eurycea bislineata* is a semi-aquatic salamander with a range extending from southeastern Canada, throughout New England, to Ohio, West Virginia, and Virginia (Conant and Collins 1998). *Eurycea bislineata* typically inhabit first- through third-order

streams, although the adults frequently use the terrestrial forest adjacent to streams (MacCulloch and Bider 1975; Conant and Collins 1998). Typically, an *E. bislineata* female will attach eggs together as a clutch to the bottom of a rock in the stream (Ferguson et al. 2014). Conservative estimates for the maximum number of embryos a female can produce in a given egg clutch is 60 (Ferguson et al. 2014), however, clusters of *E. bislineata* eggs from throughout the geographic range of the species contain between 21 and 296 embryos (Ferguson et al. 2014). This suggests that communal ovipositing on the same rock nest is common, with egg clusters often being composed of multiple clutches (Ferguson et al. 2014). Additionally, females regularly brood these egg clutches (Ferguson et al. 2014). Larvae are fully aquatic with external gills and undergo metamorphosis after two to three years in New England (MacCulloch and Bider 1975).

Study Streams.—I selected nine first-order streams in the towns of Mansfield and Coventry, Connecticut, USA with similar percent landcovers as quantified by the Connecticut Center for Land Use Education and Research (CLEAR) 2010 landcover layers (CLEAR 2010). I chose streams near road crossings that had a minimum forest buffer width of 25-meters to accommodate my sampling methods. I selected streams based on the first private landowner who provided access to the stream, and thus sampling segments fit within the property boundaries. The goal was to examine forested streams that had a gradient of housing development ages and development densities in the watershed. Therefore, all selected sites had watersheds that were primarily composed of mixed deciduous and coniferous forest with forest totals ranging from 42.2% to 99.4% (Table 1). Development made up between 0% and 35.9% of each watershed and included roads, roofs, and other impervious surfaces associated with residential development (Table 1). I attempted to eliminate streams with watersheds containing other non-forest cover types, but agriculture (i.e. crops or pasture) and grass associated with large residential lawns

made up a small proportion of the stream watersheds (Table 1). Next, I overlaid the delineated watersheds with a parcel layer, recorded the age of every home in each watershed, and calculated an average housing age (referred to as development age) for each watershed, which ranged from 1963 to 1992 across all watersheds (Table 1). I also used this parcel layer to ensure that the streams I selected across the development gradient were composed almost exclusively of residential, rather than commercial or industrial, development. Lastly, I used a forest vegetation layer developed for the Connecticut Department of Energy and Environmental Protection (Rittenhouse 2014) to calculate the percent of each watershed consisting of regenerating forest (0% to 14%) and persistent forest (55% to 98%) as an alternative metric to average development age. Streams studied here are a subset of streams used in an occupancy study (Chapter 1), and the aforementioned coarse-scale watershed features were calculated from the base of the sampled reaches in that study.

Field Sampling.—I conducted area-constrained stream surveys once a month from May 2015 to August 2015. I previously designated a 30-meter stream segment as part of an earlier sampling effort at these sites (Chapter 1). I extended the sampling segment to 200-meters for the current study, and, for all but two sites, the extension was mostly upstream of the original 30-meter segment. I marked 200-meter segments using wire flags and completed all surveys within these segments. To perform surveys, two observers simultaneously sampled on opposite sides of the stream bank, starting downstream at 0 meters and working upstream to 200 meters. Observers lifted any natural cover objects (rocks, logs, leaf litter) while holding an aquarium dipnet (6 in) directly downstream to increase successful capture. We replaced all disturbed cover objects to the original position. Sampling protocol differed depending on whether an adult *E. bislineata* or a cluster of eggs was found. When an adult *E. bislineata* was captured, one observer

stopped to process the individual while the second observer continued to survey the entire stream. Once the animal processing was complete, the first observer returned to survey with the second observer. At the point of capture, the processor marked each adult using a cohort-specific visible implant elastomer (VIE) tag such that the month and year of capture could be determined. Cohort marking prevented repeated processing of the same individual. When a rock with eggs was found, both observers stopped to individually count the number of independent clusters of eggs on the rock and the number of eggs in each cluster. If observer counts of the number of eggs in a cluster differed, the two counts were averaged. In most cases, differentiation of unique clutches within a cluster of eggs was not possible because the developmental stage was uniform throughout the cluster (Ferguson et al. 2014), though we noted when developmental stages differed within a cluster. I photographed each rock nest, noted if a brooding female was present, and recorded whether multiple egg clusters were found on the rock. We returned all salamanders and egg clusters on rocks to their original location in the stream.

I also used transects of artificial cover-boards to capture *E. bislineata* use of the terrestrial habitat in a consistent and minimally invasive manner at every study site for each of the 2014, 2015, and 2016 sampling periods (Hesed 2012). White oak trees were harvested from the University of Connecticut Forest to create a total of 60 artificial cover-boards, which were weathered for more than six months before sampling at the streams. All artificial cover-boards measured 60.96 cm X 30.48 cm X 3.81 cm, a size sufficient to retain moisture and a stable thermal environment (Hesed 2012). I placed four artificial cover-boards perpendicular to the streambed at each of my 15 sites. I positioned a cover-board at distances of 5, 10, and 20 meters from the streambed and the fourth cover-board at a distance of 5 meters on the opposing side of the streambed. I placed the transect of three cover-boards on the side of the stream with the

largest forest buffer. I checked all of the boards at a site on the same days that I performed area-constrained surveys of the stream. I marked and measured any salamanders under the cover-boards using the same methodology as the salamanders captured during the stream surveys.

Habitat data.—I identified sediment distribution, turbidity, specific conductivity, dissolved oxygen concentration, temperature, and stream discharge as stream-scale habitat variables important to salamander reproduction. I recorded water, soil, and air temperatures from the original 30-meter mark at each stream during each sampling period using a Taylor Instant Read Digital Thermometer (9840N). I wanted to capture the upper threshold of dissolved oxygen (DO), discharge, and conductivity experienced by the stream. Thus, I recorded conditions during April 2015 to capture a “snapshot” of each stream after a period of spring rain, snowmelt, and runoff containing high concentrations of road salt. During this time, I measured specific conductivity and DO concentrations in the streams using a handheld sonde (Yellow Springs Instruments, YSI 556 MPS). I calculated stream discharge by measuring wetted channel width and using a SonTek FlowTracker Handheld Acoustic Doppler Velocimeter to measure mean water-column velocity and depth at regular intervals across the stream width according to USGS guidelines (Fitzpatrick et al. 1998). In May 2015, I also collected water samples from each stream in acid washed and field rinsed bottles, which I transported to the lab on ice and kept frozen until analysis. I measured the turbidity in each of these samples using the DRT 100B Turbidimeter from HF Instruments (HF Instruments, Inc.) and following the protocol specified for the equipment. Finally, I collected sediment distribution measurements in June 2015 at each stream. I walked the length of each stream segment, randomly collecting as many particles as possible. I measured particles along the intermediate axis and recorded the corresponding size

class according to Dunne and Leopold (1978) such that I could produce a distribution curve of particle size and provide a quantifiable habitat covariate.

Data Analysis.— I used an information theoretic approach to determine how coarse-scale watershed features and fine-scale stream features influence *E. bislineata* reproduction (Akaike 1973; Burnham and Anderson 2002). My goal was to quantify three aspects of *E. bislineata* reproduction: reproductive output, communal ovipositing, and brooding behavior. To measure reproductive output, I used the number of eggs per stream, the number of egg clusters per stream, the average number of eggs per egg cluster, and an estimation of the number of clutches per stream based on a conservative estimate of 60 eggs per female clutch (Ferguson et al. 2014). I included an additional four reproductive output responses that controlled for the number of adults in each stream. I created these four responses by dividing the four previous reproductive output responses by the minimum number known alive adult count, referred to as adult count for the remainder of the manuscript, in each stream. These responses represent an estimate of reproductive output for each individual in a stream rather than the reproductive productivity of the stream reach. To measure ovipositing behaviors, I examined the number of eggs laid communally, which I defined as any cluster of eggs with greater than 60 eggs (Ferguson et al. 2014), and the proportion of eggs that were communally laid. In addition, I considered the number of clusters laid with other clusters under the same rock, the proportion of clusters that were laid with other clusters under the same rock, the number of clusters that I presumed to be composed of multiple clutches, and the proportion of clutches that I presumed to be laid communally. Only two streams exhibited rocks with multiple clusters, thus I did not perform model selection on those two responses, but I do provide anecdotal evidence. To measure brooding behavior, I quantified the following responses: the number of egg clusters brooded by

one or more females, the number of egg clutches brooded by one or more females, the number of egg clusters brooded by one or more females, the proportion of individual embryos in a stream brooded by one or more females, the proportion of estimated egg clutches brooded by one or more females, and the proportion of egg clusters brooded by one or more females. I included an additional six brooding behavior responses that controlled for the number of adults in each stream. I divided these six responses by the adult count in each stream. These responses represent an estimate of brooding behavior for each individual in a stream rather than the brooding behavior of the stream reach. Lastly, I used the adult count as a response to determine how the adult count would be influenced by the coarse- and fine-scale metrics of interest. I created linear regression models for each of my response variables using R version 3.1.2 through the interface RStudio version 0.98.1091 (R Core Team 2014; RStudio, Inc. 2014).

I began the model selection process by creating an a priori candidate model set that aimed to clarify the importance of watershed (i.e. coarse-scale) features such as development and development age on reproduction. The candidate model set included models for four possible development age metrics. The first metric, average house age, was the average of the year a residence was built for all parcels falling within a watershed boundary. For three streams with 0% development, I used imputation to assign the mean housing age of the remaining streams to these three locations. The age metric tests the hypothesis that reproductive output, communal ovipositing, and brooding behavior will be lowest in watersheds with older housing developments due to the cumulative and persistent effects of urbanization. The second metric, average house age², is the quadratic of average house ages within a stream watershed and tests the hypothesis that reproductive output, communal ovipositing, and brooding behavior in streams with new developments decline following the initial construction but then increase in streams

with the oldest developments as they recover. As salamanders depend on the surrounding forests for nutrients, water filtration, and regulation of temperature and moisture (Vannote et al. 1980; Allan 2004), I also included two forest metrics that quantify relative forest age in the stream watershed. The third metric, regeneration, is the percentage of regenerating forest (up to 20 years) within a stream watershed and tests the hypothesis that the forest regeneration that occurs following construction contributes to recovery after the initial construction disturbance, increasing reproductive output, communal ovipositing, and brooding behaviors. The last metric, persistent, is the percentage of persistent forest within a stream watershed and represents the antithesis to my previous hypotheses—if a stream contains a high percentage of persistent forest, then there has not been housing development or any other form of canopy cover disturbance recently; therefore, salamander reproductive output, communal ovipositing, and brooding behavior should be high. Lastly, I included the percent of development within each stream watershed to test the hypothesis that increasing watershed development reduces reproductive output, communal ovipositing, and brooding behavior.

I created a second candidate model set to examine the importance of stream-scale (i.e. fine-scale) features associated with increasing urbanization and amphibian abundance and reproduction (Paul and Meyer 2001; Wenger et al. 2009). I included models that compared the main effects of conductivity (Orser and Shure 1972; Turtle 2000; Willson and Dorcas 2003; Karraker et al. 2008; Brand et al. 2010; Price et al. 2012), DO (Willson and Dorcas 2003; Sacerdote and King 2009; Small et al. 2014; Bourne 2015; Jordan et al. 2016), turbidity (Lowe and Bolger 2002; Brannon and Purvis 2008; Brand et al. 2010), temperature (Orser and Shure 1972; Kuramoto 1985; Griffiths and de Wijer 1994; Willson and Dorcas 2003; Barrett et al. 2010; Campbell Grant et al. 2014), discharge (Orser and Shure 1972; Barrett et al. 2010), and

sediment distribution (Orser and Shure 1972; Smith 2002; Brannon and Purvis 2008; Rizzo et al. 2016). I assigned the mean turbidity across all sites to one site because the turbidity value was an extreme outlier, suggesting a collection error. I included a model of soil temperature rather than water temperature because I was unable to record water temperatures during sample periods in which ephemeral streams had dried, resulting in uninformative average water temperatures. The soil temperature covariate represented the three-year average soil temperature, measured monthly at the 30-meter stream reach location at each stream from May 2014 to August 2014, April 2015 to September 2015, and April 2016 to September 2016. All temperature measurements from the sixth sampling period in 2015 and the fourth sampling period in 2016 were removed due to equipment failure.

In a third candidate model set, I ranked the top-ranking coarse- and fine-scale models to each other and to a model of adult count to identify the scale at which the response variables are most strongly influenced. I only compared top-ranking coarse- and fine-scale models for the adult count response and the 10 reproductive output and brooding behavior responses controlled for the adult count.

I ranked models using Akaike information criterion corrected for finite sample sizes (AICc) (Akaike 1973; Akaike 1974; Hurvich and Tsai 1989). Top models were selected on the basis of having the lowest AICc score and being at least two ΔAICc smaller than the next top model (Burnham and Anderson 2002). I presented the results for all model selections but only provided further inference for top-ranking and competing models (Arnold 2010). I assessed output from the linear regression analyses of the top-ranking models to determine the significance, magnitude, and direction of the relationship.

RESULTS

I captured a total of 220 unique adult *E. bislineata* from May 2015 to August 2015 and processed a total of 56 egg clusters in May 2015. The number of adults at each stream ranged from 6 to 60 (Mean: 24.4; SD: 16.7). No adults were recaptured during the study. I observed a range of reproductive output, communal ovipositing, and brooding behavior responses, which varied considerably across streams (Table 2). I documented only two streams with multiple egg clusters on a single rock (Table 2). Notably, these two streams had the highest number of clusters per adult count and the highest number of clutches per adult count. Moreover, 100% of the clusters observed in one of these streams came from rocks with two or more clusters. This stream also had the highest number of eggs in the stream per adult count as well as the highest average number of eggs per cluster per adult count.

Reproductive Output.—The responses, total number of egg clusters and total number of eggs per stream, were not well-predicted by any of the covariates of interest (Table 3). The fine-scale sediment distribution model outranked the intercept-only and abundance models to best predict the estimated number of clutches per stream (Table 3). However, the 95% confidence interval for the β estimate of sediment distribution overlapped zero, indicating that the association is weak (Table 4). The average number of eggs per cluster was best predicted by a negative relationship with average soil temperature (Table 3; Table 4; Figure 1).

When controlling the reproductive output responses for the adult count, I found that coarse-scale models incorporating metrics of development age ranked highest (Table 3). Three responses, the number of eggs per stream per adult count, the number of egg clutches per stream per adult count, and the number of egg clusters per stream per adult count, were best predicted by a negative relationship with average housing age although the 95% confidence interval for the β estimates overlapped zero (Table 4). The average number of eggs per cluster per adult count

was best predicted by the percent of regenerating forest in the watershed (Table 3). The amount of regenerating forest was negatively related to the response (Table 4; Figure 1).

Communal Ovipositing.— The number of communally laid eggs was negatively related to sediment distribution (Table 4; Table 5; Figure 2), with more eggs being laid communally in streams with medium-sized sediments such as cobbles and pebbles rather than boulders. Notably, none of the streams measured were predominantly composed of fine sediments such as gravel, sand, or silt. Similarly, the number of clutches laid communally was best predicted by the fine-scale model including sediment distribution (Table 5). However, the 95% confidence interval for the β estimate of sediment distribution overlapped zero, indicating that the association is weak (Table 4). In contrast, the proportion of communally laid eggs was negatively related to the adult count (Table 4; Table 5; Figure 2). The proportion of clutches laid communally was also negatively related to the adult count (Table 4; Figure 2), outranking both the top-ranking coarse-scale regeneration model and the top-ranking fine-scale soil temperature model (Table 5).

Brooding Behavior.—The responses, number of clusters brooded and proportion of eggs brooded, were not well-predicted by any of the covariates of interest (Table 4). The number of clutches brooded, given a 60 egg per cluster estimate, and the proportion of clutches brooded were both best predicted by fine-scale covariates (Table 6). The number of clutches brooded was related to sediment distributions while the proportion of clutches brooded was related to average soil temperatures (Table 4). However, the 95% confidence interval for the β estimates overlapped zero (Table 4). The proportion of clusters brooded response was best predicted by the coarse-scale percent persistent forest model, which outranked both the fine-scale turbidity model and the adult count model (Table 6). The proportion of clusters brooded was positively related to the percent of persistent forest (Table 4; Figure 3). The fine-scale turbidity model was also

within two ΔAICc of the top-ranking persistent forest model. The proportion of clusters brooded was negatively related to turbidity, but the 95% confidence interval overlapped zero ($\beta = -0.105$, 95% CI: -0.224, 0.013; Table 4).

When controlling the brooding behavior responses for the adult count, I found that coarse-scale models incorporating metrics of development age ranked highest. Five responses, the number of eggs brooded per adult count, the number of egg clutches brooded per adult count, the number of eggs clusters brooded per adult count, the proportion of eggs brooded per adult count, and the proportion of egg clutches brooded per adult count, were negatively related to average housing age (Table 4; Table 6; Figure 4). In other words, individual brooding behavior was high in watersheds with a predominance of new housing development. The proportion of egg clusters brooded per adult count was negatively related to the percent of forest regeneration in the watershed (Table 4; Table 6; Figure 4).

Adult Count.—The adult count was best predicted by the quadratic of average housing age (Table 4; Table 7; Figure 5). Discharge was also within two ΔAICc of the top-ranking model and was positively related to the adult count ($\beta = 607.844$, 95% CI: 93.868, 1121.820; Table 4).

DISCUSSION

This study provides evidence that the reproductive output, communal ovipositing, and brooding behaviors of *E. bislineata* vary greatly among streams. This variation is explained by housing development age, fine-scale features of the stream reach, and counts of adults in the stream. In accordance with my expectation, the adult count was highest in newly developed watersheds and declined with average year since housing construction. Contrary to my expectations, however, all three reproductive responses were highest in watersheds with old housing developments or low adult counts. This result suggests that development in the

watershed, regardless of the density, influences the reproductive responses of *E. bislineata*. Intraspecific competition strongly influenced reproduction. Adult counts were lowest in streams with old housing developments, and females in these watersheds increased communal nesting and brooding, suggesting that reproductive strategies may have shifted in response to development. Reproductive output, communal ovipositing, and brooding behavior responses that were not standardized by adult count were influenced by fine-scale features. Reproductive responses were high in streams with cooler soil temperatures and a predominance of mid-ranged sediments such as cobble and pebbles. Ultimately, this research highlights the variability in reproduction exhibited by *E. bislineata* and provides evidence of housing development age influencing the reproduction of an amphibian. The variation documented may be a plastic response to development that could serve to improve embryo and/or adult survival and fitness in disturbed environments.

Fine-scale features and adult counts explained variation in *E. bislineata* reproductive responses between streams while coarse-scale features influenced reproductive responses that were standardized by adult counts. Contrary to expectation, percent development within watersheds was not a strong predictor of the reproductive responses. Rather, I found that average housing age or the percent of regenerating forest related to all reproductive output and brooding responses standardized by adult count. In other words, individual reproductive output and brooding behaviors were highest in streams containing old housing developments. This result suggests that development, regardless of the amount, influences the reproductive responses of *E. bislineata*. However, because adult counts were lowest in streams with old housing developments, the reproductive output and brooding responses related to average housing age may actually be a response to low intraspecific competition. Responses for reproductive output,

communal ovipositing, and brooding behavior that were not standardized by adult count were most strongly determined by adult counts and fine-scale features of the stream such as average soil temperature and sediment distribution. The exception was the proportion of clusters brooded, which was positively related to the percent persistent forest in the watershed. These results indicate that reproductive output, communal ovipositing, and/or brooding behaviors were increased at streams with cooler soil temperatures, a predominance of mid-ranged sediments such as cobble and pebbles, and a high percentage of persistent forest. Previous research has described the importance of temperature and stream particle sizes to amphibian reproduction (Kuramoto 1985; Griffiths and de Wijer 1994; Bernhardt and Palmer 2007; Brannon and Purvis 2008). While I do not have nest-level covariates to fully assess microhabitat selection, I expect that predictors important at the fine-scale will also be important determinants of rock selection. For example, studies have found that intermediate-sized sediments provide refugia from predators and microhabitats for egg deposition; thus, I expect that intermediate-sized sediments would be more likely to contain an egg clutch or cluster than sand or boulders (Orser and Shure 1972; Smith 2002; Bernhardt and Palmer 2007, Brannon and Purvis 2008; Rizzo et al. 2016).

One explanation for the high reproductive output, communal ovipositing, and brooding behaviors in streams with old development and low adult counts is the theory that urbanized landscapes are likely to have clustered resources, which leads to clumped distributions of females (Emlen and Oring 1977). Embryos may initially have been laid communally to improve embryo and larval survival by taking advantage of limited resources in a disturbed habitat. I suggest that the availability of ovipositing rocks or ovipositing rocks with suitable microhabitats were limited. First, the number of eggs laid communally was highest in streams with medium sized particles. Further, communal ovipositing behaviors were inversely related to adult count. I

expect that streams with high adult counts would have increased intraspecific competition for limited resources, and thus increased communal ovipositing. However, I observed the opposite pattern, which could suggest that resource clustering is the mechanism leading to communal ovipositing.

Brooding behaviors could have been highest in streams with old development and low adult counts for a number of reasons. First, when multiple females contribute to a rock nest, the probability that at least one female contributor is brooding increases. I recorded two nests that contained more than one female brooding, and I observed more than 30 individuals under rocks with at least one other *E. bislineata* throughout the study. Intraspecific interactions are therefore common. Second, females could also be taking advantage of a limited resource within the stream habitat that results in clustering (Emlen and Oring 1977). Brooding behaviors in streams were related to sediment distribution and average soil temperature, which suggests that females could be more likely to brood in streams with cooler temperatures that are composed primarily of cobbles and pebbles. Ultimately, communal brooding or shared brooding has been shown to minimize the foraging and predation trade-offs experienced by each individual female (Townsend 1986, Stearns 1992; Delia et al. 2013). Moreover, by mitigating or sharing the parental investment, the probability of females in the population producing larger clutches more frequently increases (Salthe and Duellman 1973; Church 2007).

A second explanation for the high reproductive output, communal ovipositing, and brooding behaviors in streams with old development and low adult counts is that urbanization alters the biotic community such that predator-prey interactions are driving the trade-off between reproduction and female maintenance (Lima 1998a; Freeman and Schorr 2004; Miner et al. 2005; Roy et al. 2007; Barrett et al. 2010; Canessa and Parris 2013). Predator-prey interactions

are strong drivers of population dynamics and population distributions and provide another possible mechanism for shaping the reproductive strategies exhibited during this study (Townsend et al. 1984; Duellman and Trueb 1986; Townsend 1986; Magnusson and Hero 1991; Stearns 1992; Lima 1998b; Hero et al. 2001; Eterovick and Barata 2006). The trend towards increased reproductive output, communal ovipositing, and breeding behavior in streams with older housing developments and low adult counts would suggest a release from predation pressures (Lima 1998b). In a predator-free stream, communal ovipositing is thought to be preferred, because communal ovipositing takes advantage of favorable microhabitat conditions and spreads the energetic costs of brooding among females. Conversely, the presence of predators would promote a more dispersed ovipositing distribution because communal ovipositing could make prey more accessible to predators (Lima 1998b). Additionally, complex habitat structures could further promote dispersed ovipositing distributions in streams with predators by providing refugia that allow predator and prey populations to coexist (Ellner et al. 2001; Eterovick and Barata 2006). Reproductive output and brooding behaviors may be reduced in streams with natural predators due to the nonlethal costs of predation threats and predator avoidance that add energetic costs to the parent (Stearns 1992; Lima 1998a; Lima 1998b; Binckley and Resetarits 2003; Church et al. 2007; Winandy et al. 2015; Winandy et al. 2017). A number of studies have found reduced sexual activity and egg production in amphibians in the presence of predators (Binckley and Resetarits 2003; Winandy et al. 2015; Winandy et al. 2017).

This research demonstrates the effect of urbanization on amphibian adult counts and reproductive strategies. Future research should determine how variation in these reproductive responses affects N_e/N such that true population declines can be recognized and populations can be targeted for conservation. Moreover, identifying whether communal ovipositing and brooding

behaviors influence embryo and clutch survival will be important to assess how variation in these responses could contribute to population recovery in streams with low adult counts. Our results beg the question as to whether the variation documented is actually a plastic response to housing development. Reproductive plasticity has the potential to increase the resilience of populations affected by urbanization (Miner et al. 2005). I predict that the increased reproductive output, communal ovipositing, and brooding behavior we observed in streams with low adult counts and old housing developments could improve embryo and/or adult survival and fitness (Miner et al. 2005), which could be particularly important if populations are experiencing declines due to urbanization. Ultimately, this work provides evidence of housing development age influencing salamander reproduction and contributes to scientific understanding of reproductive responses to anthropogenic influences.

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Tables

Table 1. Watershed features and the range, mean, and standard deviation values of these features for the nine sampling streams.

Feature	Range	Mean	SD
Average Year Built	1963-1992	1977	9.1
% Developed	0.0-35.9	10.8	12.8
% Deciduous	40.1-99.4	70.3	21.6
% Coniferous	0.0-14.0	3.2	5.7
% Total Forest	42.2-99.4	73.4	21.1
% Regenerating Forest	0.0-14.3	6.3	5.0
% Persistent Forest	54.6-98.5	80.0	14.9
% Grass and Turf	0.0-29.8	8.2	9.8
% Agriculture	0.0-14.6	3.9	4.9
Total Area km²	0.08-0.78	0.35	0.20

Table 2. Summary of adult count, reproductive output, communal ovipositing, and brooding behavior response data including the total count, the range of counts, the mean count, and one standard deviation around the mean for all streams. Also included are the range, mean, and standard deviation of the proportion of eggs, clutches, and clusters that were communally laid or brooded in each stream.

Response Category	Response	Total	Range	Mean	SD
Adult Count	Adult Count	220	6-60	24.4	16.7
Reproductive Output	Number of Eggs	3635	45-868	403.9	287
	Number of Clutches	91	2-21	10.1	6.6
	Number of Clusters	56	2-13	6.2	3.9
	Average Number of Eggs per Cluster	-	22.5-95.4	65.4	31.5
Communal Ovipositing	Number of Eggs Laid Communally	2593	0-720	288.1	251.7
	Number of Clutches Laid Communally	19	1-5	2.1	1.8
	Number of Clusters Laid Communally	2	0-9	1.2	3
	Proportion of Eggs Laid Communally	-	0-1	0.64	0.34
	Proportion of Clutches Laid Communally	-	0-0.55	0.33	0.19
	Proportion of Clusters Laid Communally	-	0-1	0.15	0.34
Brooding Behavior	Number of Eggs Brooded	2060	23-478	228.9	160.7
	Number of Clutches Brooded	48	1-10	5.3	3.2
	Number of Clusters Brooded	26	1-6	2.9	1.8
	Proportion of Eggs Brooded	-	0.22-0.88	0.6	0.24
	Proportion of Clutches Brooded	-	0.24-0.80	0.55	0.18
	Proportion of Clusters Brooded	-	0.23-0.60	0.48	0.11

Table 4. Linear regression output for top-ranking models with the number of model parameters (k), β estimates, and 95% confidence intervals.

Predictor Estimates for Top-Ranking Models	k	β Estimate	95% CI
Adult Count			
Adult Count			
AveHouseAge ²	2	0.000	(0.000, 0.000)
Reproductive Output			
Number of Eggs			
Intercept-only	1	403.889	(183.315, 624.463)
Number of Clutches			
SedimentDist	2	-1.018	(-2.313, 0.277)
Number of Clusters			
Intercept-only	1	6.222	(3.201, 9.243)
Average Number of Eggs per Cluster			
SoilTemp	2	-27.826	(-52.354, -27.826)
Number of Eggs/Adult Count			
AveHouseAge	2	-1.941	(-4.297, 0.414)
Number of Clutches/Adult Count			
AveHouseAge	2	-0.049	(-0.107, 0.010)
Number of Clusters/Adult Count			
AveHouseAge	2	-0.024	(-0.053, 0.004)
Average Number of Eggs per Cluster/Adult Count			
Regeneration	2	-51.964	(-98.649, -5.279)
Communal Oviposition			
Number of Communal Eggs			
SedimentDistribution	2	-47.055	(-90.791, -3.318)
Number of Communal Clutches			
SedimentDistribution	2	-0.282	(-0.645, 0.081)
Proportion of Eggs Laid Communally			
AdultCount	2	-0.015	(-0.027, -0.003)
Proportion of Clutches Laid Communally			
AdultCount	2	-0.008	(-0.016, -0.001)
Brooding			
Number of Eggs Brooded			
SedimentDistribution	2	-26.360	(-57.103, 4.376)
Number of Clutches Brooded			
SedimentDistribution	2	-0.527	(-1.150, 0.096)
Number of Clusters Brooded			
Intercept-only	1	2.889	(1.480, 4.298)
Proportion of Eggs Brooded			
Intercept-only	1	0.601	(0.416, 0.786)
Proportion of Clutches Brooded			
SoilTemp	2	-0.141	(-0.294, 0.011)
Proportion of Clusters Brooded			
Persistent	2	0.517	(0.039, 0.995)
Number of Eggs Brooded/Adult Count			
AveHouseAge	2	-1.516	(-3.010, -0.021)
Number of Clutches Brooded/Adult Count			
AveHouseAge	2	-0.032	(-0.062, -0.002)
Number of Clusters Brooded/Adult Count			
AveHouseAge	2	-0.016	(-0.031, -0.002)
Proportion of Eggs Brooded/Adult Count			
AveHouseAge	2	-0.002	(-0.004, -0.001)
Proportion of Clutches Brooded/Adult Count			
AveHouseAge	2	-0.002	(-0.003, -0.001)
Proportion of Clusters Brooded/Adult Count			
Regeneration	2	-0.397	(-0.766, -0.029)

Table 7. AICc ranking of coarse-, fine-, and the combined management-scale model sets for the adult count response. Models were weighted with respect to the top-ranking model (ΔAICc), which is bolded, and Akaike weights were calculated ($w\text{AICc}$). The number of parameters, K, for each model is also included.

Adult Count Model Selection	K	AICc	ΔAICc	$w\text{AICc}$
Coarse-Scale Model Ranking				
Intercept + AveHouseAge	2	75.373	0.016	0.441
Intercept + AveHouseAge ²	2	75.356	0.000	0.445
Intercept + Regeneration	2	80.241	4.885	0.039
Intercept + Persistent	2	82.685	7.328	0.011
Intercept + Developed	2	82.463	7.107	0.013
Intercept	1	79.686	4.329	0.051
Fine-Scale Model Set				
Intercept + Conductivity	2	82.761	6.398	0.015
Intercept + Discharge	2	76.363	0.000	0.364
Intercept + DO	2	80.126	3.762	0.056
Intercept + Turbidity	2	77.940	1.576	0.166
Intercept + SoilTemp	2	76.665	0.301	0.313
Intercept + SedimentDistribution	2	82.529	6.166	0.017
Intercept	1	79.686	3.322	0.069
Management-Scale Model Set				
<i>Top Coarse-Scale Model</i>	-	75.356	0.000	0.582
<i>Top Fine-Scale Model</i>	-	76.363	1.007	0.352
Intercept	1	79.686	4.329	0.067

Figure List

Figure 1. The reproductive output responses, average number of eggs per cluster and the average number of eggs per cluster per the adult count, were related to average soil temperature and the percent of regenerating forest, respectively.

Figure 2. The communal ovipositing responses, the number of eggs laid communally, the proportion of eggs laid communally, and the proportion of communal clutches, were related to sediment distribution, the adult count, and the adult count, respectively.

Figure 3. The top-ranking stream-level brooding behavior response, proportion of clutches brooded, which was related to the percent of persistent forest.

Figure 4. Estimate of individual brooding behaviors, the number of eggs brooded per adult count, and the proportion of eggs brooded per adult count, the number of clutches brooded per adult count, the proportion of clutches brooded per adult count, the number of clusters brooded per adult count, and the proportion of clusters brooded per adult count. The strongest predictors for all of the response variables was the average house age (i.e. year of construction) with the exception of the proportion of clusters brooded per adult count, which was related to the percent of regenerating forest.

Figure 5. The adult count response was related to average house age² and discharge.

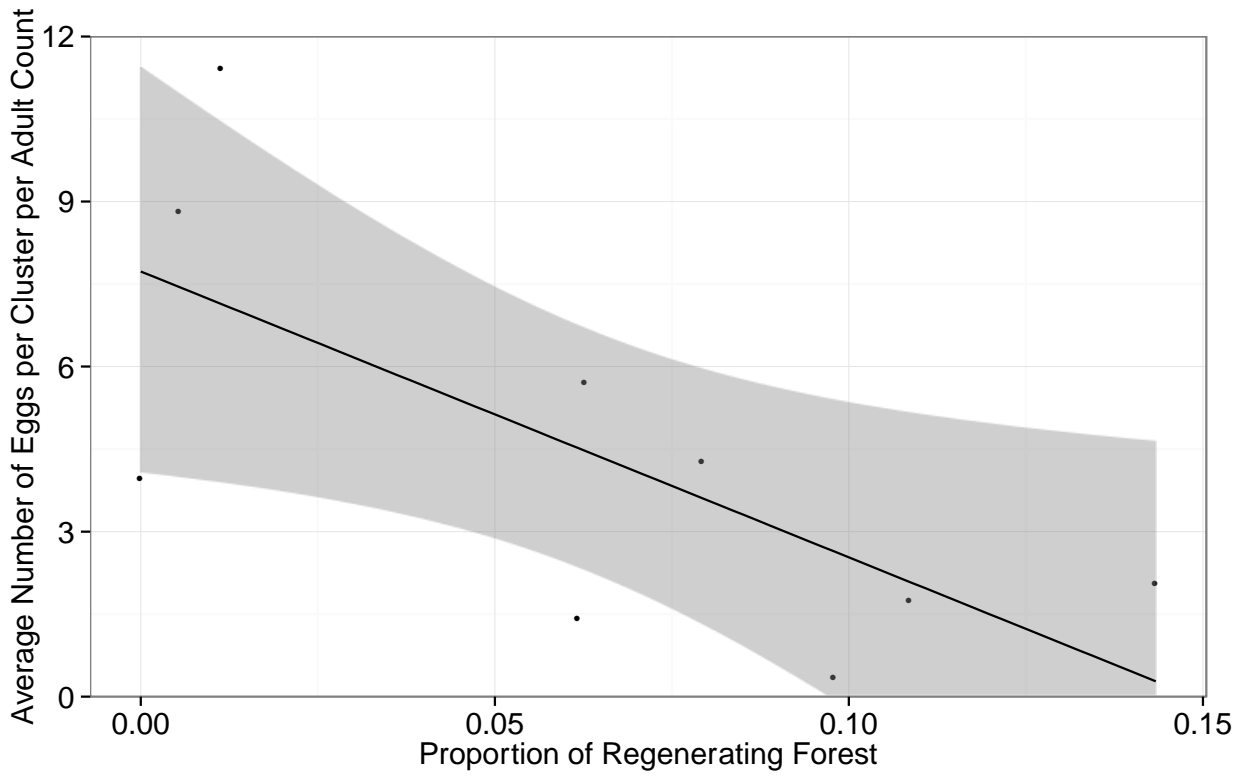
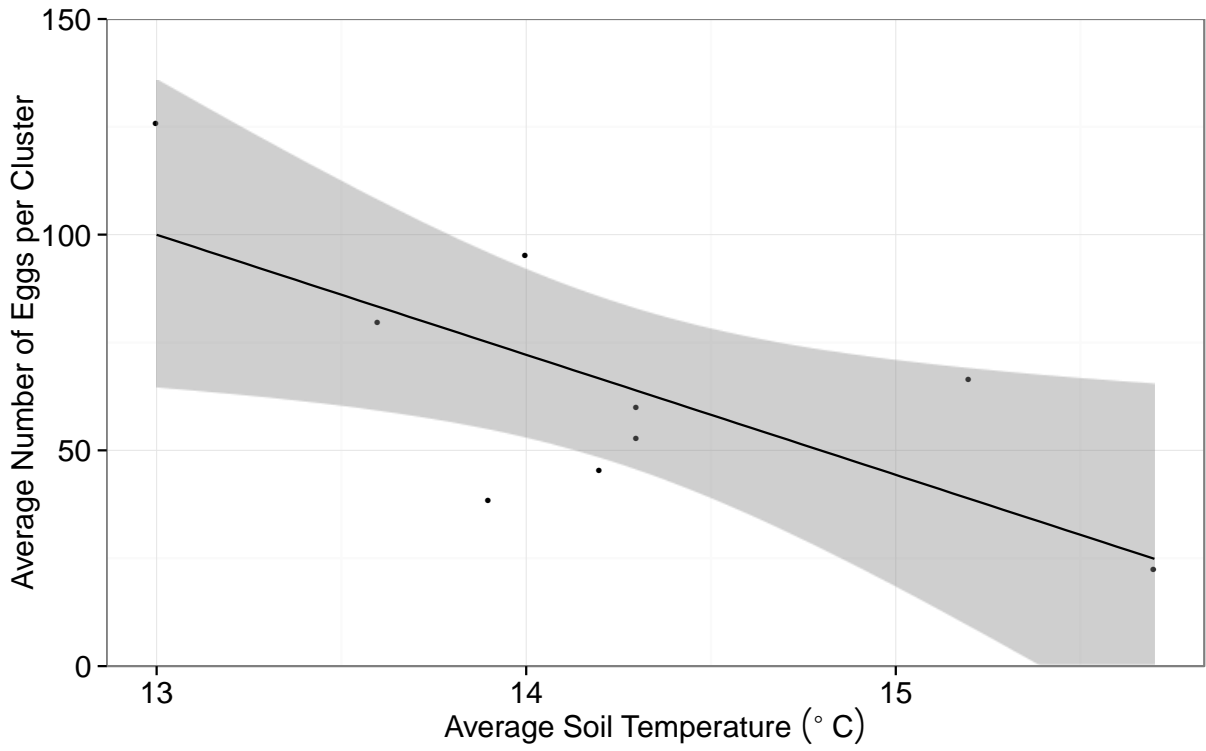


Figure 1.

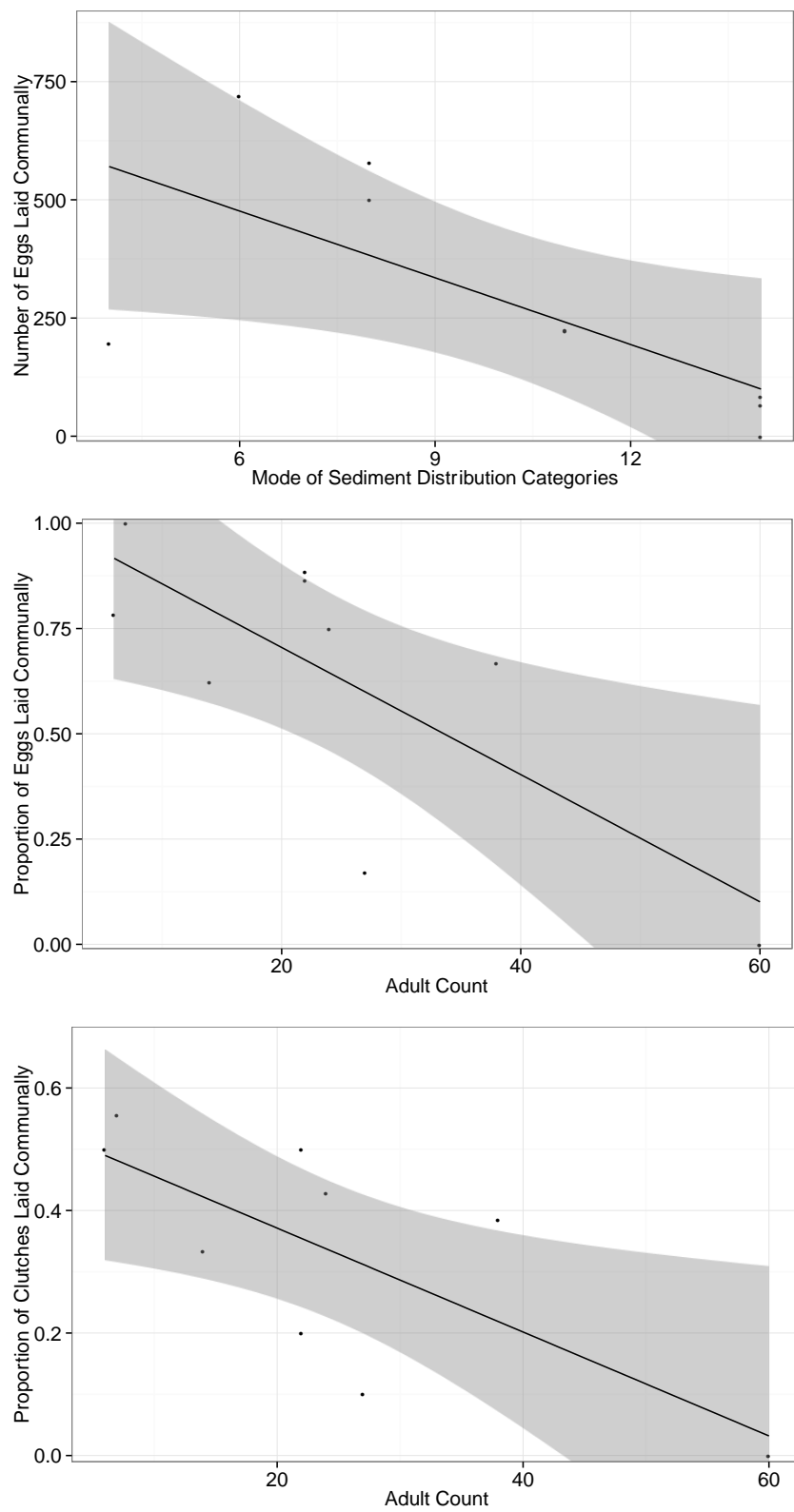


Figure 2.

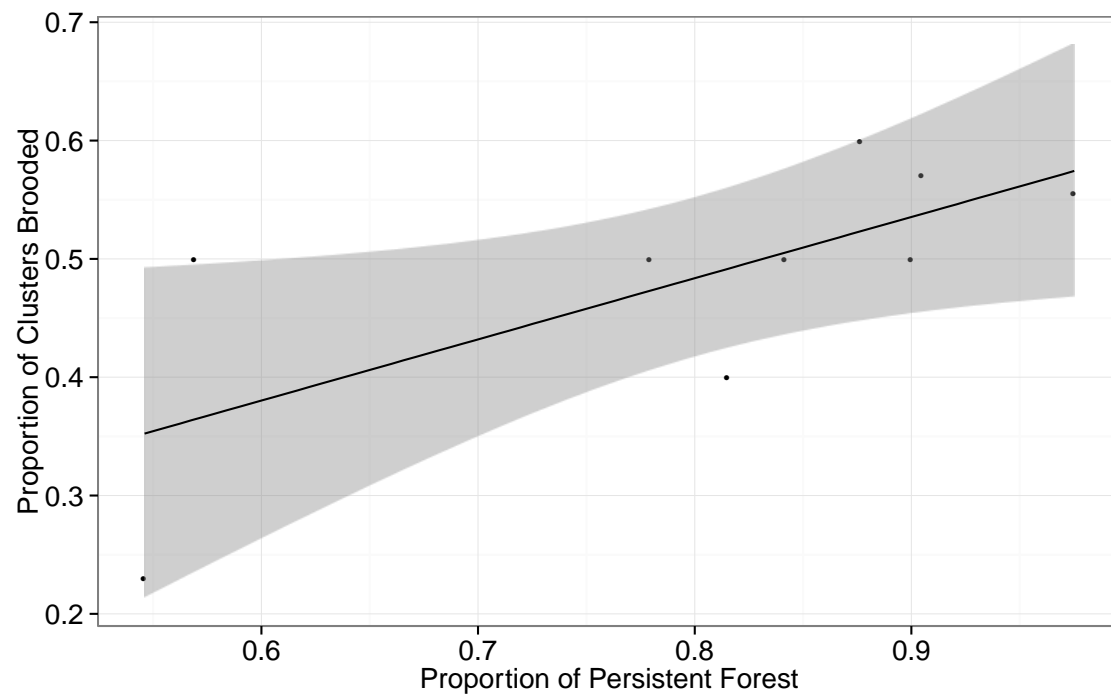


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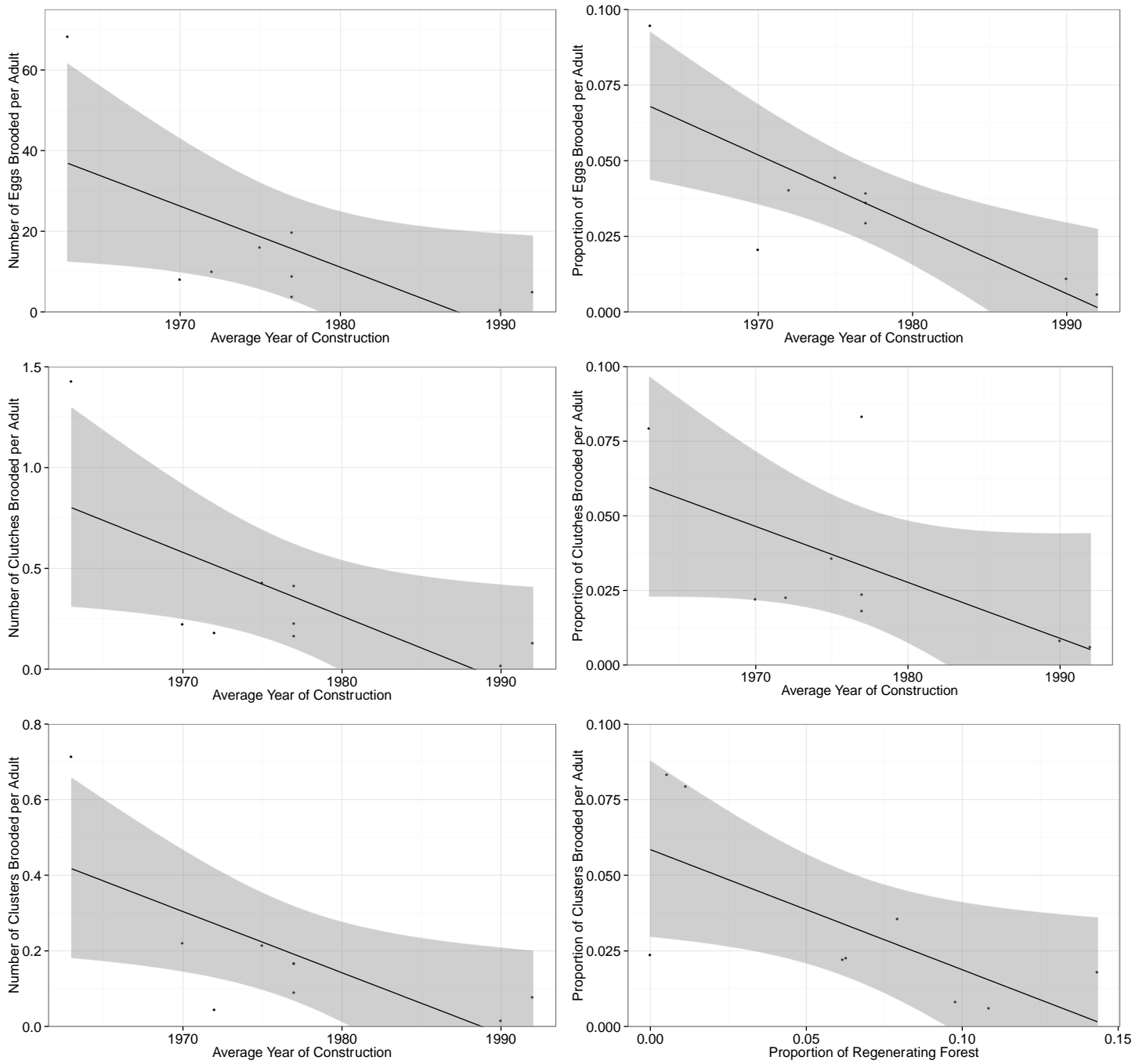


Figure 4.

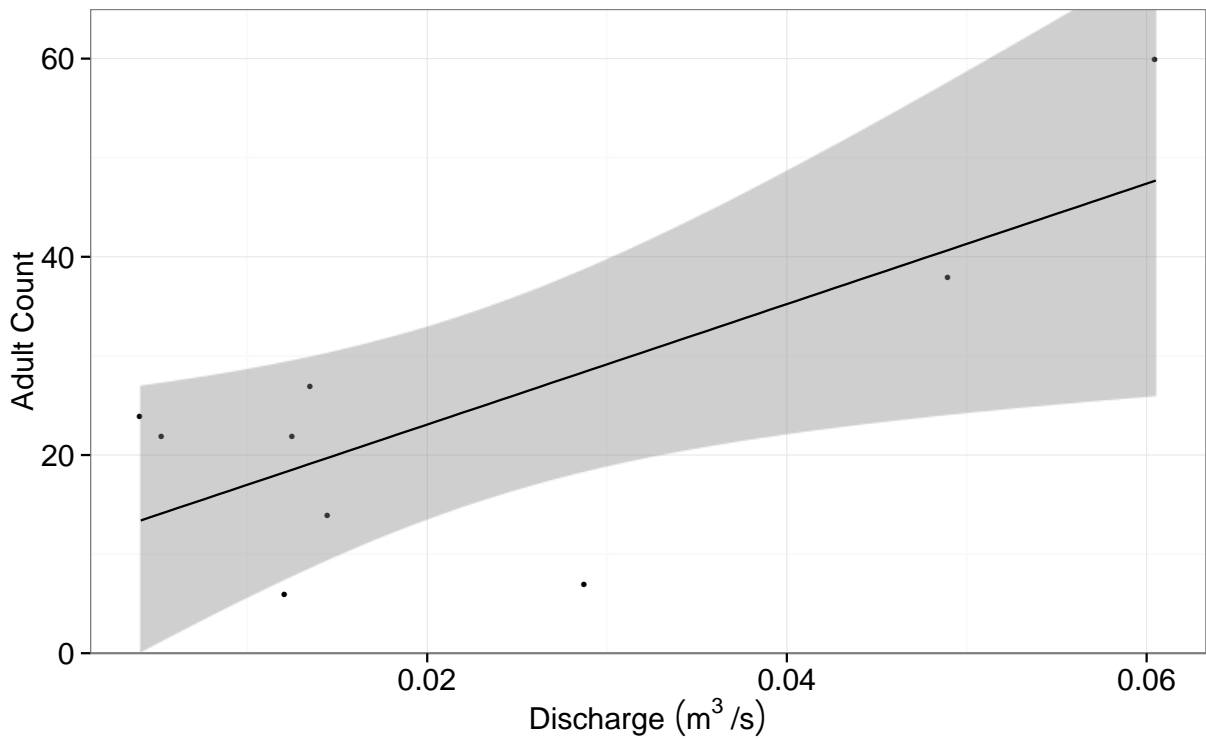
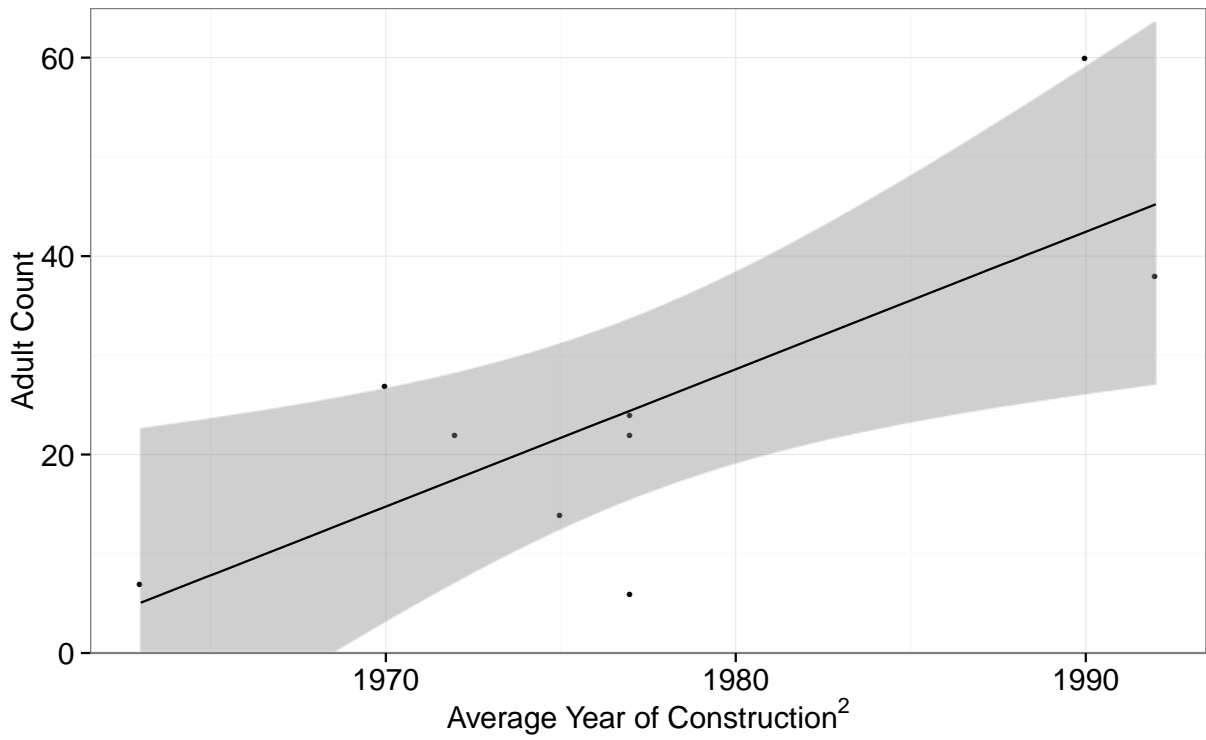


Figure 5.