
REPRODUCTION OF *EURYCEA BISLINEATA* WITHIN WATERSHEDS WITH EXURBAN DEVELOPMENT

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Abstract.—Amphibians exhibit many reproductive and parental-care strategies due to trade-offs between reproductive success and enhanced growth and survival. Phenotypic plasticity of traits associated with these strategies can allow amphibian populations to persist in volatile environments. Urbanization results in immediate and long-term changes to environmental conditions at several ecological scales. Thus, we chose to examine how coarse- (i.e., watershed) and fine-scale (i.e., riparian habitat) ecological changes associated with exurban housing development (6–25 houses/km²) influence the reproductive strategies of a stream-dwelling salamander, *Eurycea bislineata*. Egg production, as measured by the average number of eggs per egg cluster weighed by the adult count of the stream, was best predicted by a negative relationship to the proportion of regenerating forest. Communal ovipositing behaviors, such as the number of eggs laid communally and the proportion of eggs and clutches laid communally, were best predicted by stream sediment distribution and adult counts, respectively. Communal ovipositing increased in streams with a high proportion of mid-sized sediments or lower adult counts. Brooding behaviors, such as the proportion of eggs and clutches brooded weighed by the adult count and the proportion of egg clusters brooded weighed by the adult count, were best predicted by development age and the percentage of regenerating forest, respectively. Brooding rates were higher in watersheds with older development or less regenerating forest. Ultimately, this research highlights the reproductive variability of *E. bislineata* and provides evidence that exurban development can influence the reproductive strategies of an amphibian.

Key Words.—amphibian; conservation; egg clutch; exurban development; Northern Two-lined Salamander; oviposit; parental care; reproductive strategy

INTRODUCTION

Amphibians have evolved various reproductive and parental care strategies based on the trade-off between reproductive success with enhanced growth and survival (Salthe 1969; Townsend et al. 1984; Duellman and Trueb 1986; Townsend 1986; Crump 1996). Therefore, parental care evolves 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) but can reduce parental survival due to the 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 by limiting mating opportunities and through care-giving females producing fewer or smaller clutches in subsequent reproductive periods (Salthe and Duellman 1973; Townsend 1986; Church et al. 2007; Delia et al. 2013).

Independent of evolved reproductive strategies, many amphibians also exhibit phenotypic plasticity within reproduction responses (e.g., timing or location of oviposition, egg number, and parental care investment), and this plasticity often enhances reproductive success in variable environments (Kaplan 1987; Touchon and Warkentin 2008; Takahashi and McPhee 2016). For example, iteroparous amphibians can defer breeding in years when the risk of adult mortality is high (Church et al. 2007). Oviposition can be facultative to avoid potentially desiccating conditions (Takahashi and McPhee 2016), and the location of oviposition within the aquatic and terrestrial environments can be influenced by habitat disturbance and shade (Touchon and Warkentin 2008). The characteristics of amphibian egg clutches are also plastic. Within species, egg size for most amphibians is relatively 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). For example, temperature and food availability can influence the number and size of eggs produced by some female

frogs (Kaplan 1987). Parental care behaviors are also plastic responses in amphibians with transport, feeding, nest care, and temporal commitments to nest attendance strongly influenced by environmental variation (Ringler et al. 2013; Delia et al. 2014; Ferguson et al. 2014). For example, the frequency of parental care may be adjusted based on weather conditions and egg dehydration (Delia et al. 2013), and the intensity of parental care may be influenced by intra-specific competition and proximity to nesting locations (Ringler et al. 2013). Ultimately, the outcome of plastic reproductive responses can influence future adult reproduction as well as the hatching time, survival, and hatchling size of offspring (Kaplan 1989; Church et al. 2007; Delia et al. 2013, 2014). While amphibians have evolved complex reproductive strategies for their environments, the plasticity of reproductive responses exhibited can help guard against environmental volatility.

Anthropogenic factors 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 Mountain Brushtail Possums (*Trichosurus cunninghami*) 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 the Italian Agile Frog (*Rana latastei*) with larger census sizes had greater rates of polygyny, increased variance in male mating success, and reduced effective population sizes 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 in the population (Bateman 1948; Emlen and Oring 1977; Wade and Arnold 1980). Substantial population declines and reductions in the number of breeding individuals, which are likely to occur as a result of urbanization (Hitchings and Beebee 1997, 1998; Price et al. 2006, 2012; Hamer and McDonnell 2008), can make populations more susceptible to stochastic events, inbreeding depression, and genetic drift (Hitchings and Beebee 1998; Jehle et al. 2001; Ficetola et al. 2010; Palstra and Fraser 2012; Munshi-South et al. 2013). Ultimately, altered reproductive strategies in response to anthropogenic disturbances can influence population dynamics, reduce population resilience, and make populations vulnerable to extirpation (Miner et al. 2005; Lane et al. 2011).

Another form of anthropogenic disturbance that could influence reproduction is housing development. Exurban development, defined as human housing density of approximately 6–25 houses/km², has been

the fastest growing form of land use in the USA since the 1950s (Brown et al. 2005; Hansen et al. 2005). Increasing urbanization is associated with prescriptive changes to the watershed and riparian habitat, that are collectively referred to as urban stream syndrome (Paul and Meyer 2001; Meyer et al. 2005; Walsh et al. 2005). These changes include increased impervious surfaces, flashier hydrographs, increased nutrient and pollutant contamination, altered sedimentation processes, and a homogenization of the biotic community (Paul and Meyer 2001; Allan 2004; Meyer et al. 2005; Walsh et al. 2005). The ecological effects can be felt by amphibian populations at every life stage, even at housing development densities below 15% (Riley et al. 2005; Hamer and McDonnell 2008; Barrett et al. 2010; Barrett and Price 2014; Macklem et al. 2019). Urbanization has the potential to influence reproductive responses by reducing adult abundance (Barrett et al. 2010; Price et al. 2012), breeding success (Fahrig et al. 1995), and genetic viability (Nöel et al. 2007; Munshi-South et al. 2013). Urbanization can also alter the foraging and habitat resources available to adults through changes in sedimentation, hydrology, and biotic communities (Hamer and McDonnell 2008; Barrett and Price 2014). It may also reduce the performance and survival of early life stages through alterations to water chemistry, hydrology, genetic diversity, and resource availability (Barrett et al. 2010; Karraker et al. 2008; Barrett and Price 2014; Okamiya and Kusano 2018). There also appear to be strong legacy effects, with noticeable signatures affecting occupancy and abundance several decades after the initial disturbance (Gagné and Fahrig 2010; Price et al. 2012; Macklem 2019).

Our goal was to examine how exurban housing development influences the reproductive strategies of the Northern Two-lined Salamander (*Eurycea bislineata*), a plethodontid salamander recently found to exhibit variability in ovipositing and parental care reproductive responses (Ferguson et al. 2014). We sought to quantify egg production, communal ovipositing, and brooding behaviors and then model how these metrics of reproduction were influenced by coarse- (i.e., watershed) and fine-scale (i.e., riparian habitat) features of exurban housing development, and identify which ecological scale would be most effective for management actions. We anticipated that levels of egg production, communal ovipositing, and brooding would mirror patterns observed with adult abundance in watersheds with exurban development (see Macklem et al. 2019). Thus, we expected that coarse-scale features would be better predictors of reproductive responses than fine-scale features and that levels of egg production, communal ovipositing, and brooding behaviors would be highest in watersheds with the oldest housing developments, the lowest densities of

housing developments, the least regenerating forests, or the highest number of observed adults.

MATERIALS AND 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 in the USA (Conant and Collins 1998). *Eurycea bislineata* typically inhabit first-through third-order streams, and adults frequently use the terrestrial forest adjacent to streams (MacCulloch and Bider 1975; Conant and Collins 1998). Typically, female *E. bislineata* 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 (Server 2005; 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). These embryo numbers suggest 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 2–3 y in New England (MacCulloch and Bider 1975).

Study streams.—We selected nine first-order streams in the towns of Mansfield and Coventry, Connecticut, USA with similar percentage landcovers as quantified by the Connecticut Center for Land Use Education and Research (CLEAR) 2010 landcover layers (CLEAR 2010; Fig. 1). The nine selected streams were a sub-set

TABLE 1. Range, mean, and standard deviation of watershed features recorded for nine streams in Mansfield and Coventry, Connecticut, USA, where we sampled Northern Two-lined Salamander (*Eurycea bislineata*) adults and egg masses. The abbreviation SD = standard deviation, and % = percentage.

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	6.30	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 km ²	0.08–0.78	0.35	0.2

of 15 streams used in a study that estimated salamander abundance and occupancy (see Macklem et al. 2019). The goal here was to select forested streams with a gradient of housing age and densities in the watershed. Therefore, streams had watersheds that were composed of 42.2–99.4% mixed deciduous and coniferous forest (Table 1). Development ranged from 0%, which includes three control sites, to 35.9% of each watershed and was defined by roads, roofs, and other impervious surfaces (Table 1). We attempted to eliminate streams in 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, we overlaid the delineated watersheds with a parcel layer, determined the age of every house in each watershed,

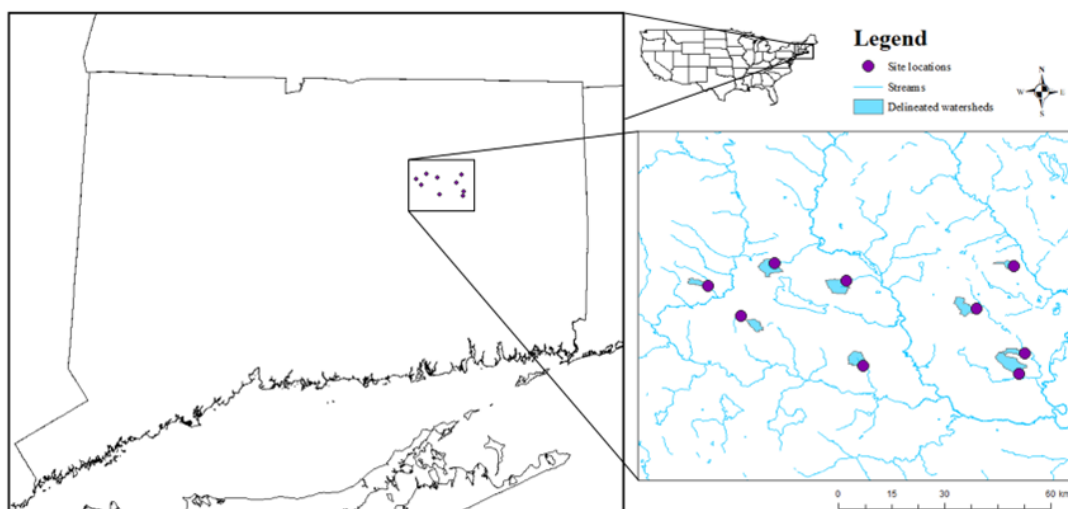


FIGURE 1. Survey stream locations in Mansfield and Coventry, Connecticut, USA, with the most downstream portion of surveyed stream segments depicted as purple points and delineated watersheds calculated from each point.

and then calculated an average housing age (referred to as development age) for each watershed, which ranged from 1963 to 1992 across all watersheds (Table 1). We also used this parcel layer to ensure that the streams were composed almost exclusively of residential, rather than commercial or industrial, development. Lastly, we used a forest vegetation layer (Rittenhouse et al. 2022) to calculate the percentage of each watershed consisting of regenerating forest (0–14%) and persistent forest (55–98%) as an alternative metric to average development age.

Field sampling.—We conducted area-constrained stream surveys once a month from May to August 2015. We only performed surveys on days without heavy rain so that detection probabilities were similar across surveys. We used a 30-m stream segment used in Macklem et al. (2019) and extended the sampling segment to 200 m. The extension was upstream of the original 30-m segment, except for two sites due to inaccessibility of adjacent properties. To perform surveys, two observers simultaneously sampled on opposite sides of the stream bank, starting downstream at 0 m and working upstream to 200 m. Observers lifted any natural cover objects (rocks, logs, leaf litter) while holding an aquarium dipnet (15.24 cm width) directly downstream to increase successful capture. We replaced all 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 was captured, one observer stopped to process the salamander while the second observer continued the survey. Once the animal processing was complete, the first observer returned to survey with the second observer. We marked each adult using Visible Implant Elastomer (VIE) and a cohort-mark that indicated the month and year of capture. When a rock with eggs was found, both observers stopped and individually counted 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), but we noted when developmental stages differed within a cluster. We photographed each rock nest, recorded 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.

We 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 stream for each of the 2014, 2015, and 2016 sampling periods (Hesed 2012). We created 60 artificial cover-

boards from White Oak (*Quercus alba*) harvested from the University of Connecticut Forest and weathered them for more than 6 mo. All artificial cover-boards measured 60.96 × 30.48 × 3.81 cm, a size sufficient to retain moisture and a stable thermal environment (Hesed 2012). We placed four artificial cover-boards perpendicular to the streambed at each stream. We positioned a cover-board at distances of 5, 10, and 20 m from the streambed and the fourth cover-board 5 m on the opposing side of the streambed. We placed the transect of three cover-boards on the side of the stream with the largest forest buffer. We checked *cover-boards* on the same days as the area-constrained surveys. We marked and measured any salamanders under the cover-boards using the same methodology as the salamanders captured during the stream surveys.

Habitat data.—We measured sediment distribution, turbidity, specific conductivity, dissolved oxygen concentration, temperature, and stream discharge as fine-scale habitat variables important to salamander reproduction. We recorded soil temperatures using a Taylor Instant Read Digital Thermometer (Model 9840N; Taylor, Oak Brook, Illinois, USA) during each stream from May to August 2014, April to September 2015, and April 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. We wanted to capture the upper threshold of dissolved oxygen (DO), discharge, and conductivity experienced by the stream. Thus, we recorded conditions during April 2015 to capture the seasonal conditions of each stream after a period of spring rain, snowmelt, and runoff containing high concentrations of road salt. During this time, we measured specific conductivity and DO concentrations in the streams using a handheld sonde (Model YSI 556 MPS; Yellow Springs Instruments, Yellow Springs, Ohio, USA). We calculated stream discharge by measuring wetted channel width and using a SonTek FlowTracker Handheld Acoustic Doppler Velocimeter (SonTek-A Xylem Brand, San Diego, California, USA) to measure mean water-column velocity and depth at regular intervals across the stream width according to U.S. Geological Survey guidelines (Fitzpatrick et al. 1998). In May 2015, we collected water samples from each stream in acid washed and field rinsed bottles, transported samples to the laboratory on ice, and then froze samples until analysis. We measured the turbidity in each of these water samples using the DRT 100B Turbidimeter (HF Scientific-A WATTS Brand, Fort Myers, Florida, USA). In June 2015, and as outlined by Dunne and Leopold (1978), we collected sediment distribution measurements by haphazardly collecting approximately 100 standard particles at each stream.

We measured each particle along the intermediate axis and sorted each particle into a corresponding size class. We used the mode particle size class for each stream.

Data analysis.—We used an information theoretic approach to determine how coarse-scale watershed features and fine-scale stream features influence *E. bislineata* reproduction and which ecological scale should be targeted for management purposes (Akaike 1973; Burnham and Anderson 2002). Our goal was to quantify three aspects of *E. bislineata* reproduction: egg production, communal ovipositing, and brooding behavior. For the purposes of this study, we refer to any group of eggs as a cluster of eggs. We defined a clutch as any independent cluster of eggs containing 60 or fewer eggs. This definition is in accordance with previous research examining the natural history and reproductive biology of the species, which suggests that 60 eggs is a conservative maximum threshold for a clutch of eggs by a single adult female (Server 2005; Ferguson et al. 2014). The maximum ovum count for the species is 86 (Stewart 1968), and mean egg count for solitary clutches was reported to be 40 (Ferguson et al. 2014). Thus, 60 eggs was selected as an appropriate benchmark. If a cluster of eggs exceeded 60 eggs, we defined this cluster as a communal nest. We estimated the number of clutches contributing to a communal nest by determining the maximum number of clutches that could have contributed using our 60-egg limit. From that, we calculated the average number of eggs for each of these clutches. For example, a cluster of 100 eggs would indicate two clutches of 50 eggs. We also anticipated that the number of adults observed would be an important variable to consider because salamander abundance varies greatly with the density and age of housing developments (Price et al. 2006; Gagné and Fahrig 2010; Macklem et al. 2019), and because the abundance of reproductively receptive females is a strong predictor of reproductive strategies (Ficetola et al. 2010). Thus, we accounted for the number of adults observed by either weighting our responses by adult count or including adult count as a model during the model selection process.

To measure egg production, we 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 our 60-egg limit (Server 2005; Ferguson et al. 2014). We weighted the four response variables by dividing each response by the adult count of each stream. These weighted responses can be used to represent an estimate of the average number of eggs produced by adult individuals, the likelihood of communal ovipositing, average clutch size, and the proportion of breeding females in a stream, respectively. To measure communal

ovipositing behaviors, we examined the number of eggs laid communally, which we defined as any cluster of eggs with greater than 60 eggs (Server 2005; Ferguson et al. 2014), and the proportion of eggs that were communally laid based on this limit. In addition, we considered the number of clusters that we presumed to be composed of multiple clutches, and the proportion of clutches that we presumed to be laid communally. We also wanted to examine the number of clusters laid with other clusters under the same rock and the proportion of clusters that were laid with other clusters under the same rock. Only two streams, however, exhibited individual rocks with multiple clusters, thus we did not perform model selection on those two responses, but we report observations. We made a distinction between the number and proportion of these responses to clarify potential differences between the individual and stream scale. For example, a stream with one very large clutch laid communally and several very small clutches laid separately, you would see a relatively high number of eggs laid communally but the proportion of clutches laid communally would be quite low.

We defined brooding as any egg-attendance by a female (i.e., the presence of a female under the same cover object as the eggs). To measure brooding behavior, we 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 eggs 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. As with the egg production responses, we weighted these responses by the number of adults, and these responses represent an estimate of brooding behavior at the scale of each adult in a stream and the stream as a whole. We created univariate Linear Regression models for each of the response variables and confirmed that no coarse-scale and only two fine-scale predictor variables (soil temperature and discharge) were correlated using a Pearson Correlation Coefficient ($r = 0.70$). We performed all analyses using R version 3.1.2 through the interface RStudio version 0.98.1091 (R Core Team 2014; RStudio, Inc. 2014).

We began the model selection process by creating an *a priori* candidate model set that aimed to clarify the importance of coarse-scale features on salamander reproduction. The candidate model set included two models that directly quantified exurban development age and two models that quantified forest metrics that could also represent development age. The first metric, average house age, was the average year a residence was built for all parcels within a watershed boundary. For three streams with 0% development, we used imputation

to assign a housing age to these three watersheds. We ran 1,000 simulations that randomly replaced these values with a number pulled from a uniform distribution bounded by the minimum and maximum observed housing ages in our samples. Then we took the mean of the output and assigned it to the three watersheds. The age metric tests the hypothesis that egg production, communal ovipositing, and brooding behavior will be lowest in watersheds with newer housing developments due to the acute 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 responses in streams with new developments may initially decline due to disturbance caused by construction but then the reproductive responses in streams with the oldest developments may recover as the forest and stream return to pre-disturbance conditions. The third metric, regeneration, is the percentage of regenerating forest (up to 20 y) 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 egg production, 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 egg production, communal ovipositing, and brooding behavior should be high. Lastly, we included the percentage of development within each stream watershed to test the hypothesis that increasing watershed development reduces reproductive responses.

We created a second candidate model set that aimed to clarify importance of stream-scale (i.e., fine-scale) features of urbanization on salamander reproduction (Paul and Meyer 2001; Wenger et al. 2009). We included models with main effects of conductivity, DO, turbidity, soil temperature, discharge, and sediment distribution. The turbidity value at one stream was an extreme outlier that may be an error in data collection; therefore, we assigned the mean turbidity across all sites to this one stream. The soil temperature was the three-year average soil temperature at each stream.

The third candidate model set consisted of the top-ranked coarse- and fine-scale models from the previous models sets to identify the scale at which the response variables are most strongly influenced and where management decisions would be most effective to influence a specific parameter. In other words, this model set identifies the true top-ranking model for a given parameter, regardless of ecological scale. For

the communal ovipositing models where scaling the response variable by adult count was inappropriate for our research questions, we also included a model with adult count as an alternative way to assess the importance of adult counts to the response variables.

We ranked models using Akaike Information Criterion (AIC) corrected for finite sample sizes (AICc; Akaike 1973; Akaike 1974; Hurvich and Tsai 1989). For the three sites with 0% development, we used the 1,000 randomly imputed housing age values to simulate 1,000 AICc model scores. We used the mean AICc score of the simulations to compare to the scores from other models. Top models were identified based on the lowest AICc score and being at least two Δ AICc smaller than the next top model (Burnham and Anderson 2002). We presented model ranking, but only make inference for top-ranking and competing models (Arnold 2010). When the intercept-only model was the top-ranking model, we did not provide any additional inference because it indicated that our models did not rank meaningfully higher than the null model. We assessed output from the Linear Regression analyses of the top-ranking models to determine the significance, magnitude, and direction of the relationship.

RESULTS

We observed a range of adult counts as well as egg production, communal ovipositing, and brooding behavior responses, which varied considerably across streams (Table 2). We captured 220 unique adult *E. bislineata* from May 2015 to August 2015, with no recaptures (Table 2). The number of adults at each stream ranged from 6 to 60 (mean = 24.4, standard deviation = 16.7; Table 2). We processed 3,635 eggs, 91 clutches, and 56 clusters in May 2015 (Table 2, Fig. 2). We note that, using our 60-egg benchmark, only 21% of the clutches assessed were subjected to this calculation. We found that, on average, 64% of eggs were laid communally (Table 2, Fig. 3); however, communal ovipositing was facultative, as one stream exhibited no communal oviposition (Table 2). We documented only two streams with multiple egg clusters on a single rock (i.e., the number of clusters laid communally), which accounted for about 15% of egg clusters (i.e., the proportion of clusters laid communally; Table 2, Fig. 4). 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. We also found that, on average, 60% of eggs across all study streams were brooded (Table 2). We

TABLE 2. Summary of adult count, egg production, communal ovipositing, and brooding behavior response data of Northern Two-lined Salamanders (*Eurycea bislineata*) including the total count, the range of counts, the mean count, and one standard deviation (SD) around the mean for all streams. Also included are the range, mean, and SD of the proportion of eggs, clutches, and clusters that were communally laid or brooded in each Connecticut, USA, stream.

Response Category	Response	Total	Range	Mean	SD
Adult Count	Adult Count	220	6–60	24.4	16.7
Egg Production	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	3.0
	Proportion of Eggs Laid Communally	—	0–1	0.64	0.34
	Proportion of Clutches Laid Communally	—	0.00–0.55	0.33	0.19
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	0.60	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

observed that at least one cluster of eggs was brooded in every stream (i.e., none of the streams we surveyed exhibited a complete absence of brooding behavior; Table 2).

Egg production.—The intercept-only models ranked highest for all but one response (Appendix Table 1). Three responses that were best predicted by the intercept-only model include 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 (Tables 3 and 4). The average number of eggs per cluster per adult count was best predicted by the percentage of regenerating forest in the watershed (Appendix Table 1). The amount of regenerating forest was negatively related to the response (Table 3, Fig. 5).

Communal ovipositing.—The number of eggs laid communally was negatively related to sediment distribution (Tables 4 and 5; Fig. 6), 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 sampled 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 (Appendix

Table 2); however, the model was $< 2 \Delta AICc$ from the intercept-only model, and the 95% confidence interval for the β estimate of sediment distribution overlapped zero, indicating that the model was no better than the null and the association was weak (Table 3; Appendix Table 2). In contrast, the proportion of eggs laid communally was negatively related to the adult count (Table 3; Appendix Table 2; Fig. 6). The proportion of clutches laid communally was also negatively related to the adult count (Table 3; Fig. 6). This model of adult count outranked both the top-ranked coarse-scale and the top-ranked fine-scale models for both responses (Appendix Table 2).

Brooding behavior.—Coarse-scale, watershed models of development age ranked highest for most brooding behavior responses. The number of eggs brooded per adult count and the number of egg clutches brooded per adult count were best predicted by a negative relationship to average housing age followed by a competing model with the quadratic of housing age, while the number of egg clusters brooded per adult count was best predicted by the quadratic of average housing age followed by a competing model with a negative relationship to average housing age (Table 3; Appendix Table 3). The models for all three responses, however, were $< 2 \Delta AICc$ away from the intercept-only model



FIGURE 2. Examples of single clusters (A, F) or single clutches (B, C, D, E) of Northern Two-lined Salamander (*Eurycea bislineata*) eggs. These photographs depict various embryonic development stages (in order A-F). Early stages are devoid of pigment, and the embryo is spherical. As the embryo develops, it elongates and grows into a larger and larger C shape. During later stages of embryonic development, external gills become visible as well as pigmentation on the dorsal side of the embryo. (Photographed by D. Cristina Macklem).

(Appendix Table 3). The proportion of eggs brooded per adult count was best predicted by a negative relationship to average housing age and a competing model with the quadratic of housing age (Table 3; Appendix Table 3; Fig. 7). Top-ranking models for the proportion of egg clutches brooded per adult count included a negative relationship to housing age, a model with the quadratic of housing age, and a negative relationship to turbidity with higher proportions of brooding when housing developments were older and when average turbidity was lower, respectively (Table 3; Appendix Table 3; Fig. 7). The proportion of egg clusters brooded per adult count was negatively related to the percent of forest regeneration in the watershed with the highest proportion of brooding in watersheds with the least regenerating forest (Table 3; Appendix Table 3; Fig. 7). Moreover, the fine-scale model including average turbidity was a competing model at 0.634 Δ AICc from the top-ranking model (Appendix Table 3), with the

proportion of egg clusters brooded per adult having a negative relationship with average turbidity such that the highest proportion of egg clusters brooded per adult occurred when average turbidity was lowest.

DISCUSSION

Our study provides evidence that the reproductive responses (i.e., egg production, communal ovipositing, and brooding behaviors) of *E. bislineata* can vary across streams. For many responses, this variation was best explained by parameters from across the ecological scales we examined including coarse-scale features such as housing development age and regenerating forest in watersheds, fine-scale features such as sediment distribution within the stream reach, and population-level features such as adult counts in the stream. Contrary to our expectation, the density of development within watersheds was not a strong



FIGURE 3. Example of an embryo cluster of a Northern Two-lined Salamander (*Eurycea bislineata*), composed of at least two clutches at visibly different developmental stages. (Photographed by D. Cristina Macklem).

predictor of the reproductive responses. In accordance with our expectations, the egg production response, average number of eggs per cluster per adult count and the brooding behavior responses of the proportion of eggs, clutches, and clusters brooded per adult count were best predicted by coarse-scale features and were highest in watersheds with less regenerating forest or old housing developments. This result suggests that exurban development in the watershed, regardless of the density, can influence the reproductive responses of *E. bislineata* nearly 60 y following peak development disturbance. Communal ovipositing occurred at higher rates in streams with low adult counts, which was contrary to our expectation. One explanation for these responses is that females are clustering around limited resources in a disturbed habitat. Another possible explanation is that urbanization altered the biological community by reducing or eliminating predators that would otherwise deter such behaviors. The remainder of our egg production and brooding behavior responses were not well explained by variables associated with exurban development, which suggests that other biotic



FIGURE 4. Examples of multiple egg clusters of Northern Two-lined Salamanders (*Eurycea bislineata*) under a single rock. (A) One rock contained two egg clusters with eggs at similar developmental stages. (B) This rock contained four egg clusters. The top-most cluster is composed of at least two clutches at visibly different developmental stages. (Photographed by D. Cristina Macklem).

or abiotic characteristics of the environment are more strongly driving these responses. Overall, this research highlights the variability in reproduction exhibited by *E. bislineata* and provides evidence that housing development could influence the reproductive responses of an amphibian. The variation documented here, combined with our previous finding that adult abundance is influenced by an interaction between exurban housing age and density such that watersheds with low densities of old development have higher abundance relative to watersheds with high densities of new development (see Macklem et al. 2019), suggests that reproductive

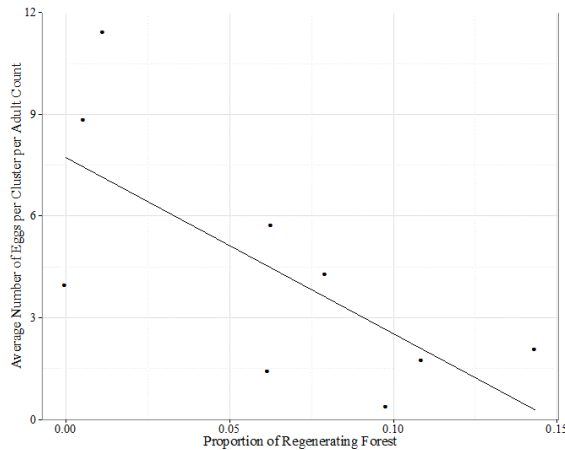


FIGURE 5. The average number of eggs per cluster per the adult count of Northern Two-lined Salamanders (*Eurycea bislineata*) was negatively related to the proportion of regenerating forest.

plasticity could contribute to population recovery following disturbance from housing development.

We observed patterns indicating a potential increase in some salamander egg production and brooding behaviors in streams containing old housing developments or low percentages of regenerating forest. Contrary to expectation, the density of development within watersheds was not a strong predictor of the reproductive responses. Rather, we found that, when models were weighted by adult count, average housing age, the quadratic of average housing age, and the percentage of regenerating forest predictors were related to all egg production and brooding responses. Previous work on *E. bislineata* suggests strong legacy effects from housing development disturbances with abundance increasing several years following peak disturbance (Macklem et al. 2019). In accordance with this pattern, we suggest that as the riparian habitat has time to recover from the disturbance of housing developments, important abiotic and biotic resources may also recover and be replenished. As resources such as optimal forage become more available and abundant, adult salamanders may have more energy to put towards reproduction and parental care such that egg production and brooding responses also increase with time. Increased parental investment, such as egg production and brooding, can greatly increase reproductive success; however, it comes at a cost to the parent (Salthe and Duellman 1973; Duellman and Trueb 1986; Clutton-Brock 1991). Thus, if resources are reduced following disturbance from housing development, the cost of egg production and parental care could exceed the potential increase in survival and fitness of the embryos, favoring reduced parental investment. Our data support *E. bislineata* exhibiting this type of reproductive plasticity. Our results indicate that even if adult abundance is not changed

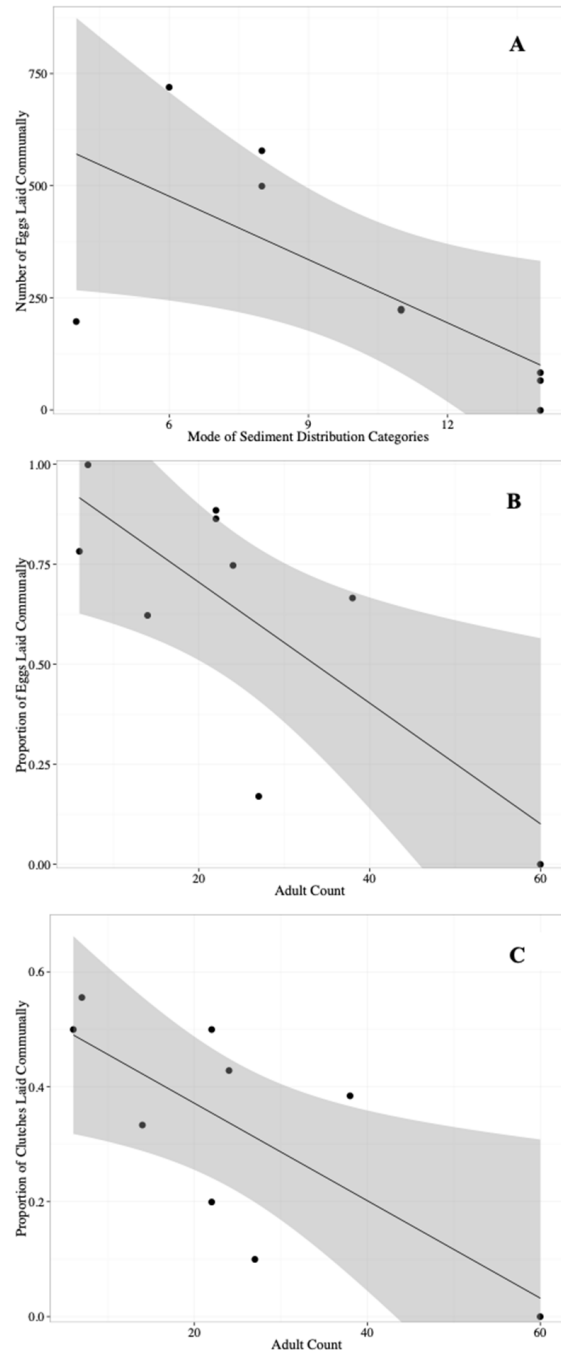


FIGURE 6. The communal ovipositing responses of Northern Two-lined Salamanders (*Eurycea bislineata*) as determined by (A) the number of eggs laid communally, (B) the proportion of eggs laid communally, and (C) the proportion of communal clutches. Responses were related to sediment distribution, the adult count, and the adult count, respectively.

by housing development, any amount of disturbance resulting from new housing can influence certain reproductive responses of *E. bislineata*. Additional research is needed to understand how small but repeated

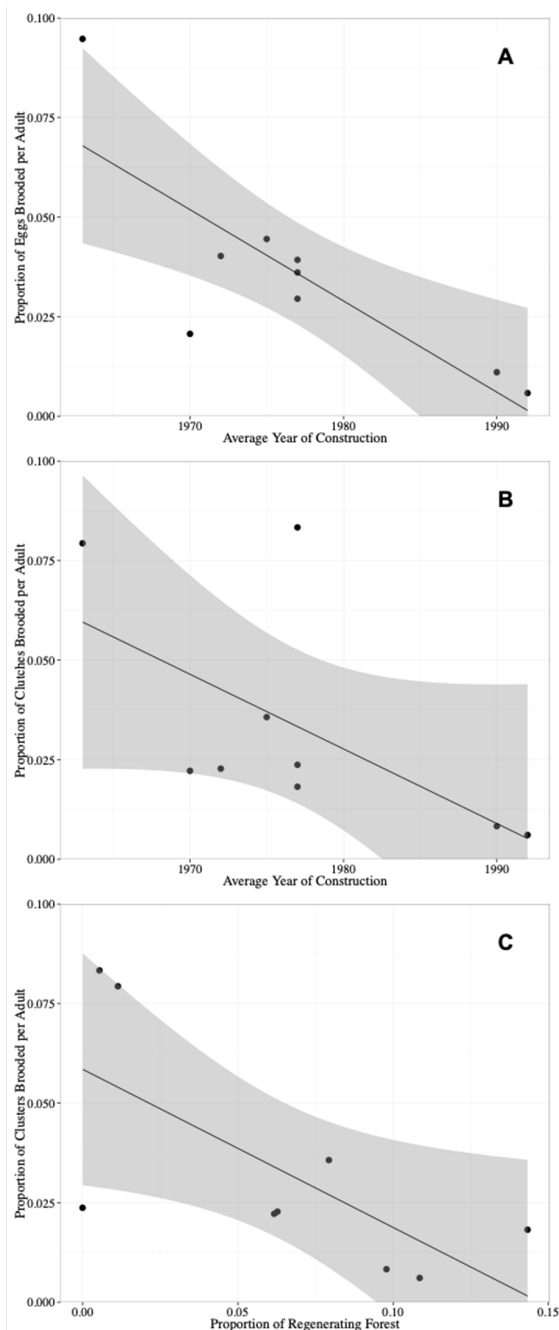


FIGURE 7. Estimate of brooding behavior responses of Northern Two-lined Salamanders (*Eurycea bislineata*) as determined by (A) the proportion of eggs brooded per adult count and (B) the proportion of clutches brooded per adult count, and (C) proportion of clusters brooded per adult count. Responses from top-ranking models included the average age of house construction, the average age of house construction, and the proportion of regenerating forest, respectively.

disturbances affect reproduction over time. Perhaps more concerning is the magnitude that egg production and brooding behavior is reduced in watersheds with

new housing developments. Our models estimated fewer than one egg per cluster for every individual and zero eggs, clutches, and clusters brooded in recently developed watersheds. Thus, mitigating the acute effects of housing development and protecting nearby watersheds with little development that could act as source populations should be an important consideration for maintaining stream salamander populations (Semlitsch 2000; Macklem et al. 2019).

One explanation for the high communal ovipositing in streams with low adult counts is the hypothesis that urbanized landscapes are likely to have clustered resources, which leads to clumped distributions of females and/or embryos (Emlen and Oring 1977). In this case, embryos may initially have been laid communally to improve embryo and larval survival by taking advantage of limited resources in a disturbed habitat. One potential limited resource in urbanized streams is the availability of ovipositing rocks or ovipositing rocks with suitable microhabitats. While we do not have nest-level covariates to fully assess microhabitat selection, many studies have described the importance of intermediate-sized sediments for refugia from predators and microhabitats for egg deposition (Orser and Shure 1972; Smith 2002; Bernhardt and Palmer 2007, Brannon and Purvis 2008; Rizzo et al. 2016). Urbanization, however, often leads to increased sedimentation and altered stream hydrology that can reduce the availability of preferred large sediments (Walsh et al. 2005). Our data support this hypothesis of clustered nesting resources. 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. We expected that communal ovipositing rates were driven by high adult counts leading to increased intraspecific competition, although we observed the opposite pattern, which could suggest that resource clustering is the mechanism leading to communal ovipositing. In this scenario, large ovipositing rocks may be limited in the streams we sampled, perhaps due to alterations in the riparian habitat from housing developments, such that a higher proportion of females selected to oviposit under the few suitable rocks in the stream.

We also observed several intraspecific interactions over the course of the study. We recorded two nests that contained more than one female brooding, and we observed more than 30 individuals under rocks with at least one other *E. bislineata* throughout the study. Communal brooding could simply be the result of high adult abundance within a watershed, therefore increasing the chance of intraspecific interactions, or communal brooding could provide some benefit to the individual and/or to clutch survival. For example, communal brooding or shared brooding has been

TABLE 3. Linear regression output for top-ranking reproduction models for Northern Two-lined Salamanders (*Eurycea bislineata*) across all candidate model sets, in rank order, with the number of model parameters (k), β estimates, and 95% confidence intervals.

Predictor Estimates for Top-Ranking Models	k	β Estimate	95% CI
Egg Production			
Number of Eggs/Adult Count			
Intercept only	1	26.540	(3.549, 49.537)
Number of Clutches/Adult Count			
Intercept only	1	0.653	(0.082, 1.225)
Number of Clusters/Adult Count			
Intercept only	1	0.378	(0.098, 0.658)
Average Number of Eggs per Cluster/Adult Count			
Regeneration	2	-51.964	(-98.649, -5.279)
Communal Oviposition			
Number of Communal Eggs			
Sediment Distribution	2	-47.055	(-90.791, -3.318)
Number of Communal Clutches			
Sediment Distribution	2	-0.282	(-0.645, 0.081)
Intercept only	1	2.111	(0.702, 3.520)
Proportion of Eggs Laid Communally			
Adult Count	2	-0.015	(-0.027, -0.003)
Proportion of Clutches Laid Communally			
Adult Count	2	-0.008	(-0.016, -0.001)
Brooding			
Number of Eggs Brooded/Adult Count			
Average House Age	2	-1.516	(-3.010, -0.021)
Average House Age ²	2	-0.000	(-0.001, -0.000)
Intercept only	1	15.627	(-0.223, 31.478)
Sediment Distribution	2	-2.735	(-7.062, 1.593)
Number of Clutches Brooded/Adult Count			
Average House Age	2	-0.032	(-0.062, -0.002)
Average House Age ²	2	-0.000	(-0.000, -0.000)
Intercept only	1	0.358	(0.033, 0.682)
Number of Clusters Brooded/Adult Count			
Average House Age ²	2	-0.000	(-0.000, -0.000)
Average House Age	2	-0.016	(-0.031, -0.002)
Intercept only	1	0.191	(0.030, 0.352)
Regeneration	2	-2.150	(-5.365, 1.065)
Proportion of Eggs Brooded/Adult Count			
Average House Age	2	-0.002	(-0.004, -0.001)
Average House Age ²	2	-0.000	(-0.000, -0.000)
Proportion of Clutches Brooded/Adult Count			
Average House Age	2	-0.002	(-0.003, -0.001)
Average House Age ²	2	-0.000	(-0.000, -0.000)
Turbidity	2	-0.024	(-0.048, 0.000)
Proportion of Clusters Brooded/Adult Count			
Regeneration	2	-0.397	(-0.766, -0.029)
Turbidity	2	-0.029	(0.011, 0.055)

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), which is also in accordance with egg production exhibiting similar patterns to brooding behavior in our study.

The overall trend we observed of certain increased egg production and brooding behavior responses in streams with older housing developments and decreased communal ovipositing in streams with high adult counts could also suggest a release from predation pressures (Lima 1998b). We hypothesize that an altered biotic community caused by increasing urbanization could result in predator-prey interactions driving the trade-off between reproduction and female maintenance (Lima 1998a; Freeman and Schorr 2004; Miner et al. 2005; Roy et al. 2007; Canessa and Parris 2013). In streams with natural predators, we predict that reproductive output and brooding behaviors would be reduced due to the nonlethal costs of predation threats and predator avoidance that add energetic costs to the parent (Stearns 1992; Lima 1998a,b; Winandy et al. 2015, 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, 2017). Moreover, our observation of increased adult abundance in watersheds with old development combined with decreased communal ovipositing in streams with high adult counts could further indicate a lack of predation on the adult population and a reduced incentive for *E. bislineata* to employ a strategy of communal ovipositing. Thus, a reduction in the predator community in watersheds with old housing developments could produce the reproductive patterns we observed.

We also note that several of our egg production and brooding behavior responses were not well explained by the variables we selected to examine the influence of exurban housing development. It is possible that other abiotic characteristics of the environment or biotic interactions in the stream habitat are more strongly influencing these responses. Predation pressures, altered hydrology, and other types of habitat disturbance can all influence the reproductive responses of amphibians (Kaplan 1987; Touchon and Warkentin 2008; Takahashi and McPhee 2016). We had a limited sample size, with just nine streams, and only collected data over the course of a single reproductive season, so it is also possible that the variability between streams and/or across an individual breeding season were greater than the potential influence that exurban development had on these responses. Additional survey locations across

several breeding seasons could help to differentiate the sources of reproductive variability more clearly in *E. bislineata* in the future.

Quantifying the magnitude and extent of reproductive plasticity in response to housing development and urbanization will be important to conservation strategies because reproductive plasticity has the potential to increase the resilience of populations affected by urbanization (Miner et al. 2005). Here we demonstrated potential effects of urbanization and adult counts on the reproductive strategies of *E. bislineata*. *Eurycea bislineata* is a common species known to persist in more urbanized watersheds than many other stream salamanders. Additional studies with other stream salamanders across greater geographic ranges are necessary to determine if reproductive plasticity contributes to salamander persistence in disturbed habitats. Future research should aim to quantify how egg production, communal ovipositing, and brooding behaviors influence reproductive success and population structure. Ultimately, this information could help identify populations vulnerable to decline and extirpation as well as contribute to population conservation and recovery strategies for amphibians affected by housing development and/or low adult counts. This work provides evidence of housing development influencing salamander reproduction and contributes to scientific understanding of reproductive responses to anthropogenic influences.

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APPENDIX TABLE 1. Egg production models of Northern Two-lined Salamander (*Eurycea bislineata*) for coarse-scale (average housing age and the percentage of regenerating forest, persistent forest, and development in watersheds), fine-scale (conductivity, discharge, dissolved oxygen, turbidity, soil temperature, and sediment distribution in riparian habitats), and management model sets. The model sets were the same for all responses. For each model, the table reports the number of parameters (K), AIC value corrected for small samples size (AICc), as well as the calculated change in AICc ($\Delta AICc$), and model weight (w). Competing models are indicated by an asterisk (*).

	K	Number of Eggs/Adult Count			Number of Clutches/Adult Count			Number of Clusters/Adult Count			Average Number of Eggs per Cluster/Adult Count		
		AICc	$\Delta AICc$	w	AICc	$\Delta AICc$	w	AICc	$\Delta AICc$	w	AICc	$\Delta AICc$	w
Coarse-Scale Model Set													
Intercept + Average House Age	2	90.569	0.347*	0.212	24.033	0.304*	0.228	10.986	0.114*	0.247	51.780	2.033	0.161
Intercept + Average House Age ²	2	90.617	0.395*	0.207	24.062	0.333*	0.224	11.013	0.140*	0.244	51.777	2.030	0.162
Intercept + Regeneration	2	90.875	0.653*	0.182	25.080	1.351*	0.135	12.387	1.515*	0.123	49.747	0.000	0.446
Intercept + Persistent	2	92.515	2.293	0.080	26.057	2.328	0.083	13.435	2.562	0.073	54.143	4.396	0.050
Intercept + Developed	2	92.912	2.690	0.066	26.057	2.798	0.065	14.096	3.334	0.052	53.483	3.736	0.069
Intercept	1	90.222	0.000	0.252	23.729	0.000	0.265	10.872	0.000	0.262	52.510	2.763	0.112
Fine-Scale Model Set													
Intercept + Conductivity	2	92.757	2.535	0.103	26.361	2.632	0.097	13.971	3.099	0.080	54.125	54.125	0.108
Intercept + Discharge	2	93.650	3.428	0.066	27.158	3.429	0.065	14.297	3.425	0.068	55.216	55.216	0.063
Intercept + Dissolved Oxygen	2	93.348	3.126	0.077	26.844	3.115	0.076	13.853	2.981	0.085	54.335	54.335	0.097
Intercept + Turbidity	2	92.802	2.580	0.101	26.193	2.464	0.105	12.877	2.005	0.138	52.745	52.745	0.216
Intercept + Soil Temperature	2	92.485	2.263	0.118	26.094	2.365	0.110	13.376	2.504	0.107	52.660	52.660	0.225
Intercept + Sediment Distribution	2	91.755	1.533*	0.170	25.040	1.311*	0.187	12.744	1.872*	0.147	55.717	55.717	0.049
Intercept	1	90.222	0.000	0.366	23.729	0.000	0.360	10.872	0.000	0.376	52.510	0.000	0.243
Management-Scale Model Set													
Top Coarse-Scale Model	-	-	-	-	-	-	-	-	-	-	49.747	0.000	0.799
Top Fine-Scale Model	-	-	-	-	-	-	-	-	-	-	-	-	-
Intercept	1	90.222	0.000	1.000	23.729	0.000	1.000	10.872	0.000	1.000	52.510	2.763	0.201

APPENDIX TABLE 2. Communal oviposition models of Northern Two-lined Salamanders (*Eurycea bislineata*) for coarse-scale (average housing age and the percentage of regenerating forest, persistent forest, and development in watersheds), fine-scale (conductivity, discharge, dissolved oxygen, turbidity, soil temperature, and sediment distribution in riparian habitats), and management model sets. For each model, the table reports the number of parameters (K), AIC value corrected for small samples size (AICc), as well as the calculated change in AICc ($\Delta AICc$), and model weight (w). Competing models are indicated by an asterisk (*).

	K	Number of Eggs Laid Communally				Number of Clutches Laid Communally				Proportion of Eggs Laid Communally				Proportion of Clutches Laid Communally			
		AICc	$\Delta AICc$	w	AICc	AICc	$\Delta AICc$	w	AICc	$\Delta AICc$	w	AICc	$\Delta AICc$	w	AICc	$\Delta AICc$	w
Coarse-Scale Model Set																	
Intercept + Average House Age	2	131.578	3.014	0.106	43.251	3.289	0.096	11.258	1.839*	0.134	1.426	2.598	0.103				
Intercept + Average House Age ²	2	131.590	3.026	0.105	43.258	3.295	0.096	11.281	1.862*	0.132	1.453	2.625	0.102				
Intercept + Regeneration	2	131.229	2.666	0.126	42.878	2.915	0.116	12.157	2.738	0.085	-1.172	0.000	0.378				
Intercept + Persistent	2	131.980	3.416	0.086	43.105	3.142	0.104	12.821	3.403	0.061	2.890	4.062	0.049				
Intercept + Developed	2	131.673	3.110	0.101	43.391	3.428	0.090	9.996	0.577*	0.252	1.521	2.693	0.098				
Intercept	1	128.563	0.000	0.477	39.963	0.000	0.498	9.419	0.000	0.336	-0.499	0.673*	0.270				
Fine-Scale Model Set																	
Intercept + Conductivity	2	131.432	5.333	0.043	43.326	3.471	0.060	10.658	3.207	0.075	1.970	2.624	0.073				
Intercept + Discharge	2	131.960	5.860	0.080	43.117	3.262	0.066	10.248	2.798	0.093	1.781	2.435	0.080				
Intercept + Dissolved Oxygen	2	131.806	5.707	0.033	42.921	3.066	0.073	10.287	2.837	0.091	-0.038	0.616*	0.200				
Intercept + Turbidity	2	131.219	5.119	0.036	42.605	2.750	0.085	12.642	5.192	0.028	2.677	3.331	0.051				
Intercept + Soil Temperature	2	131.623	5.523	0.039	43.364	3.509	0.058	8.733	1.283*	0.140	-0.654	0.000	0.272				
Intercept + Sediment Distribution	2	126.100	0.000	0.620	39.855	0.000	0.338	7.451	0.000	0.375	1.982	2.636	0.073				
Intercept	1	128.563	2.464	0.181	39.963	0.108*	0.320	9.419	1.968*	0.198	-0.499	0.155*	0.251				
Management-Scale Model Set																	
Top Coarse-Scale Model	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Top Fine-Scale Model	-	126.100	0.000	0.730	39.855	0.000	0.459	7.451	2.006	0.244	-0.654	3.265	0.120				
Intercept + Adult Count	2	131.211	5.111	0.057	42.783	2.928	0.106	5.445	0.000	0.665	-3.919	0.000	0.612				
Intercept	1	128.563	2.464	0.213	39.963	0.108*	0.435	9.419	3.974	0.091	-0.499	3.420	0.111				

APPENDIX TABLE 3. Brooding models of Northern Two-lined Salamanders (*Eurycea bislineata*) for coarse-scale (average housing age and the percentage of regenerating forest, persistent forest, and development in watersheds), fine-scale (conductivity, discharge, dissolved oxygen, turbidity, soil temperature, and sediment distribution in riparian habitats), and management model sets. The model sets were the same for all responses. For each model, the table reports the number of parameters (K), AIC value corrected for small samples size (AICc), as well as the calculated change in AICc (Δ AICc), and model weight (w). Competing models are indicated by an asterisk (*).

	Number of Eggs Brooded/ Adult Count			Number of Clutches Brooded/Adult Count			Proportion of Eggs Brooded/ Adult Count			Proportion of Clutches Brooded/Adult Count			Proportion of Clusters Brooded/Adult Count						
	K	AICc	Δ AICc	w	AICc	Δ AICc	w	AICc	Δ AICc	w	AICc	Δ AICc	w	AICc	Δ AICc	w			
Coarse-Scale Model Set																			
Intercept + Average House Age	2	82.728	0.000	0.288	12.521	0.000	0.302	0.305	-40.000	0.000	0.410	-41.428	0.000	0.358	-35.151	2.245	0.143		
Intercept + Average House Age ¹	2	82.760	0.032*	0.283	12.546	0.025*	0.298	0.311	-39.951	0.050	0.400	-41.414	0.014*	0.356	-35.345	2.050	0.157		
Intercept + Regeneration	2	84.771	2.043	0.104	14.710	2.188	0.101	1.586	1.982*	0.115	-35.136	4.864	0.036	2.152	-37.396	0.000	0.438		
Intercept + Persistent	2	85.379	2.650	0.077	15.529	3.008	0.067	2.533	2.929	0.072	-35.070	4.930	0.035	-36.726	4.702	0.122	-33.898	3.497	0.076
Intercept + Developed	2	86.032	3.304	0.055	16.117	3.596	0.050	4.052	4.449	0.034	-35.312	4.688	0.039	-37.283	4.145	0.045	-33.401	3.994	0.059
Intercept	1	83.525	0.797*	0.193	13.528	1.007*	0.182	0.906	1.303*	0.162	-36.713	3.287	0.079	-38.544	2.884	0.085	-34.919	2.477	0.127
Fine-Scale Model Set																			
Intercept + Conductivity	2	85.975	2.450	0.097	16.034	2.506	0.095	3.337	2.431	0.076	-34.865	2.540	0.082	-36.721	3.634	0.095	-33.088	3.675	0.080
Intercept + Discharge	2	86.904	3.379	0.061	16.867	3.339	0.063	4.266	3.360	0.066	-34.210	3.195	0.059	-36.667	3.688	0.063	-32.230	4.532	0.052
Intercept + Dissolved Oxygen	2	86.879	3.354	0.061	16.854	3.326	0.063	4.132	3.226	0.070	-33.918	3.487	0.051	-36.177	4.177	0.063	-32.331	4.432	0.055
Intercept + Turbidity	2	86.030	2.505	0.094	15.771	2.243	0.109	2.010	1.104*	0.203	-36.852	0.553*	0.220	-40.354	0.000	0.109	-36.762	0.000	0.504
Intercept + Soil Temperature	2	85.053	1.528*	0.153	15.173	1.645*	0.147	2.901	1.995*	0.130	-37.405	0.000	0.291	-38.879	1.475*	0.147	-32.858	3.905	0.072
Intercept + Sediment Distribution	2	84.462	0.936*	0.206	14.661	1.133*	0.189	3.337	2.431	0.104	-35.108	2.297	0.092	-35.488	4.867	0.189	-31.500	5.262	0.036
Intercept	1	83.525	0.000	0.329	13.528	0.000	0.334	0.906	0.000	0.352	-36.713	0.691*	0.206	-38.544	1.810*	0.334	-34.919	1.843*	0.201
Management-Scale Model Set																			
Top Coarse-Scale Model	-	82.728	0.000	0.598	12.521	0.000	0.623	-0.396	0.000	0.657	-40.000	0.000	0.682	-41.428	0.000	0.549	-37.396	0.000	0.495
Top Fine-Scale Model	-	-	-	-	-	-	-	-	-	-	-37.405	2.595	0.186	-40.354	1.074*	0.321	-36.762	0.634*	0.361
Intercept	1	83.525	0.797*	0.412	13.528	1.007*	0.377	0.906	1.303*	0.343	-36.713	3.287	0.132	-38.544	2.884	0.130	-34.919	2.477	0.143