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Cover Photograph: A female Southern Two-lined Salamander (*Eurycea cirrigera*) with a clutch of eggs. Photograph by Todd W. Pierson.

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Abstract – Urbanization alters many aspects of stream ecosystems, and its effects upon wildlife will likely increase as more watersheds become developed. This may be particularly true for species with complex life histories, which could be vulnerable in different life stages. *Eurycea cirrigera* (Green) (Southern Two-lined Salamanders) are common members of many stream communities in the southeastern United States, and they prefer to nest in cobble with little sedimentation—a microhabitat that is threatened by stream degradation. We collected data on the nesting ecology of this amphibian species in urban streams in Atlanta, Georgia, to evaluate microhabitat availability, nest-site selection, and the influence of impervious surface cover—a proxy for urbanization—upon nesting behaviors and life history parameters. We confirmed that these salamanders preferentially nest in shallow riffles with cobble, and we found higher embeddedness (i.e., the percentage of coarse substrate buried in or surrounded by fine substrate) and lower nest density in streams with higher impervious surface cover. We also found preliminary evidence for a small, positive effect of impervious surface cover on female body size—which itself is predictive of clutch size. Together, these results add to our understanding of how urbanization-driven changes in substrate and other habitat characteristics can influence the life history of stream salamanders.

Introduction

Urban sprawl in the southeastern United States is projected to more than double in the next several decades (Terando et al. 2014). As of 2009, 8% of small streams by length in the Piedmont ecoregion were found in watersheds with predominantly urban land use; by 2060, this number is expected to triple, jeopardizing the health of over 20,000 stream kilometers (Van Metre et al. 2019). Urbanization can have profound consequences in stream ecosystems, including the burial of small streams; changes in temperature, nutrients, and pollutant concentrations; and changes in the frequency and intensity of floods (e.g., Espey et al. 1966, Paul and Meyer 2001, Walsh et al. 2005). Changes that result in stream degradation often drive declines in the biodiversity and abundance of native flora and fauna (McKinney and Lockwood 1999, McKinney 2002, Shochat et al. 2006, Van Metre et al. 2019).

One ecologically important taxon that is threatened by stream degradation is salamanders, which can be the most abundant vertebrates in stream and forest ecosystems and provide a link between aquatic and terrestrial food webs (e.g., Davic and Welsh 2004). In the southeastern United States, stream salamander communities are dominated in abundance and diversity by the lungless salamanders of the family Plethodontidae. Within these communities, *Eurycea cirrigera* (Green) (Southern Two-lined Salamanders) are quite resilient to environmental changes and are often found in degraded streams from which other species have disappeared (Barrett and Guyer 2008, Rittenburg 2023). Many populations of this species (and its close relatives in the larger *Eurycea bislineata* [Green] [Two-lined Salamander] species complex) in urban streams are characterized by lower abundance (Wilson and Dorcas 2003, Miller et al. 2007, Price et al. 2011, Macklem et al. 2020) but faster growth

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and metamorphosis (Barrett et al. 2010a, Murphy et al. 2016, Rittenburg and Pierson 2024) than populations in rural or less-urbanized streams, although support for these trends is not universal (Rizzo et al. 2016). One possible mechanism through which urbanization might influence these ecological and life history characteristics is the loss of microhabitat complexity due to increased sedimentation and embeddedness of substrate—changes that are associated with decreased abundance in various stream salamanders (Orser and Shure 1972, Lowe and Bolger 2002, Smith and Grossman 2003).

Because Southern Two-lined Salamanders have a complex life history, it is important to consider the impacts of urbanization upon all life stages (Scheffers and Paszkowski 2012, Barrett and Price 2014). Females typically nest by attaching eggs in a single layer to the bottom of a cover object, preferentially in shallow water with cobble substrate (Guy et al. 2004, Oswald et al. 2015). Furthermore, females often tend nests—which are sometimes laid communally with those from other females (e.g., Pierson and Bayona-Vásquez 2017)—and the frequency of nest attendance and communal nesting may vary with urbanization (as estimated by time since development and forest cover) in a close relative (Macklem et al. 2022). Here, we evaluated microhabitat availability, nest-site selection, and the influence of urbanization upon nesting behaviors and life history characteristics of Southern Two-lined Salamanders in Atlanta, Georgia.

Materials and Methods

Field-site description

We collected data from the same sites sampled in Rittenburg and Pierson (2024). In brief, these included 14 streams—found within public parks, private property, and golf courses—in the Peachtree Creek watershed in metro Atlanta, Georgia, USA. This watershed covers 240 km^2, and as of 2011, it was 83% developed with 32% impervious surface cover (U.S. Geological Survey [USGS] 2019).

Field methods and data collection

We visited each stream between 22 January 2022 and 04 February 2022. At each stream, we returned to the transects delimited by Rittenburg and Pierson (2024), who haphazardly selected the location of these 10 x 1 m transects, requiring only that they contain at least one riffle and follow the bank. However, we expanded our search effort at each stream to a larger 30 x 1 m stream transect that included within it the same 10 x 1 m transect delineated in Rittenburg and Pierson (2024). Within each 30 x 1 m transect, we started downstream and overturned all cover objects (e.g., rocks and logs) to search for nests and adult Southern Two-lined Salamanders. When we discovered a nest, we quickly took a photograph of the nest with a smartphone and attempted to capture any adult associated with it. We then replaced the cover object with the nest to its original orientation in the water. Following the capture of an adult, we placed the salamander in an 11 x 18 x 5.75 cm rectangular plastic container with an approximately 12.5 x 9 cm ColorChecker Passport Photo color palette standard (MSCCPPCC0319; X-Rite Inc.; MI, USA) and approximately 3 cm of stream water. Again using a smartphone, we took a photograph of the salamander from the dorsal view, making sure to the best of our ability that the container was level, glare was minimal, the entire color palette and salamander were visible, and the plane of the camera lens was parallel to the salamander. In the container or in a plastic bag, we checked for primary and secondary sexual characters (e.g., yolked ova in females, and the presence of cirri, mental glands, and/or hypertrophied jaw musculature in males) and noted the sex of each salamander; when we could not discern sex, we recorded “unknown”. After data collection, we immediately returned each salamander to the rock under which it was found. Following the search of each standardized transect, we opportunistically searched adjacent stream reaches for additional nests and salamanders to maximize our sample size for analyses that did not depend upon a standardized transect.

We collected stream habitat data from 25 random points within each 30 x 1 m transect (hereafter "random points") and from all nests. To do this, we constructed a 0.5 x 0.5 m PVC square quadrat, placed it in the stream, and used it to visually estimate the percent coverage of substrate type (i.e., inorganic, wood, vegetative debris, or artificial debris [e.g., trash or concrete]), percent coverage of substrate size (i.e., silt, sand, pebble, cobble, boulder, or bedrock; Wentworth 1922), and percent embeddedness within the quadrat (i.e., the percentage of coarse substrate buried in or surrounded by fine substrate; Smith and Grossman 2003). We noted whether each point was found within a riffle (i.e., relatively shallow with high stream velocity), run (i.e., intermediate in depth and velocity), or pool (i.e., deeper with low stream velocity) (as in Pierson et al. 2021) and measured stream depth. To determine where the 25 random points should be, we used a random number generator to determine a linear distance from the beginning of each transect. For nests, we placed the quadrat so that the nest was centered within it.

Measurements of clutch size and adult female size

To determine clutch size, two of us (LR and ED) manually counted eggs in the photographs of salamander nests after we had returned from the field so that the amount of time an adult salamander spent away from its nest could be minimized. If our counts differed, we reviewed the photographs together and reached a consensus. We adapted the methods outlined by Aragón-Sánchez et al. (2017) to approximate the snout-girdle length (SGL, the distance from the tip of the snout to the middle of the pelvic girdle) of adult female *E. cirrigera* from photographs using the ImageJ.JS online application v0.5.7 (Schneider et al. 2012, Ouyang et al. 2019). We used SGL instead of snout-vent length (SVL) because the location of the distal end of the vent is hard to approximate from photographs of the dorsal side of *Eurycea*. We used the 50 mm ruler on the color palette visible in each photo as a standard for measuring SGL.

Statistical analyses

For all statistical analyses, we used R v4.4.2 (R Core Team 2024). First, we evaluated whether nest sites were randomly distributed within streams by conducting a principal components analysis (PCA) on the characteristics of all stream points (i.e., nests and random points); this analysis included scaled measurements (z-scores) of substratum type, substratum size, depth, and embeddedness. We included all nests within the standardized transects, but we excluded all sampling points with missing data (n = 1 random point) for any of these parameters. To test whether nests and random points were differentiated across the first PC axis (PC1), we conducted a Welch's two-sample *t*-test to compare PC1 values between these two groups ($\alpha = 0.05$). We also evaluated whether nests were randomly distributed among stream habitats (i.e., riffles, runs, and pools) by arranging counts of quadrat survey points in a contingency table—with stream habitats as columns and point type (i.e., nest or random) as rows—and comparing the distribution of habitats between random points and nests with a chi-square test ($\alpha = 0.05$), excluding any points (n = 3 nests and 3 random points) that were missing these data.

Second, we evaluated whether degree of urbanization influenced the quality of available nesting habitat and the number of nests we observed. To do this, we used percent impervious surface cover (ISC) as calculated in Rittenburg and Pierson (2024); that study used Stream-

Stats v4.8.1 (USGS 2019), which derives ISC from watershed boundaries, digital elevation layers, and the National Land Cover Database. We then calculated the average embeddedness (i.e., the percentage of coarse substrate buried in or surrounded by fine substrate) for each stream, using only the values from the random points, and we summed the total number of nests found in each stream, counting only those found within the standardized transect. To evaluate whether urbanization alters the quality of nesting sites available, we modeled embeddedness as a function of ISC. Because both of these variables are bounded between 0% and 100%, we rescaled both to be between 0 and 1 and used a generalized additive model (GAM) with a beta error distribution and logit link function using the packages gam v1.22-5 (Hastie 2024) and mgcv v1.9-1 (Wood 2011). To evaluate whether the number of nests we observed was influenced by degree of urbanization, we modeled these nest counts as a function of ISC. We did this using a generalized linear model with a Poisson error distribution.

Third, we evaluated whether nesting behaviors (i.e., nest attendance and communal nesting) varied with degree of urbanization. To do this, we used all nests (i.e., even those from outside of the standardized transects), and for each stream, we calculated the proportion of nests that were tended (i.e., that had at least one adult with them) and the proportion of nests that were laid communally (i.e., under the same rock as another nest). In the case of communal nests, all were either discontiguous on the rock and/or at (subtly) different stages of development. We again rescaled variables to be between 0 and 1 and fit GAMs with beta error distributions using the methods described above.

Finally, we evaluated the relationship between urbanization, female body size, and clutch size. First, we calculated the mean female SGL for each stream, using all captures of mature females that we made throughout the study, and then fit a linear model of female SGL as a function of ISC. Next, we used data from non-communal nests in which a single female was unambiguously present (n = 30) to evaluate the relationship between female size and clutch size by fitting a linear model of clutch size as a function of female SGL. All data and code are available from Zenodo (https://doi.org/10.5281/zenodo.15553592)

Results

We located and collected data from a total of 92 nests (71 within transects, 21 opportunistically located nearby). In the PCA, the first axis (PC1) explained 23% of variation; random points were spread across the full range of PC1 values, while nests were clustered at lower PC1 values (Figure 1A). The loadings revealed that points with high PC1 values were deeper, had more sand and silt, and had higher embeddedness, while points with low PC1 values had more cobble (Figure 1B). Nests had lower PC1 scores (mean = −1.10 ± 0.85 [sd]) than random points (0.22 ± 1.69; $P < 0.001$). We found 45 nests in riffles, 17 nests in runs, and 6 nests in pools; in comparison, 116 random points were located in riffles, 162 in runs, and 68 in pools. Thus, nests were overrepresented in riffles (66% of nests) compared to the prevalence of riffles among random points (34%; $\chi^2 = 25.57$; $P < 0.001$). We found a positive relationship between ISC and embeddedness (coefficient [95% confidence interval] = 4.71 [0.94, 8.48]; $P = 0.01$; adjusted $R^2 = 0.16$), indicating that streams with higher ISC have higher average embeddedness (Figure 2A). We found a negative relationship between ISC and nest counts (coefficient [95% CI] = −0.04 [−0.07, −0.02]; $P < 0.001$; McFadden's pseudo $R^2 = 0.16$), indicating that streams with higher ISC had lower nest counts (Figure 2B).

Although it appeared that nest attendance decreased with ISC (Figure 3A), this relationship was not statistically significant (coefficient [95% CI] = −4.00 [−9.46, 1.46]; $P = 0.15$; adjusted $R^2 = 0.16$). Similarly, we found no relationship between ISC and communal

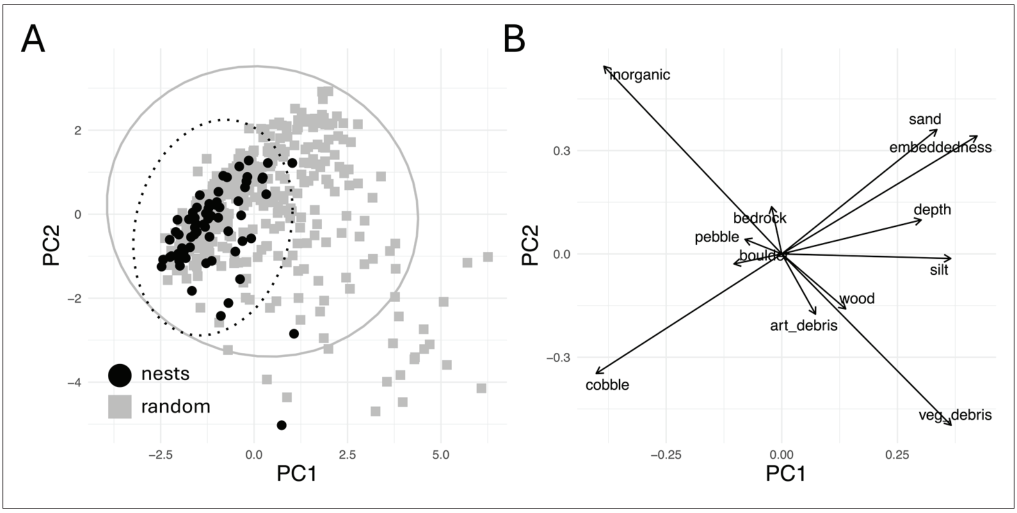

Figure 1. a) The first two axes from a principal components analysis (PCA) of Southern Two-lined Salamander nest microhabitat data from Atlanta, Georgia. Symbol shapes and colors indicate whether observations were from random points within stream transects (i.e., representative of total available habitat) or from nests. 95% confidence ellipses for random points and nests are shown with solid gray and dotted black lines, respectively. b) Loadings from the PCA in (a), showing that high scores on PC1 were associated with greater sand and silt, depth, and embeddedness, and that low scores were associated with greater cobble.

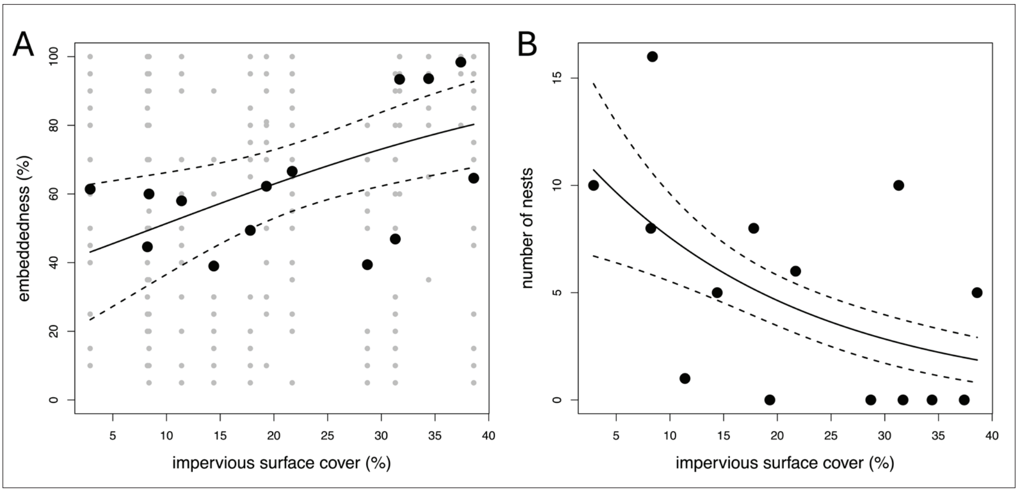

Figure 2. a) The relationship between percent impervious surface cover for a watershed and the percent embeddedness of random points within stream transects in Atlanta, Georgia. Large black points indicate averages per stream, from which the model was built. The solid black line shows the fitted model, and the dashed black lines indicate the 95% confidence interval. The smaller gray points indicate individual measurements from each stream, from which the averages were calculated. b) The relationship between percent impervious surface cover and the number of Southern Two-lined Salamander nests that we encountered in standardized 30 x 1 m stream transects. Points indicate counts from each stream, the solid line shows the fitted model, and the dashed black lines indicate the 95% confidence interval.

nesting (coefficient [95% CI] = −0.94 [−6.55, 4.68]; P = 0.74; adjusted R^2 = −0.10; Figure 3B). We found a small positive relationship between ISC and female size (coefficient [95% CI] = 0.05 [0.01, 0.08]; P = 0.01; adjusted R^2 = 0.42); that is, for every 20% increase in ISC, we estimated a 1 mm increase in average female SGL (i.e., ~3% of mean SGL; Figure 4A). We also found a positive relationship between female size and clutch size (coefficient [95% CI] = 5.41 [2.76, 8.05]; $P < 0.001$; adjusted R^2 = 0.36); for every increase of 1 mm in SGL, we estimated an increase in clutch size of approximately 5 eggs (Figure 4B).

Discussion

We found clear evidence that Southern Two-lined Salamanders select nesting sites in shallow riffles with cobble and low embeddedness. This is consistent with previous work also conducted in the Georgia Piedmont, but in a less urbanized environment (Guy et al. 2004). This microhabitat selection may indicate a preference for environments with low sedimentation and high oxygen availability, facilitating gas exchange for developing embryos (Mills and Barnhart 1999). Alternatively, it could reflect biotic factors like competition with other salamander species or the relative risks of predation in each habitat. In nearby streams where Southern Two-lined Salamanders are syntopic with *Eurycea* cf. *wilderae* Dunn (Blue Ridge Two-lined Salamander), the large majority of larvae collected from pools are Southern Two-lined Salamanders, while the large majority of larvae in riffles are Blue Ridge Two-lined Salamanders—a pattern that may be explained by character displacement in nest-site selection (Pierson et al. 2021).

Consistent with our expectations, streams with higher ISC had higher embeddedness. For example, our model estimated approximately 45% embeddedness for streams with 5% ISC and 77% embeddedness for streams with 35% ISC (Figure 2A). These results are concordant with broader evidence for increased sedimentation in urban streams—especially in streams with continuing disturbance and urbanization (e.g., Finkenbine et al. 2000, Paul and Meyer 2001). A few caveats and limitations of our study are worth mentioning. First, we chose to use ISC as a proxy measurement for urbanization. Although this approach is very common in urban ecology (e.g., Arnold and Gibbons 1996, Paul and Meyer 2001), it may not perfectly capture all the ways in which urbanization can alter stream environments (e.g., changes in pollutants or productivity), and our broader conclusions about urbanization should be interpreted with caution. Second, although we selected the placement of our stream transects haphazardly and interpret them as representative of the full streams, it is possible that this is not true—a potential bias perhaps amplified by practical need to sample within permitted areas (e.g., parks).

We also expected that nest density would be lower in more urbanized streams, and our results supported this prediction. Indeed, our model estimated nest density approximately five times higher in streams with 5% ISC than in streams with 35% ISC (Figure 2B). Although we interpret this as a logical consequence of the reduction in suitable nesting habitat, it could also reflect a lower overall population abundance—a variable that we did not measure, but which would be consistent with previous studies (Wilson and Dorcas 2003, Miller et al. 2007, Price et al. 2011, Macklem et al. 2020). Alternatively, our results could be misleading if confounded by differences in nesting phenology (e.g., if our sampling window was too early to detect nests in more urban streams). However, we view this as unlikely. Rittenburg and Pierson (2024) inferred a positive (but statistically insignificant) effect of ISC on stream temperature at these same sites, and across a broad geography, oviposition occurs earlier in warmer streams (Pierson et al. 2023). Thus, if there were such a bias, we would expect it to be in the opposite direction of our results.

We found no conclusive evidence for a change in nest attendance across an urbanization gradient. In Connecticut, Macklem et al. (2022) found that nest attendance in *Eurycea*

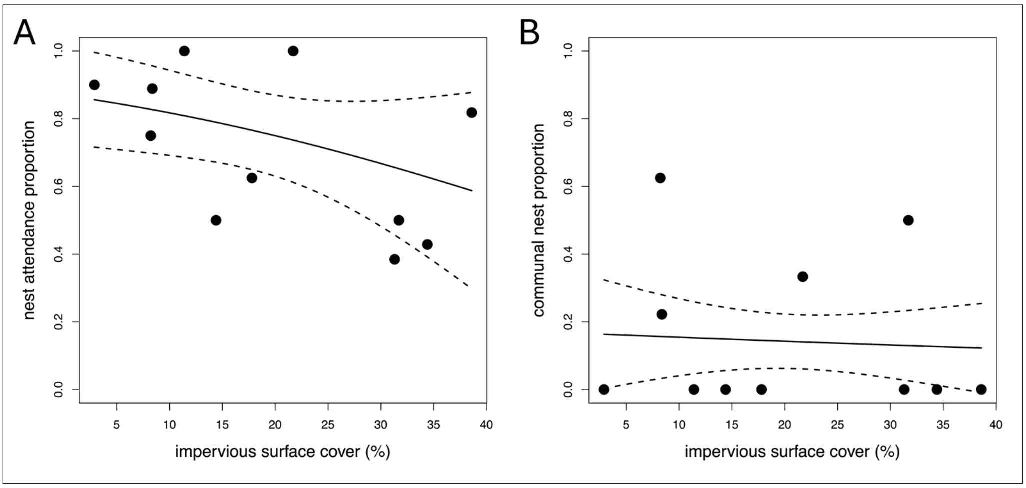

Figure 3. a) The relationship between percent impervious surface cover and the proportion of Southern Two-lined Salamander nests that had at least one adult found with them. b) The relationship between percent impervious surface cover and the proportion of Southern Two-lined Salamander nests that were laid communally. In both, points show proportions from individual streams, the solid black line shows the fitted model, and the dashed black lines indicate the 95% confidence interval.

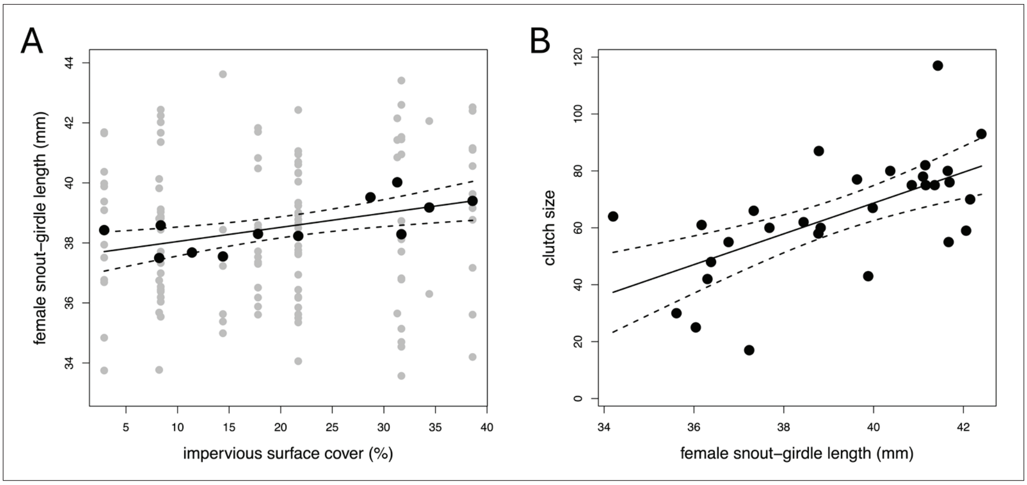

Figure 4. a) The relationship between percent impervious surface cover and the snout–girdle length (SGL) of adult female Southern Two-lined Salamanders. Large black points indicate averages per stream, from which the model was built. The solid black line shows the fitted model, and the dashed black lines indicate the 95% confidence interval. The smaller gray points indicate measurements of individual females, from which the averages were calculated. b) The relationship between female SGL and clutch size. The solid black line shows the fitted model, and the dashed black lines indicate the 95% confidence interval.

bislineata (Green) (Northern Two-lined Salamander) decreased with urbanization, with the proportion of clutches attended ranging between 24% and 80% among streams. We observed a similarly large range of values, but our negative point estimate of the relationship between ISC and nest attendance probability was not statistically significant. However, we caution that our sample size was small (n = 11 streams with nests), and our results may still be consistent with this previous study. Similarly, we found no relationship between ISC and the probability of communal nesting, although Macklem et al. (2022) did. This relationship was unexpected in that previous study, which assumed that any nest with >60 eggs was communal (Macklem et al. 2022). We are therefore hesitant to draw strong conclusions from the results of either study.

Southern Two-lined Salamanders are notable for their persistence in many urban environments. In our broader fieldwork (i.e., beyond the surveys described in this study), we have observed their near ubiquity in permanent streams in Atlanta—perhaps missing only from streams entirely lacking loose substrate (e.g., channelized streams fully encased in concrete), in which mortality following scouring events caused by heavy rainfall is likely very high (Barrett et al. 2010b). Although many factors likely help explain their persistence in urban environments, one intriguing possibility is the existence of compensatory life history responses. For example, Cayuela et al. (2022) demonstrated that although *Bombina* frogs have shorter lifespans in urban environments, they have higher reproductive rates—with the magnitude of this "compensatory recruitment" sufficient to overcome the lower adult survival. Several studies have now documented higher growth and developmental rates in urban salamanders (Barrett et al. 2010a, Murphy et al. 2016, Rittenburg and Pierson 2024), and here, we provide preliminary evidence for a very modest increase in adult female size in response to increased ISC, a proxy for urbanization. Because female size is predictive of clutch size, this could lead to higher per-capita reproductive rates. We emphasize that our results are far too preliminary to conclude that compensatory recruitment exists in these populations, but we encourage future researchers to explore these ideas.

In conclusion, our results confirm that Southern Two-lined Salamanders preferentially nest in shallow riffles with cobble substrate. These results also demonstrate that embeddedness is higher and nest density is lower in streams with higher impervious surface cover (ISC). We found no conclusive evidence for a relationship between ISC and nest attendance or communal nesting, but we found preliminary evidence for a small influence of ISC on female body size (female body size itself is predictive of clutch size). Together, these results add to our understanding of how potential measures of urbanization can influence the life history of stream salamanders.

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Literature Cited

Aragón-Sánchez, J., Y. Quintana-Marrero, C. Aragón-Hernández, and M.J. Hernández-Herero. 2017. ImageJ: A free, easy, and reliable method to measure leg ulcers using digital pictures. International Journal of Lower Extremity Wounds 16:269–273.

Arnold Jr., C.L., and C.J. Gibbons. 1996. Impervious surface coverage: the emergence of a key environmental indicator. Journal of the American Planning Association 62:243–258.

Barrett, K., and C. Guyer. 2008. Differential responses of amphibians and reptiles in riparian and stream habitats to land use disturbances in western Georgia, USA. Biological Conservation 141:2290–2300.

Barrett, K., and S.J. Price. 2014. Urbanization and stream salamanders: A review, conservation options, and research needs. Freshwater Science 33:927–940.

Barrett, K., B.S. Helms, S.T. Samoray, and C. Guyer. 2010a. Growth patterns of a stream vertebrate differ between urban and forested catchments. Freshwater Biology 55:1628–1635.

Barrett, K., B.S. Helms, C. Guyer, and J.E. Schoonover. 2010b. Linking process to pattern: Causes of stream-breeding amphibian decline in urbanized watersheds. Biological Conservation 143:1998–2005.

Cayuela, H., B. Monod-Broca, J.-F. Lemaître, A. Besnard, J.M.W. Gippet, B.R. Schmidt, A. Romano, T. Hertach, C. Angelini, S. Canessa, G. Rosa, L. Vignoli, A. Venchi, M. Carafa, F. Giachi, A. Tiberi, A.M. Hantzschmann, U. Sinsch, E. Tournier, E. Bonnaire, G. Gollmann, B. Gollmann, A. Spitzen-van der Sluijs, H. Buschmann, T. Kinet, A. Laudelout, R. Fonters, Y. Bunz, M. Corail, C. Biancardi, A.R. Di Cerbo, D. Langlois, J.-M. Thirion, L. Bernard, E. Boussiquault, F. Doré, T. Leclerc, N. Enderlin, F. Laurenceau, L. Morin, M. Skrzyniarz, M. Barrioz, Y. Morizet, S.S. Cruickshank, J. Pichenot, A. Maletzky, T. Delsinne, D. Henseler, D. Aumaître, M. Gailledrat, J. Moquet, R. Veen, P. Krijnen, L. Rivière, M. Trenti, S. Endrizzi, P. Pedrini, M. Biaggini, S. Vanni, D. Dudgeon, J.-M. Gaillard, and J.-P. Léna. 2022. Compensatory recruitment allows amphibian population persistence in anthropogenic habitats. Proceedings of the National Academy of Sciences 119:e2206805119.

Davic, R.D., and H.H. Welsh Jr. 2004. On the ecological roles of salamanders. Annual Review of Ecology, Evolution, and Systematics 35:405–434.

Espey, W.H. Jr., C.W. Morgan, and F.D. Masch. 1966. Study of some effects of urbanization on storm runoff from a small watershed. University of Texas, Center for Research in Water Resources Report 44D 07–6501 CRWR-2. 110 p.

Finkenbine, J.K., J.W. Atwater, and D.S. Mavnic. 2000. Stream health after urbanization. Journal of the American Water Resources Association 36:1149–1160.

Guy, C.J., R.E. Ratajczak, and G.D. Grossman. 2004. Nest-site selection by Southern Two-lined Salamanders (*Eurycea cirrigera*) in the Georgia Piedmont. Southeastern Naturalist 3:75–88.

Hastie, T. 2024. gam: Generalized Additive Models. R package version 1.22-5. Available online at https://CRAN.R-project.org/package=gam.

Lowe, W.H., and D.T. Bolger. 2002. Local and landscape□scale predictors of salamander abundance in New Hampshire headwater streams. Conservation Biology 16:183–193.

Macklem, D.C., A.M. Helton, M.W. Tingley, J.M. Dickson, and T.A. Rittenhouse. 2020. Stream salamander persistence influenced by the interaction between exurban housing age and development. Urban Ecosystems 23:117–132.

Macklem, D.C., J.M. Dickson, and T.A. Rittenhouse. 2022. Reproduction of *Eurycea bislineata* within watersheds with exurban development. Herpetological Conservation and Biology 17:229–248.

McKinney, M.L. 2002. Urbanization, biodiversity, and conservation. BioScience 52:883–890.

McKinney, M.L., and J.L. Lockwood. 1999. Biotic homogenization: A few winners replacing many losers in the next mass extinction. Trends in Ecology & Evolution 14:450–453.

Miller, J.E., G.R. Hess, and C.E. Moorman. 2007. Southern Two-lined Salamanders in urbanizing watersheds. Urban Ecosystems 10:73–85.

Mills, N.E., and M.C. Barnhart. 1999. Effects of hypoxia on embryonic development in two *Ambystoma* and two *Rana* species. Physiological and Biochemical Zoology 72:179–188.

Murphy, M.O., M. Agha, T.A. Maigret, S.J. Price, and M.E. Dorcas. 2016. The effects of urbanization on body size of larval stream salamanders. Urban Ecosystems 19:275–286.

Orser, P.N., and D.J. Shure. 1972. Effects of urbanization on the salamander *Desmognathus fuscus fuscus*. Ecology 53:1148–1154.

Oswald, H.R., J.L. Waldron, S.M. Welch, S.H. Bennett, and T.A. Mousseau. 2015. Environmental effects on Southern Two-lined Salamander (*Eurycea cirrigera*) nest-site selection. Copeia 103:7–13.

Ouyang, W., F. Mueller, M. Hjelmare, E. Lundberg, and C. Zimmer. 2019. ImJoy: An open-source computational platform for the deep learning era. Nature Methods 16:1199–1200.

Paul, M.J., and J.L. Meyer. 2001. Streams in the urban landscape. Annual Review of Ecology and Systematics 32:333–365.

Pierson, T.W., and N.J. Bayona-Vásquez. 2017. *Eurycea cirrigera* (Southern Two-lined Salamander). Communal Nesting. Herpetological Review 50:544.

Pierson, T.W., B.M. Fitzpatrick, and C.D. Camp. 2021. Genetic data reveal fine-scale ecological segregation between larval plethodontid salamanders in replicate contact zones. Evolutionary Ecology 35:309–322.

Pierson, T.W., J. Blake-Sinclair, L.T. Rittenburg, and Y. Kalki. 2023. Geographic variation in the reproductive phenology of a widespread amphibian. Journal of Herpetology 57:125–132.

Price, S.J., R.A. Browne, and M.E. Dorcas. 2011. Evaluating the effects of urbanisation on salamander abundances using a before-after control-impact design. Freshwater Biology 57:193–203.

R Core Team. 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available online at https://www.R-project.org/.

Rittenburg, L. 2023. Variation in salamander life history and community composition across an urban gradient in Atlanta, Georgia, USA. M.S. Thesis.

Rittenburg, L.T., and T.W. Pierson. 2024. Stream temperature shapes the larval life history of an urban plethodontid salamander. Herpetologica.

Rizzo, A.A., R.L. Raesly, and R.R. Hilderbrand. 2016. Stream salamander responses to varying degrees of urbanization within Maryland's piedmont physiographic province. Urban Ecosystems 19:397–413.

Scheffers, B.R., and C.A. Paszkowski. 2012. The effects of urbanization on North American amphibian species: Identifying new directions for urban conservation. Urban Ecosystems 15:133–147.

Schneider, C.A., W.S.Rasband, and K.W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9:671–675.

Shochat, E., P.S. Warren, S.H. Faeth, N.E. McIntyre, and D. Hope. 2006. From patterns to emerging processes in mechanistic urban ecology. Trends in Ecology & Evolution 21:186–191.

Smith, S., and G.D. Grossman. 2003. Stream microhabitat use by larval southern two-lined salamanders (*Eurycea cirrigera*) in the Georgia piedmont. Copeia 2003:531–543.

Terando, A.J., J. Costanza, C. Belyea, R.R. Dunn, A. McKerrow, and J.A. Collazo. 2014. The southern megalopolis: Using the past to predict the future of urban sprawl in the Southeast U.S. PLoS ONE 9:e102261.

U.S. Geological Survey. 2019. The StreamStats program. Available online at http://streamstats.usgs.gov.

Van Metre, P.C., I.R. Waite, S. Qi, B. Mahler, A. Terando, M. Wieczorek, M.R. Meador, P.M. Bradley, C.A. Journey, T.S. Schmidt, and D. Carlisle. 2019. Projected urban growth in the southeastern USA puts small streams at risk. PLoS ONE 14:e0222714.

Walsh, C.J., A.H. Roy, J.W. Feminella, P.D. Cottingham, P.M. Groffman, and R.P. Morgan. 2005. The urban stream syndrome: Current knowledge and the search for a cure. Journal of the North American Benthological Society 24:706–723.

Wentworth, C.K. 1922. A scale of grade and class terms for clastic sediments. The Journal of Geology 30:377–392.

Wilson, J.D., and M.E. Dorcas. 2003. Effects of habitat disturbance on stream salamanders: Implications for buffer zones and watershed management. Conservation Biology 17:763–771.

Wood, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society (B) 73:3–36.