

Growth patterns of a stream vertebrate differ between urban and forested catchments

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SUMMARY

1. Urban development results in the decline of amphibian density and species richness. A logical next step towards understanding why urbanisation negatively impacts amphibians is to track species-specific demographic responses to urbanisation.
2. We monitored growth of two-lined salamander (*Eurycea cirrigera* Green) larvae over two complete cohorts (2006 and 2007) in nine western Georgia, U.S.A. streams.
3. We found that salamanders in streams surrounded by urbanised and developing catchments hatched at the same size as their reference-stream counterparts, but achieved larger sizes within the first few months of growth. We evaluated the effect of four variables that correlate with the urban-forest gradient and found that elevated temperatures in the urban environment, coupled with decreased intraspecific competition because of lower survivorship in these same habitats, were two of the most likely explanations for increased growth rates.
4. Such an increase in growth of surviving larvae may maintain population viability in urban areas where it has been shown survival is difficult because of increased in-channel flow during flood events. Because larvae that do survive in urban streams undergo metamorphosis at large sizes, they may recoup a component of fitness (i.e. increased adult survivorship and reproduction) through growth.

Keywords: amphibian, competition, growth rate, predator avoidance, resource availability

Introduction

A global decline in amphibian species richness has brought considerable attention to the need for studies that enhance our understanding of which species are imperilled and what factors put these species at risk (Stuart *et al.*, 2004; Brito, 2008). Habitat loss ranks high on the list of contributors to the loss of amphibian species (Cushman, 2006), and urbanisation, in particular, has been cited as a key threat to this group (Hamer & McDonnell, 2008). To date, many studies have noted an overall decline in amphibian species

richness or in abundances of species examined across areas of increasing urbanisation (Willson & Dorcas, 2003; Miller, Hess & Moorman, 2007; Barrett & Guyer, 2008). Documentation of such trends is vital; however, in a review on the impact of urban areas on amphibians, Hamer & McDonnell (2008) suggest biotic consequences of urbanisation should not be assessed solely by composite community measures such as diversity. Likewise, Cushman (2006) suggests an urgent need for noting species-specific responses to fragmentation, which can offer key insights into conservation strategies applicable to a particular species.

Among amphibians (particularly larval stages), differential growth in body size of individuals in urban and forested habitats is a species-specific response that could prove important to evaluate for

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some species. Growth differences along the urban-forest gradient, as with other habitat gradients, may arise because of differential resource availability (Bernardo & Agosta, 2003) or habitat quality (Gillespie, 2002; Johnson & Wallace, 2005; Peterson, Peterson & Mendonça, 2008). For example, Johnson & Wallace (2005) found that *Eurycea wilderae* larvae had reduced growth rates, density and biomass after leaf litter was experimentally reduced in streams. Their results strongly indicated that habitat alterations can induce bottom-up impacts on higher trophic levels. In addition to resource availability and habitat quality, several studies have noted the importance of temperature on amphibian larval growth (Newman, 1998; Alvarez & Nicieza, 2002; Gillooly *et al.*, 2002). This factor has particular relevance in urban habitats, where stream temperatures may be elevated because of heat pulses from run off during rain events (Pluhowski, 1970) and decreased riparian vegetation, both of which may elevate stream temperatures in urban habitats above regional norms (Pluhowski, 1970; Paul & Meyer, 2001). Warmer stream temperatures in urbanised habitats could lead to faster larval growth (Voss, 1993). Finally, presence of predators reduce larval growth (Currens, Liss & Hoffman, 2007; Collier *et al.*, 2008), a response that is thought to represent a trade-off between foraging time and predator avoidance. If predator density is altered in urban streams, then larvae in these streams would be expected to exhibit correspondingly altered growth rates.

Two previous studies (Barrett & Guyer, 2008; Barrett, 2009) suggest the two-lined salamander (*Eurycea cirrigera* Green) would be well suited for assessing urban land use effects on growth of a stream-dwelling species. Barrett & Guyer (2008) indicated that salamanders and frogs were particularly sensitive to urban development. The two-lined salamander was one of the few amphibian species persisting in urban habitats. A second study (Barrett, 2009) demonstrated two-lined salamanders hatch in urban streams in equal or higher numbers than conspecifics in reference (forested) streams, but larval survivorship appears to decline more rapidly in urban environments than forested ones. These data suggest any negative effects of urbanisation are not detectable via reproductive output of the terrestrial adult, but instead are manifest within the larval stage. While two-lined salamanders may persist more effectively in

urban environments than many amphibian species, they must overcome decreased survival to metamorphosis in urban streams to do so. If factors associated with growth lead to larger size at metamorphosis for larvae that can survive in urban areas, then one component of overall fitness (higher reproduction resulting from larger size) might offset effects of another, allowing persistence of two-lined salamanders in urban habitats (Semlitsch, Scott & Pechmann, 1988; Beck & Congdon, 1999). Conversely, if there is no such compensatory growth, then the probable decrease in reproduction coupled with decreased survivorship would represent overall reduced fitness in urban habitats.

We used data from nine streams representing varying levels of urbanisation to assess growth in larval salamanders. Specifically, we compared growth of two-lined salamander larvae between urban and forested streams. In addition, we evaluated specific mechanisms that could alter growth by testing four select hypotheses derived from the literature (Table 1). First, we predicted a positive correlation between temperature and growth, and we anticipated temperatures to be highest in urban streams. Second, we predicted that the lower survivorship in urban streams would allow for increased growth of hatchlings in a density-dependent manner. Third, we predicted that growth would increase with prey availability, which increases with urbanisation. Finally, we evaluated the hypothesis that increased predator density in urban streams could decrease growth by reducing foraging. We use data from fish density surveys and data on foraging success to test this hypothesis.

Methods

We collected *E. cirrigera* larvae from nine-second- or third-order streams in western Georgia, U.S.A. (Table 2). Stream order was determined by examining visible drainages on 1-m resolution maps of the study area. Streams and their surrounding catchments were categorised as either reference, urban or developing ($n = 3$ for each category). These streams were categorised based on a 1-m resolution land cover analysis of the entire catchments for each stream. Reference sites were those sites with at least 75% of the overall land cover as forest, the urban land cover category contained at least 25% of the catchment as impervious

Table 1 Hypotheses relating to factors effecting increased salamander growth in urbanised catchments, and results from linear regressions used to evaluate each hypothesis

Hypothesis	Predictor variable Response variable	N	Slope	r ²	P
Elevated temperatures in urban environments lead to increased growth in these habitats	Median temperature (April–July 2007) Hatchling growth (2007 cohort)	5	0.87	0.53	0.17
Low survivorship of larvae in urban streams results in less inter-cohort competition for hatchlings emerging during the spring	06 cohort density of pre-metamorphs Hatchling growth (2007 cohort)	7	−0.43	0.31	0.19
Increased prey availability increases growth of hatchlings	Aquatic invertebrate density Hatchling growth (2006 cohort)	7	5.14	0.25	0.31
Increased prey availability increases growth of hatchlings	Aquatic invertebrate density Hatchling growth (2007 cohort)	6	1.98	0.22	0.29
High predator density reduces larval foraging rate, which results in slower growth	Centrarchidae density Hatchling growth (2006)	7	8.27	0.57	0.08
High predator density reduces larval foraging rate, which results in slower growth	Centrarchidae density Hatchling growth (2007)	6	2.38	0.35	0.16
High predator density reduces larval foraging rate, which results in less food consumed	Centrarchidae density Number of prey items in stomach	9	−1.43	0.04	0.60

Table 2 Land cover and physical characteristics of study catchments

Site	Catchment size (km ²)	IS	Pasture	Forest	LU/LC
SB1	20.1	2	20	73	Developing
SB2	6.3	3	20	73	Developing
SB4	26.6	3	28	64	Developing
BLN	3.6	1	19	76	Forest
MO	9	2	13	81	Forest
MU3	10.4	2	15	78	Forest
BU1	25.5	40	23	34	Urban
BU2	24.7	25	25	46	Urban
RB	3.7	30	27	39	Urban

IS, % impervious surface cover; forest, % total forest cover; LU/LC, dominant land cover in catchment (defined in Methods).

surface, and finally the developing category referred to streams selected to represent catchments with recent low-density residential development (average impervious surface = 3%). Developing sites were in Harris County, Georgia, one of the fastest growing counties in the United States (Lockaby *et al.*, 2005). Detailed methods of the spatial analysis and quantitative justification for land use categories are detailed in Lockaby *et al.* (2005) and Barrett & Guyer (2008).

Salamander and environmental sampling

Animals were collected from each stream during density surveys (separate study) conducted along

five, 15-m transects distributed in a stratified random manner along a 500-m representative stream reach. We used a small 15-cm wide aquarium net to scoop salamanders seen on the surface of the stream bed as well as to capture salamanders exposed from under rocky cover or root masses along the bank. We sampled each transect five consecutive times or until three consecutive passes yielded no animals. Animals caught on each pass were placed in a small plastic bag until all passes were complete. Captured animals were measured [snout-vent length (SVL) and total length (TL)] and weighed prior to release. These surveys were conducted at five regularly spaced intervals throughout the duration of both the 2006 and 2007 cohort. Sampling of a cohort of larvae began in spring (April), just after hatching from eggs, and continued through summer (July), autumn (October), winter (January) and the following spring (April of the next year, when larvae were of pre-metamorphic size). During spring and summer sampling periods, representatives of two cohorts often were captured. We were able to separate individuals into respective cohorts for analyses by visual inspection of SVL histograms (Bruce, 1995). Salamander densities were estimated using the variable probability removal estimator (Pollock & Otto, 1983) option of the Removal task in Program Capture (software available online at <http://www.mbr-pwrc.usgs.gov/software.html>). During each season, we attempted to capture, euthanise and preserve at least five individuals from

each stream for gut content analysis, which we used to characterise the influence of food availability on growth rate (details in the following paragraphs).

We collected temperature data from January 2007 through June 2008 using OnSet Hobo H8 temperature data loggers (Onset Computer Corporation, Bourne, MA, U.S.A.). One logger was placed in each study stream (5–8 cm under the water's surface), and we programmed loggers to record at 1-h intervals.

Resource availability and predator presence also are known to influence salamander growth, so we measured both aquatic invertebrate density and the density of fishes in the family Centrarchidae, the most likely predators of two-lined salamander larvae (Hecnar & M'Closkey, 1997). We quantified benthic macroinvertebrates and fishes in three pools and three runs per stream reach during summer (September), winter (February) and spring (April–May) samples during 2003 and 2004. These data predate our salamander sampling, so the results of our analysis must be viewed cautiously. Nevertheless, they were the most recent resource and predator data available, and we felt they provided an adequate opportunity to evaluate our hypotheses.

For macroinvertebrates, we used a Surber sampler (250- μ m mesh; 0.093-m² sampling area), consolidating multiple Surber collections in each habitat (three for pools, four for runs), resulting in a 0.27- and 0.36-m² sample from each pool and run, respectively (1.89 m² total area sampled for each study reach per stream and season). We identified macroinvertebrates to lowest possible taxonomic level, usually genus. We sampled fishes in each habitat to depletion with block nets, a backpack electroshocker (Smith-Root LR-24; Vancouver, WA, U.S.A.) and seines. We identified and measured TL of all fishes captured and returned them near the point of collection, except for voucher specimens of each species, which were deposited in the Auburn University Museum Fish Collection.

Gut content surveys

To determine the relative foraging success of larvae among streams and land cover categories, we examined the gut contents of two to five individuals from each stream during the summer 2006 and spring and summer of 2007. Larvae were euthanised shortly after capture (typically within 5 h) with MS-222 and then frozen until they could be examined. To determine

gut contents of specimens, we made a sagittal incision along the ventral midline of each individual and subsequently opened the digestive tract so that contents could be removed by flushing with 70% ethanol (Bardwell, Ritzi & Parkhurst, 2007). We sorted prey items under a dissecting scope, counted individuals and identified them to the lowest possible taxonomic level (typically order).

Data analysis

Our primary interest was in determining if larvae differed in size among land cover categories. To evaluate this, we compared the change in SVL within land cover categories across seasons. It is possible that the differences in size, if observed among land use categories, could relate directly to differential survivorship. We hypothesise two mechanisms by which differential survivorship could occur. First, intense flood events in urban streams (Schoonover, Lockaby & Helms, 2006) could selectively wash the smallest larvae downstream. Second, fish, which are gape-limited predators, are known to actively select prey based in part on a trade-off between handling time and energetic reward (Mittelbach, 1981). During the spring, newly hatched fish are denser in the urban streams (Helms, 2008). As a result, it is possible that the dense assemblage of gape-limited predators could be actively selecting the smallest hatchlings in urban streams. To evaluate these possibilities, we compared the variances in urban streams between spring and summer sampling periods for 2006 and 2007 cohorts. We hypothesised that differential survival in urban streams would yield lower variances during summer samples relative to spring samples of newly hatched individuals. We found no significant difference between variances for either the 2006 (*F*-test, *P* = 0.56) or 2007 (*F*-test, *P* = 0.19) cohort. As a result of this finding, we conclude that changes in size from one season the next in these populations represent growth and not differential survival based on larval size.

We compared mean SVL of larvae from the three land cover categories within seasons for each of two cohorts (2006 and 2007). We included land cover categories in comparisons only when a given category contained at least five individuals. Comparisons among or between land cover categories were made using two-sample *t*-tests or one-way ANOVA as

appropriate. For the 2006 cohort, enough data were available from urban and reference sites to compare the residuals from a regression of mass against SVL for the pre-metamorphic stage using a *t*-test. In essence, positive residuals represent individuals that are heavier than expected given their SVL, while negative residuals would represent the opposite. We refer to the residuals as a measure of body condition index, and we assessed it for the pre-metamorphic stage as another way to evaluate size (and potential fitness) as the larvae enter the terrestrial phase of the life cycle.

To evaluate the effect of the factors hypothesised to influence growth, we used linear regression. For analyses described in the following paragraphs that incorporate hatchling growth, we used the mean change in SVL between hatch and summer as a response variable to approximate this growth. This time period represents the interval with the greatest mean difference in SVL for any two consecutive seasons (Fig. 1). We examined the impact of temperature on growth using the 2007 cohort. We plotted hatchling growth against the median temperature for that same time period. We used the median because it was a better measure of central tendency in our temperature data set, which had a few outliers on the left side (lower temperatures) of the distribution. We also hypothesised an effect of competition on growth. Specifically, we tested for an effect of inter-cohort competition by examining the regression of hatchling growth against the density of pre-metamorphic individuals from the 2006 cohort (as measured during spring 2007; see Barrett, 2009 for methods).

To evaluate the impact of either predation pressure or resource availability on growth, we coupled hatchling growth data from 2006 and 2007 with survey data on aquatic invertebrate and centrarchid density from the same streams. Resource availability (bottom-up effect) was evaluated by regressing hatchling growth against log aquatic invertebrate density for each stream. Similarly, we used linear regression to assess the effect of predator density on hatchling growth. This analysis was a means to assess top-down regulation of larval salamander growth. We also evaluated the relationship, for each stream, between the number of prey items in salamander guts and the density of centrarchids to further evaluate the hypothesis that predators influence foraging behaviour.

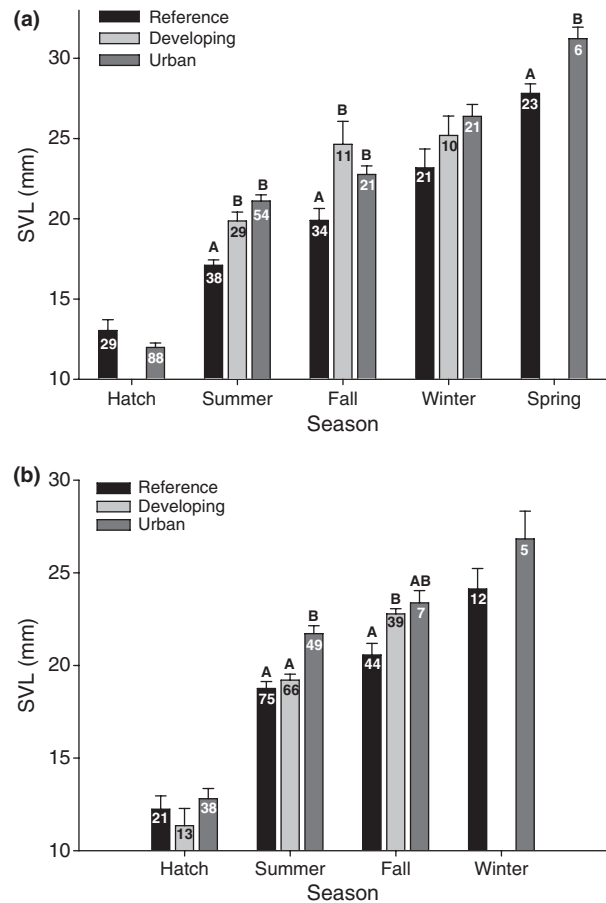


Fig. 1 Mean (\pm SE) larval two-lined salamander size comparisons within land cover categories by season for (a) 2006 and (b) 2007 cohorts. The first set of bars labelled Hatch on the x-axis represent the newly hatched individuals sampled in April of the given cohort year. Letters above the bars represent significant differences from two-sample *t*-tests or a one-way ANOVA followed by Tukey's pair-wise comparison, as appropriate. Where there are no letters above bars, none of the means were significantly different from one another. Sample sizes are listed inside the bars. We did not plot the means for or statistically compare larvae from land cover categories with fewer than five captures within a given season.

Results

The 2006 cohort of larvae provided a more complete data set than the 2007 cohort for evaluating size differences between land cover categories, as the number of captures was far lower in all land cover categories during autumn, winter and pre-metamorphic spring samples of the 2007 cohort. In 2006 and 2007, there was no significant size difference among land cover categories for the newly emerged (spring) hatchlings (Fig. 1). By the following summer

(4 months after initial measurements), urban larvae for both cohorts and larvae for developing sites for the 2006 cohort had achieved larger sizes than larvae at reference sites (ANOVA, $P < 0.0005$ for both comparisons; Fig. 1). Larvae from urban and developing sites continued to be larger than those from reference streams during autumn samples of both cohorts (ANOVA, $P \leq 0.004$ for both cohorts), but this difference vanished during winter 2006 and 2007. By the following spring, pre-metamorphic larvae of the 2006 cohort were larger for urban sites than reference sites (t -test, $P = 0.003$; Fig. 1). There was no significant difference in the body condition index for larvae at this stage (t -test, $P = 0.63$). Larval capture success was too low in 2007 to compare sizes among land cover categories during the pre-metamorphic stage.

Linear regressions indicated none of the evaluated factors were correlated with larval growth (Table 1). Of our *a priori* hypotheses, the regression of temperature on growth had the highest r^2 value (Table 1); however, the failure of one temperature logger resulted in low statistical power. The test for an effect of centrarchid density on growth had the strongest statistical support, but was a positive relationship, thus in the opposite direction of our *a priori* hypothesis.

Discussion

We observed that hatchling larvae of two-lined salamanders from urban, developing and reference streams did not differ in size. However, larvae in developing and urban habitats attained larger SVL than their reference counterparts within a few months. Size differences remained throughout the larval period and at metamorphosis, although it was not statistically significant during the winter months when growth probably slows because of lower temperatures. Our observations provided a foundation for evaluating existing hypotheses regarding factors that influence the growth of amphibians and, more generally, all ectotherms, in the context of an urban-forested gradient.

Increased growth of two-lined salamander larvae from developing and urban catchments could partially offset lower survivorship known to occur in these same habitats during the larval phase (Barrett, 2009). An increase in spate frequency and magnitude that accompanies urbanisation in these streams

(Schoonover *et al.*, 2006) probably dislodges many developing larvae from the stream (Barrett, 2009). Those that do survive appear to grow faster, although they are no heavier than expected based on their length. Nevertheless, increased growth could allow larvae to undergo metamorphosis earlier and/or at larger sizes, which would presumably provide a fitness benefit during the terrestrial phase of the life cycle (Semlitsch *et al.*, 1988; Beck & Congdon, 1999). Specifically, such a benefit would be conferred because larger females have, on average, more offspring than smaller conspecifics (Scott & Fore, 1995; Verrell, 1995).

We investigated relationships between salamander growth and four major abiotic and biotic factors (Table 1) to identify potential mechanisms driving observed patterns. None of the factors we evaluated had a statistically significant relationship with change in SVL, but we believe our results provide data that can help guide future studies. First, despite the fact that perceived predation risk has been found to reduce foraging and/or activity rates of larval amphibians in experimental trials (Laurila, Pakkasmaa & Merilä, 2006; Currens *et al.*, 2007), we found no evidence to support the hypothesis that Centrarchidae density would negatively influence growth of two-lined salamander larvae. In fact, there was no statistically significant relationship between hatchling growth and predatory fish density or between the amount of food in larval stomachs and fish density. We do not believe further tests of this hypothesis in an urban-rural context would be fruitful. Second, from previous work (Helms, Schoonover & Feminella, 2009), we knew prey availability increased with urbanisation and hypothesised this would increase larval growth in these streams relative to reference environments. The direction of the relationship was consistent with our prediction, but a greater number of streams will need to be evaluated before differential growth in an urban-rural setting can be attributed to resource availability. Third, we found only very weak support for the prediction that inter-cohort competition would decrease growth of hatchling larvae. This prediction was based on the fact that hatchlings emerge in the presence of, and potentially compete with, larvae from the previous year's cohort that have yet to undergo metamorphosis. Survivorship of larvae is low in urban streams (Barrett, 2009), so hatchlings in these streams may be

released from inter-cohort competitive pressures. We were only able to assess this hypothesis with data from a single year, and the overall trend was consistent with our hypothesis; however, the relationship was not statistically significant. We would suggest that this hypothesis cannot confidently be rejected. Finally, we hypothesised that the elevated water temperatures from run off and decreased riparian vegetation in urban habitats would result in higher larval growth relative to cooler, reference environments (Pluhowski, 1970; Paul & Meyer, 2001). This relationship was the most consistent with our *a priori* predictions, and the environments with the highest temperatures were, in fact, the urban stream systems.

Anthropogenically elevated temperatures in urban streams may offer a growth advantage to two-lined salamander larvae (i.e. they achieve larger size at metamorphosis or emerge into the terrestrial environment quicker than conspecifics in other habitats); however, elevated temperatures may be detrimental to other salamander species. Previous studies (Price *et al.*, 2006; Barrett & Guyer, 2008) noted a decline in amphibian species richness and/or species abundances with urbanisation. There are many factors that contribute to such declines, but the low thermal tolerances of some stream amphibians may explain the loss of some species from streams subject to urbanisation (Bury, 2008). Plethodontids (*Eurycea* and other genera of lungless salamanders) probably evolved in cool, mountain stream-type habitats (Wilder & Dunn, 1920; Beachy & Bruce, 1992); as such, these species may not be able to cope with the elevated temperatures and more open canopies that accompany urbanised stream channels (Barrett & Guyer, 2008).

There are myriad factors that influence a biological response as complicated as growth, and identifying which factors are most important in the context of urbanisation will take a very large-scale effort. Our study offers a foundation upon which larger-scale efforts can build and test hypotheses that will offer insights regarding demography shifts in amphibians (i.e. growth and metamorphosis). Understanding which environmental changes in an urbanised environment translate to demographic shifts in stream-breeding amphibians would allow for a more focused, species-specific approach to amphibian conservation (Hamer & McDonnell, 2008).

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