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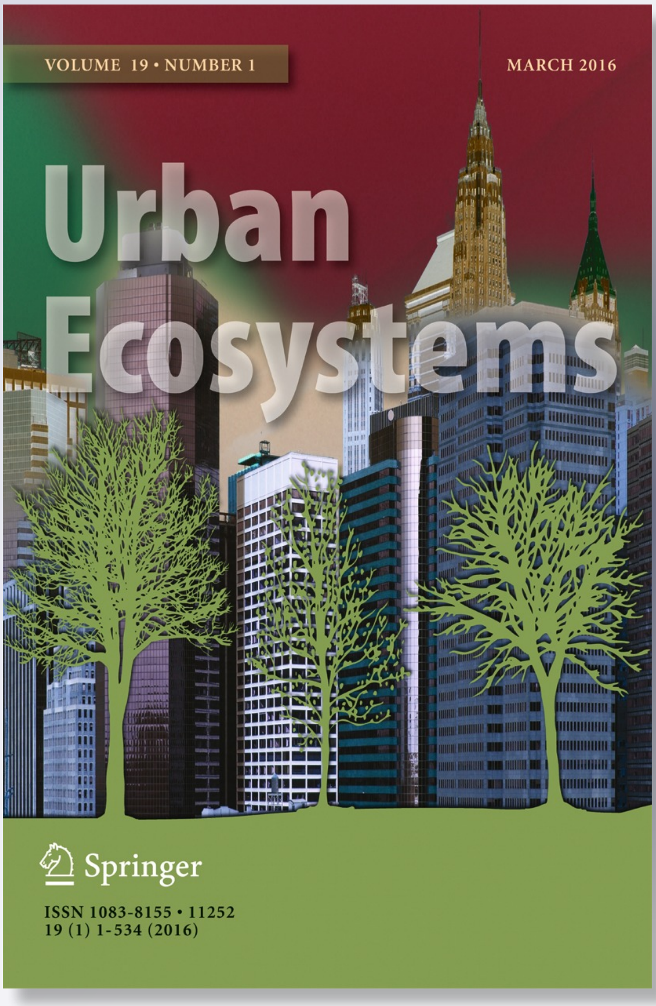

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The effects of urbanization on body size of larval stream salamanders

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Abstract Animal body sizes in urban areas often differ from nearby rural areas, which may impact population fitness and dynamics. We examined the effects of urbanization on larval body sizes of two species of salamanders, the two-lined salamander (*Eurycea cirrigera*) and the northern dusky salamander (*Desmognathus fuscus*). Specifically, we utilized a before-after control-impact (BACI) study design which allowed for the assessment of differences in larval body size between multiple control and impacted sites over a 5 year period. We found a decrease in larval body size in both species at the impacted sites compared to control sites in the first year after urbanization, followed by generally larger body sizes in urban sites compared to control sites in years 3–5, and significantly so in year 4. Using generalized linear models, we found support that larger body sizes post impact in urbanized streams may be due to warmer stream water temperature and decreased abundance of larvae. Both *E. cirrigera* and *D. fuscus* are well known for their ability to persist in urbanized streams; our data suggest that despite overall lower abundances in urban streams, persistence may be due to increases in larval body size and, potentially, post-metamorphic benefits.

Keywords Abundance · Before-after control-impact (BACI) · *Desmognathus* · *Eurycea*

Introduction

Body size of animals, defined as the length, width or weight of individuals, is often used to assess fitness of individuals in a population (Calder 1996). In urban areas, animal body sizes often differ from surrounding rural areas with both increases and decreases in body size noted

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(Liro 1985; Richner 1989; Ovaska 1991; Luiselli et al. 2002; Ruiz et al. 2002; Rasner et al. 2004). Differences in the thermal environment of urban areas (i.e., warmer urban environments) can result in smaller body sizes resulting from dissipation of heat and lower cell growth (Brown and Lee 1969; Walters and Hassall 2006), or larger body sizes resulting from increased metabolic rate and growth (Barrett et al. 2010a). Other potential mechanisms include differences in resources (i.e., food, water) between urban and rural areas, which can result in either larger or smaller body sizes in urban areas relative to species-specific resource requirements (Zeveloff and Boyce 1988; Luiselli et al. 2002; Kozłowski et al. 2004). Despite freshwater systems in urban environments being well-studied, few previous investigations have examined the impact of urbanization on body size in aquatic or semi-aquatic species (Walsh et al. 2001; Chadwick et al. 2006; Price et al. 2014).

Body sizes of larval amphibians are influenced by both abiotic and biotic factors. Increased temperatures and changes in water chemistry have been shown to decrease body sizes (Carey and Bryant 1995; Sanzo and Hecnar 2006; Reading 2007, but see Barrett et al. 2010a). Relative abundance or density of larval amphibians within a given population also influences body size of individuals; for example, low densities often result in larger individual body sizes due to decreased competition for limited resources (Damuth 1981; Petranka and Sih 1986). Urbanization of stream watersheds can lead to increased water temperatures, changes in stream water chemistry (e.g., increased specific conductance, decreased pH; Walsh et al. 2005) and overall decreases in population density of larval amphibians (Barrett and Price 2014).

In this study, we examined the impact of urbanization on changes in the larval body size of two stream salamander species, the southern two-lined salamander (*Eurycea cirrigera*), and the northern dusky salamander (*Desmognathus fuscus*). We used a before-after control-impact (BACI) design, which allowed for comparisons within the same sites before and after urbanization, as well as comparisons between designated control sites. This design reduced the impact of stochastic differences among sites and among years. In this study we asked: 1) Does urbanization affect body size in larval salamanders, and how do these changes compare to control sites both pre- and post-disturbance? 2) Within urbanized sites, do changes in water temperature and relative abundance from year to year (accounting for site to site variation) influence body size of larval salamanders? We hypothesized that both species would exhibit larger body sizes following urbanization in the impacted streams. We also expected that these changes in body size in impacted streams would be a response to decreased abundances (as measured by counts) after urbanization, and to a lesser extent, increases in water temperature.

Methods

Study species

We focused on two species, *E. cirrigera* and *D. fuscus*, that have been studied extensively in relation to urbanization (Barrett and Price 2014). Both species inhabit low-order streams, a class of stream considered highly vulnerable to urbanization (Elmore and Kaushal 2008). *Eurycea cirrigera* display a 1–2 year aquatic larval stage (Bruce 1985), and typically attain sizes of 18.5 mm to 26.4 mm before metamorphosis (Bruce 1982). *Desmognathus fuscus* exhibits a 9–14 month aquatic larval stage (Petranka 1998), and typically attain sizes of 9 mm to 20 mm before metamorphosing in late spring (Petranka 1998). Size at metamorphosis was found to follow latitudinal clines for *D. fuscus*, while differences in *E. cirrigera* were found to be better supported as a response to greater competition and predation pressure (Juterbock 1990; Bruce 1982).

Experimental design

We used a BACI study design to examine the effects of urbanization on larval body size. We conducted our study at 30 first order streams over a 5 year period (2005–2009) in the greater Charlotte metropolitan area of North Carolina, USA. Catchments (i.e., watersheds) ranged from 16 to 70 ha, and land cover within stream catchments was primarily forested prior to urbanization. Urbanization occurred within the catchments of 13 of the 30 study sites following the first year of sampling. The amount of the catchment urbanized in these 13 sites ranged from 1 to 78 %, with a mean of 35 %. Our 17 control catchments did not experience land use change during the study period (see Price et al. 2010, 2011 for in-depth description of the study sites).

Salamanders were sampled at each site during March and again in April or early May along a one permanently marked 10 m transect per site, and these transects were selected for similarity in width, depth and velocity. However, we used animals captured in April or early May in this study. We captured larval salamanders via dip-netting (i.e., turning over rocks and debris), and subsequently measured via calipers each individual by its snout-to-vent length (SVL), which we used to assess body size, before counting and release. Actual salamander abundances were not calculated in this study; we used counts as a surrogate. While we recognize that counts are not an ideal measure of abundance due to imperfect detection of individuals (e.g., Dodd and Dorazio 2004), we believe our consistent sampling design allows for counts to serve as an adequate proxy. Additionally, we measured water temperature (°C) at each visit (i.e., March and April/early May) using a handheld YSI 85 m (YSI, Inc., Yellow Springs, OH, U.S.A.). We conducted sampling at each site every year, with exception of a single control site, which was not sampled during year five. Though *E. cirrigera* exhibits a larval stage of over 1 year in our study region, only body sizes of late stage larval salamanders were included in this study.

Data analysis

To address question (1), we compared mean SVL between impact and control sampling sites, accounting for a year effect, by conducting repeated measures analyses of variance (ANOVA) with unbalanced data. We measured the effects of time (year), type (whether the site was a control or impacted catchment), and the interaction of these two effects on body size for both species. To account for variation between sites and types, we nested the effect of type within site. We then conducted a post-hoc Tukey's HSD to compare body sizes between all year and type combinations; *E. cirrigera* and *D. fuscus* were analyzed separately.

To examine question (2), we conducted stepwise regressions for both species, testing each variable (i.e., abundance, maximum March temperature, site and year) as predictors of body size. Prior to the regression analysis, we first performed a Pearson's pairwise correlation between our abiotic variables to examine for multicolliniearity. Lastly, to achieve normality within the residuals of our count data, we log-10 transformed our salamander counts at each site. Finding no correlation, we then conducted generalized linear models (GLM) for each study species at urbanized sites post impact using restricted maximum likelihood as an estimation method to assess each variable's effect on body size. Within each GLM, we accounted for repeated site visits and year to year correlation with a compound symmetry covariance structure (Wolfinger 1993). All analyses had an a priori alpha of 0.05 and were conducted using SAS 9.3 software package (SAS Institute, Cary, NC).

Results

Between April 2005 and early May 2009, we captured and measured 730 *E. cirrigera* larvae and 474 *D. fuscus* larvae, with average body sizes of 24.35 (Standard deviation±4.49) mm and 18.42 (±3.86) mm respectively. Water temperatures averaged 16.0 °C (±2.7 °C) at all sites across all years. A summary of yearly count and temperature data for each species can be found in Fig. 1.

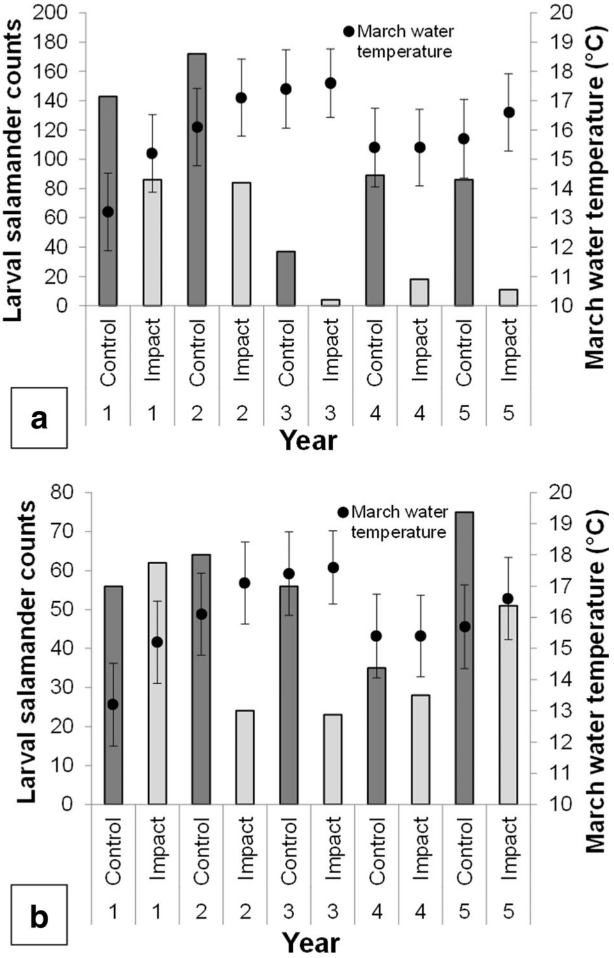

Fig. 1 Total *E. cirrigera* (**a**) and *D. fuscus* (**b**) counts at each site for control and impacted sites across 5 years. *Circles* represent mean March water temperatures at each site class. *Error bars* represent the standard deviation around the mean

The body sizes of larval *E. cirrigera* were significantly different among years ($df=4$, $F=11.35$, $P<0.001$) and between urbanized and control sites ($df=24$, $F=10.50$, $P<0.001$). There was, however, an interaction between site and year, indicating changes in body size at impacted sites from control sites over time ($df=4$, $F=7.31$, $P<0.001$). Comparing mean body size between impact and control sites within years, we found no difference between control and impact sites at year one (i.e., body sizes were similar pre-urbanization). *Eurycea cirrigera* exhibited significantly smaller body sizes in year two at impacted sites relative to control sites ($P<0.05$). Mean body sizes at impacted sites were generally larger in years three through five, but this difference was only significant in year four (Table 1). Examining year to year comparisons, *E. cirrigera* exhibited a significant ($P<0.05$) decrease in body size from year one to two, and a significant increase from year two to three at impact sites. At control sites, body size decreased significantly ($P<0.05$) from year two to three (Tables 2 and 3, Fig. 2).

The mean body sizes of larval *D. fuscus* were different among years ($df=4$ $F=17.36$, $P<0.001$), and between sites ($df=28$, $F=10.96$, $P<0.001$). However, we found no interaction between site and year ($df=4$, $F=1.12$, $P=0.3486$). Comparing mean body size between impact and control sites within years, we found no difference between control and impact sites at year one (i.e., body sizes were similar pre-urbanization). *Desmognathus fuscus* exhibited smaller body sizes in year two at impacted sites compared to control sites ($P<0.05$). *Desmognathus fuscus* at impacted sites exhibited significantly larger body sizes relative to control sites in year three, followed by a shift to smaller body sizes compared to control sites by year five (Table 4). Examining year to year comparisons, *D. fuscus* exhibited a decrease ($P<0.05$) in body size from year one to two, and a significant increase from year two to three at impact sites. At control sites, body size decreased ($P<0.05$) from years one to two (Tables 5 and 6, Fig. 2).

Using generalized linear models, we found that both maximum March water temperature and abundance influenced salamander body size at urbanized sites. We found a positive relationship between maximum water temperature in March and larval salamander body size for both species, as well as a negative relationship between abundance and body size for both *E. cirrigera* ($P<0.0001$, $P=.083$) and for *D. fuscus* ($P<.0.0001$, $P=0.037$), though the relationship between abundance and body size was not significant at the 0.05 level in *E. cirrigera*. Furthermore, we also found a Year ($P=0.039$) and Site ($P<0.001$) effect for *D. fuscus*, but not for *E. cirrigera* (Tables 7 and 8).

Table 1 Tukey's post hoc comparisons: Mean body size differences and confidence intervals for *E. cirrigera* comparing control and impacted sites within years. Salamander body sizes at impacted sites were significantly smaller than at control sites during year two, while overall body sizes at impacted sites were larger in years three through five, significantly so during year four. Difference represents difference between means in each year. Abbreviation CI stands for confidence interval. When 95 % CI does not overlap zero, it is significant at 0.05 level

Control	Impact	Difference	95 % CI
Year 1	Year 1	−0.180	(−1.879, 1.519)
Year 2	Year 2	3.327	(1.786, 4.869)
Year 3	Year 3	−5.777	(−11.848, 0.294)
Year 4	Year 4	−4.545	(−7.526, −1.564)
Year 5	Year 5	−2.421	(−6.114, 1.273)

Table 2 Tukey's post hoc comparisons examining body size differences for *E. cirrigera* between years at impacted sites. Larval salamander body sizes decreased significantly from year one to year two, and increased significantly from year two to year three (Alpha of 0.05 value=4.4891). Difference represents difference between means in each year. Abbreviation CI stands for confidence interval. When 95 % CI does not overlap zero, it is significant at 0.05 level

Impact	Impact	Difference	95 % CI
Year 1	Year 2	2.768	(0.881, 4.655)
Year 2	Year 3	−6.136	(−12.040, −0.231)
Year 3	Year 4	−0.978	(−7.353, 5.398)
Year 4	Year 5	0.819	(−3.595, 5.233)

Discussion

Urbanization often leads to changes to stream habitat structure and results in population declines of stream biota (Paul and Meyer 2001; Morgan and Cushman 2005; Price et al. 2010; Price et al. 2011; Price et al. 2014). In this study, we demonstrated a multi-year effect of urbanization on body size of larval *E. cirrigera* and *D. fuscus* through a dynamic response to urbanization at impact sites relative to control sites. We found an initial decrease in body size of larvae at the urbanized sites in year two, followed by an increase in mean body size in larvae in years three through five. Observed increases in larval body sizes in urban sites 3, 4 and 5 years after urbanization may be related to elevated water temperatures or low abundance of individuals at these sites.

The immediate decrease in body size 1 year after urbanization was likely the result of proximate changes in the affected watersheds, such as modification to the physical makeup of the stream bed. Urbanization has been shown to cause decreased water quality via altered channel and bed characteristics, altered flow patterns in streams, runoff from urbanized lands, and increased flood potential (Paul and Meyer 2001; Riley et al. 2005; Wenger et al. 2009). Increased sedimentation, in particular, has been cited as a potential cause for decreased occupancy of salamanders after urbanization (Price et al. 2010). By eliminating streambed heterogeneity, sediment can both reduce microhabitat for larval salamanders and increase the potential for floods to wash individuals downstream (Barrett et al. 2010b). Similar disturbances within our study could have led to short-term effects on growth and fitness in the year immediately post-impact. Neckel-Oliveira and Gascon (2006) found size differences between male frogs in forests that were previously cleared from those that were undisturbed, and

Table 3 Tukey's post hoc comparisons examining body size differences for *E. cirrigera* between years at control sites. Larval salamander body size did not change from year one to year two, though mean body size did decrease from year two to year three (Alpha of 0.05 value=4.4891). Difference represents difference between means in each year. Abbreviation CI stands for confidence interval. When 95 % CI does not overlap zero, it is significant at 0.05 level

Control	Control	Difference	95 % CI
Year 1	Year 2	−0.739	(−2.044, 0.566)
Year 2	Year 3	2.969	(0.879, 5.059)
Year 3	Year 4	−2.210	(−4.466, 0.046)
Year 4	Year 5	−1.305	(−3.049, 0.439)

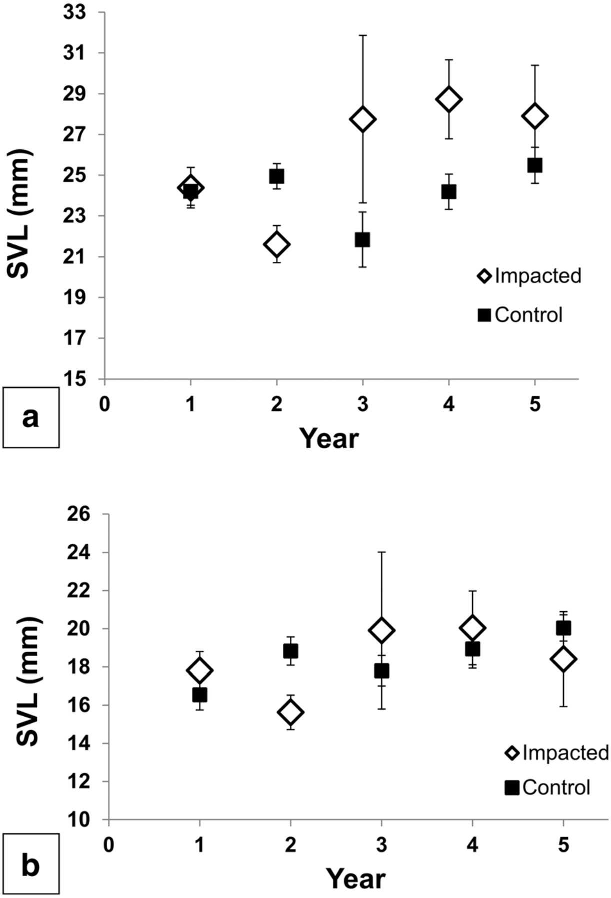

Fig. 2 Mean *E. cirrigera* (**a**) and *D. fuscus* (**b**) SVL (mm) for control and impacted sites across 5 years. *Diamonds* represent averaged control site values, and squares represent averaged urbanized site values. *Error bars* represent the 95 % confidence interval around each mean

Table 4 Tukey's post hoc comparisons: Mean body size differences and confidence intervals for *D. fuscus* comparing control and impacted sites within years. Salamander body sizes at impacted sites were significantly smaller than at control sites during year two, while impacted body sizes in year three were significantly higher, though a downward trend is noted where body sizes at impacted sites decreased in years four and five relative to the control sites. Difference represents difference between means in each year. Abbreviation CI stands for confidence interval. When 95 % CI does not overlap zero, it is significant at 0.05 level

Control	Impact	Difference	95 % CI
Year 1	Year 1	−1.261	(−2.667, 0.145)
Year 2	Year 2	3.203	(1.387, 5.019)
Year 3	Year 3	−2.110	(−3.989, −0.230)
Year 4	Year 4	−1.093	(−3.017, 0.831)
Year 5	Year 5	1.628	(0.251, 3.005)

Table 5 Tukey's post hoc comparisons: Tukey's post hoc comparisons examining body size differences for *D. fuscus* between years at impact sites. Larval salamander body sizes decreased significantly from year one to year two, and increased significantly from year two to year three (Alpha of 0.05, Critical value=4.4975). Difference represents difference between means in each year. Abbreviation CI stands for confidence interval. When 95 % CI does not overlap zero, it is significant at 0.05 level

Impact	Impact	Difference	95 % CI
Year 1	Year 2	2.182	(0.357, 4.006)
Year 2	Year 3	−4.288	(−6.502, −2.074)
Year 3	Year 4	−0.123	(−2.258, 2.013)
Year 4	Year 5	1.624	(−0.161, 3.409)

Karraker and Welsh (2006) found lower overall body conditions in terrestrial amphibians following timber harvest. In the preceding investigations, the documented changes in body condition post-impact were linked to increased abundances, which caused competition for resources, resulting in lower overall body condition.

In contrast to the declines exhibited in year two, during years three to five, larval body size generally increased relative to control sites for *E. cirrigera* (significantly so in year 4), and increased to similar control site body sizes in *D. fuscus*. Barrett et al. (2010b) found that growth patterns of *E. cirrigera* were accelerated in urbanized streams relative to non-impact reference streams. The variation in growth patterns in that study were not found to be linked to factors measured, such as elevated water temperatures, low survivorship of larvae, increased prey availability, or high predator density, though it was hypothesized that lower abundances in urban streams would lead to reduced competition and increased growth rates. In our study, we showed a relationship between body size and water temperature as well as abundance. Temperature induced changes in body size are well studied (Angilletta et al. 2004). Walters and Hassall (2006) noted that increased cold environment cellular growth in ectotherms leads to overall larger body size, though lower overall growth rates. We found a positive relationship between March water temperature and body size. Though temperatures were only measured at time of sampling and not over a longer period, our findings are in line with claims that the thermal profile of impacted streams could alter larval salamander growth patterns and body sizes by increasing metabolic rates and leading to larger larval salamanders. Barrett et al. (2010a) found a link between increased temperatures in urbanized streams and increased growth rates, though overall body size was not assessed.

Table 6 Tukey's post hoc comparisons examining body size differences for *D. fuscus* between years at control sites. Larval salamander body size increased from year one to year two, but did not change significantly in the subsequent years (Alpha of 0.05, Critical value=4.4975). Difference represents difference between means in each year. Abbreviation CI stands for confidence interval. When 95 % CI does not overlap zero, it is significant at 0.05 level

Control	Control	Difference	95 % CI
Year 1	Year 2	−2.283	(−3.678, −0.888)
Year 2	Year 3	1.025	(−0.364, 2.413)
Year 3	Year 4	−1.139	(−2.774, 0.496)
Year 4	Year 5	−1.097	(−2.650, 0.456)

Table 7 Generalized linear model explaining larval body size in *E. cirrigera*. Parameters examined include year, site, abundance, and maximum March water temperature (°C). For each parameter, parameter estimates, standard error, t value and P value are listed

Parameter	Estimate	Standard error	t Value	Pr>|t|
Intercept	12.361	4.086	3.02	0.003
Year	0.372	0.402	0.93	0.356
Site	0.233	0.159	1.46	0.146
Abundance	−1.938	1.108	−1.75	0.083
Max March water temperature	0.964	0.217	4.45	<0.001

We also found a negative relationship between salamander abundance and body size in salamanders. The negative relationship between density and body size or condition has been previously studied in experimental amphibian larval populations (Semlitsch and Caldwell 1982). In natural populations, Petranka and Sih (1986) found that streamside salamander (*Ambystoma barbouri*) growth, development, and survivorship was linked to population densities, and more specifically that body size varied inversely with density. In their study, floods destroyed 90 % of stream dwelling salamander populations, but those that survived exhibited a faster growth rate and obtained larger body sizes at metamorphosis. This trend was further supported by experimental studies conducted by Petranka (1989) with *Ambystoma opacum* larvae in ephemeral ponds, which attributed the inverse relationship between growth rates and density to intraspecific aggression as opposed to resource limitations. Furthermore, Karraker and Welsh (2006) found similar trends in terrestrial salamander populations (*Ensatina eschscholtzii*) in commercially thinned forests, though they hypothesized that the increased abundances resulted in increased competition for cover objects, which resulted in poorer body condition. Thus, our study compliments the existing research which demonstrates an inverse relationship between population density and larval body size, and extends these findings to stream Plethodontid populations, though it remains unclear whether the body size increases are due to reduced competition, reduced intraspecific aggression, or another factor.

Both *E. cirrigera* and *D. fuscus* are well known for their greater ability to persist relative to other salamander species in urbanized streams (Barrett and Guyer 2008; Price et al. 2011; Barrett and Price 2014). This resistance may be due, in part, to increases in body size despite overall lower abundances in urban streams. Increased body size at metamorphosis has been linked to increased survivorship (Semlitsch et al. 1988), and while we did not measure or record resource availability in the study streams, prey availability has been shown to increase

Table 8 Generalized linear model explaining larval body size in *D. fuscus*. Parameters examined include year, site, abundance, and maximum March water temperature (°C). For each parameter, parameter estimates, standard error, t value and P value are listed

Parameter	Estimate	Standard error	t Value	Pr>|t|
Intercept	12.679	2.359	5.38	<0.001
Year	0.350	0.168	2.08	0.039
Site	−0.446	0.062	−7.15	<0.001
Abundance	−1.632	0.764	−2.14	0.035
Max March water temperature	0.606	0.109	5.55	<0.001

under similar urban stressors (Liro 1985; Luiselli et al. 2002; Helms et al. 2009; Barrett et al. 2010b). Individual salamanders may be able to take advantage of lower abundances (and potentially reduced competition) and therefore have access to a larger portion of resources. While certain species, like *E. cirrigera* and *D. fuscus*, have been shown to persist in higher numbers in impacted areas, the exact mechanisms for species specific survival are not clear (Barrett and Price 2014), and should be a focus of future study.

Broad scale urbanization has the potential to not only alter species diversity, but also significantly impact individual characteristics. Our results suggested fewer but larger larvae as urbanization progresses, though patterns of body size shifts were species specific. We believe our study provides a basis for future research on the effects of urbanization on individual life history characteristics. To foster a more comprehensive understanding of the effects of urbanization on aquatic vertebrates, future studies should focus on two areas: 1) Examining broader life history datasets, including traits such as growth, fecundity, diet, and age at first reproduction and 2) Examining species-specific differences across these traits, looking for relationships between specific life history traits and a species' relative resilience in urban environments (i.e., urban adapters vs. avoiders; Blair 1996). Furthermore, future studies should continue to focus on using multi-year BACI data, which will provide a more complete picture of life history changes after impact. Additionally, experimental studies should play significant roles in isolating the effects of variables such as temperature, water chemistry, and abundance on body size and other life history traits. Ultimately, studies on species' life history characteristics and responses of these characteristics will give us a better understanding of why some species persist in urbanized areas where others cannot.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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