

APPLIED ISSUE

Evaluating the effects of urbanisation on salamander abundances using a before-after control-impact design

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SUMMARY

1. Urbanisation represents a significant threat to semi-aquatic amphibian populations, especially stream-dwelling salamanders. Although studies of urbanisation effects on amphibians have been conducted, there is an urgent need to follow populations over longer time periods, account for imperfect detection and determine the response time to urbanisation. Consequently, we used a before-after control-impact (BACI) study design to estimate changes in abundances of larval and adult salamanders in streams affected by urbanisation.

2. From 2005 to 2009, we used standard sampling techniques to obtain a count of salamanders in 13 first-order streams that underwent urbanisation of their catchments after the first year of sampling. Simultaneously, we counted salamanders in 17 streams that experienced no disturbance within stream catchments. Additionally, we measured environmental variables at each stream.

3. We used Royle's binomial mixture model to estimate annual mean abundances and individual detection probabilities, and Bayesian inference was used to estimate population parameters for each stage and species.

4. Although mean abundance estimates varied among years in control and urbanised streams, we found that urbanisation had a negative effect on larval and adult salamander abundances. Larval salamander abundances at sites 1 year after urbanisation were significantly lower than abundances from control sites. Abundances of adult two-lined salamanders (*Eurycea cirrigera*) at urbanised sites were lower than abundances at control sites 2 years post-urbanisation, and adult dusky salamander (*Desmognathus fuscus*) abundances at urbanised sites were lower than abundances at control sites 3 years post-urbanisation. Maximum conductivity, sedimentation level and maximum stream channel width differed between urban and non-urban streams.

5. Our results suggest that stream-dwelling salamanders exhibit little resistance to urbanisation. Our study also highlights the use of the BACI design to study how urbanisation affects populations in semi-aquatic habitats. We emphasise that inferences regarding urbanisation effects on population response may be compromised unless urban populations are compared to populations in control sites, especially for species in which populations fluctuate.

Keywords: *Desmognathus*, development, *Eurycea*, first-order streams, response time

Introduction

Understanding the response of freshwater animal populations to urbanisation has become one of the most critical issues in conservation biology. Globally, urbanisation represents one of the most ubiquitous forms of land

conversion and represents a major threat to ecosystems and biodiversity (McKinney, 2002; Liu *et al.*, 2003; Lepczyk, Hammer & Stewart, 2007). Urbanisation has numerous effects on aquatic ecosystems including altered hydrology and decreased water quality because of increases in impervious surfaces (Paul & Meyer, 2001),

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climatic differences (Leblanc, Brown & Fitzgibbon, 1997) and increased establishment of non-native species (Pickett *et al.*, 2001). Aquatic systems in urban areas have lower abundances of native species, decreases in overall species richness and lower species occupancy rates compared with non-urban areas (Willson & Dorcas, 2003; Burcher & Benfield, 2006; Scott, 2006; Barrett & Guyer, 2008).

Streams are sensitive to urbanisation because of the link between stream properties and terrestrial processes within stream catchments. Urban streams often have highly altered hydrologic patterns, channel characteristics, water chemistry and substrata compared with streams within non-urban catchments (Paul & Meyer, 2001). Owing to complex life cycles and incorporation of both terrestrial and aquatic habitats into their life histories, stream salamanders are vulnerable to urban development within stream catchments. For example, Barrett & Guyer (2008) found that urban streams in western Georgia, U.S.A., harboured only one species of stream salamander, whereas up to four species were found in catchments with forested, agricultural or developing land-cover. Similarly, Orser & Shure (1972), Willson & Dorcas (2003) and Miller, Hess & Moorman (2007) identified a strong, negative correlation between the number of salamanders captured and the amount of urban land-cover in stream catchments.

Although previous studies provide important insights into the effects of urbanisation on stream salamanders, they are temporally limited and rely solely on correlations between urban land-cover and salamander numbers to determine response. An informative alternative to previous studies is to evaluate population dynamics before, during and after urbanisation, and compare these dynamics to those of populations in streams that have not undergone urbanisation. This approach can provide better information on resistance of salamander populations to urbanisation.

Examining the response of stream salamander populations to disturbances can be challenging. Salamanders are extremely cryptic; individuals often remain under cover or within underground refugia (Bailey, Simons & Pollock, 2004), and activity is limited to particular seasons and/or climate conditions (Hyde & Simons, 2001). Therefore, at any given time, the majority of individuals may be undetectable to survey efforts, confounding estimates of abundance. However, Royle's binomial mixture models (Royle, 2004; Royle & Dorazio, 2008) account for imperfect detection of individuals and estimate abundance, but this technique has not been used in previous studies investigating the effects of urbanisation on animal populations.

In this study, we examined the effects of urbanisation on the abundances of adult and larval stages of two

salamander species, northern dusky salamander (*Desmognathus fuscus*) (Rafinesque) and southern two-lined salamander (*Eurycea cirrigera*) (Green). Based on previous studies (e.g. Green, 2003; Willson & Dorcas, 2003), we expected that salamander abundance would decrease in urbanised streams, whereas abundances in control sites would remain relatively stable throughout the 5 years of sampling. Specifically, we hypothesised dusky salamanders, which are strongly associated with aquatic habitats, would exhibit less population decrease than two-lined salamanders. Two-lined salamanders use aquatic habitat for larval development and reproduction, but forested, terrestrial habitat during the non-breeding season (Petranka, 1998), and therefore, we expected that changes to stream catchment and in-stream habitat conditions would result in a significant population declines. We also predicted that stage-specific differences would be apparent with larvae being less resistant than adults, as larvae may be more vulnerable to modifications in stream habitat, particularly sedimentation, changes in stream channel morphology and altered hydrologic regimes, associated with urbanisation. In addition to testing the effects of urbanisation on salamander abundances, we compared environmental characteristics of streams to document the effects of urbanisation on stream attributes.

Methods

Study sites

We sampled salamanders annually from 2005 to 2009 in 30 first-order, semi-permanent streams in the Charlotte-Metropolitan area of North Carolina, U.S.A., specifically within Cabarrus, Gaston, Iredell, Lincoln and Mecklenburg counties (Fig. 1). During our study, land-cover within the Charlotte-Metropolitan area consisted of second growth, mixed forests, agricultural and pasture land, and urban land. Significant decreases in forests and agricultural lands over the last 40 years have occurred because of increases in urban land-cover, with some counties within the region losing up to 60% of undeveloped land to urban development (Price *et al.*, 2006; D. Shoemaker pers. comm.).

We used a geographic information system (GIS, ArcGIS V 9.2; ArcHydro Extension, Redlands, CA, U.S.A.) to delineate catchments for each stream. Catchment areas ranged from 16 to 70 ha. Of the 30 streams in our study, catchments of 13 streams were developed during summer 2005, after our first year of sampling salamanders (see Fig. 1). Urbanisation consisted of grading land and removal of some vegetation, road building, and construc-

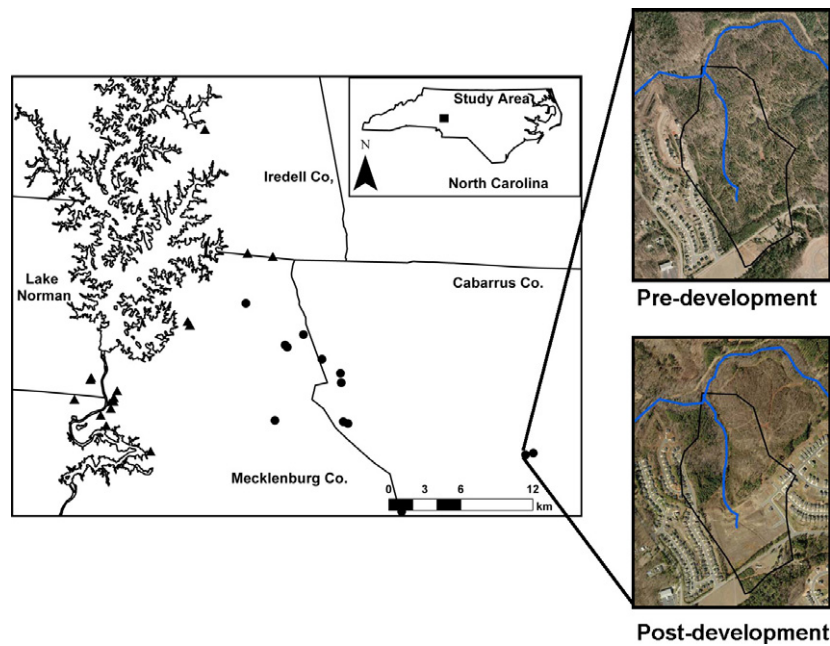


Fig. 1 Location of control and urbanised stream catchments in the Charlotte-metropolitan area, NC, U.S.A., with an example of a stream before and after urbanisation of the stream catchment. The circles represent stream locations that were urbanised after the first year of sampling (2005). Triangles represent control study streams. Stream catchments are represented by black outlines.

tion of homes, shopping centres and other buildings. The conversion of land and construction continued throughout the duration of the study. The total area urbanised in each catchment at the end of the study (i.e. 2009) averaged 35% (range from 1 to 78%). The remaining 17 streams comprised the controls and were located on protected land, and land-cover changes to their catchments did not occur during our study.

Salamander data collection

We conducted counts of salamanders in four, linear transects in each stream annually from 2005 to 2009. Sample transects were chosen based on similarity in stream width, depth and current velocity. Using systematic dip-netting and bank searches, we sampled salamanders in one 10-m transect during March/early April and a second 10-m transect in April/early May. We also trapped salamanders in each stream for 2, 1-week sessions; we trapped one 10-m section in March/early April and a second 10-m section in mid-April to early May; see the study by Price *et al.* (2011) for more information on sampling methods. We counted all salamander species captured and identified life stage (larva or adult) prior to release. The same four transects in each stream were sampled every year of the study with the exception that we were unable to sample one control study site during 2008 and 2009 and another two control study sites in 2009.

Environmental data collection

We sampled environmental attributes at each stream during each salamander survey to evaluate the effects of urbanisation on stream condition and to account for these conditions on salamander detection probability. To evaluate the effects of urbanisation on aquatic conditions, we recorded dissolved oxygen (% saturation), conductivity (μS) and water temperature ($^{\circ}\text{C}$) (e.g. Willson & Dorcas, 2003). Dissolved oxygen, conductivity and water temperature were measured with a hand-held YSI 85 meter (YSI, Inc., Yellow Springs, OH, U.S.A.) before each dip-net sample and before setting traps and checking traps. We also recorded stream depth (cm) and width (cm) at the beginning, midpoint and end of each 10-m transect prior to dip-netting and setting traps. Finally, we visually estimated the proportion of silt within each transect to the nearest 5% (modified from Lowe & Bolger, 2002). We defined silt as any fine sediment accumulated in the stream bed. We categorised siltation based on the total percentage of transect areas embedded with silt. Specifically, our silt categories included (i) 0–20% of transects covers with silt (low siltation), (ii) 21–40% of transects covered with silt, (iii) 41–60% of transects covered with silt and (iv) >61% of transects covered with silt (high siltation).

We also recorded habitat conditions that may be particularly relevant in salamander detection. We assumed detectability of salamanders may differ among

sites and among visits owing to the varying amount of cover objects (rocks, logs, branches, etc.) and detritus (primarily leaf litter) within the sampling transect. Thus, we counted all cover objects including rocks >50 mm in diameter as well as logs and other woody debris within the sampling transects. The amount of detritus was estimated visually within each transect to the nearest 5%. We also noted whether precipitation occurred within 24 h prior to our sample, as precipitation events may result in higher activity (and thus higher detection), especially after flow levels stabilise (Johnson & Goldberg, 1975).

Statistical analyses

To estimate salamander abundances, we used the binomial mixture model developed by Royle (2004). This model estimates abundance and individual detection rate, can incorporate site-level and survey covariates and provides estimates of the uncertainty associated with each parameter. The field protocol, as described by Royle (2004) and Royle & Dorazio (2008), consists of replicate counts conducted at a set of spatially distinct sites (i) during temporally indexed surveys (j), denoted as c_{ij} . The counts are modelled as J -independent outcomes of binomial sampling with index N_i and success or detection probability, p_i , resulting in the product-binomial model:

$$[y_i|N_i, p_i] = \prod_{j=1}^J \text{Bin}(y_{ij}|N_i, p_i) \quad (1)$$

Additional modelling, including the introduction of parameters, is needed to specify the relationship between the local-level parameters (i.e. N_i , p_i). Abundances (λ) at the local-level are often modelled with the Poisson distribution such that:

$$N_i|\lambda_i \sim \text{Poi}(\lambda_i) \quad (2)$$

To model heterogeneity in abundance among populations, a Poisson regression formulation of local mean abundances, given by $\log(\lambda_i) = \beta_0 + \beta_1 x_i$, can be used to estimate the regression slope parameter β_1 to quantify the association between λ_i and a habitat covariate (x_i) at the i th sample location. Royle & Dorazio (2008) refer to the regression coefficients (β_0 and β_1) as metapopulation-level parameters of the hierarchical model.

The per-individual detection probability (p) follows a binomial distribution and is modelled according to:

$$c_{ij}|N_i \sim \text{Bin}(N_i, p_{ij}) \quad (3)$$

Sources of heterogeneity in detection can also be identified by modelling associations between sampling covari-

ates and p_i such that $\text{logit}(p_{ij}) = \alpha_0 + \alpha_1 x_{ij}$, where x_{ij} equals the sampling covariate value at site i survey j .

To conduct our analysis, we first separated salamander count data for each species and stage (i.e. larvae or adult). We used the following models for inferences about N_i and p involved in the origin of the observed counts of salamanders. We assumed that the number of salamanders may differ between urban and control catchments. Thus, we considered the site-level abundance of salamanders to be specified by:

$$\begin{aligned} N_i|\lambda_i &\sim \text{Poi}(\lambda_i) \\ \log(\lambda_i) &= \beta_0 + \beta_1 * \text{urban} \end{aligned} \quad (4)$$

where *urban* is a vector of 1 or 0 dependent on if a site was urbanised (1) or control (0).

We assumed that the detectability of salamanders may differ among sites and among visits because of the number of cover objects, detritus within the sampling transect and recent (i.e. 24 h prior to sampling) precipitation events. These three covariates, *cover*, *detritus* and *rain*, were used to model heterogeneity in detectability such that:

$$\begin{aligned} c_{ij}|N_i &\sim \text{Bin}(N_i, p_{ij}) \\ \text{logit}(p_{ij}) &= \alpha_0 + \alpha_1 * \text{cover} + \alpha_2 * \text{detritus} + \alpha_3 * \text{rain} \end{aligned} \quad (5)$$

The covariates *cover* and *detritus* were matrices of the number of cover objects and visually estimated proportion of detritus in each sampling transects. We standardised both *cover* and *detritus*, so the mean of the population was 0 and the standard deviation was 1. Rain was a matrix of either 1 or 0 dependent on if a precipitation event occurred 24 h prior to sampling salamanders.

To estimate population parameters for each stage and species, we used WinBUGS Version 1.4 in batch mode with data handling in R (Spiegelhalter *et al.*, 2003) (version 2.10) (Ihaka & Gentleman, 1996) (add-in library R2WinBUGS). Our models used uninformative priors for the metapopulation-level parameters (Royle & Dorazio, 2008). Specifically, we assumed $\beta \sim N(0, 10^2)$, $\alpha_0 \sim N(0, 1.6^2)$, $\alpha_1 \sim N(0, 10^2)$, $\alpha_2 \sim N(0, 10^2)$ and $\alpha_3 \sim N(0, 10^2)$. The α_0 prior approximates a $U(0, 1)$ prior for $\text{expit}(\alpha_0)$, where expit represents the inverse logit function (i.e. $\exp(\alpha)/[1 + \exp(\alpha)]$). Posterior summaries for each parameter were based on 300 000 Markov chain Monte Carlo iterations with a 30 000 sample burn-in and a thinning rate of 5. The mean and standard deviation of the model coefficients were calculated, along with the 2.5 and 97.5 percentiles of the distribution, which represent 95% Bayesian credible intervals. Abundance estimates were derived using the log transformation [i.e. $\exp(\beta_0) * \exp(\beta_1 * \text{urban})$].

We used a repeated measures multivariate analysis of variance (MANOVA) with site type (urban versus non-urban) as a blocking factor and time as repeated measures to evaluate the effects of urbanisation on environmental data collected at each stream. Specifically, we determined whether differences were apparent between minimum dissolved oxygen content, minimum and maximum conductivity, minimum and maximum water temperature recorded in both the first (March) and second (April) samples, and amount of silt between urban and non-urban sites. All data were examined for assumptions prior to analysis and we used appropriate transformations if needed to correct for non-normality or heteroscedasticity.

Results

We counted a total of 6558 dusky and two-lined salamanders between 2005 and 2009 [3889 two-lined salamanders (298 adults and 3591 larva) and 2669 dusky salamanders (974 adults and 1695 larva)]. Detection probabilities for salamanders varied among years, with covariates *cover*, *detritus* and *rain* having positive, negative or no effects (i.e. 95% CI overlaps with zero) dependent on stage and

species (Table 1). We did, however, find some consistent associations between sample covariates and salamander detection. The relationship between salamander detection and *rain* was always negative (i.e. lower detection if rain occurred within 24 h of sampling) if 95% credible intervals of α estimates did not contain zero (Table 1). Detection of salamanders was influenced by other covariates; however, these relationships were not consistent among species. For example, detection of larval and adult two-lined salamanders was enhanced in transects with greater number of cover objects. However, detection of larval and adult dusky salamanders was occasionally reduced as the number of cover objects increased in the stream (Table 1).

We found considerable temporal, species and stage-specific variation in our estimates of salamander abundance, with most estimates having large credible intervals (Tables 2 & 3). For example, in non-urban stream catchments, annual abundance estimates of adult dusky salamanders ranged from 12.2 (95% CI = 6.80, 29.0) to 46.6 (95% CI = 15.9; 166), whereas in urban catchments abundances of adult dusky salamanders ranged from 9.9 (95% CI = 3.52; 44.9) to 40.7 (95% CI = 8.70; 216). Other species

Table 1 Detection parameters including the posterior mean and 95% credible intervals for adult and larval dusky salamanders (*Desmognathus fuscus*) and adult and larval two-lined salamanders (*Eurycea cirrigera*) in first-order streams near Charlotte, NC, U.S.A. Annual variation in detection was modelled with covariates *cover*, *detritus* and *rain*, which we define as the total number of rocks and logs within the sampling transect, the percentage of each sampling transect covered in detritus and rain within 24 h of sampling, respectively. Posterior means represent the parameter estimate for the covariates, where 95% credible intervals reflect the probable range of posterior means given the evidence in the observed data

Year	Parameter	Dusky salamander adult		Dusky salamander larva		Two-lined salamander adult		Two-lined salamander larva	
		Posterior mean	95% credible interval	Posterior mean	95% credible interval	Posterior mean	95% credible interval	Posterior mean	95% credible interval
2005	α_0	-1.10	-2.51, -0.10	-0.87	-1.83, -0.16	-2.28	-3.62, -1.25	0.42	0.14, 0.70
	<i>Cover</i>	-0.09	-0.29, 0.10	-0.1	-0.30, -0.12	0.66	0.36, 1.01	0.15	0.005, 0.30
	<i>Detritus</i>	-0.04	-0.22, 0.12	-0.07	-0.25, 0.12	-0.16	-0.49, 0.15	0.10	-0.01, 0.21
	<i>Rain</i>	-0.43	-0.80, -0.06	-0.39	-0.71, -0.07	0.22	-0.33, 0.79	-0.78	-1.01, -0.56
2006	α_0	-1.80	-3.10, -0.85	-0.76	-1.45, -0.18	-2.66	-4.46, -1.32	-0.43	-0.74, -0.13
	<i>Cover</i>	0.21	0.08, 0.39	-0.33	-0.55, -0.13	0.32	0.03, 0.73	0.70	0.47, 0.94
	<i>Detritus</i>	0.05	-0.13, 0.24	0.01	-0.16, 1.89	0.19	-0.07, 0.46	-0.14	-0.26, -0.02
	<i>Rain</i>	-0.52	-0.92, -0.13	-0.08	-0.42, 0.27	0.04	-0.56, 0.60	0.20	-0.036, 0.43
2007	α_0	-2.22	-3.59, -0.97	-1.15	-1.77, -0.69	-1.14	-1.69, -0.68	-2.14	-2.78, -1.45
	<i>Cover</i>	0.04	-0.12, 0.19	0.13	0.01, 0.27	0.13	0.001, 0.27	0.31	0.23, 0.40
	<i>Detritus</i>	-0.15	-0.32, 0.02	0.58	0.42, 0.74	0.58	0.43, 0.74	-0.06	-0.14, 0.02
	<i>Rain</i>	-0.36	-0.68, -0.06	-0.68	-0.92, -0.46	-0.68	-0.92, -0.45	-0.25	-0.40, -0.09
2008	α_0	-2.50	-3.90, -1.13	0.001	-0.90, 0.84	-0.19	-1.50, 1.03	-2.22	-2.56, -1.88
	<i>Cover</i>	0.23	0.07, 0.44	-0.15	-0.31, 0.001	0.23	-0.24, 0.77	0.63	0.51, 0.76
	<i>Detritus</i>	-0.30	-0.50, -0.10	-0.31	-0.63, -0.02	-0.49	-1.03, 0.01	-0.17	-0.31, -0.04
	<i>Rain</i>	-0.38	-0.75, -0.02	0.28	-0.29, 0.83	-1.04	-2.20, -0.02	0.03	-0.23, 0.30
2009	α_0	-1.05	-2.12, -0.22	-0.73	-1.33, -0.19	-0.75	-2.05, 0.60	-1.28	-1.94, -0.76
	<i>Cover</i>	0.14	-0.05, 0.35	0.07	-0.09, 0.22	1.98	0.42, 3.80	0.30	0.18, 0.45
	<i>Detritus</i>	-0.05	-0.26, 0.15	0.36	0.20, 0.54	-0.41	-1.38, 0.47	-0.08	-0.19, 0.02
	<i>Rain</i>	-0.13	-0.51, 0.26	-0.01	-0.32, 0.30	0.27	-1.36, 1.96	-0.13	-0.35, 0.08

Table 2 Abundance estimates with 95% credible intervals (in parentheses) of northern dusky salamander (*Desmognathus fuscus*) adults and larvae in streams that did not undergo urbanisation of catchments and in stream catchments that were urbanised after 2005

Year	Non-urban catchments		Urbanized catchments	
	Adult	Larva	Adult	Larva
2005	12.2 (6.8, 29.0)	13.9 (8.3, 29.8)	16.7 (6.7, 54.5)	27.0 (12.4, 76.1)
2006	40.6 (12.2, 154.5)	16.9 (11.5, 27.9)	40.7 (8.7, 216.0)	8.4 (4.1, 19.1)
2007	46.6 (15.9, 165.8)	56.8 (40.7, 93.7)	39.3 (10.2, 184.6)	30.5 (17.9, 61.3)
2008	23.2 (10.7, 74.8)	5.7 (4.1, 8.8)	13.1 (4.2, 60.4)	5.7 (2.8, 12.6)
2009	24.4 (12.3, 78.6)	26.8 (19.4, 38.1)	9.9 (3.5, 44.9)	12.6 (7.1, 23.9)

Table 3 Abundance estimates with 95% credible intervals (in parentheses) of southern two-lined salamander (*Eurycea cirrigera*) adults and larvae in streams that did not undergo urbanisation of catchments and in stream catchments that were urbanised after 2005

Year	Non-urban catchments		Urbanized catchments	
	Adult	Larva	Adult	Larva
2005	8.9 (3.9, 29.4)	37.0 (33.0, 42.2)	15.1 (3.9, 83.9)	32.9 (25.0, 43.4)
2006	16.5 (5.4, 93.2)	32.6 (27.8, 38.6)	9.7 (1.6, 103.8)	21.6 (15.2, 31.1)
2007	56.4 (40.8, 87.4)	221.9 (124.1, 397.8)	30.2 (17.9, 57.1)	41.1 (18.7, 90.5)
2008	2.7 (1.6, 5.9)	49.3 (38.3, 65.0)	1.0 (0.3, 4.5)	17.4 (10.2, 30.2)
2009	1.6 (0.8, 3.4)	77.6 (54.1, 128.9)	0.4 (0.1, 2.9)	12.2 (6.4, 26.8)

and stages exhibited similar variation in estimated abundances (Tables 2 & 3). In general, however, abundance estimates in urbanised streams were lower than those of non-urban control streams, particularly as the number of years post-urbanisation increased (Tables 2 & 3).

Despite the variation in abundance estimates, we documented a negative effect of urbanisation on salamander abundances. Prior to urbanisation of stream catchments (i.e. 2005), we found that larval dusky salamanders were more abundant in urban (i.e. to be urbanised) than non-urban streams, whereas adult dusky salamanders, adult two-lined salamanders and larval two-lined salamander had similar abundances in urban and non-urban streams (Tables 2 & 3; Fig. 2). Abundances of larval two-lined salamanders and larval dusky salamanders in urban sites were different from control sites 1 year post-urbanisation of stream catchments (Fig. 2) and remained, for the most part, significantly lower throughout the duration of the study. Mean abundances of adult dusky salamanders and two-lined salamanders were similar in urban and non-urban streams 1 year post-urbanisation. However, by 2007, adult two-lined salamander abundances were lower in urban streams than in non-urban streams and remained significantly lower throughout the duration of the study. Mean abundances of dusky salamanders in urban streams were not less than abundances from control stream until 2008 (Fig. 2). Adult dusky salamander abundances were also lower in urban streams in 2009 (Fig. 2).

Maximum conductivity increased progressively over time in urban locations but remained relatively stable in our control sites from 2005 to 2009 (maximum conductivity: $F_{1,4} = 3.76$, $P = 0.007$, Fig. 3a). Similarly, siltation level within urban streams increased considerably over time, peaking in years three and four (i.e. 2008 and 2009) post-urbanisation, whereas siltation levels in non-urban streams varied little over time (siltation level: $F_{1,4} = 15.44$, $P = 7.24 \times 10^{-10}$, Fig. 3b). Maximum stream width also differed between urban and control locations and varied over time (maximum stream width: $F_{1,4} = 3.24$, $P = 0.02$, Fig. 3c). Maximum stream width decreased in urban streams one and 2 years post-urbanisation; however by 2009 (i.e. 4 years post-urbanisation), the maximum stream width in urban streams was significantly greater than the stream width of non-urban streams (Fig. 3c). The time-by-treatment interactions in the MANOVA comparing minimum DO₂, minimum and maximum March and April temperatures and maximum stream depth between urban and non-urban locations were not significant ($P > 0.05$).

Discussion

Our findings generally supported our expectations that salamander abundances would decrease in urban streams and remain relatively stable in control streams. However, estimated salamander abundances varied temporally,

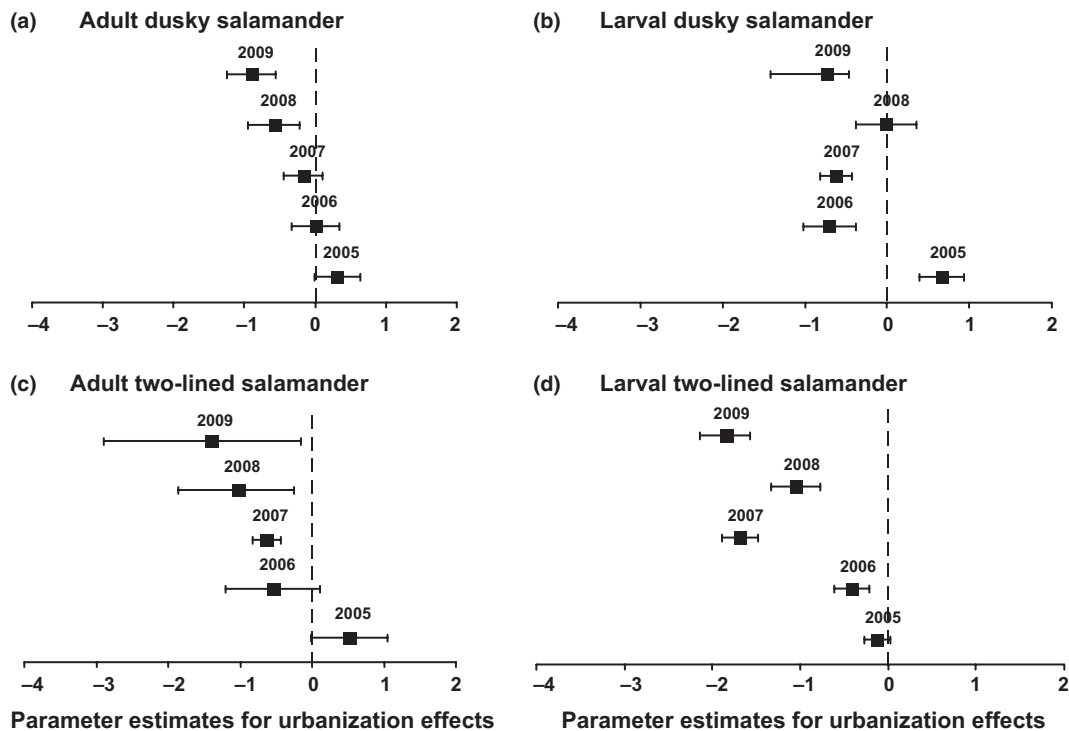


Fig. 2 Estimates of β (effect of urbanisation) on abundances of (a) adult northern dusky salamanders (*Desmognathus fuscus*), (b) larval northern dusky salamanders (*D. fuscus*), (c) adult southern two-lined salamanders (*Eurycea cirrigera*) and (d) larval southern two-lined salamanders (*E. cirrigera*) detected in 30 streams in the Charlotte-metropolitan area, North Carolina, U.S.A. Error bars indicate 95% credible intervals. Species and/or stages with parameter estimates (including 95% credible intervals) below zero declined after urbanisation.

between species and stages and between stream types. The high degree of variability in our abundance estimates contradicts investigations by Green (2003) and Hairston (1987), which suggest streamside salamander populations are generally stable, both in size and in temporal variability. Our study confirms the findings by Dodd & Dorazio (2004), which used a similar analytical method and found a high degree of variation in abundances of several salamander species in the Great Smoky Mountains National Park, U.S.A. Similar to Dodd & Dorazio (2004), however, we had a relatively limited number of samples each year (i.e. two); a greater number of samples may have decreased the variance in our estimates.

Incorporating detection estimates and covariates that affect detection can be important when investigating the responses of secretive species, like salamanders, to disturbances. Our models showed that stream salamander detection was influenced by several sampling covariates; however, these relationships varied temporally and between species and stages. These findings support the conclusions provided by Bailey *et al.* (2004) who indicated that terrestrial salamanders exhibit temporal and spatial variation in detection. Reasons for the inconsistent relationship between *cover*, *rain* and *detritus* and detection are

not readily apparent, although local abundance of species are likely influenced by several abiotic and biotic factors (i.e. McKenny, Keeton & Donovan, 2006; Connette, Price & Dorcas, 2011).

Despite the variation in abundances and detection, our results clearly demonstrated negative effects of urbanisation on salamander abundances. Four years after urbanisation of stream catchments, adult two-lined salamanders exhibited population declines of 98%, larval two-lined salamanders declined by approximately 60%, adult dusky salamanders declined by 45% and larval dusky salamanders declined by 49%. More importantly, however, estimates of abundance in non-urban streams were significantly greater than those from urbanised streams. In fact, abundances in urban streams differed from non-urban streams within 1 year post-urbanisation for larval dusky and two-lined salamanders, 2 years post-urbanisation for adult two-lined salamanders and 3 years post-urbanisation for adult dusky salamanders. With the exception of larval dusky salamanders in 2008, differences between urban and non-urban streams were evident throughout the study. By 2009, estimates of adult dusky salamanders, larval dusky salamanders, adult two-lined salamanders and larval two-lined salamanders were,

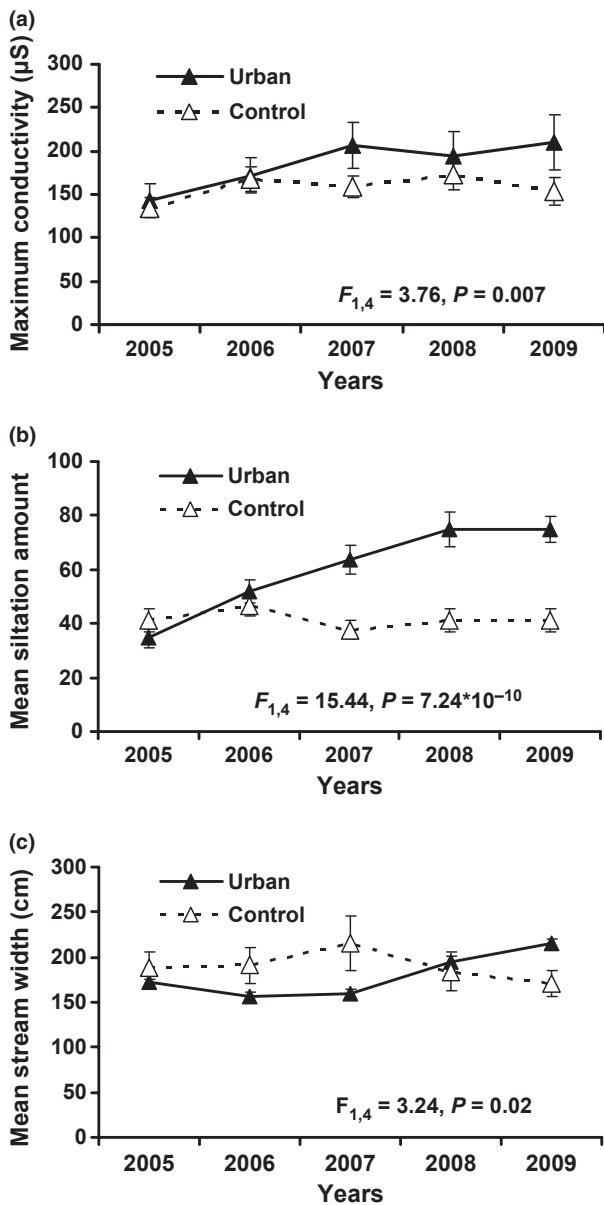


Fig. 3 Environmental conditions, including (a) mean maximum conductivity (μS), (b) mean siltation level and (c) mean stream width (cm), in urban and non-urban streams in the Charlotte-metropolitan area, NC.

respectively, 59, 53, 75 and 84% greater in non-urban streams than in urban streams. These findings indicate that for stream salamanders response time to urbanisation is rapid.

Consistent with our hypothesis, we found that abundances of larval salamanders differed between control and urban streams within 1 year of urbanisation. We speculate the rapid change in larval salamander abundances in urbanised catchments was the result of deterioration of in-stream conditions, particularly increases in sediment, modifications to stream flow (as measured

through changes in channel morphology) and possibility changes to water chemistry. We found siltation level increased significantly over time in our urbanised streams. Larval salamanders use in-stream cover objects, such as rocks, leaf litter and logs, and associated interstitial spaces as a diurnal refuge (Petranka, 1998; Smith & Grossman, 2003). The integrity of in-stream microhabitat conditions can deteriorate because of increased levels of sedimentation (Corn & Bury, 1989; Welsh & Ollivier, 1998; Lowe, Nislow & Bolger, 2004; Peterman & Semlitsch, 2008) and result in a simpler stream-bed structure, which could ultimately influence abundances (Barrett *et al.*, 2010).

Urbanisation of catchments also results in hydrologic alteration (Schoonover, Lockaby & Helms, 2006), typically rapid flood peaks and low base flows, which change channel morphology. As shown in previous studies (Booth, 1990), we also detected changes in maximum width of urban streams, almost on a year-to-year basis, with the streams significantly more narrow and then finally significantly wider than non-urban streams. Combined with simplified stream-bed structure, altered hydrology has been shown to lead to downstream drift of larval salamanders (Barrett *et al.*, 2010), which may lead to decreases in local abundances.

We also found that maximum conductivity increased in urban streams, with 2009 maximum conductivity levels 27% greater in urban streams than in non-urban streams. Conductivity, which is directly proportional to the concentrations and types of positively and negatively charged ions present in the water, can result from both natural and anthropogenic sources, but the likely contributors in our urban streams include fertilisers, pesticides, herbicides and possibly road salt entering the stream from runoff. Amphibians are sensitive to increased conductivity because it results in changes to their osmolar environments and possibly their macroinvertebrate prey (Demers, 1992). Indeed, previous studies focusing on pond-breeding amphibians have documented a negative relationship between high conductivity and abundance (Glooschenko *et al.*, 1992; Knutson *et al.*, 2004; Karraker, Gibbs & Vonesh, 2008; Schmutzer *et al.*, 2008); however, conductivity values were generally greater in these previous studies than values we observed in urban streams.

In addition to in-stream changes, reductions in salamander abundances in urban streams may also be due to changes within the stream catchments. We hypothesised that differences between species would occur, with two-lined salamanders being more sensitive to urbanisation because they use both aquatic and terrestrial habitats. Our data support this hypothesis, as two-lined salamanders

declined more than dusky salamanders in urbanised streams. Two-lined salamanders inhabit forested habitats surrounding streams (MacCulloch & Bider, 1975; Petranka, 1998) where they may be susceptible to land clearing in the stream catchment. In contrast, dusky salamanders generally do not move far (<5 m) from aquatic habitat (Petranka, 1998) and thus may be less reliant on terrestrial habitat within stream catchments. Our results are consistent with previous studies which suggest amphibians that require multiple habitats are more sensitive to habitat disturbance than species associated with a single habitat type (Rubbo & Kiesecker, 2005; Becker *et al.*, 2007; Harper, Rittenhouse & Semlitsch, 2008; Peterman & Semlitsch, 2008).

Our study implies that when investigating the effects of urbanisation on species with complex life cycles and variation in habitat use, consideration of the impacts on vital rates of both adult and larval stages is required to fully assess response to disturbance. Specifically, maintaining populations of some amphibian species in urban environments will require the preservation of both aquatic and terrestrial habitats and the implementation of appropriate measures to control for siltation and other effects of urbanisation on aquatic habitats. Our results also support the contention by many researchers (e.g. Welsh & Ollivier, 1998; Davic & Welsh, 2004; Lowe *et al.*, 2004; Welsh & Hodgson, 2008) that stream amphibians are sensitive ecologic indicators of ecosystem condition. Ecologic indicators, as defined by Niemi & McDonald (2004), are measurable characteristics of the structure, composition or function of ecologic conditions that measure the response of a system to environmental disturbance. We found that larval salamander abundances in urbanised streams differed from control streams 1 year post-urbanisation of stream catchments, indicating salamander abundance may be a useful, short-term indicator of anthropogenic stressors on stream ecosystems. However, our results also highlighted that salamander abundances exhibit some fluctuation among years and that application of abundance-based indicators may not be appropriate if population monitoring cannot be conducted before and after a disturbance, over a number of years or at many sites including both control locations and impacted locations.

Assessing the impacts of urbanisation on populations of stream biota has led to an increasing number of correlative studies documenting patterns of species occupancy, abundance and community composition along urban/rural gradients and/or comparisons between urban and non-urban sites. Our findings generally corroborate research conducted on urbanisation effects on stream invertebrates and fishes, where urban streams often have lower abun-

dances than non-urban streams (i.e. Morgan & Cushman, 2005; Burcher & Benfield, 2006; Scott, 2006). However, our study differs from those conducted previously as we employed the before-after control-impact (BACI) design to study the effects of urbanisation. Without the use of the BACI study design, the response of salamander abundances might have been less apparent or not detectable. For example, salamander abundances peaked in 2007 (i.e. 2 years post-urbanisation), with more larval two-lined salamanders and larval and adult dusky salamanders captured in urbanised streams than were captured prior to urbanisation (i.e. 2005). Without comparing data collected at urban sites to data collected at non-urban, control streams' salamander abundances would appear to increase after urbanisation. By using a BACI design, however, we were able to separate variability in salamander counts among populations because of natural fluctuations from variability in salamander counts among populations because of urbanisation. Thus, we could effectively calculate the effects of urbanisation on stream salamanders in the light of natural population fluctuations. By employing a BACI study design and using models that account for imperfect detection, this is the first study to track the temporal dynamics of animal abundances throughout the urbanisation process. Furthermore, our study is among the first to take advantage of the urbanisation process, which includes land clearing, land modification and construction, to 'experimentally' assess the effects of urbanisation on populations of stream biota.

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References

- Bailey L.L., Simons T.R. & Pollock K.H. (2004) Estimating detection probability parameters for Plethodon salamanders using the robust capture–recapture design. *Journal of Wildlife Management*, **68**, 67–79.
- Barrett K. & Guyer C. (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., Helms B.S., Guyer C. & Schoonover J.E. (2010) Linking process to pattern: causes of stream-breeding amphibian decline in urbanized watersheds. *Biological Conservation*, **143**, 1998–2005.
- Becker C.G., Fonseca C.R., Haddad C.F.B., Batista R.F. & Prado P.I. (2007) Habitat split and the global decline of amphibians. *Science*, **318**, 1775–1777.
- Booth D.B. (1990) Stream channel incision following drainage-basin urbanization. *Water Resources Bulletin*, **26**, 407–417.
- Burcher C.L. & Benfield E.F. (2006) Physical and biological responses of streams to suburbanization of historically agricultural watersheds. *Journal of North American Benthological Society*, **25**, 356–369.
- Connette G.M., Price S.J. & Dorcas M.E. (2011) Influence of abiotic factors on activity in a larval stream salamander assemblage. *Southeastern Naturalist*, **10**, 109–120.
- Corn P.S. & Bury R.B. (1989) Logging in Western Oregon: responses of headwater habitats and stream amphibians. *Forest Ecology and Management*, **29**, 39–57.
- Davic R.D. & Welsh H.H. (2004) On the ecological roles of salamanders. *Annual Review of Ecology and Systematics*, **35**, 405–434.
- Demers C.L. (1992) Effects of road deicing salt on aquatic invertebrates in four Adirondack streams. In: *Chemical Deicers and the Environment* (Ed. F.M. D'Itri), pp. 245–251. Lewis Publishers, Boca Raton, FL.
- Dodd C.K. Jr & Dorazio R.M. (2004) Using counts to simultaneously estimate abundance and detection probabilities in a salamander community. *Herpetologica*, **60**, 468–478.
- Glooschenko V., Weller W.F., Smith P.G.R., Alvo R. & Archbold J.H.G. (1992) Amphibian distribution with respect to pond water chemistry near Sudbury, Ontario. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**(Suppl. 1), 114–121.
- Green D.M. (2003) The ecology of extinction: population fluctuation and decline in amphibians. *Biological Conservation*, **111**, 331–343.
- Hairston N.G. Sr (1987) *Community Ecology and Salamander Guilds*. Cambridge University Press, Cambridge.
- Harper E.B., Rittenhouse T.A.G. & Semlitsch R.D. (2008) Demographic consequences of terrestrial habitat loss for pool-breeding amphibians: predicting extinction risk from inadequate size of buffer zones. *Conservation Biology*, **22**, 1205–1215.
- Hyde E.J. & Simons T.R. (2001) Sampling plethodontid salamanders: sources of variability. *Journal of Wildlife Management*, **64**, 624–632.
- Ihaka R. & Gentleman R. (1996) R: A language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, **5**, 299–314.
- Johnson J.E. & Goldberg A.S. (1975) Movement of larval two-lined salamanders (*Eurycea bislineata*) in the Miller River, Massachusetts. *Copeia*, **1984**, 684–688.
- Karraker N.E., Gibbs J.P. & Vonesh J.R. (2008) Impacts of road deicing salt on the demography of vernal pool-breeding amphibians. *Ecological Applications*, **18**, 724–734.
- Knutson M.G., Richardson W.B., Reineke D.M., Gray B.R., Parmelee J.R. & Weick S.E. (2004) Agricultural ponds support amphibian populations. *Ecological Applications*, **14**, 669–684.
- Leblanc R.T., Brown R.D. & Fitzgibbon J.E. (1997) Modeling the effects of land use change on water temperature in unregulated urban streams. *Journal of Environmental Management*, **49**, 445–469.
- Lepczyk C.A., Hammer R.B. & Stewart S.I. (2007) Spatiotemporal dynamics of housing growth hotspots in the North Central US from 1940 to 2000. *Landscape Ecology*, **22**, 939–952.
- Liu J., Daily G.C., Ehrlich P.R. & Luck G.W. (2003) Effects of household dynamics on resource consumption and biodiversity. *Nature*, **421**, 530–533.
- Lowe W.H. & Bolger D.T. (2002) Local and landscape-scale predictors of salamander abundance in New Hampshire headwater streams. *Conservation Biology*, **16**, 183–193.
- Lowe W.H., Nislow K.H. & Bolger D.T. (2004) Stage-specific and interactive effects of sedimentation and trout on a headwater stream salamander. *Ecological Applications*, **14**, 164–172.
- MacCulloch R.D. & Bider J.R. (1975) Phenology, migrations, circadian rhythm and effect of precipitation on the activity of *Eurycea b. bislineata* in Quebec. *Herpetologica*, **31**, 433–439.
- McKenny H.C., Keeton W.S. & Donovan T.M. (2006) Effects of structural complexity enhancement on eastern red-backed salamander (*Plethodon cinereus*) populations in northern hardwood forests. *Forest Ecology and Management*, **230**, 186–196.
- McKinney M.L. (2002) Urbanization, biodiversity and conservation. *BioScience*, **52**, 883–890.
- Miller J., Hess G. & Moorman C. (2007) Southern two-lined salamanders in urbanizing watersheds. *Urban Ecosystems*, **10**, 73–85.
- Morgan R.P. & Cushman S.F. (2005) Urbanization effects on stream fish assemblages in Maryland, USA. *Journal of the North American Benthological Society*, **24**, 643–655.
- Niemi G.J. & McDonald M.E. (2004) Application of ecological indicators. *Annual Review of Ecology, Evolution and Systematics*, **35**, 89–111.
- Orser P.N. & Shure D.J. (1972) Effects of urbanization on the salamander *Desmognathus fuscus fuscus*. *Ecology*, **53**, 1148–1154.

- Paul M.J. & Meyer J.L. (2001) Streams in the urban landscape. *Annual Review of Ecology, Evolution and Systematics* **32**, 333–365.
- Peterman W.E. & Semlitsch R.D. (2008) Efficacy of riparian buffers in mitigating local population declines and the effects of even-aged timber harvest on larval salamanders. *Forest Ecology and Management*, **257**, 8–14.
- Petranka J.W. (1998) *Salamanders of the United States and Canada*. Smithsonian Institution Press, Washington, D.C., 587 pp.
- Pickett S.T.A., Cadenasso M.L., Grove J.M., Nilon C.H., Pouyat R.V., Zipperer W.C. *et al.* (2001) Urban ecological systems: linking terrestrial ecological, physical, and socio-economic components of metropolitan areas. *Annual Review of Ecology, Evolution and Systematics*, **32**, 127–157.
- Price S.J., Dorcas M.E., Gallant A.L., Klaver R.W. & Willson J.D. (2006) Three decades of urbanization: estimating the impact of land cover change on stream salamander populations. *Biological Conservation*, **133**, 436–441.
- Price S.J., Cecala K.K., Browne R.A. & Dorcas M.E. (2011) Effects of urbanization on occupancy of stream salamanders. *Conservation Biology*, **27**, 547–555.
- Royle J.A. (2004) N-mixture models for estimating population size from spatially replicated counts. *Biometrics*, **60**, 108–115.
- Royle J.A. & Dorazio R.M. (2008) *Hierarchical Modeling and Inference in Ecology: The Analysis of Data from Populations, Metapopulations and Communities*. Academic Press, New York, NY.
- Rubbo M.J. & Kiesecker J.M. (2005) Amphibian breeding distribution in an urbanized landscape. *Conservation Biology*, **19**, 504–511.
- Schmutzer A.C., Gray M.J., Burton E.C. & Miller D.L. (2008) Impacts of cattle on amphibian larvae and the aquatic environment. *Freshwater Biology*, **53**, 2613–2625.
- Schoonover J.E., Lockaby B.G. & Helms B.S. (2006) Impacts of land cover on stream hydrology in the West Georgia Piedmont, USA. *Journal of Environmental Quality*, **35**, 2123–2131.
- Scott M.C. (2006) Winners and losers among stream fishes in relation to land use legacies and urban development in the southeastern US. *Biological Conservation*, **127**, 301–309.
- Smith S. & Grossman G.D. (2003) Stream microhabitat use by larval two-lined salamanders (*Eurycea cirrigera*) in the Georgia Piedmont. *Copeia*, **2003**, 531–543.
- Spiegelhalter D.J., Thomas A., Best N.G. & Lunn D. (2003) *WinBUGS Version 1.4 User Manual*. MRC Biostatistics Unit, Cambridge, UK.
- Welsh H.H. Jr & Hodgson G.R. (2008) Amphibians as metrics of critical biological thresholds in forested headwater streams of the Pacific Northwest. *Freshwater Biology*, **53**, 1470–1488.
- Welsh H.H. Jr & Ollivier L.M. (1998) Stream amphibians and ecosystem stress: a case study from California's redwoods. *Ecological Applications*, **8**, 1118–1132.
- Willson J.D. & Dorcas M.E. (2003) Effects of habitat disturbance on stream salamanders: implications for buffer zones and watershed management. *Conservation Biology*, **17**, 763–771.

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