

Effects of Urbanization on Occupancy of Stream Salamanders

STEVEN J. PRICE,*†‡ KRISTEN K. CECALA,*§ ROBERT A. BROWNE,† AND MICHAEL E. DORCAS*

*Department of Biology, Davidson College, Davidson, NC 28035-7118, U.S.A. †Department of Biology, Wake Forest University, Winston-Salem, NC 27109, U.S.A.

Abstract: Urban development is the most common form of land conversion in the United States. Using a before-after control-impact study design, we investigated the effects of urbanization on larval and adult stages of southern two-lined salamanders (Eurycea cirrigera) and northern dusky salamanders (Desmognathus fuscus). Over 5 years, we estimated changes in occupancy and probabilities of colonization and survival in 13 stream catchments after urbanization and in 17 catchments that were not urbanized. We also examined effects of proportion of urbanized area in a catchment and distance of the salamander population to the nearest stream on probabilities of colonization and survival. Before urbanization, adult and larval stages of the two salamander species occupied nearly all surveyed streams, with occupancy estimates ranging from 1.0 to 0.78. Four years after urbanization mean occupancy of larval and adult two-lined salamanders had decreased from 0.87 and 0.78 to 0.57 and 0.39, respectively. Estimates of mean occupancy of larval northern dusky salamanders decreased from 1.0 to 0.57 in urban streams 4 years after urbanization; however, adult northern dusky salamander occupancy remained close to 1.0 in urban streams over 5 years. Occupancy estimates in control streams were similar for each species and stage over 5 years. Urbanization was associated with decreases in survival probabilities of adult and larval two-lined salamanders and decreases in colonization probabilities of larval dusky salamanders. Nevertheless, proportion of impervious surface and distance to nearest stream had little effect on probabilities of survival and colonization. Our results imply that in the evaluation of the effects of urbanization on species, such as amphibians, with complex life cycles, consideration of the effects of urbanization on both adult and larval stages is required.

Keywords: amphibian decline, before-after control-impact study, *Desmognathus*, development, dynamic occupancy model, *Eurycea*, northern dusky salamander, southern two-lined salamander

Efectos de la Urbanización sobre la Ocupación de Salamandras de Arroyo

Resumen: El desarrollo urbano es la forma más común de conversión de suelo en los Estados Unidos. Mediante el diseño de un estudio previo y posterior del impacto del control, investigamos los efectos de la urbanización sobre la fase larvaria y adulta de dos especies de salamandras (Eurycea cirrigera y Desmognathus fuscus). A lo largo de 5 años estimamos los cambios en ocupación y las probabilidades de colonización y supervivencia en el área de influencia de 13 arroyos después de la urbanización y en 17 que no fueron urbanizados. También examinamos los efectos de la proporción de superficie impermeable en cada área de influencia y de la distancia de la población de salamandras al arroyo más cercano sobre las probabilidades de colonización y supervivencia. Previo a la urbanización, la fase adulta y larvaria de las dos especies de salamandras ocuparon casi todos los arroyos muestreados, las estimaciones de ocupación variaron entre 1.0 y 0.78. Cuatro años después de la urbanización, la ocupación media de larvas y adultos de E. cirrigera disminuyó de 0.87 a 0.78 a 0.57 y 0.39, respectivamente. Las estimaciones de la ocupación media de larvas de D. fuscus disminuyó de 1.0 a 0.57 en arroyos urbanos 4 años después de la urbanización; sin embargo, la ocupación de adultos de D. fuscus permaneció cercana a 1.0 en arroyos urbanos durante los 5 años. Las estimaciones de ocupación en los arroyos control fueron similares para cada especie y fase a lo largo de los 5 años. La urbanización fue asociada con la disminución en las probabilidades de supervivencia de adultos y larvas de E. cirrigera y con la disminución en las probabilidades de colonización de D. fuscus. Sin embargo, la proporción de superficie impermeable y la distancia al arroyo más cercano tuvo poco efecto sobre las probabilidades de supervivencia y colonización. Nuestros resultados implican, que en la evaluación de los efectos de la urbanización sobre especies, como los anfibios, que es necesario de considerar los efectos de la urbanización tanto sobre la fase adulta y como la larvaria.

Palabras Clave: declinación de anfibios, desarrollo, *Desmognathus*, estudio previo y posterior del impacto del control, *Eurycea*, modelo de ocupación dinámica

Introduction

Urbanization of terrestrial environments affects nearby stream ecosystems (Paul & Meyer 2001; Allan 2004). During the initial phase, building can add sediments to streams and lead to changes in stream-channel morphology (Paul & Meyer 2001). As impervious surface area increases within the stream catchment, the patterns of flow may change and widen and deepen stream channels (Booth & Jackson 1997). Clearing of vegetation in riparian zones, decreased groundwater recharge, and runoff from heated impervious surfaces can result in changes in stream temperature (Nelson & Palmer 2007). Storm water runoff from impervious surfaces often includes chemicals, such as heavy metals, fertilizers, pesticides, and hydrocarbons (Paul & Meyer 2001), which decrease water quality.

Urbanization of stream catchments also can affect stream amphibians (Orser & Shure 1972; Willson & Dorcas 2003a; Miller et al. 2007). Unlike fish and some aquatic invertebrates, most stream amphibians have two life-history stages and occupy both terrestrial and aquatic habitats (Becker et al. 2009). Previous investigations of the effects of urbanization on amphibian populations generally relied on gradient analysis or comparisons between urban and nonurban sites to infer the effects of urbanization (Hamer & McDonnell 2008). Furthermore, in many investigations of the effects of urbanization on amphibians researchers focused on one life stage or did not discriminate stages. Studies of a single species, stage, or combined stages cannot fully elucidate the response of populations to change because one stage may be more responsive to changes in the environment and have a disproportionate effect on probabilities of local extinction (Biek et al. 2002; Lowe et al. 2004).

To evaluate the effects of urbanization on stream amphibians, we monitored larvae and adults of northern dusky salamander (*Desmognathus fuscus*) and southern two-lined salamander (*Eurycea cirrigera*) over 5 years. We estimated changes in occupancy and probability of colonization (i.e., probability a vacant site in year x would be occupied in year x+1) and survival (i.e., probability a site occupied in year x would be occupied in year x+1) after urbanization of stream catchments and compared occupancy in urbanized catchments with occu-

pancy in stream catchments that were not urbanized. We also examined whether the proportion of urbanized area and distance to nearest first-order streams affected probabilities of survival and colonization in urbanized catchments.

Methods

Study Sites

Our study was conducted in Cabarrus, Gaston, Iredell, Lincoln, and Mecklenburg counties (part of the Charlotte metropolitan area) in the western Piedmont of North Carolina (U.S.A.). During our study, regional land cover was a mixture of second-growth forests, agricultural fields, pasture, and urbanized areas. There have been substantial increases in urban cover and simultaneous decreases of forested and agricultural cover in the area (Price et al. 2006; D. Shoemaker, personal communication). For example, from 1976 to 2006 within a 24-county area near Charlotte approximately 809,400 ha were converted from agricultural fields and forests to urban uses, an increase in urban land cover of approximately 27% (D. Shoemaker, personal communication).

We sampled salamanders in 30 first-order streams annually from 2005 to 2009. Catchments of 13 streams were cleared of some vegetation and graded in June, July, August, or September of 2005, after our first season of sampling (Fig. 1). Road building, construction of homes, and landscaping continued throughout the study. Seventeen study sites that were not developed during the study served as control sites. In general streams were semipermanent (i.e., contained flowing surface water for the majority of the year); however, in 2008 a severe drought resulted in the partial or complete lack of surface water in both control and urbanized study streams for 1–3 months.

We delineated catchments for each stream with a geographic information system (GIS) (ArcGIS, version 9.2, ArcHydro Extension, ESRI, Redlands, California). Catchment areas of the 30 streams ranged from 16 to 70 ha. At the end of the study (2009) we used GIS and aerial photographs of our study sites to calculate the proportion

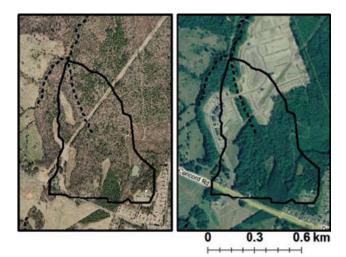


Figure 1. Example of a stream (dashed line) catchment (black polygon) before (2005, left) and after (2009, right) urbanization.

of the catchment area that had been converted to urban uses.

Salamander Sampling

We sampled salamanders in four transects in each stream. We surveyed two transects in March through early April and the other two transects in April through early May. We sampled in spring because adult and larval salamanders are concentrated around streams during this time (Petranka 1998). Transects in each stream were chosen on the basis of their similarity of width, depth, and current velocity.

We used a combination of funnel trapping, systematic dipnetting, and bank searches to sample salamanders in each stream. We trapped each stream for two, 1-week sessions, once the beginning of March through early April and once the middle of April through early May. Trapping sessions were at least 3 weeks apart. During each trapping session, we deployed 12 plastic funnel traps in a 10-m transect of the stream according to the protocol described in Willson and Dorcas (2003b). We checked traps every other day. We determined the species and development stage of salamanders and captured and released salamanders into the same sampling transect after the session was complete.

Twice in each stream we also used systematic dipnetting and bank searches to capture salamanders. One dipnetting and bank-search session was conducted from the beginning of March through early April and the other was conducted between the middle of April to early May. These sampling sessions were separated by at least 3 weeks. One person trained in sampling and identifying salamanders conducted the bank searches, searching for salamanders in leaf litter, rocks, logs, and other cover objects within 0.5 m of the stream margin. While dipnetting, one person moved upstream and actively searched for salamanders around submerged leaves, rocks, logs, and other cover within the stream (Willson & Dorcas 2003b). All salamanders captured in dipnets or found on banks were recorded, identified to species, and released when the session was complete. Each dipnetting and bank-search session was in a different 10-m transect, and each dipnetting and bank-search transect was separate from each funnel-trap transect. The same dipnetting and bank-search transects and trapping transects were sampled each year of the study. We did not sample one study site in 2008 and 2009, and in 2009 we did not sample two study sites. These three study sites were control streams.

Statistical Analyses

We used dynamic occupancy models (Royle & Kéry 2007; Royle & Dorazio 2008) to evaluate the stage and speciesspecific effects of urbanization on stream salamanders. These models allow for estimation of occupancy, colonization, survival, and detection; incorporation of site-level and survey covariates; approximation of the uncertainty associated with parameter estimates; and can accommodate missing observations. Dynamic occupancy models use the "robust design" (Pollock 1982) sampling design in which repeated presence-absence surveys of sites occur across a number of primary sampling periods. Secondary sampling periods occur within primary sampling periods and are assumed to be demographically closed. Occupancy status may change among primary periods as a result of extinction or colonization events, but occupancy status does not change among secondary sampling periods.

We had five primary sampling periods (years 2005-2009) and two secondary sampling periods in each primary sampling period. We categorized the outcome of sampling in each secondary period as either detection or nondetection separately for each stage and species category (e.g., larval *D. fuscus*, adult *E. cirrigera*). Following Royle and Dorazio (2008), z(i, t) is the true occupancy status of site *i* during time *t* and has possible states of occupied (z = 1) or not occupied (z = 0) for each species and stage. Because species are rarely detected perfectly, z(i, t) is unobserved or partially unobserved.

To account for imperfect detection, we used the two secondary sampling periods at each site, denoted as $y_j(i,t)$ for samples j = 1,2 of site *i* during season *t*. We assumed samples $y_j(i,t)$ were independent and identically distributed (i.i.d.) Bernoulli trials with parameter p_{it} (detection probability). We defined $\mathbf{y}(i, t) = y_1(i, t), y_2(i,$ $t), \ldots, y_{30}(i, t)$ as the vector of all salamander samples for site *i* and primary period *t*. Secondary sampling periods yielded detection and nondetection data from the three sampling methods (i.e., trapping and dipnetting and bank searching) used at each stream during the first (early March through early April) and second (middle of April through early May) sampling periods. The two secondary samples resulted when we condensed our sampling data from trapping, dipnetting, and bank searching for the first sampling period so that data would reflect detection by at least one method or nondetection by all methods for the first sample period. Similarly, detection of a salamander by at least one method during the second sampling period was considered a detection.

The dynamic occupancy model is formulated as a hierarchical or state-space model, expressed by two component processes: a submodel for the observations conditional on the unobserved state process (i.e., $\mathbf{y}(i, t)$ | z(i, t)) and a submodel for the unobserved or partially observed state process (z(i, t); i = 1, 2, ..., t = 1, 2,...). The state model is formulated in terms of initial occupancy probability (ψ_1), local survival probabilities of populations ($\Phi_t, ..., \Phi_{T-1}$), and colonization probabilities ($\gamma_t, ..., \gamma_{T-1}$). We assumed the initial occupancy states were i.i.d. Bernoulli random variables,

$$z(i, 1) \sim \text{Bern}(\psi_1) \text{ for } i = 1, 2, \dots, M,$$
 (1)

where M is the total number of sites, whereas in subsequent periods

$$z(i, t)|z(i, t-1) \sim \text{Bern}[\pi(i, t)] \text{ for } t = 2, 3, \dots, T, (2)$$

where T is the number of primary sampling periods and

$$\pi(i,t) = z(i,t-1) \Phi_{T-1} + [1 - z(i,t-1)] \gamma_{T-1}.$$
 (3)

The observation model is

$$y(i,t)|z(i,t) \sim \operatorname{Bern}\left[z(i,t)\,p_t\right].\tag{4}$$

For the observation model, if a site is occupied at time t, the data are Bernoulli trials with parameter p_t . If a site is not occupied at time t, then the data are Bernoulli trials with Pr(y[i,t] = 1) = 0.

Primary parameters of the dynamic occupancy model include initial occupancy probability (ψ_i), survival probability (Φ_i), colonization probability (γ_t), and detection probability (p_i). We derived occupancy probability for each species and stage during each year according to

$$\psi_t = \psi_{t-1} \ \Phi_{t-1} + (1 - \psi_{t-1})\gamma_{t-1}.$$
(5)

Because our scope of inference was the sites at which our data were collected as opposed to a theoretically infinite population of sites, we used finite sample estimates of population parameters (e.g., $\psi_t^{(fs)}$) (Royle & Kéry 2007).

To evaluate the stage- and species-specific effects of urbanization on salamander occupancy, we included the term $\alpha * \mathbf{urban}(i)$ in the occupancy model so that

log it(
$$\pi_{i,t}$$
) = $\alpha_0 (t-1)$
+ $\alpha_1(t-1) * z(i, t-1)$ (6)
+ $\alpha_2 * urban(i)$,

where **urban** is a vector of zero if the catchment within which a site was located was not urbanized or 1 if the catchment was urbanized and α_2 is the species- and stagespecific effect of urbanization, which we assumed to be random such that $\alpha_i \sim N(\mu_{\alpha_i}, \sigma_{\alpha_i}^2)$ (*N*, population; μ , mean; σ^2 , variance). We used 14 parameters (i.e., five year-specific *p*, four year-specific intercepts, four yearspecific autologistic regression parameters, one parameter to describe the effects of location on occupancy) to describe the occupancy dynamics.

We also used the autologistic parameterization of the dynamic occupancy model (Royle & Dorazio 2008) to evaluate effects of urbanization on colonization and survival probability for each species and stage. We included the term $\alpha * \mathbf{urban}(i)$ in the occupancy model so that

$$\log \operatorname{it}[\pi(i, t)] = \alpha_0(t - 1) + \alpha_1(t - 1) * z(i, t - 1) + \alpha_2 * \operatorname{urban}(i) + \alpha_3 * \operatorname{urban}(i) * z(i, t - 1),$$
(7)

where $\alpha_2 * \mathbf{urban}(i)$ and $\alpha_3 * \mathbf{urban}(i) * z(i,t-1)$ indicate the interaction of the covariates with z(i,t-1). We used 15 parameters (i.e., five year-specific p, four year-specific intercepts for γ , four year-specific intercepts for Φ , location effects on γ and Φ) in this model.

We also used the autologistic parameterization of the dynamic occupancy model to parameterize the effects of proportion of the catchment that was urbanized and Euclidean distance to the neighboring stream on probabilities of colonization and survival in the 13 streams with urbanized catchments. Amount of urbanization and distance to nearest stream were calculated with GIS and standardized prior to statistical analyses. To include separate effects of each covariate on colonization and survival probability, the occupancy model was

$$\log it[\pi(i, t)] = \alpha_0(t - 1) + \alpha_1(t - 1) * z(i, t - 1) + \alpha_2 * amount (i) + \alpha_3 * distance (i) + \alpha_4 * amount (i) * z(i, t - 1) + \alpha_5 * distance (i) * z(i, t - 1),$$
(8)

where $\alpha_4 * \operatorname{amount}(i) * z(i,t-1)$ and $\alpha_5 * \operatorname{distance}(i) * z(i, t-1)$ indicate the interaction of the covariates with z(i,t-1).

Bayesian Inference

To estimate population parameters for each stage and species, we performed a Bayesian analysis of dynamic occupancy in the software package WinBUGS (version 1.4) (Spiegelhalter et al. 2003). We organized data in R (version 2.10) (Ihaka & Gentleman 1996) and executed WinBUGS in batch mode with the R add-in library

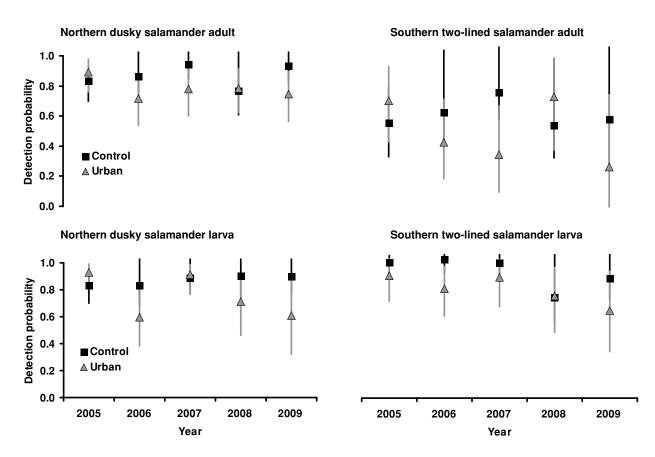


Figure 2. Estimated annual probabilities of detection of larval and adult salamanders at 30 first-order streams in the study area (urban, 13 streams in catchments in which urbanization occurred; control, 17 streams in catchments in which urbanization occurred; control, 17 streams in catchments in which urbanization did not occur during the study; error bars, 95% CIs).

R2WinBUGS. Our models used uninformative priors, following the standard uniform distribution. Using uninformative priors places equal probability on parameter values, which may be particularly useful in analyzing ecological data where little prior information is available (Royle & Dorazio 2008). Posterior summaries were based on 35000 Markov chain Monte Carlo iterations, in which we disregarded the first 5000 iterations as burn-in, and a thinning rate of 10. We calculated the mean and standard deviation of the model coefficients and the 95% Bayesian credible intervals (CI).

Results

On average 35% (range 1–78%) of each catchment was converted to urban uses. Throughout the study, estimates of detection probability for stream salamanders at control sites were relatively stable (Fig. 2), whereas detection probability at sites in urbanized catchments was, in general, slightly lower for both species and stages. Nevertheless, 95% CI for urbanized and control streams overlapped in all years for each stage and species, which indicates there was little effect of urbanization on our ability to detect salamanders (Fig. 2).

Estimated occupancy for each stage and species remained relatively stable in control sites throughout the study, although relative to occupancy at the beginning of the study, occupancy by larval dusky salamanders in 2008 and adult two-lined salamanders in 2009 decreased (Fig. 3). Overall the trend was toward decreased occupancy from 2005 to 2009 for adult and larval two-lined salamanders and larval northern dusky salamanders in urbanized catchments (Fig. 3). Estimates of occupancy of control sites and urbanized sites differed for larval twolined salamanders in 2007 (95% CI: control, 0.941-0.942; urban, 0.77-0.923) and 2009 (control, 0.88-1.00; urban, 0.46-0.85); adult two-lined salamanders in 2007 (control, 0.94-1.00; urban, 0.38-0.92) and 2008 (control, 0.65-1.00; urban, 0.38-0.62); and larval dusky salamanders in 2007 (control, 1.00-1.00; urban, 0.84-0.92) and 2009 (control, 0.88-1.00; urban, 0.46-0.85). Occupancy rates of adult dusky salamanders remained stable at both control and urbanized sites throughout the study.

Urbanization of stream catchments was associated with a decrease (i.e., 95% CI of parameter estimates of urbanization effect did not contain zero) in occupancy of adult

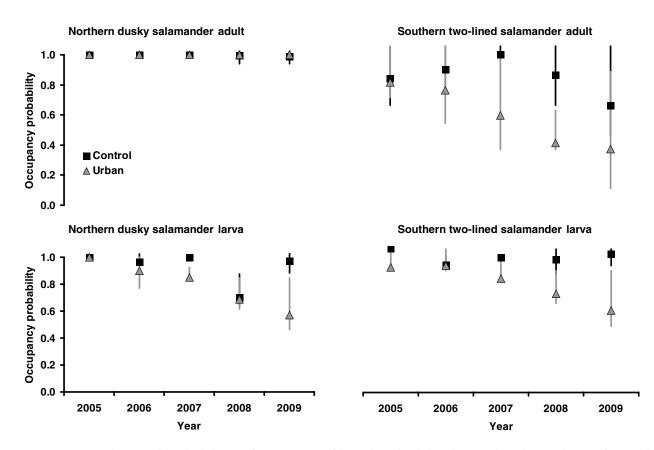


Figure 3. Estimated annual probabilities of occupancy of larval and adult salamanders detected at 30 first-order streams in the study area (urban, 13 streams in catchments in which urbanization occurred; control, 17 streams in catchments in which urbanization did not occur during the study; error bas, 95% CIs).

two-lined salamanders, larval two-lined salamanders, and larval dusky salamander (Fig. 4a). Urbanization was not associated with a decrease in occupancy of adult dusky salamanders (Fig. 4a). Urbanization was associated with a decrease in survival probabilities of adult two-lined salamanders and larval two-lined salamanders (Fig. 4b). Urbanization was associated with a decrease in colonization probabilities for larval dusky salamanders (Fig. 4c). Probabilities of colonization and survival of adult dusky salamanders did not differ between sites in urbanized and control catchments (Fig. 4a,b).

Despite the association between urbanization and decreases in occupancy of adult two-lined, larval two-lined, and larval dusky salamanders, our models estimated these species would continue to occupy sites in some urbanized catchments (Fig. 3). Nevertheless, the proportion of the catchment that was urbanized was associated with decreases in survival of only larval northern dusky salamanders (-1.95; 95% CI -4.49 to -0.04) and suggested that higher proportions of urbanization within a catchment were associated with decreases in probability of survival. Distance to nearest stream did not explain substantial variance in colonization for any species

or stage (95% CI of all parameter estimates contained zero).

Discussion

Our results suggest that stream salamander occupancy decreased in response to urbanization. Nevertheless, species and developmental stage differed in their responses to urbanization. Occupancy of larval stages of dusky and two-lined salamanders were high (i.e., $\psi_t^{(fs)} = 1.0$ prior to urbanization, but decreased by approximately 40% 4 years after urbanization, whereas occupancy in control sites remained stable. Likewise, occupancy of adult two-lined salamanders decreased, on average, by 40% 4 years after urbanization but remained relatively stable at control sites. Occupancy of adult dusky salamanders at urbanized and control sites, however, did not change throughout the study. Our results indicate changes in occupancy were likely due to reductions in survival probabilities of adult and larval two-lined salamanders and reduced

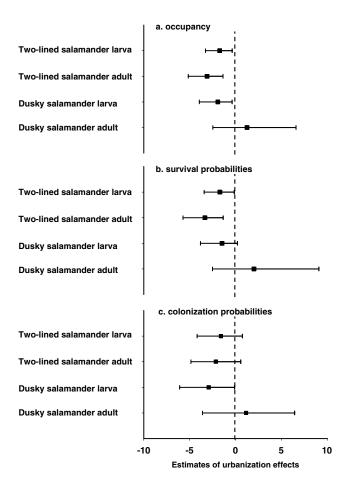


Figure 4. Estimates of α (effect of urbanization [i.e., conversion of undeveloped land to developed land]) on (a) occupancy, (b) survival probabilities, and (c) colonization probabilities of larval and adult salamanders detected at 30 streams in the study area (error bars, 95% CIs).

colonization probability of larval dusky salamanders in urbanized catchments. With the exception of decreased survival of larval dusky salamanders in catchments in which a greater proportion of area was urbanized, our results also suggest that proportion of catchment that was urbanized and distance to nearest stream had little effect on probabilities of colonization and survival of salamanders.

Differences in the apparent response of species and stages to urbanization reflect the species' biological attributes and life histories. Rubbo and Kiesecker (2005) suggest amphibian species that require different habitat types, particularly forests and water, at different life stages are more responsive to urbanization than species associated strictly with aquatic habitats. We believe that decreases in occupancy rates of adult two-lined salamanders in urbanized stream catchments were due, at least in part, to the decreased probability of survival in those catchments. Conversely, occupancy of adult dusky salamanders remained stable in streams in urbanized catchments. These species differ considerably in their use of terrestrial areas.

Northern dusky salamanders generally do not leave their aquatic habitat (Petranka 1998). Two-lined salamanders, in contrast, migrate from their aquatic habitat to forests (MacCulloch & Bider 1975; Petranka 1998), where they may be negatively affected by clearing of trees in the stream catchment. Our findings are consistent with those of Peterman and Semlitsch (2008), who found that the abundance of the semi-aquatic Blue Ridge two-lined salamander (*E. wilderae*) decreased 2 years after tree harvest, whereas the aquatic black-bellied salamander (*D. quadramaculatus*) did not. Peterman and Semlitsch (2008) suggest black-bellied salamanders may be more resistant to the immediate effects of forest harvest because they occur primarily within 5 m of streams.

Our results highlight that adult and larval stages may have different responses to urbanization. Annual occupancy of larval salamanders of both species decreased following urbanization, whereas adult occupancy decreased for only two-lined salamanders. We suspect the greater response of larvae to urbanization reflects increased levels of sedimentation within streams, which likely reduces interstitial spaces and availability of cover (Welsch & Ollivier 1998; Lowe et al. 2004). This explanation is consistent with results of several previous studies on the effects of sedimentation on stream amphibians (Welsch & Ollivier 1998; Lowe et al. 2004). The increase in sedimentation may also reduce the availability of nesting sites for two-lined and dusky salamanders, which could lead to a reduction in larval abundance. Both species regularly nest under cover, and Guy et al. (2004) found that two-lined salamanders avoid nesting in areas with high levels of silt substratum.

Urbanization of catchments modifies the hydrology of streams and results in rapid flood peaks and low base flows (Paul & Meyer 2001; Schoonover et al. 2006). These factors may also influence survival of larval and potentially adult stream salamanders. Severe flood events can wash away cover objects (Pratt et al. 1981), such as leaves and logs, destabilize channels (Snodgrass et al. 2007), and potentially lead to downstream drift of larval salamanders, which may reduce local survival and ultimately occupancy. Barrett et al. (2010) found that southern twolined salamanders on substrate typical of streams in urban catchments (i.e., sand) are displaced downstream at significantly lower water velocities than larvae on substrates (i.e., rocks) typical of streams in catchments that have not been urbanized. Additionally, the reduction in base-flow conditions, as a result of a greater proportion of precipitation leaving urbanized catchments via drainage sewers, may influence larval survival. To complete development, larvae of dusky and two-lined salamanders must survive through at least one period of low water, usually occurring in late summer. If the stream lacks surface water for

prolonged periods during larval development, survival of larval salamanders may decrease.

We found that proportion of urban land cover in a catchment and distance of the salamander population to neighboring streams had little effect on probabilities of survival and colonization of stream salamanders. Both covariates are positively correlated with salamander occupancy and abundance (Lowe & Bolger 2002; Willson & Dorcas 2003a; Grant et al. 2009) and may mitigate the effects of urbanization on occupancy. We found the proportion of catchment converted to urban cover had an effect only on larval dusky salamander survival, and distance to nearest stream did not significantly affect either of our study species or stages. This suggests that other factors besides proportion of urban area and spatial arrangement of streams in the landscape influence probabilities of colonization and survival. It is possible, however, that the effects of proportion of urban cover and spatial arrangement of streams on probabilities of colonization and survival of salamanders are not yet apparent within 4 years after urbanization.

Our results augment inferences from correlative studies on urbanization and stream salamanders, especially within the Piedmont region. Price et al. (2006) used predictive models developed by Willson and Dorcas (2003a) and found that the increased rate of urbanization from 1972 to 2000 near Davidson, North Carolina, may have led to the declines in abundance of stream salamanders in this region. Price et al. (2006) could not clarify, however, whether a time lag existed between salamander decline and urbanization. Our results indicate that occupancy for some stream salamander species decreases immediately following urbanization events and continues to decline 4 years after urbanization. We found that 4 years after urbanization, the occupancy of the populations we studied did not return to preurbanization levels. Thus, our results do not support the notion that there may be a lag time of several decades between changes to amphibian habitat and a species-specific response, as other researchers suggest (Findlay & Bourdages 2000; Löfvenhaft et al. 2004). We acknowledge, however, that differences between regions and amphibian species (i.e., pond breeding vs. stream breeding) likely exist.

Our results suggest that the relative response of larval and adult salamanders to urbanization varies among species. Populations may be more likely to persist over the moderate to long term if adults are less sensitive to urbanization than larvae. Conversely, if both adult and larval stages are sensitive to disturbance, populations may decrease over a relatively short time.

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