



Effects of even-aged timber harvest on stream salamanders: Support for the evacuation hypothesis

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ABSTRACT

Habitats worldwide are increasingly threatened by degradation and conversion. Critical to the process of habitat loss is the organismal response, which can have effects on immediate conservation measures or future restoration. Among the most threatened and underappreciated habitats are headwater streams, which are small but abundant features of montane forests. These habitats comprise a significant proportion of the total stream length, can harbor remarkable biodiversity, and are critical for numerous ecosystem processes. One of the most abundant organisms in montane headwater ecosystems are salamanders, and therefore what happens to salamanders when the forest habitats surrounding headwater streams are altered? Three main hypotheses exist: (1) mortality hypothesis; (2) retreat hypothesis; and (3) evacuation hypothesis. To examine these hypotheses we evaluated the impacts of even-aged riparian timber harvest on stream-breeding salamanders. Riparian forests along headwater streams were logged, leaving riparian buffers of 0 m, 9 m, and 30 m. Responses to each riparian alteration were measured in terms of salamander terrestrial habitat use and growth in the riparian habitat, as well as changes in population density within headwater streams. Adult and juvenile salamander densities measured in headwater streams were significantly greater in logged riparian treatments than in unaltered riparian treatments. In addition, salamanders significantly reduced their terrestrial habitat use following riparian logging with both the average distance from the stream and the relative abundance of salamanders decreasing. It is unlikely that salamanders will persist in highly modified riparian habitats, as we measured significantly reduced body conditions over short periods of time at these sites. We present corroborative evidence that salamanders evacuate the riparian habitat following intensive riparian logging, emigrating to adjacent headwater streams. Our results underscore the sensitivity of stream salamanders to riparian habitat alteration as well as the importance of riparian buffers in preserving amphibian assemblages.

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1. Introduction

Headwater streams are generally small, lotic waterways that conservatively account for more than 70% of the total stream length (Meyer and Wallace, 2001; Naiman et al., 2005; Peterman et al., 2008). Though seemingly insignificant in size, headwaters provide important services such as flood control, recharge of groundwater, recycling nutrients, maintenance of biological diversity, and resources for the biological productivity of downstream rivers, lakes, and estuaries (Meyer et al., 2003). Despite these benefits and services, headwater streams in the United States have been largely overlooked in policy and management guidelines

(e.g., Adams, 2007; Olson et al., 2007), making them susceptible to development and forestry. The majority of existing stream-riparian management guidelines have arisen around the resources and needs of fish species (Naiman et al., 2000). This restricted scope leaves shallow, fishless headwater systems vulnerable to degradation or alteration (Lowe and Likens, 2005), and it is these habitats throughout the Pacific Northwest and the Appalachian Mountains of the eastern United States that harbor numerous endemic amphibians, especially salamanders (Petranka, 1998; Welsh and Hodgson, 2011). Many salamanders have complex life histories that depend on aquatic habitats for reproduction and larval development, and riparian habitats for foraging and over-wintering (Barbour et al., 1969; Ashton and Ashton, 1978; Petranka, 1998). These life history traits can make some salamanders useful for monitoring the health and integrity of ecosystems (Welsh and Droege, 2001; Southerland et al., 2004).

There has been minimal research in the Appalachians addressing the effects of logging or other land uses on stream-dependent

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salamander populations. Terrestrial salamander populations are known to decrease following logging (de Maynadier and Hunter, 1995; Harpole and Haas, 1999; Grialou et al., 2000; Knapp et al., 2003), but the majority of these studies (e.g., Petranksa, 1993; Ash and Bruce, 1994; Crawford and Semlitsch, 2008b) do not provide direct evidence of the ultimate fate of salamanders. In order to develop effective management practices that preserve biodiversity and ecosystem health, processes leading to population declines must be understood. Three primary hypotheses have been suggested regarding the response of amphibians following logging that include (Semlitsch et al., 2008): (1) mortality hypothesis—reduced abundance from the death of salamanders as a result of desiccation, starvation, or loss of refuge (e.g., Petranksa, 1993, 1994); (2) retreat hypothesis—salamanders remain and survive in cut forests after logging in underground refugia, exhibiting reduced or limited activity (e.g., Johnston and Frid, 2002); and (3) evacuation hypothesis—salamanders leave logged areas seeking more suitable habitat and microclimates (e.g., Reichenbach and Sattler, 2007; Semlitsch et al., 2008). None of these hypotheses are mutually exclusive and their applicability likely depends on the type and intensity of logging and the species affected (Semlitsch et al., 2008).

To identify which of these processes is occurring, it is important to understand the responses of salamanders in both aquatic and terrestrial stages following riparian forest alteration. Here, we focus on the near term patterns that would likely emerge for each hypothesis following riparian logging. Stream salamanders in the Appalachians are predictably distributed up to 100 m away from streams into the surrounding riparian forest (Organ, 1961; Crawford and Semlitsch, 2007). If salamanders suffer high rates of direct mortality as a result of logging, we would expect to see an overall decrease in salamander abundance (Petranksa, 1993). Additionally, terrestrial habitat use will likely become confined to remaining forested areas near streams, resulting in a contraction of the terrestrial habitat use. The retreat hypothesis is likely to be indistinguishable from the mortality hypothesis in the short term, as salamander abundance will also appear depressed and terrestrial habitat use will be reduced, with the exception that salamanders still persist, but are less active and visible. Lastly, the evacuation hypothesis is likely to be characterized by a behavioral response of salamanders moving off and away from unsuitable habitat. Like the previous two hypotheses, this movement will result in a reduced number of salamanders in altered terrestrial habitat as well as a contraction of the terrestrial habitat occupied. The key differences are that mortality will be limited and surface activity will not be reduced, meaning that animals previously found away from the stream will actively seek more favorable habitat, potentially causing an increase in abundance in the remaining suitable habitat (Reichenbach and Sattler, 2007; Semlitsch et al., 2008). In stream-dependent salamanders this will likely mean that salamanders will leave altered terrestrial habitat and move toward or even into the stream. Once in the stream, salamanders may continue to disperse up or down stream. Although not mutually exclusive, the preponderance of evidence will likely support one hypothesis more than another. It is important to distinguish among the three primary hypotheses in order to mitigate the effects that land uses have on populations. By identifying the mechanisms underlying the population declines we can better anticipate and understand future patterns of recovery. For example, if the response is retreat or evacuation, declines may not be irreversible. Populations may be only temporarily depressed until vegetation and microclimates are restored, and salamanders may recolonize the area and/or resume normal surface activity.

We assessed the effectiveness of riparian buffers in mitigating riparian logging effects on adult and juvenile stream salamanders in the first two years following even-aged riparian forest removal. Specifically, we measured the abundance, terrestrial habitat use, growth, in-stream capture frequency, and in-stream population

density of adult and juvenile stream salamanders in relation to riparian buffers. These measurements were evaluated in terms of current hypotheses predicting the fate of salamanders following even-aged timber harvest, allowing for assessment of current riparian buffer regulations.

2. Methods

2.1. Study area

Five southern Appalachian headwater streams were monitored to determine the effects that riparian buffer width has on adult salamander populations. These sites represented independent streams, and were chosen by the US Forest Service for their similar gradients, catchment sizes, and previous logging history as part of a larger research project assessing riparian buffer management. Streams drained small watersheds (<10 ha) within the Wine Spring Creek study area of the Wayah Ranger District, Nantahala National Forest, Macon County, North Carolina, USA (35.20°N, –83.51°W). Sites were located at elevations of 800–900 m, and flowed through closed-canopy upland hardwood and cove hardwood forests that primarily consisted of an oak (*Quercus* spp.), hemlock (*Tsugacanadensis*), tulip popular (*Liriodendron tulipifera*), and hickory (*Carya* spp.) overstory, with rhododendron (*Rhododendron* spp.) dominating the understory along streams. All sites had forest of similar stand age (70–80 yr; O’Keefe, 2009). Sites were logged using a 2-age shelter wood harvest (hereon even-aged timber harvest), where a few mature trees were left for regeneration purposes, but all other harvestable timber was felled and removed. Tower logging was utilized to minimize on-the-ground impacts of machinery on steep mountain slopes; no logs or machinery ever entered or cross the study streams during timber harvesting. Logging resulted in one of four riparian zone alterations: 0 m forest retained (complete upland forest harvest; $N = 1$), 9 m forest retained ($N = 1$), 30 m forest retained ($N = 1$), and control (no upland forest removal; $N = 2$). Target residual basal area and stem density outside the buffers following harvest ranged from 3.4–4.6 m² ha⁻¹ and 20–30 stems ha⁻¹ of 30–40 cm diameter at breast height overstory vegetation. Logging treatments were completed on both sides of the stream and extended for 200 m parallel to the stream and up to 200 m away from the stream. Logging of the 0 m and 9 m sites occurred from October 2005 to May 2006 and logging of the 30 m site occurred from June 2006 to September 2006. After logging, roads were reshaped and seeded with grass. Subsequent road use has been restricted to light-weight vehicles traveling to the experimental areas.

2.2. Sampling protocol

We used three different methods (leaf litter bag sampling, removal sampling, and line transects) to survey metamorphosed salamanders within the stream and surrounding riparian forest. None of these sampling methods were conducted on the same day. Sampling locations of litter bags and origins of terrestrial transects were spatially separated ≥ 10 m. Removal sampling did not commence until litter bag and transect sampling was complete. With the exception *Eurycea wilderae*, focal salamanders of this study are known to be relatively philopatric (home ranges < 8.5 m²), and move only short distances between observations (Huheey and Brandon, 1973; Kleeberger, 1984; Camp and Lee, 1996; Peterman et al., 2008). As such, salamanders observed using each method can be considered independent observations with little to no double counting.

2.2.1. Leaf litter bag sampling

To sample in-stream salamander populations, each stream was divided into three 40 m sampling blocks that were each subdivided

into four 10 m subsections; each block was separated by 40 m (see Peterman, 2008 for figure of block layout). Salamanders were captured using leaf litter bags (Pauley and Little, 1998; Waldron et al., 2003) made from 1.9 cm² polypropylene mesh. Four litter bags were systematically distributed in each 10 m subsection ($n = 16$ per 40 m section) and a total of 48 leaf bags were deployed at each study site. Bags were checked by shaking them over a white tray for approximately 20 s. Water and sediments collected in the trays were then poured through a 15 × 20 cm baitnet. In 2006, only the 0 m, 9 m, and Control 1 streams were monitored. Trapping intensity differed between years; there were eight trapping periods in 2006 and five periods in 2007. To account for these differences, relative abundance estimates were converted into rates (salamanders captured per trapping period).

2.2.2. Removal sampling

To estimate in-stream population sizes of metamorphosed salamanders, removal sampling was conducted from 11 to 16 July 2007 following the completion of leaf bag trapping and riparian transect searches. Three 3 m blocks were randomly selected at each stream without regard to previous litter bag sampling; each block included 1 m of riparian habitat on each bank. Sampling blocks were spaced at least 10 m apart, and were at least 50 m from the forest-cut edge. Each 3 m removal block was searched at night by one researcher until no salamanders were found for 5 min. Only surface-active salamanders were captured and no cover objects were disturbed during the searches. Each block was surveyed twice in a night at least 2 h apart, and sites were surveyed six times total in a six day period. Removal surveys were conducted from 2200–0330 EST, with survey times rotating on each subsequent visit to a site. Captured salamanders were retained in climate-controlled chambers at Highlands Biological Station until the completion of the study, but were returned to the site of capture following the sixth and final removal sampling period.

2.2.3. Riparian transects

To determine stream salamander distribution in the terrestrial riparian habitat, one line transect was established perpendicular to the stream edge from 2004 to 2007 at four of the five sites (0 m, 9 m, 30 m, and Control 1). Nighttime sampling was conducted using visual encounter searches to capture surface-active salamanders. Three night transects were conducted at each site during each field season. During each sample, two researchers walked the line transect from the stream edge out to 100 m, recording distance from the stream edge for each salamander encountered. Each researcher searched 2.5 m to the right and left of the transect line, respectively. All salamanders were identified to species, measured for snout-vent length and total length, weighed, and released at the point of capture (Crawford and Semlitsch, 2007).

2.2.4. Salamander enclosures

To assess body condition due to buffer treatments over time, we experimentally caged 10 *Desmognathus ocoee* in the terrestrial riparian habitat at each of three study sites in 2006 (0 m, 9 m, and Control 1). Salamanders were housed individually in rectangular Rubbermaid® containers (61 × 41 × 22 cm) that had the lid, bottom and the upper half of the long edges cut away. Cut-out areas were covered with 3.2 mm screening to permit water and nutrient flow, but retain salamanders. Enclosures were placed 8 m from the stream edge. This distance corresponded with the mean distance that *D. ocoee* were found from the stream in 2004 and 2005 across all sites prior to logging (Crawford, 2007). Enclosures were buried so that the surrounding soil surface was flush with the top screen of the cage. After excavating the hole to bury the enclosure, the soil was returned to the enclosure to make it

level with the surrounding soil; leaf litter was added to the approximate depth of the surrounding area. A small square of carpet (15 × 15 cm) was saturated in water and placed in the upslope, left corner of the cage to provide a moist microhabitat and to facilitate recapture of salamanders during daytime data collection.

One adult male salamander with an intact tail was randomly assigned to each enclosure. All salamanders were weighed prior to stocking using a portable digital balance (Acculab Pocket-Pro® Model PP-62). Enclosures were checked bi-weekly for eight weeks and the mass and length of salamanders recorded. All cages were checked during each sample period whether or not a salamander was found on the previous search.

2.3. Environmental data

Environmental data were collected at all sites except Control 2 during the day at monitoring stations located at 1, 3, 7, 10, 15, 25, 50, and 100 m from the stream bank. Monitoring station distances were selected based on the home range sizes and potential distances traveled by the target species of stream-breeding salamanders (Crawford and Semlitsch, 2007). Data was collected at each monitoring station for four environmental variables: (1) leaf litter depth—measured six times per station using a ruler for an average leaf litter depth value; (2) surface soil temperature—measured six times per station using an infrared Raytek® MT4 temperature gun for an average temperature value; (3) soil moisture—measured six times per station using an Aquaterr® M300 soil moisture meter for an average soil moisture value; and (4) Canopy cover—measured two times per station using a spherical crown densiometer for an average canopy cover value. Data was collected at each station three times per season in each of the four field seasons (2004–2007).

2.4. Data analysis

2.4.1. Leaf litter bag sampling

We used a general linear model analysis of variance to test for significant differences in the three main factors (buffer treatment, species, and year). Because we lacked site replication, we only assessed the significance of these main effects, and used the remaining interaction terms to estimate our error mean square (Cochran and Cox, 1957, pp. 218–219). Although we cannot state with certainty, we assume that interaction terms are not significant. Capture rates (salamanders captured per trapping period) were square-root transformed to meet assumptions of normality.

2.4.2. Removal sampling

Salamander removal data were analyzed using Huggins closed captures with heterogeneity (Huggins, 1989) in program MARK (Version 4.2). Prior to analysis, capture histories for each of the three removal blocks were pooled together to create a single capture history for each study stream. Because time varied with each sampling period and nocturnal activity of salamanders varies throughout the night (Hairston, 1949; Keen, 1984), an individual covariate of sample time was incorporated into removal models. Due to the discrete sampling period (6 days) and relative philopatry of salamanders (Huheey and Brandon, 1973; Kleeberger, 1984; Camp and Lee, 1996; Peterman et al., 2008), we are confident that births and deaths are a nonissue, while immigration and emigration can be considered negligible. In another removal experiment, Hairston (1986) found no evidence for immigration into removal plots by either *Desmognathus monticola* or *Desmognathus ochrophaeus* (now recognized as *D. ocoee*). Assumptions of closure can never be perfectly met in biological populations (White et al., 1982), but through our temporal and spatial sampling design the major assumptions for using closed population models have been adequately met (White et al., 1982). Violation of closure could result

in biased estimates (increased population estimation). Simulation studies of capture–recapture estimation methods have suggested that random movement into and out of populations do not introduce bias, but precision of population estimates will be reduced (Kendall, 1999). The best fit model was determined using second order Akaike's information criterion (AICc; Burnham and Anderson, 2002) as calculated within MARK.

Population estimates from MARK for all salamanders combined and for individual species were converted into densities (salamanders m^{-2}) to create a standardized measure that accounted for the variable stream width across sample blocks. Significant differences between treatments were determined by comparing 95% confidence intervals about the estimated population densities.

2.4.3. Riparian transects

To estimate terrestrial habitat use by salamanders for each sample, we used the mean distance of captured salamanders from the stream edge. For all years, data from the three sample periods were pooled together to generate a mean value for each year. Terrestrial habitat use and salamander abundance were calculated for the assemblage of four species (*D. monticola*—seal salamanders; *D. ocoee*—Ocoee salamanders; *D. quadramaculatus*—black-bellied salamanders; and *E. wilderae*—Blue Ridge two-lined salamanders) and each individual species (except for *D. quadramaculatus*, which had sample sizes too small for separate analysis). It was determined preliminarily via *t*-tests that pre-cut years (2004–2005) did not differ from each other. As such, we pooled data from pre-cut years for each site together to establish a baseline. We then calculated the percent change from baseline for both salamander abundance and mean distance from stream for each post-cut year. After arc-sine square root transforming data, these measures became our response variables used in two-way between-group ANOVA models to test whether retained riparian buffers preserved terrestrial habitat use and maintained stream salamander abundance. In order to use the two-way ANOVA model and test hypotheses about species and treatments, it was necessary to use post cut years (2006 and 2007) as independent replicates in the model. We acknowledge that years may not be independent, but due to the scale of our project and limitations in treatment replication, this was necessary. Significant site and species differences were determined using Tukey's HSD post hoc analyses. To explore significant ANOVA model terms in more detail, we utilized independent samples *t*-tests. These *t*-tests were also used to determine pre- and post-cut differences in environmental variables. Tests with $P < 0.05$ were considered statistically significant. Only salamanders that were captured 2 m or more from the stream edge were included in analyses in an attempt to create a dataset representative of the riparian salamanders, and independent of the within stream measures made using leaf litter bags and removal sampling.

2.4.4. Salamander enclosures

To measure the impact that different riparian forest buffer treatments had on body condition, mean change in mass for salamanders at each site were compared using a univariate general linear model. Post hoc analyses to determine significant site differences were performed using Tukey's HSD test. Survival rates could not be definitively determined in this study due to the possibility of trespass out of the enclosure or enclosure failure.

3. Results

3.1. Leaf litter bag sampling

In-stream salamander capture rates increased from 2006 to 2007 at all treatments, but the rate of increase was greatest at

the 0 m and 9 m sites (35% and 59% greater, respectively; Fig. 1). All three main effects were significant in the general linear model (buffer: $F_{4,16} = 6.85$, $P = 0.008$; year: $F_{1,16} = 8.06$, $P = 0.019$; species: $F_{1,16} = 12.88$, $P = 0.006$). Due to lack of replication and incomplete sampling across all sites and years, we were unable to conduct post hoc tests of significant site differences. In general, the Control 1 and 2 treatments and the 30 m site did not differ in captures of *D. ocoee* or *D. monticola*, and the Control 1 site did not differ appreciably between 2006 and 2007. In contrast, the 0 m and 9 m buffer treatments had a greater number of in-stream salamander captures. The 0 m and 9 m sites also differed by year. *Desmognathus ocoee* at the 0 m buffer treatment had the greatest in-stream capture rate of all salamanders and sites in 2006, but were the only species and site to decrease in 2007. Rate of *D. ocoee* captures at the 9 m site increased from 2006 to 2007, while the rate of *D. monticola* captures increased at both the 0 m and 9 m sites from 2006 to 2007 (Fig. 1; see Peterman, 2008 for data tables).

3.2. Removal sampling

Over six in-stream removal periods, a total of 387 adult and juvenile salamanders were captured in removal plots. Salamander captures declined with each successive sampling period, suggesting that removal efforts were effective. The best fit removal model for all species as well as individual species had constant capture and detection probability. In both data sets, all other competing models had a $\Delta AIC > 4$, indicating little support. Salamanders were more abundant at the 0 m and 9 m sites, the majority of which were *D. monticola* and *D. quadramaculatus* (Fig. 2; see Peterman, 2008 for data tables). Because these two sites were the narrowest streams with the smallest search areas, they correspondingly had the greatest estimated population densities. Only the 0 m site had a significantly greater population density than the other sites, though the 9 m site had the second greatest density, which was substantially greater than the 30 m or control sites. These trends were driven by *D. monticola* density, which was nearly twice as high at the 0 m and 9 m sites than at the other sites. *D. quadramaculatus* showed a much more erratic pattern across the treatments, with the highest density occurring at the 0 m site and the lowest density at the 9 m site. While the 0 m buffer treatment had significantly higher densities of *D. monticola* and *D. quadramaculatus*, there were significantly fewer *D. ocoee* at the 0 m site than at the 30 m or control sites.

3.3. Riparian transects

Prior to riparian forest removal, the mean number of salamanders found along transects was 10.6 (± 2.74 SD). Following riparian forest modification the relative abundance of salamanders along transects decreased 71–100% across treatments (Fig. 3a; see Crawford, 2007 for data tables). Salamander abundance differed significantly in relation to the width of the riparian buffer ($F_{3,28} = 33.04$, $P < 0.001$). The effect size of riparian buffer on relative abundance was large. Partial eta squared was 0.89, which means that riparian buffer by itself accounted for 89% of the overall variance (effect + error). Post hoc tests showed that the 0 m and 9 m sites had significantly fewer salamander than the Control 1 site ($P < 0.001$), and the 30 m site also had fewer salamanders, although this test was only marginally significant ($P = 0.047$). The 30 m site had more salamanders than the 0 m site and 9 m sites, but 0 m and 9 m sites showed no differences in relative abundances. Species did not significantly differ in relative abundance among treatments ($F_{3,28} = 1.19$, $P = 0.356$).

Pre-cut, the mean distance of salamanders from the stream was 32.2 m (± 1.98 SD). Post-cut, the mean distance from the stream for salamanders decreased 72–95% (Fig. 3b; see Crawford, 2007 for

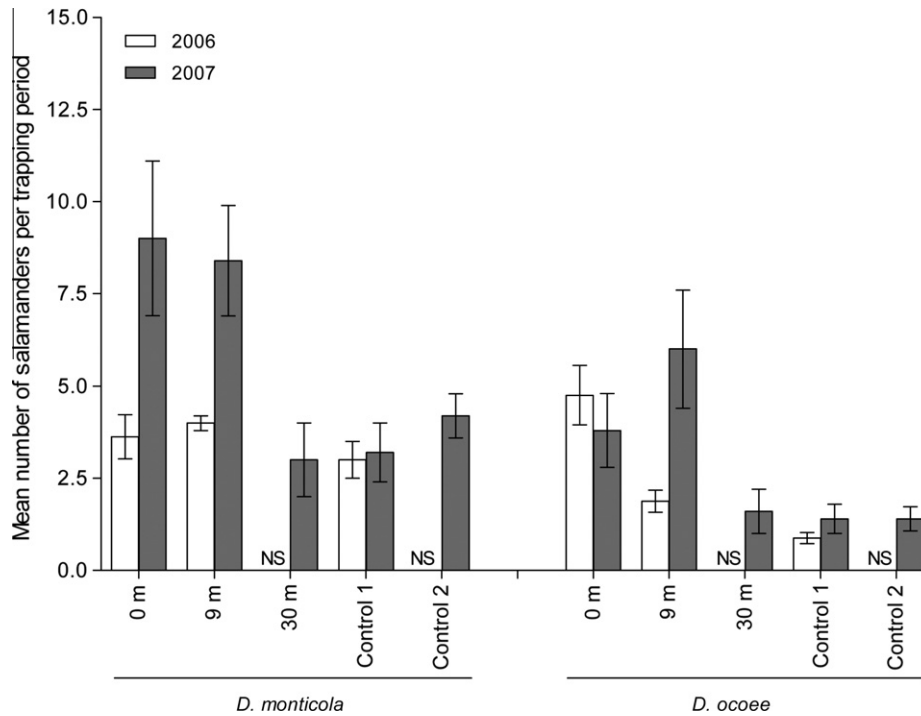


Fig. 1. Adult and juvenile *D. monticola* and *D. ocoee* captures from leaf litter bags. Values represent the mean number of salamanders captured per trapping period (\pm SD). There were eight trapping periods in 2006 and 5 in 2007. NS signifies sites that were not sampled in 2006.

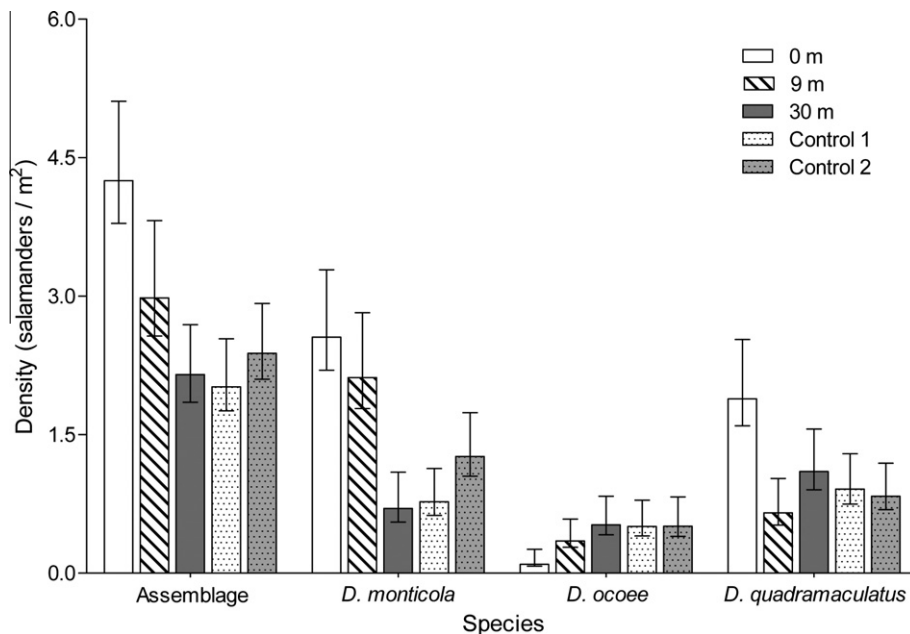


Fig. 2. Salamander density measured within the stream through removal sampling (\pm 95% confidence intervals). Sites with non-overlapping 95% CI were considered statistically different. The assemblage of salamanders encompasses the three species depicted separately.

data tables). The interaction term (species \times buffer) was significant ($F_{9,28} = 3.05$, $P = 0.038$), as well as the main effect of riparian buffer ($F_{3,28} = 22.85$, $P < 0.001$). Species were marginally nonsignificant ($F_{3,28} = 3.133$, $P = 0.066$). Both the interaction term and riparian buffer had large effect sizes in the model (partial eta squared = 0.70 and 0.85, respectively). Post hoc analysis of the one-way ANOVA model assessing the effect of riparian buffer on distance from the stream showed that the Control 1 and 30 m sites did not differ, nor did the 0 m or 9 m sites differ, but all comparisons between

these groups were significant, showing that at the 0 m and 9 m sites salamanders were found closer to the stream. The significant interaction term indicates that species responded differently to riparian buffer treatments, and was evident in the more terrestrial *E. wilderae* and *D. ocoee*. We found that the most terrestrially dependent species, *E. wilderae*, had a significantly contracted distribution away from the stream at the 30 m site ($t = 8.44$, $df = 7$, $P < 0.001$). At the 9 m site *D. monticola* (the least terrestrial species) were not significantly closer ($t = 1.58$, $df = 10$, $P = 0.145$), but both

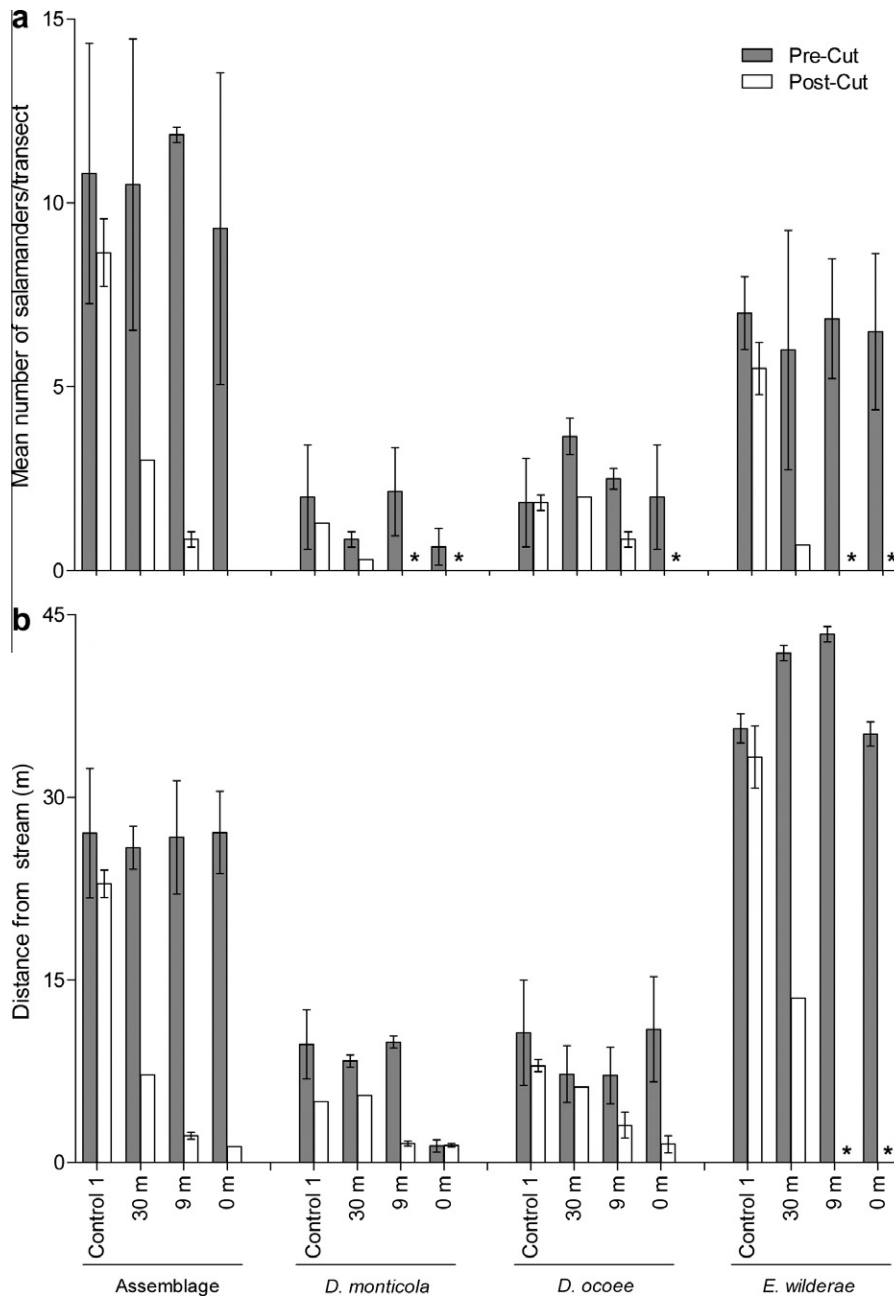


Fig. 3. Results from riparian transects showing salamander responses to riparian timber harvest pre- and post-cut. (a) Mean number of salamanders per transect (\pm SD); (b) distance from the stream that encompassed 50% of the observed population (\pm SD). The assemblage of salamanders includes all other species in the figure, as well as *D. quadramaculatus*. Asterisks indicate zero values.

D. ocoee and *E. wilderae* were closer ($t = 3.92$, $df = 10$, $P = 0.003$; $t = 16.09$, $df = 10$, $P < 0.001$, respectively).

Prior to riparian forest modification, no significant differences were seen among the Control 1, 30 m, 9 m, or 0 m sites for the environmental variables of leaf litter depth (mean, \pm SE; 31.2 mm, ± 1.98), soil temperature (19.6 °C, ± 0.74), percent soil moisture (36.0%, ± 1.70), and canopy cover (91.3%, ± 1.03). All of these variables remained constant over all years at the Control 1 site, but all differed significantly at the treatment sites following riparian modification (see Crawford, 2007 for summary data tables). Specifically, leaf litter depth declined by an average of 56% ($t = 15.78$, $df = 10$, $P < 0.001$), soil moisture declined by an average of 58% ($t = 7.10$, $df = 10$, $P < 0.001$), canopy cover declined by an average of 79% ($t = 15.74$, $df = 10$, $P < 0.001$), while surface soil temperatures increased by an average of 43% ($t = 4.80$, $df = 10$, $P = 0.001$).

3.4. Salamander enclosures

Of the 30 *D. ocoee* at the 0 m, 9 m, and Control 1 treatments, 20 were found and measured at the end of the 8 week study (7 salamanders—0 m site; 6 salamanders—9 m site; 7 salamanders—Control 1). We cannot definitively say that survival rates are equivalent among treatments, but there was not an appreciable difference among treatments in number of salamanders at the end of the experiment. The initial mass of salamanders used at each site did not differ among treatments ($F_{2,27} = 0.48$; $P = 0.625$), yet at the end of the study, the body mass of salamanders changed significantly ($F_{2,17} = 39.20$; $P < 0.001$). Post hoc analyses showed that salamanders from both the 0 m and 9 m buffer treatments lost a significant amount of weight compared to the Control 1 ($P < 0.001$ for both), but the loss of mass in salamanders at the

0 m and 9 m buffer treatments did not differ from each other ($P = 0.362$). Salamanders in the 0 m and 9 m site lost 20.1% and 16.0% of their original body mass, respectively, while the mass of salamanders in the Control 1 site increased by 3.4%.

4. Discussion

Even-aged riparian timber harvest had clear impacts on stream-breeding salamanders. First, riparian transects showed that salamander distributions away from the stream were significantly reduced. Second, the relative abundance of salamanders in the riparian habitat was significantly reduced. Third, removal sampling revealed that salamander densities within streams were significantly greater at the 0 m buffer treatment and were substantially higher at the 9 m buffer treatment. Lastly, there was a significant increase in the capture rate of adult and juvenile salamanders within the stream using litter bags, with the greatest increases occurring at the 0 m and 9 m buffer treatments.

In terms of the three hypotheses, our results collectively provide support for the evacuation hypothesis—the first such evidence in stream salamander systems. Stream-breeding salamanders at our study sites appeared to actively leave the modified riparian forest and enter the stream, suggesting that observed population declines in the terrestrial habitat are at least partially due to emigration to the stream. Further, we provide evidence suggesting that the retreat hypothesis is unlikely in at least one stream salamander species, *D. ocoee*. At the 0 m and 9 m sites, *D. ocoee* lost a significant amount of body mass over an eight week period, but *D. ocoee* at the Control 1 site gained weight over the study period. The observed losses in weight are likely due to a combination of water, fat, and muscle loss, but water loss alone is unlikely as Littleford et al. (1947) showed that body mass reductions of 18–25% due to water losses were lethal in some Plethodontid salamanders over short time periods (<120 min). Salamanders appear capable of surviving in logged habitat, but at a great cost to body condition. Long-term demographic fitness consequences of timber harvest are likely for individuals attempting to retreat and persist in the logged riparian habitat. Homyack and Haas (2009) found that *D. ochrophaeus* (a sister species to *D. ocoee*) in the central Appalachians produced fewer eggs in the first six years following timber harvest.

Although we provide multiple lines of evidence converging on support for evacuation, it is unlikely to be the sole cause of reduced salamander populations following logging. It is likely that some portion of the population retreats underground (retreat hypothesis) or dies (mortality hypothesis), and species may be differentially affected by riparian logging. Only with time can these hypotheses be definitively excluded. For instance, it could be argued that an increase in habitat complexity resulting from increased coarse woody debris following logging may ameliorate effects of canopy loss (McKenny et al., 2006; Rittenhouse et al., 2008), but direct benefits to salamanders would likely not be realized until woody debris began to decompose (McKenny et al., 2006). In the future, the retreat hypothesis could be identified through a more rapid increase in population size following forest succession and reestablishment of suitable microclimates (Johnston and Frid, 2002). Retreat may also lead to a skewed population size distribution following recovery from persistence in suboptimal conditions due to differential survival. Previous studies with salamanders (Ash, 1997; Sattler and Reichenbach, 1998) and turtles (Bodie and Semlitsch, 2000) suggest that larger individuals may better survive or recolonize following habitat perturbations, although a study by Winne et al. (2010) on aquatic snakes found that intermediate-sized individuals were most likely to survive. Again, only with time will these alternative scenarios play out, but we do know that southern Appalachian salamander assemblages are predictably distributed

from the stream into the surrounding forest with larger species tending to be more aquatic and smaller species more terrestrial (Hairston, 1949, 1980; Organ, 1961; Crawford and Semlitsch, 2007). This distribution and partitioning of the riparian habitat was clearly altered following even-aged timber harvest and the life history of each species likely leads to differential responses and survival.

D. monticola exhibited the strongest measurable response to even-aged riparian timber harvest. In-stream densities at the 0 m and 9 m buffer treatments were nearly twice the observed densities at the 30 m buffer or Control treatments (Fig. 3). *D. monticola* generally utilize terrestrial habitat for nighttime foraging, but following logging, terrestrial habitat use and relative abundance of *D. monticola* decreased (Fig. 1). Immigration into the stream may serve as an initial step toward dispersal off of logged habitat via the stream itself, but Crawford and Semlitsch (2008b) reported that abundance and terrestrial habitat use by *D. monticola* were significantly reduced in even-aged forest stands less than 40 years old as compared to older forested stands. This indicates that our observation of *D. monticola* evacuation into the stream is the proximal response to even-aged timber harvest, and that in the long-term, local populations will likely decline, and remain depressed for up to 40 years (Crawford and Semlitsch, 2008b).

The two most terrestrially dependent and smallest species in our assemblage are *D. ocoee* and *E. wilderae*. *D. ocoee* were significantly less abundant and had significantly reduced distributions at the 0 m and 9 m buffer treatments, while *E. wilderae* also had significantly reduced riparian habitat use at the 30 m buffer treatment (Fig. 2). It is unknown if the decline in *D. ocoee* capture and density within the stream at the 0 m site is a result of in-stream dispersal, depredation by larger heterospecific salamanders (Hairston, 1986), or due to competition for resources in an assemblage with elevated salamander density. Both interference competition (Ransom and Jaeger, 2006) and predation (Hairston, 1986) have been suggested as possible mechanisms in structuring salamander assemblages, so the increased density of *D. monticola* and high densities of *D. quadramaculatus*, both larger species, at the 0 m and 9 m buffer treatments may have suppressed surface activity of the smaller *D. ocoee* or reduced their population through depredation. Being faced with multiple stressors such as predation or competition within the stream, *D. ocoee* may be forced back into the riparian habitat where they become more susceptible to desiccation (Spotila, 1972).

Temporal and species-specific responses to riparian forest loss were also measured. *D. ocoee* were found more frequently in the stream at the 0 m buffer treatment immediately after harvesting in 2006 than at any other treatment (Fig. 1). The rate of capture for *D. ocoee* continued to be higher than at the 30 m or Control 1 and 2 treatments in 2007, while *D. ocoee* captures increased nearly 70% at the 9 m buffer treatment from 2006 to 2007. Being the most terrestrially dependent *Desmognathus* species, *D. ocoee* at the 0 m buffer treatment may have been immediately forced into the stream following logging, but *D. ocoee* at the 9 m buffer treatment may have been able to persist in the minimal remaining riparian habitat longer, thus delaying emigration until 2007 (Fig. 1). A similar delay in evacuation was observed with *D. monticola*, which are less dependent on riparian habitat than *D. ocoee*; *D. monticola* were more frequently encountered within both the 0 m and 9 m buffered streams in 2007 than in 2006.

D. quadramaculatus were a significant component of the salamander density at the 0 m buffer treatment (Fig. 2), but we do not believe that the high density observed is in response to riparian timber harvest. *D. quadramaculatus* is the largest species in the assemblage and are most abundant in the stream and along its banks, rarely venturing more than 5 m into the riparian habitat (Peterman et al., 2008). Anderson et al. (2007) found that headwater

streams have a significant capacity to buffer against clear cut microclimate changes. As such, *D. quadramaculatus* are likely less susceptible to changes in microclimate that may have a greater effect on the more terrestrial species. The observed *D. quadramaculatus* densities at our five study streams are within the natural variation of population densities previously reported (Davic and Orr, 1987; Camp, 1997; Peterman et al., 2008). Although *D. quadramaculatus* were likely buffered from riparian timber harvest, as dominant competitors or predators, they may be influential in shaping the composition of the rest of the salamander assemblage, particularly *D. ocoee*, which were conspicuously absent from the 0 m buffer treatment during nighttime removal sampling and were less frequently encountered in leaf litter trapping in 2007.

Previous research has shown that terrestrial plethodontid salamanders (genus *Plethodon*), which do not require streams for reproduction, show extreme population declines following even-aged timber harvest (Petranka, 1993; Ash, 1997; Harpole and Haas, 1999; Knapp et al., 2003). Petranka et al. (1993) speculated that these declines represented direct mortality of salamanders inhabiting cut forests. Our data on stream salamanders do not fully support these findings, and we suggest that responses are likely dependent on species-specific attributes and the severity of habitat change following logging. By measuring *D. ocoee* body mass at the 0 m and 9 m buffer and Control 1 treatments we have shown that salamanders are able to survive within the treatments for eight weeks despite significant changes to environmental variables, although their body condition deteriorated significantly. An important habitat characteristic in predicting salamander abundance is leaf litter depth (Crawford and Semlitsch, 2008a), which was significantly reduced following even-aged timber harvest (Crawford, 2007). Leaf litter is essential for terrestrial invertebrate species richness (Seastedt and Crossley, 1981); invertebrates are the predominant prey source for stream salamanders (Petranka, 1998), and therefore, measured weight loss is most likely due to a decrease in available prey items. These changes to forest communities provide incentive for a large proportion of the stream salamander population to evacuate the cut forest, but we recognize that an unknown portion of the population perhaps not able to evacuate likely died following logging, and others may have sought refuge, continuing to persist.

4.1. Conclusions

4.1.1. Caveats and limitations

It is important to draw conclusions cautiously from our data. First, we were limited in our replication of stream buffer treatments, so inferences beyond our study streams must be made cautiously. Second, we utilized multiple sampling approaches in both the terrestrial and aquatic environments without any explicit account of detection or capture probability, which if used, can lead to more accurate abundance measures (Bailey et al., 2004a,c, 2004b). In order to ensure that the greatest proportion of the salamander population was sampled, we conducted transect surveys and in-stream removal sampling at night when salamanders are surface active. While relative abundance measures of surface active salamanders can generally be assumed to proportionally correspond to the absolute population size (Hairston, 1986; Petranka, 1994), we do not know how surface activity varied among sites as a result of riparian timber harvest. As such, observed reduced abundance and terrestrial habitat use could, in part, be due to decreased surface activity. Even with these caveats, we maintain that multiple lines of independent evidence converging on a common pattern goes beyond circumstantial evidence and is indicative of a real phenomenon (Semlitsch et al., 2008).

To an extent, we can generalize some of our findings based on other literature and data. Peterman et al. (2008) and Camp and

Lee (1996) report densities of *D. quadramaculatus* to be 1.13 and 1.41 m⁻² (this study = 0.83–1.88 m⁻²). Kleeberger (1984) estimated densities of *D. monticola* to be 0.72–1.4 m⁻². In this study, the Control 1, Control 2, and the 30 m sites fell within this range (0.70–1.26 m⁻²), while the 0 m and 9 m treatment sites exceeded it (2.55 and 2.11 m⁻², respectively). Lastly, looking at unpublished data (Crawford), we can compare our pre-treatment transect count data with 14 other southern Appalachian sites with similar characteristics and communities, surveyed using identical techniques (see Crawford and Semlitsch, 2007 for site descriptions). In our study, mean *D. monticola* abundance per transect ranged from 0.65 to 2.15 (grand mean = 1.41), *D. ocoee* ranged from 1.85 to 3.65 (grand mean = 2.5), and *E. wilderae* abundance ranged from 6.00 to 7.00 (grand mean = 6.59). In comparison, 14 other sites had mean transect abundance of 0.33–8.00 *D. monticola* (grand mean = 2.24), 1.00–5.00 *D. ocoee* (grand mean = 2.79), and 3.67–8.33 *E. wilderae* (grand mean = 6.12). In summary, our study streams all fall within the range of variation observed across a broader sample of sites, and exhibit nearly identical mean abundance per transect for *D. ocoee* and *E. wilderae*.

4.1.2. Summary and management implications

We have provided evidence for the evacuation hypothesis of stream salamanders following even-aged timber harvest, but we have shown that species differ with regard to timing and severity of their responses. Our findings add stream salamanders (*Desmognathus* and *Eurycea* spp.) to terrestrial salamanders (*Plethodonhubrichti*), mole salamanders (*Ambystoma* spp.), and anurans (*Rana* and *Bufo* spp.) that exhibit active movement away from altered habitat (Reichenbach and Sattler, 2007; Semlitsch et al., 2008). We are still lacking detailed information on the mechanism behind the patterns we observed, and future research should attempt to characterize species-specific behaviors following riparian forest modification as well as monitor patterns of recolonization as riparian forests recover. It is imperative that management of riparian headwater habitats attempt to preserve salamander assemblages, and not just single species. Recommendations based on *D. monticola* alone for instance, would likely compromise the more terrestrial *D. ocoee* and *E. wilderae*. By developing guidelines encompassing the community of species that inhabit and differentially utilize riparian habitat, ecosystem processes such as leaf litter decomposition and nutrient cycling will be better preserved.

Current guidelines for this region of the Appalachians require that 100 ft (~30 m) buffer be maintained surrounding intermittent streams when rare plants are present, but only require 30 ft (~9 m) buffer surrounding streams with no rare plants (USDA 2000). These buffers are likely inadequate, as Crawford and Semlitsch (2007) recommend a core terrestrial habitat of 42.6 m with an additional 50 m buffer to protect against edge effects (92.6 m total). We found that a 9 m buffer was functionally no different than complete removal of the riparian habitat with regard to stream salamander abundance, density, distribution, and growth. The 9 m buffer treatment was also unable to maintain environmental conditions necessary for terrestrial habitat use by salamanders (Crawford and Semlitsch, 2007, 2008a). Retention of a 30 m buffer seemed to ameliorate the immediate effects of even-aged riparian timber harvest for the majority of the salamander assemblage, although highly terrestrial *E. wilderae* had significantly reduced abundance and distribution even at the 30 m buffer treatment because they use terrestrial habitat out to a mean distance of 42.6 m (Crawford and Semlitsch, 2007). Salamander responses to riparian logging were delayed one year at the 9 m buffer site, and it is likely that population responses would also be further delayed in the 30 m buffer treatment. As significant components of headwater ecosystems, salamanders should not be neglected in land management policy. Healthy, functional headwater ecosystems in the eastern

United States may be highly dependent on salamanders (Welsh and Droege, 2001; Davic and Welsh, 2004). To preserve these habitats while allowing for continued land use, sufficient riparian buffers must be maintained.

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