

**EFFECTS OF FOREST REGENERATION METHODS ON SALAMANDER
POPULATIONS IN CENTRAL APPALACHIA**

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ABSTRACT

In forested ecosystems, salamanders occupy important ecological roles as predator, prey and as potential regulators of ecological processes. The effects of forest management, particularly clearcut harvesting, on salamanders have been well documented; removal of overstory trees negatively affects abundances of salamanders. However, the length of time that salamander populations remain depressed following forest harvesting and factors limiting population recovery have been a source of controversy in the literature and are the goal of this dissertation. As part of the Southern Appalachian Silviculture and Biodiversity (SASAB) project (Chapter 1), a long-term replicated field experiment designed to evaluate a range of silvicultural treatments on biodiversity, I evaluated specific hypotheses related to salamander populations, their prey, and their habitat.

First, I examined long-term trends in salamander abundances across a range of silvicultural treatments to determine whether negative effects of forest harvesting persisted for 13-years after harvest (Chapter 2) and to document the effects of multiple harvests on salamanders (Chapter 3). The relative abundances of terrestrial salamanders were quantified in six silvicultural treatments and an unharvested control and on six replicated field sites with night-time, area-constrained searches. Across 13-years of post-harvest data, terrestrial salamander abundances generally were lower in silvicultural treatments with some disturbance to the canopy (group selection harvest through silvicultural clearcut). Further, a comparison of demography of

common species of salamanders suggested that differences in habitat quality existed between harvested and unharvested experimental units (EUs). A second harvest in the shelterwood plots to remove overwood had a cumulative negative effect on salamanders at one of two sites studied. Additionally, I conducted a sensitivity and elasticity analysis for eastern red-backed salamanders (*Plethodon cinereus*) and modeled population growth to evaluate the contribution of demographic parameters to population recovery. These analyses indicated that adult survival was the parameter with the greatest influence on the population growth rate and that >60 years would be required for recovery of salamander populations to preharvest levels even if habitat conditions were restored to preharvest conditions immediately.

Next, I quantified the bioenergetics of salamanders across a disturbance gradient to evaluate whether changes to (1) invertebrate prey, (2) energy expenditure for basic maintenance costs, and or (3) an index to body condition could help explain observed changes to abundances or demography of salamanders from forest harvesting (Chapter 4). Although I did not detect a difference in abundances of invertebrates along the disturbance gradient, I determined that salamanders in recently disturbed forest stands expended approximately 33% more energy for basic maintenance costs in an active season and the body condition of salamanders was greater at one of two sites in disturbed EUs. Thus, the bioenergetics of terrestrial salamanders may have been affected by increasing temperatures from silvicultural disturbance and may cause salamanders to allocate less energy to reproduction or growth because of increased maintenance costs.

In collaboration with Eric Sucre, Department of Forestry at Virginia Tech, I examined the effects of salamanders on invertebrates and ecosystem processes, specifically leaf litter decomposition. We constructed 12 *in situ* field mesocosms and I manipulated densities of red-

backed salamanders into zero, low, and high density treatments. From June 2006-June 2008, I estimated invertebrate abundances, rates of leaf litter decomposition and food habits of salamanders across treatments. I found that invertebrate abundances were more affected by season than by the density of salamanders and that rates of leaf litter decomposition did not differ among salamander treatments. Salamanders were euryphagic and consumed more (by abundance and volume) herbivorous invertebrates than predators or detritivores.

Finally, I modeled habitat relationships of terrestrial salamanders at two spatial scales on the SASAB study sites (Chapter 6). I quantified abundance of salamanders with area-constrained searches during warm rainy nights and measured forest characteristics related to foraging or refugia habitats or that described the overstory and understory of forest stands. At the scale of the 30 m² transect and the 10 m² sub-transect, abundance of salamanders was best described by models that incorporated descriptors of canopy cover and woody and herbaceous understory vegetation. Thus, terrestrial salamanders may have responded positively to forest stands with a mature overstory and structurally diverse understory for foraging habitat.

Collectively, these data suggest that recovery of salamander populations after forest harvesting will take approximately 60 years, and that life history characteristics (low fecundity, late sexual maturity) and possibly changes to bioenergetics may contribute to the slow recovery. Further, silvicultural practices that retain some canopy trees through a rotation may have a more rapid return of salamander populations to preharvest levels and may encourage development of understory structure for salamander foraging. Although these data fill some gaps in knowledge of relationships between silviculture and terrestrial salamanders, many questions about long-term effects of disturbances on populations and habitats remain. My modeling of recovery of salamander populations depended on estimates of a survival from a congener, and I did not

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ATTRIBUTION

Chapter 2: Long-term effects of experimental forest harvesting on abundance and demography of terrestrial salamanders. Carola A. Haas (Department of Fisheries and Wildlife Sciences, Virginia Tech) co-developed the experimental design for this research, co-refined the content of this chapter, and edited all drafts of the manuscript.

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CHAPTER 1: INTRODUCTION

In his seminal work, “A Sand County Almanac,” Aldo Leopold reflected on what he perceived to be a sharp dichotomy between Group A foresters focused on economic production and Group B foresters, who considered wildlife, recreation, and aesthetics in addition to profit (Leopold 1949). To Leopold, Group B foresters embodied an ecological conscience by considering both the community response and economics as practicing managers of the land. Whether or not such a strict separation in ideology exists, it is clear that the field of natural resources is based on constantly evolving hypotheses of how human actions influence ecosystems (Seymour 1998). At the intersection of silviculture and wildlife science, questions regarding effects of forest management on wildlife populations have broadened their scope to include silvicultural regimes that may serve as alternatives to common timber harvesting practices. To continue expanding our knowledge of how extracting wood fiber influences wildlife and ecosystem functioning, natural resource professionals require large-scale, replicated field experiments followed through time (DeStefano 2002).

In the early 1990s, the Departments of Forestry and Fisheries and Wildlife Sciences at Virginia Tech in collaboration with the U.S. Department of Agriculture Forest Service’s Southern Research Station and Mead-Westvaco Corporation initiated such a replicated field experiment. Termed the Southern Appalachian Silviculture and Biodiversity (SASAB) project, this long-term field experiment was developed to study rigorously the effects of a range of oak regeneration treatments, from an unharvested control through a silvicultural clearcut, on biodiversity, ecosystem processes, and regeneration responses in hardwood forest. Silvicultural treatments represented alternative practices for regenerating oaks (*Quercus spp.*), which are foundation species (Ellison et al. 2005) and an important mast producing group (McShea et al.

2008) in the central and southern Appalachian mountains. Since the installation of the SASAB study, researchers have examined the influence of these silvicultural practices on diversity and structure of the plant community (Hammond 1997, Wender 2000, Hood 2001, Belote 2008), regeneration of oaks (Lorber 2003, Atwood 2008), abundance of salamanders (Harpole 1996, Knapp 1999), and soil properties (Parrish and Fox, unpublished data, Sucre 2008).

At each of six study sites in Virginia (Blacksburg 1, Blacksburg 2, Clinch 1, Clinch 2) and West Virginia (West Virginia 1, West Virginia 2), seven silvicultural treatments were applied randomly to adjacent 2-ha experimental units (EUs) (Table 1.1, Figure 1.1). The silvicultural treatments in order of increasing overstory removal were as follows:

1. Control: No silvicultural activity occurred in these plots, though skid trails were not entirely excluded from EUs.
2. Midstory herbicide treatment: Basal application of herbicide (triclopyr and imazapyr) was applied to reduce competition for advanced oak regeneration. Woody stems were individually treated on the lower 15-30 centimeters with an oil/herbicide solution.
3. Group selection: All stems >2.5 cm diameter at breast height (dbh) were removed from 2-3 openings (0.5 ha total) created per treatment plot and the residual stand was selectively cut to improve tree growth and quality. The target residual basal area was 15-20 m^2/ha . Additional groups are to be harvested 20 years following the initial treatment (approximately 2014-2018).
4. Shelterwood: Plots were partially harvested, with 12-14 m^2/ha of overstory basal area retained, which was an average of 41% reduction following harvest (Knapp et al. 2003). Residual stems were dominant or co-dominant stems of preferred species with dbh of 25-40 cm. Remaining overstory trees were removed during winter 2007-2008 at Blacksburg 1 and

Blacksburg 2. The remaining overwood was scheduled to be removed during winter 2007-2008 at West Virginia 1 and West Virginia 2 and during winter 2009-2010 at Clinch 1 and Clinch 2.

5. Leave-tree harvest: Plots were partially harvested, with 25-45 high-quality trees/ha (4-7 m²/ha) retained. Residual stems were distributed evenly in the plots, and were selected to have dbh of 5-25 cm. This harvest resulted in a 72% reduction in basal area (Knapp et al. 2003).
6. Commercial clearcut: This treatment was a partial overstory removal without regard to future values that retained 4-7 m²/ha of unmerchantable trees left on site. Originally, this treatment was considered a low-leave shelterwood. Basal area was reduced by 81% (Knapp et al. 2003).
7. Silvicultural clearcut: All stems >5 cm dbh were cut except for scattered wildlife trees (<10 stems/ha). Unmerchantable stems were felled and left on the plots, with 2 m²/ha residual basal area.

For this dissertation, I used previously collected data and obtained additional estimates of abundances of salamanders on the SASAB sites to examine how the disturbance gradient affected populations of terrestrial salamanders, a group of species known to be sensitive to subtle changes to forested habitats (Welsh and Droege 2001) and thought to be important contributors to ecosystem processes (Wyman 1998, Davic and Welsh 2004, Walton and Steckler 2005). Terrestrial salamanders were sampled annually since the initiation of this experiment (Table 1.2) and included both preharvest and postharvest estimates of abundance.

Prior researchers determined that silvicultural practices with even limited disturbance to the canopy negatively affected abundances of salamanders on these sites (Harpole and Haas

1999, Knapp et al. 2003). The observation of fewer salamanders after forest harvesting has been a consistent trend in the literature (Petranka et al. 1993, deMayndier and Hunter 1995, Ash 1997). What has been less well-described, however, is the length of time required for populations of salamanders to return to preharvest abundances and the mechanisms limiting their recovery. In southern Appalachian forest, recovery of salamander populations after clearcut harvesting has been estimated to be from 20-70 years (Petranka et al. 1993, Ash 1997), but these estimates have been controversial (Ash and Bruce 1994, Petranka 1994, Petranka 1999). The slow recovery of salamander populations may be explained by lasting effects of silvicultural treatments on habitat and forest structure, lasting effects on microclimate or prey availability and subsequently on energy budgets of salamanders, or to an inability for rapid rebound among species with relatively low fecundity. These hypotheses serve as core research questions for this dissertation.

Specifically, I documented effects of oak regeneration treatments on abundances and population performance of salamanders (Chapter 2), evaluated effects of a repeated-entry harvest on salamanders and their habitat (Chapter 3), compared microclimate profiles and bioenergetics of salamanders across a disturbance gradient (Chapter 4), investigated the role of salamanders in structuring invertebrate communities and their influence on rates of leaf litter decomposition (Chapter 5), and modeled habitat relationships of salamanders (Chapter 6). This dissertation aims to fill a void in information regarding the effects of forest management on a group of sensitive and ecologically important species. By focusing on how this information may be applied, I hope to provide relevant information for natural resource practitioners.

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Table 1.1. Location and site descriptions of the Southern Appalachian Silviculture and Biodiversity project study sites, where seven silvicultural treatments were experimentally applied to 2-ha blocks in southwestern Virginia, and north-central West Virginia, 1994-1998.

	Study site					
	Blacksburg 1	Blacksburg 2	West Virginia 1	West Virginia 2	Clinch 1	Clinch 2
Location	Montgomery Co., VA	Montgomery Co., VA	Randolph Co., WV	Randolph Co., WV	Scott Co., VA	Wise Co., VA
Pre- treatment Basal Area (m ² /ha) ^a	25.5	26.8	35.2	32.5	29.2	29.1
Pre- treatment stems/ha ^a	847	1045	1519	1293	840	1022
Elevation (m)	710	730	880	1006	1036	1040
Aspect (°)	153	151	270	129	149	108
Slope (%)	16	21	38	9	30	16
Site Index ^b (m)	23	22	23	24	18	20
Age at treatment ^a	100	99	73	63	111	76
Date of harvest completion	March 1995	June 1996	April 1998	August 1998	October 1998	March 1998
Date of shelterwood overstory removal	Winter 2007-2008	Winter 2007-2008	n/a	n/a	n/a	n/a

^aEstimated by Hammond (1997)

^bSite Index was estimated by Hammond (1997) for *Quercus alba* at 50 years.

Table 1.2. Numbers of complete sampling occasions by year for terrestrial salamanders on the six study sites of the Southern Appalachian Silviculture and Biodiversity Project. Only sampling occasions where all experimental units within a site were sampled, where sampling selected transects were not completely duplicated within a year, and that exclude mid-summer (June-August) sampling on the Blacksburg (BB1, BB2) sites are reported. See Chapter 2 for a description of the methodology used to sample salamanders. Underlining separates pre-treatment from post-harvest sampling. The Blacksburg and Clinch (CL1, CL2) sites are located on the Jefferson National Forest and the West Virginia (WV1, WV2) sites are located on the former Mead-Westvaco Wildlife and Ecosystems Research Forest, owned by Penn-Virginia Corporation as of 2007.

Year	Site					
	BB1	BB2	CL1 ^a	CL2	WV1	WV2
1994	<u>5</u>	0	5	5	0	0
1995	7	<u>4</u>	0	0	0	0
1996	7	2	3	4	6	4
1997	8	8	7	<u>0</u>	<u>0</u>	8
1998	9	5	<u>0</u>	6	9	<u>0</u>
1999	7	7	2	1	3	3
2000	3	0	0	0	0	0
2001	4	3	0	0	2	2
2002	6	5	0	0	3	3
2003	5	4	0	0	3	4
2004	5	4	0	0	2	3
2005	4	2	0	0	4	4
2006	4	4	1	3	8	8
2007	5	4	3	4	5	4
2008	4	4	4	4	6	6

^a Some timber harvest activity site at the Clinch 1 site began late summer 1994 and continued through October 1998.

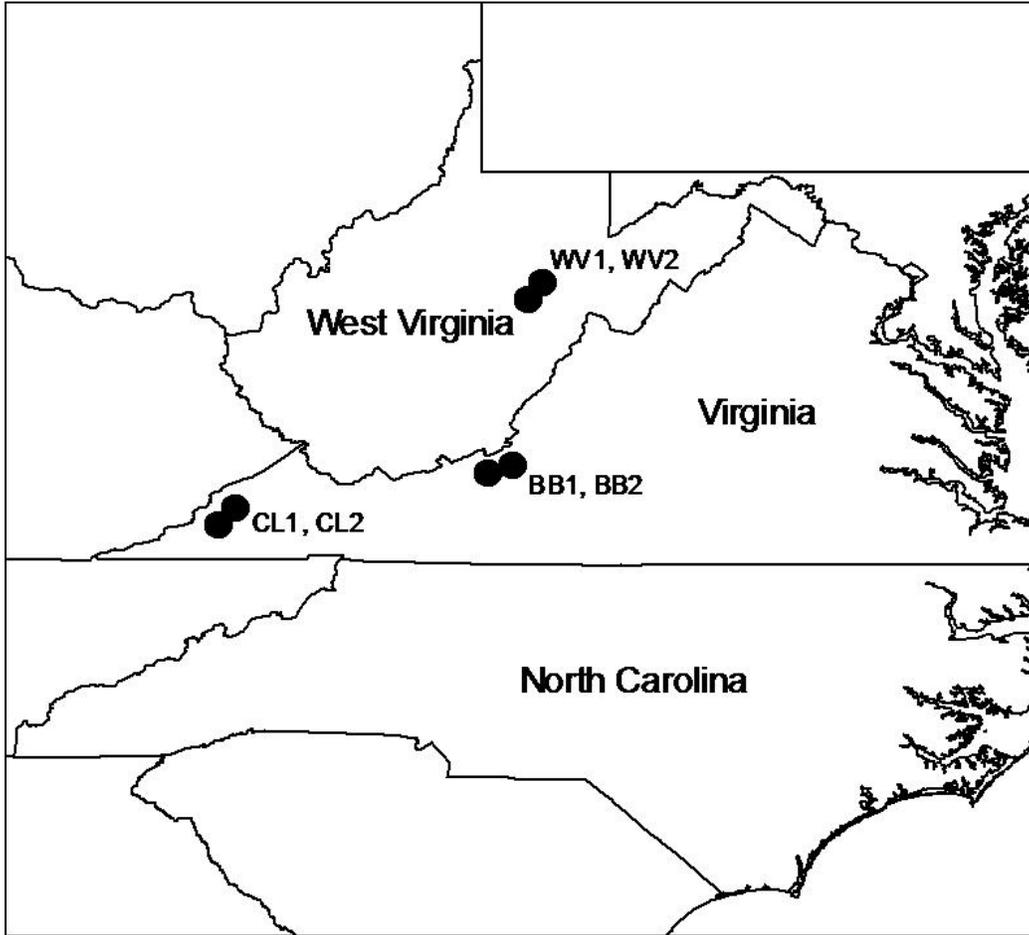


Figure 1.1. Location of six Southern Appalachian Silviculture and Biodiversity (SASAB) study sites used to evaluate effects of alternative silvicultural practices on abundance, habitat, and demography of terrestrial salamanders. The West Virginia 1 (WV1) and West Virginia 2 (WV2) sites were located on private industrial forest and sites in Virginia (BB1, BB2, CL1, and CL2) were located on the Jefferson National Forest.

CHAPTER 2: LONG-TERM EFFECTS OF EXPERIMENTAL FOREST HARVESTING ON ABUNDANCE AND DEMOGRAPHY OF TERRESTRIAL SALAMANDERS

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Abstract: Both observational and experimental studies have documented drastic reductions in salamanders after forest harvesting. Yet, the amount of time until salamander populations rebound and the factors limiting recovery after harvesting are unknown. We compared the effects of 6 oak regeneration practices to a control, representing a disturbance gradient from no treatment to silvicultural clearcut, on the relative abundance and reproductive demography of terrestrial salamanders through 13-years post-harvest. Following the experimental disturbance, relative abundance of terrestrial salamanders in treatments that opened the canopy were significantly and persistently lower than in either untreated control stands or midstory herbicide treatments. In general, this trend persisted through 9-13 years after treatment. Changes to demography of commonly captured salamanders varied by species, but *Plethodon cinereus* had a greater proportion of juveniles in unharvested treatments 7-13 years post-harvest, and *Desmognathus ochrophaeus* had a greater proportion of juveniles and a greater number of eggs/female in unharvested treatments 1-6 years post-harvest. Population modeling of *P. cinereus* indicated that adult survival had the greatest elasticity of the vital rates. Further, >60 years may be needed before *P. cinereus* reduced by the observed decline could reach pre-harvest levels of abundance. Of the treatments with canopy disturbance, the group selection harvest had the greatest abundances of salamanders 7-13 years post-harvest, but when coupled with future stand entries, the volume of wood fiber extracted, costs of harvesting, reduced sprouting of oaks,

and soil disturbances, this method may not have the best balance of ecological and economic sustainability in central Appalachian hardwood forest.

Keywords: Appalachia; demography; forest harvest; Plethodontidae; *Quercus* spp.; salamander.

Introduction

Understanding how forest harvesting affects the structure of ecosystems, ecological processes, diversity of species, and viability of populations is integral for management of forests for ecological and economic sustainability. Within both private commercial and public (state and national) forests within the United States, forest management and silvicultural systems are subject to review for alleged effects on ecological sustainability in addition to achieving economic, social, recreational, and aesthetic objectives. Despite these complex and often conflicting management goals, little research has compared effects on ecological communities from clearcut harvesting to a range of silvicultural alternatives. Even rarer are experiments that investigate long-term responses (>5 years) of plant and animal populations exposed to a gradient of silvicultural disturbances (deMaynadier and Hunter 1995, DeStefano 2002), which may represent alternative forest management practices.

In forests of eastern North America, salamanders are one of the most abundant and diverse vertebrate taxa (Burton and Likens 1975) and are considered by some as indicators of forest biodiversity (Welsh and Droege 2001) and of ecosystem health and integrity (Davic and Welsh 2004). Terrestrial salamanders may influence ecosystem processes as apex predators of invertebrates in the detrital ecosystem (Wyman et al. 1998, Walton 2005, Walton and Steckler 2005), as high-quality prey for numerous taxa (Pough 1987), and as regulators of leaf litter decomposition (Hairston 1987, Wyman et al. 1998). Plethodontid salamanders are excellent study animals in forested ecosystems because of their physiological ties to microhabitat and

microclimate, the relative ease of sampling populations, and the low variation in abundance estimates (Welsh and Droege 2001).

Although researchers generally agree that terrestrial salamanders play important roles in ecosystem processes, the strength and persistence of effects from forest harvesting on salamander populations has been more controversial. Across 16 research projects, control stands had about 4.3× more captures of salamanders than clearcut stands (deMaynadier and Hunter 1995), yet the length of time for populations to return to pre-harvest levels and comparisons of clearcut harvesting to other silvicultural regimes have not been well-documented. Recovery times of salamander populations following clearcut timber harvest reportedly range from 20-70 years in southern Appalachian forests, but these estimates represent extrapolated salamander captures through time (Ash 1997) or are from chronosequence studies without randomization (Petranka et al. 1993). Likewise, the effects of timber harvesting on demography of salamanders remains largely unstudied over long time periods and across large spatial scales (deMaynadier and Hunter 1995). Even a single disturbance to a population of salamanders with low reproductive rates may contribute to the lengthy recovery period that seems to outlast microclimatic or structural changes to managed stands (Dupuis and Bunnell 1999, Semlitsch et al. 2007). Thus, understanding how anthropogenic disturbances influence vital rates of salamanders could be important to prioritize conservation and management efforts by identifying mechanisms of population changes (Biek et al. 2002) associated with forestry practices.

We examined changes in the relative abundance and reproductive demography of plethodontid salamanders following the experimental application of a suite of forest management prescriptions designed to facilitate oak (*Quercus spp*) regeneration in a randomized design replicated across central Appalachian hardwood forests over a 13-year post-treatment period.

Based on prior research on these sites, relative abundances of salamanders decreased immediately following treatment (Harpole and Haas 1999, Knapp et al. 2003). However, we predicted that relative abundances of salamanders would increase as harvested treatments gained vertical structure and entered the stem exclusion stage (Smith et al. 1996). We further predicted that if habitat quality for salamanders remained suppressed, then demographics associated with reproduction (e.g., number of eggs/gravid female, number of gravid females) would be greater in unharvested treatments through the study period. Finally, we evaluated the relative importance of demographic parameters to the population growth rate with a sensitivity/elasticity analysis and modeled population growth of the most common salamander species in our study. These data contribute to a growing body of research documenting that human-caused disturbances to forested habitats may have lasting consequences to salamander population size and dynamics.

Materials and Methods

Study sites

Our research encompassed 6 study areas across Virginia and West Virginia, spanning \approx 300 km north to south and 200 km east to west. Study sites (blocks) were established within the Ridge and Valley and the Cumberland Plateau physiographic provinces in the Jefferson National Forest, Virginia (BB1, BB2, CL1, CL2), and the Mead-Westvaco Corporation's Wildlife and Ecosystem Research Forest (MWERF), West Virginia (WV1, WV2) (Belote et al. 2008). Sites were selected to be south-facing with moderate slopes (10-40%), and relatively uniform stocking of merchantable trees (Hammond 1997, Wender 2000). They were dominated by moderately productive mixed-hardwoods forest type with stand ages of 62-100 years. Oaks (*Quercus spp.*) dominated the overstory of study sites, and red maple (*Acer rubrum*), yellow-poplar (*Liriodendron tulipifera*), American beech (*Fagus grandifolia*), Fraser magnolia (*Magnolia*

fraseri), and sourwood (*Oxydendron arboretum*) were present (Wender 2000). At each site, 7 2-ha experimental units (EU) were established adjacent to one another.

A suite of silvicultural systems, ranging from no management (control) to silvicultural clearcut, was applied randomly to EUs within each site using the following prescriptions (in order of increasing overstory removal) during 1994-1998: (1) Control: no silvicultural activity occurred, (2) Midstory herbicide treatment: basal application of herbicide (triclopyr and imazapyr) applied to individual stems to reduce competition for oak seedlings and saplings. Woody stems were individually treated on the lower 15-30 cm with an oil/herbicide solution, (3) Group selection: all stems >2.5 cm dbh removed from 2-3 small openings (0.5 ha total) and the residual stand was selectively harvested to improve tree growth and quality. The group selection plots are intended to have additional groups harvested at 20 years following the initial treatment (approximately 2014-2018), (4) Shelterwood: partial harvest, with a 41% reduction in basal area, and the residual stems were dominant or co-dominant stems with dbh of 25-40 cm that will be removed 13-15 years after the initial entry, (5) Leave-tree harvest: partial harvest with 25-45 high-quality trees/ha retained through the rotation, (6) Commercial clearcut: partial overstory removal without regard to future values and unmerchantable trees left on site, and (7) Silvicultural clearcut: all stems >5 cm dbh cut, except for scattered wildlife trees (<10 stems/ha). WV1 had only 5 of 7 treatments; the midstory herbicide treatment and commercial clearcut were not applied. Additional details regarding study sites were reported by Belote et al. (2008) and Knapp et al. (2003). This study included those sites used by Knapp et al. (2003) but include an additional 9 years of post-harvest data and an additional 6th site.

Field methods

We applied the methods of previous investigations to quantify the relative abundances of terrestrial salamanders among treatments (Harpole and Haas 1999, Knapp et al. 2003). We sampled salamanders using night-time, area-constrained searches of 2×15 m transects to non-destructively estimate relative abundance of salamanders. Nine sampling transects per 2-ha EU were established in each study site in a 3×3 grid ($n=360$ transects). Transects were >30 m from any edge of EUs, but in some instances, transect locations had to be shifted slightly to avoid slash piles or skid trails that made salamander sampling ineffective.

For each sampling night, one randomly selected transect per treatment was sampled. Each night, we rotated the order in which transects were sampled to avoid potential biases with changing activity levels of salamanders as the night progressed. Individual transects were not searched >1 time/sampling year. Transects were searched nights (>1 hour after sunset) during or after rain events when temperatures exceeded 7° C and the leaf litter and/or soil surface were moist, April-November. Two to three observers hand-captured surface-active salamanders and marked capture locations within transects. Salamanders were measured in the lab and individuals were returned to the point of capture the following day. Salamanders active on surface habitats represent only a portion of the total superpopulation both of surface and subsurface individuals (Bailey et al., 2004). Captures or counts of individuals are a measure of relative abundance only, having a presumably positive and linear relationship to the true population size (Hairston 1983, Welsh and Droege 2001, Williams and Berkson 2004, Reichenbach and Sattler 2007). We continued to utilize relative abundance indices to provide continuity with prior data collection on EUs (Harpole and Haas 1999, Knapp et al. 2003), and we assume that expected capture probabilities were approximately equal across all EUs, years, and species complexes (Yoccoz et al. 2001, Pollock et al. 2002, Mazerolle et al. 2007). For a field

experiment of this geographic scale, the use of relative abundance estimates from a standardized, non-destructive sampling scheme rather than mark-recapture of uniquely marked salamanders had both logistical and financial benefits.

Densities of forest-dwelling wildlife populations do not always correlate positively with habitat quality (Van Horne 1983, Todd and Rothermel 2006), and additional information regarding species demographics or vital rates may strengthen inferences made from relative abundances (Welsh et al. 2008). To develop relationships among salamander relative abundances, habitat quality, and demography, we identified stage-classes (juvenile or adult) from published ranges of snout-vent lengths (SVL) (Sayler 1966, Petranka 1998), and counted eggs in gravid females of light-colored salamander species (*Plethodon cinereus*, *Desmognathus ochrophaeus*) by candling (Gillette and Peterson 2001). We followed Knapp et al. (2003) and pooled members of the slimy salamander semispecies complex (*Plethodon glutinosus* and *P. cylindraceus*) into *P. glutinosus*.

Statistical analyses for relative abundances

We averaged data from individual transects across sampling nights within a year and EU to the mean number of salamander captures/transect/EU. The study site was the unit of replication and was blocked in analyses. We used a repeated-measures Analysis of Covariance (ANCOVA) to determine effects of the silvicultural treatment, site, year of sampling, and treatment \times year interaction on relative abundances of salamanders using SAS 9.1 (SAS Institute, Cary, North Carolina, USA). EUs within study sites had 1-2 years of pre-harvest abundances, which was used as a covariate to account for spatial variation in abundances among treatment plots. We averaged across years to develop the covariate for sites with >1-year of preharvest data. Prior to analyses, data were examined for normality and homoscedasticity, and all non-

normal data and data with inconstant variance were square-root transformed to meet the assumptions of analysis of covariance (ANCOVA) (Neter et al. 1996). We used the autoregressive heterogeneous option in SAS to structure the covariance matrices.

Whereas BB1, BB2, WV1, and WV2 were sampled nearly every year since the initial harvest, CL1 was sampled during years 1, 8, and 9-post-harvest and CL2 was sampled years 1, 2, 9, and 10 post-harvest. The large number of missing cells from CL1 precluded its use in an analysis of all post-harvest sampling years. Therefore, we conducted 2 separate repeated-measures ANCOVAs for the relative abundance of all terrestrial salamanders combined: (1) from years 1-13-years post-treatment, excluding the CL1 site, and (2) using years 1-2, and 8-9 post-treatment, which included all 6 study sites. Differences among silvicultural treatments were examined after adjusting p-values with the Tukey-Kramer adjustment. We considered statistical significance at $\alpha=0.05$.

Demography

We determined the proportion of sampled populations that were juveniles, the proportion of light-vented adult females that were gravid during the pre-brooding season, and the mean number of yolked eggs of gravid females of light-vented species as metrics of demography. We addressed small sample sizes by pooling salamanders from non-harvested treatments (i.e., control and herbicide EUs) and comparing estimates to pooled harvested treatments (i.e., group selection, shelterwood, leave tree, commercial clearcut, and silvicultural clearcut), which all had decreased relative abundances up to 4-years post-harvest (Knapp et al. 2003). Further, we pooled data across years into three time periods to examine how long potential changes to demography persisted after treatment. We examined demographics within year 0, the preharvest sampling period, and divided the post-harvest periods into 2, approximately equal time periods.

We examined demographics from 1-6 years post-harvest, which we termed “early,” and from 7-13-years post-harvest, which we termed “late.”

To estimate the reproductive status of females, we only considered adult female salamanders captured prior to June 15 of each year, after which gravid females could be expected to be brooding eggs, and thus unavailable for capture. We separated adult salamanders from juveniles using maximum SVLs for juveniles reported in Petranka (1998): 34 mm for *Plethodon cinereus*, 38 mm for *P. richmondi*, 58 mm for *P. glutinosus*, and 30 mm for *Desmognathus ochrophaeus*. Demographics of less commonly captured species were not compared.

We used two-tailed binomial proportions tests to compare differences between the proportion of gravid to non-gravid females of light-vented species (i.e., *P. cinereus* and *D. ochrophaeus*) and the proportion of juveniles to adults between harvested and unharvested treatments for commonly captured species (Zar 1996). We compared the mean number of eggs/gravid female between harvested and unharvested treatments within a time period with two-tailed t-tests (Zar 1996). The number of eggs in gravid salamanders was not recorded consistently prior to treatment application, so we did not compare the mean number of eggs/female for the preharvest time period.

Population matrices and projections

Vital rates of *P. cinereus*, the most commonly captured species in our study, were examined for their influence on population growth rates and to determine the potential influence of vital rates on the long-term reduction in relative abundances in harvested treatments. We predicted that relatively low fecundity and high survival of *P. cinereus* would result in a low population growth rate and an extended recovery period. We used a pre-hatching pulse female-based, Lefkovich three-stage population matrix with pre-juvenile (egg), juveniles, and adults as

life stages based on sizes of individuals (Crouse et al. 1987, Biek et al. 2002) (Figure 2.1). *P. cinereus* are direct developers without a larval stage. Thus, we considered females <34 mm SVL as non-reproductive juveniles, and considered females ≥ 34 mm SVL adults.

We estimated the number of eggs laid/female (i.e., fecundity, F_i) from our estimates of yolked ova during the pre-brooding periods and assumed a 1:1 sex ratio of hatchlings. Egg survival is thought to be high based on a laboratory study (Highton and Savage, 1961, *but see* Yurewicz and Wilbur 2004), and our estimates of eggs/gravid *P. cinereus* ($\bar{X} = 7.03$) matched closely with an estimate of hatchlings/nest ($\bar{X} = 7.17$) from a wild population near our BB1 and BB2 sites (Angleberger and Chinnici 1975). Based on this information, we estimated egg survival as 0.9 to account for some egg mortality. Across the 13-years of post-harvest sampling, we never captured a gravid female *P. cinereus* with a SVL <34 mm, and Saylor's (1966) sampling of *P. cinereus* in Maryland only reported gravid females ≥ 34 mm. Therefore, we assumed that the probability of animals classified as juveniles laying eggs was zero, and based on the literature, females may only reproduce biennially so that the adult probability of laying eggs was 0.5 (Saylor 1966). Annual survival rates for specific stages of plethodontid salamanders have not been well-documented, but those estimates that are available range from 0.626-0.743 for adult *D. ochrophaeus* (Tilley 1980), 0.155-0.229 for *D. fuscus* (Danstedt 1975) and 0.81 for *P. jordani* (Hairston 1983). Because published juvenile survival and adult survival rates for *P. cinereus* were unavailable, we incorporated estimates from a life table analysis of the species with the most similar life history, *P. jordani* (Hairston 1983). Using demographic parameters from a congener is a commonly used technique for population modeling (Biek et al. 2002, Heppell et al. 2000). Although life tables rely on the often untenable assumptions of a stable age distribution and equal probability of being sampled among individuals (Gaillard et al.

1998), these survival estimates represented the best available information. From Hairston (1983), we estimated annual adult survival as 0.81 and annual juvenile survival as 0.574 and incorporated these values into the population matrix (Figure 2.1). We followed Crouse et al. (1987) to estimate stage-specific probabilities of surviving and remaining a juvenile (P_i) and of surviving and entering the adult stage (G_i).

We used analytical sensitivity and elasticity analysis (Caswell 2001) to determine the influence of individual vital rates on proportional changes in the population growth rate (λ) (Biek et al. 2002). Sensitivity refers to the change in λ from an infinitesimal change in an individual vital rate, and elasticity simply rescales sensitivity to a proportional change in λ with a proportional change in a single vital rate (Caswell 2001). Sensitivity and elasticity analyses are useful for estimating changes in λ when changes to survival or reproduction occur; thus, these results can be used to predict how salamander populations may respond to perturbations in survival or reproduction (Biek et al. 2002).

Secondly, to qualitatively evaluate whether observed changes to relative abundance from forest harvesting impeded population recovery to pre-harvest levels, we projected our population matrix for 15 time-steps, the approximate length of this study. First, we multiplied our female-based projection matrix by a hypothetical population-vector representing the number of individuals in the stage classes at time zero (PM1). Our vector was based on the number of juveniles: adults observed during years 1-6 post-treatment across all treatments (14:37). We assumed 1/2 of females produced 7 eggs, and 1/2 of the eggs were female, so that 64 eggs were in the population at $t=0$. We selected our starting numbers of individuals to sum to a population size close to 100 to simplify interpretation. However, we were not interested in absolute numbers of salamanders, but rather in determining the dynamics of the population over time so

that any number of eggs: juveniles: adults in the aforementioned proportions would produce the same conclusions.

From our field data, 24% of the pre-harvest abundance of *P. cinereus* was present in the silvicultural treatments with canopy disturbance by 3-years post-harvest. Assuming this reduction in relative abundance of salamanders represented the decline in the population size of *P. cinereus*, or at least of surface-active salamanders, we estimated whether a simultaneous reduction of all stage-classes by 76% would prevent populations from rebounding to pre-harvest levels of abundance within 15-years (PM2). We considered PM1 to be a baseline population unaffected by disturbance and qualitatively compared PM2 to the population structure. We projected the population prior to reaching the stable age distribution because we were interested in the initial dynamics, which represented the disruption of population age structure from forest harvesting. Population projections and associated computations were calculated with the PopTools 2.7.5 (G.M. Hood, CSIRO Corporation) add-in to Microsoft Excel 2003 (Microsoft Corporation).

Results

Overstory basal area

Overstory basal area of EUs prior to treatment, 2-years after treatment and 9-11 years after treatment averaged 29 m²/ha, 30 m²/ha, and 32 m²/ha for the control EUs, 32 m²/ha, 32 m²/ha, and 33 m²/ha for the midstory herbicide treatment EUs, 32 m²/ha, 18 m²/ha, and 20 m²/ha for the group selection EUs, 32 m²/ha, 14 m²/ha, and 16 m²/ha for the shelterwood EUs, 31 m²/ha, 8 m²/ha, and 10 m²/ha for the leave tree EUs, 34 m²/ha, 6 m²/ha, and 10 m²/ha for the commercial clearcut EUs, and 33 m²/ha, 1 m²/ha, and 2 m²/ha for the silvicultural clearcut EUs, respectively (C. Atwood, Virginia Tech, Department of Forestry, unpublished data).

Total salamander abundance

Across the 14 years of sampling, we attained >10,000 captures of plethodontid salamanders across 263 sampling nights. Data were square-root transformed prior to analyses to meet the parametric assumptions of normally distributed residuals and homogeneity of errors. Following transformation, residuals were normally distributed and variances were homogeneous ($P>0.55$). Pre-treatment estimates of abundance differed ($F_{1,21}=17.01$, $P<0.001$) and were incorporated in analyses as a covariate. For the analysis up to 13-years post-treatment, there were significant differences among years post-harvest ($F_{12,179}=9.74$, $P<0.001$) and treatments ($F_{6,21}=9.71$, $P<0.001$), but no significant treatment \times year interaction ($F_{72,179}=0.62$, $P=0.989$). In general, silvicultural treatments with canopy disturbance had lower relative abundances of salamanders than treatments without canopy disturbance (i.e., control and herbicide) (Figure 2.2, Figure 2.3). Relative abundance of salamanders in the group selection harvest was lower than the herbicide treatment, but not significantly different than any other treatment.

For the ANCOVA that included all 6 study sites, but only years 1, 2, 8, and 9 post-harvest, there were significant differences among pre-treatment estimates of abundance ($F_{1,27}=10.11$, $P<0.004$), treatments ($F_{6,27}=6.36$, $P<0.001$), but no significant effect of year ($F_{3,78}=1.04$, $P<0.379$), or year \times treatment interaction ($F_{18,78}=0.53$, $P=0.934$). Relative abundance of terrestrial salamanders was greatest in the control and herbicide treatments, which were similar to each other ($P=0.820$). Whereas the control EUs did not differ ($P>0.05$) from any treatment with canopy disturbance except for the commercial clearcut ($P=0.014$), the herbicide treatment had greater salamander abundances than all silvicultural treatments other than control EUs (Figure 2.2).

Demographic differences in treatments

No consistent patterns emerged for demographics across the four species of salamanders examined. The proportion of juvenile salamanders captured varied among the four most common species, ranging from 22% of *P. cinereus* in the harvested treatments, during the late period, to 75% of *P. glutinosus* in the harvested treatments during the late period (Table 2.1). The proportion of juvenile *P. cinereus* was greater in the unharvested than harvested treatments during the late time period and for *D. ochrophaeus* during the early period ($P < 0.05$) (Table 2.1). For *P. richmondi*, the proportion of juveniles was greater in harvested treatments during the pre-treatment period ($P = 0.039$), but this did not persist through later periods. The proportion of juvenile *P. glutinosus* did not differ between treatment classes in any time period ($P > 0.05$).

Across the entire study, we captured 512 gravid *P. cinereus* and 170 gravid *D. ochrophaeus* prior to June 15 (Table 2.1). The proportion of gravid female *P. cinereus* or *D. ochrophaeus* did not differ between harvested or unharvested treatments during any time period ($P > 0.09$) (Table 2.1). However, the proportion of gravid female *P. cinereus* did appear to decline through time since harvest. Further, the number of yolked eggs/gravid female *P. cinereus* did not differ between harvested and unharvested treatments ($P > 0.17$) (Table 2.1). During years 1-6 post-harvest, the average number of eggs/gravid female *D. ochrophaeus* was 13.8 in unharvested treatments and 11.3 in harvested treatments, which differed statistically ($t_1 = 2.64$, $P = 0.01$).

Population projections of P. cinereus

Based on the population matrix derived from estimated vital rates of *P. cinereus*, the probability of surviving and remaining a juvenile (P_i) was 0.475 and the probability of surviving and entering the adult stage class (G_i) was 0.099. Further, we estimated λ as 1.03 indicating the population was increasing by 3%. The sensitivity and elasticity analyses revealed an

infinitesimally small perturbation in adult survival would result in the greatest change of λ . Elasticity of adult survival (0.487) was $3.7-4.3 \times$ > other elements of the population matrix. Therefore, if adult survival decreased from 0.81 to 0.71, λ would be expected to decrease by 5% [$((0.71-0.81)*0.487) = -0.05$].

The two projection scenarios varied in the resulting population structure after 15 years (Figure 2.4). The baseline projection (PM1) displayed a steadily increasing population. In contrast, after a 76% reduction across stage classes to represent observed declines in abundance (PM2), only the number of juveniles grew to “pre-harvest” levels after 15 time steps. Approximately 60 years would be necessary for all stage classes to recover under PM2. Scenarios required approximately 3-4 time steps to reach the stable age distribution (Figure 2.4).

Discussion

Silvicultural treatments that disturbed the canopy in Appalachian hardwood forests had long-term negative impacts on relative abundance of terrestrial salamanders. Contrary to our prediction, we detected significant treatment effects through 13-years post-harvest and failed to detect significant treatment \times time interactions, suggesting that the negative effects of the silvicultural techniques were persistent and consistent through our study period. Similar to Harpole and Haas (1999) and Knapp et al. (2003), we observed lower total numbers of salamander captures in most treatments with canopy disturbance as compared to both the control and herbicide EUs (Figure 2.2). The exception was the group selection treatment, which only had significantly smaller numbers of salamander captures compared to the herbicide EUs.

As with worldwide losses in biodiversity, degradation of habitat has been implicated as one of a suite of factors causing global declines of amphibians (Alford and Richards 1999, Beebee and Griffiths 2005). Although North American plethodontid salamanders typically have

not displayed the wide-scale population declines of other amphibians (but see Highton 2005), these species experience local declines after anthropogenic disturbances to their habitats, such as from forest harvesting. The short-term effects of forest harvesting to terrestrial salamanders (Pough et al. 1987, deMaynadier and Hunter 1995) and longer-term consequences of clearcutting on forest amphibians (Petranka et al. 1993, Ash 1997, Herbeck and Larsen 1999, Ford et al. 2002) have been documented, but experimental comparisons of a broad range of forest regeneration techniques across broad spatial and temporal scales are lacking. Based on the results of our long-term experimental manipulation of mixed-hardwood forest, relative abundances of terrestrial salamanders showed long-term changes from the application of 6 oak regeneration techniques, and population vital rates indicate that life history characteristics may contribute to these observed patterns.

Results from our second analysis that included all 6 study sites, but only years 1, 2, 8, and 9 post-harvest were more ambiguous, presumably due in part to fewer degrees of freedom and subsequently lower power to detect differences. Further, strong declines in salamander abundances after harvesting were not evident in year 1 (Knapp et al. 2003), which also could have influenced the results. From this, only salamander abundances in the herbicide EUs were statistically greater than the other silvicultural treatments, and the control EUs could only be distinguished from the commercial clearcut (Figure 2.2).

Although our results varied depending on whether all years of post-harvest data or all sites were included, it is clear that a wide range of oak regeneration treatments had lasting negative effects to salamanders in Appalachian hardwood forest. During years 8-9 post-harvest, only the control and herbicide EUs had abundances \geq the pretreatment period; the other treatments ranged from 33% of preharvest abundances for the commercial clearcut to 70% for

the silvicultural clearcut (Figure 2.3). Overall, the harvested treatments increased from a low of 18% at year 3 post-treatment to 67% at year 9. From the perspective of terrestrial salamanders, silvicultural alternatives to clearcutting may not be suitable for maintaining abundances for an extended period of time following harvest.

During both the initial post-harvest period (Harpole and Haas 1999, Knapp et al. 2003) and during our long-term study, the herbicide treatment supported either similar or greater abundances than control EUs. We are uncertain why salamanders may have increased their abundances following the understory herbicide treatment, especially given that the understory vegetation, microclimate, and leaf litter biomass were not substantially different from control EUs (Hammond et al. 1998, Harpole and Haas 1999, Knapp 1999). It is possible that subtle changes in understory vegetation structure in herbicide EUs led to increased foraging opportunities and success for salamanders (Jaeger 1978), ultimately increasing fecundity or the proportion of juveniles surviving. Or, a slight decrease in basal area without a concurrent increase in canopy openness may have led to increased soil moisture from less evapotranspiration through woody stems.

Demography of salamanders

If the long-term decreases in relative abundances of terrestrial salamanders were caused by reductions in habitat quality from oak regeneration treatments, then differences in reproduction of salamanders should be apparent between harvested and unharvested treatments. In agreement with our prediction, some demographics associated with fecundity were greater in unharvested treatments. Both *D. ochrophaeus* and *P. cinereus* had a greater proportion of juveniles in the unharvested treatments, but the difference was evident soon after harvesting (years 1-6 post-harvest) for *D. ochrophaeus* whereas the proportion of juveniles differed for *P.*

cinereus 7-13-years post harvest. *D. ochrophaeus* brood 8-37 eggs annually (Petranka 1998) and female *P. cinereus* produce an average of 6-9 eggs every other year (Sayler 1966, Petranka 1998). Therefore, there may have been a greater time lag in the changes to demography caused by forest manipulations to *P. cinereus* as a result of lower fecundity.

Other research has noted differences in demographics of terrestrial salamanders when comparing uncut forest stands to recent clearcuts, including a smaller proportion of juvenile and fewer adult male *P. metcalfi* in reproductive condition in a 10-year-old clearcut (Ash et al. 2003). Conversely, a greater proportion of juvenile *P. cinereus* were reported in forest clearcuts harvested 2-11 years earlier than in mature stands (deMaynadier and Hunter 1998) and a greater proportion of young *P. elongatus* in young forest compared to late seral forest (Welsh et al. 2008). A change in salamander reproductive demographics was not detected within the first 1-4 years following stand treatments on these study sites (Knapp et al. 2003), but the number of sites, years of post-treatment sampling, and number of salamander captures all have increased greatly in this study.

Adult salamanders in the unharvested EUs may have been more fecund and able to maintain the number of juveniles via higher reproductive values than salamanders in the harvested EUs with reduced reproduction. The greater number of *D. ochrophaeus* eggs/gravid female in unharvested stands during years 1-6 supports the hypothesis that habitat quality for at least some species of salamanders is altered by forest harvesting, although we did not detect differences in the proportion of gravid females for light-vented species. The mechanisms altering habitat quality of salamanders from forest harvesting are not known, but changes to invertebrate prey (Mitchell et al. 1996), increased energetic requirements (Brooks and Kyker-

Snowman 2008), or limits to cutaneous respiration (deMaynadier and Hunter 1998) may negatively affect reproduction or survival of terrestrial salamanders.

Population modeling

Perturbations of vital rates and possibly λ may be a key mechanism causing reduced abundances of wildlife following a disturbance (Todd and Rothermel 2006). Our elasticity analysis indicated that disturbances that affect survival of adult *P. cinereus* would have the greatest influence on the population growth rate (Biek et al. 2002). In fact, a decrease in adult survival of as little as 10% could cause the population to decline. However, PM2, which reduced numbers of juvenile and adult salamanders by a realistic 76% with no decrease in survival, closely approximated the reduction of salamanders we observed in our experimental treatments. At 9-years post-treatment the total number of salamanders in harvested EUs was at 67% of preharvest abundances, similar to the 62% of adult and juvenile salamanders predicted by the projection matrix at year 9. Our results suggest that increased mortality as a result of a single disturbance without long-term changes in survival of *P. cinereus* from forest harvesting could explain our observed patterns of abundance. Whether increased desiccation and/or temperatures had greater effects on juvenile salamanders is unknown, but plausible, given their higher surface area: volume ratios. We stress that survival estimates for this analysis were from a congener, that those estimates may differ based on skeletochronology (Ash et al. 2003), and currently no estimates of variability in this vital rate are available, so that our projections should be viewed cautiously. Additionally, we do not have information on movement of salamanders after harvesting, and recolonization of harvested EUs could have been facilitated by immigration of individuals from outside our sites (deMaynadier and Hunter 1998, Ash et al. 2003).

With observed reduction in salamanders and the low population growth rate (3%), >60 years would be needed for all life-stages of *P. cinereus* to reach predisturbance levels. In clearcut stands, recovery of salamanders has been estimated from 20-70 years in the Appalachians based on chronosequence and observational studies (Petranka et al. 1993, Ash 1997), which encompasses this estimate. And, >80 years may be necessary for the negative effects of logging roads on terrestrial salamanders to dissipate, indicating that forest disturbances have long-lasting effects on salamanders (Semlitsch et al. 2007). Despite the potential benefits from population analyses to conservation and management of amphibians (Biek et al. 2002, Boyce et al. 2006, Todd and Rothermel 2006), ours is the first study that we are aware of to use either a sensitivity/elasticity analysis or projection matrices to model the effects of forestry practices on dynamics of terrestrial salamanders. Although our population analyses were deterministic and density independent, these results suggest that the return of salamander populations to harvested plots may not only be limited by long-term changes to habitat (deMaynadier and Hunter 1995, Ash 1997), but also by the life history characteristics and reproductive potential of salamander species.

Management Implications

To evaluate the trade-offs between economic gain and ecological stability, forest managers need results from long-term experimental manipulations. Our research indicates that a range of forest management techniques may cause lasting reductions of terrestrial salamander populations likely due to both low population growth rates and changes to habitat. Future studies of the influence of silviculture on salamanders should estimate survival rates of salamanders before and after forest harvesting and determine whether movements occur in or out of harvested stands. In the past, long-term marking techniques for small amphibians were limited, but

subcutaneous marking of *Plethodon* salamanders with elastomers can be a reliable method for mark-recapture studies (Davis and Ovaska 2001, Heemeyer et al. 2007) to estimate survival as can individual pattern recognition (Tilley 1980, Church et al. 2007). Similarly, population reconstruction of salamanders from skeletochronology (Ash et al. 2003, *but see* Bruce and Castanet 2006, Eden et al. 2007) or size distributions (Hairston 1983) can provide estimates of age-specific survival for population modeling, but life table modeling relies on assumptions difficult to reach in wild populations and does not provide estimates of variability (Gaillard et al. 1998).

Although we provide some evidence that salamanders in group selection harvests may be recovering more quickly compared with other oak regeneration options, these EUs are scheduled for a second entry in 7-9 years (approximately 20 years after the first entry). The effects of multiple stand entries on terrestrial salamander populations are unknown, but are likely to have cumulative negative impacts. Further, managers must also consider the trade-offs between the amounts of wood fiber extracted, costs of harvesting, soil erosion, and number of re-entries required when evaluating silvicultural regimes. For example, combining loss of salamanders with the area of land required to extract a given amount of wood fiber, Knapp et al. (2003) determined that the group selection harvest has 1.8× the landscape-scale effect on salamanders as the silvicultural clearcut. Additionally, the group selection harvest was estimated to have 10 tons/acre more soil loss than other treatments over a 100-year rotation (Hood et al. 2002) and may have less vigorous regeneration of oaks from stump sprouts than other silvicultural systems (Atwood 2008). Thus, implementing silvicultural clearcuts, which could limit the spatial extent of habitat alteration, could provide a method to maintain populations of terrestrial salamanders at a larger scale, given that remaining forested habitats are not disturbed. Our study only examined

the effect of a single stand entry on terrestrial salamanders on 2-ha EUs; repeated disturbances to the soil and vegetation from harvesting equipment and disturbances at a larger spatial scale may cause different effects on salamanders than what we observed.

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Table 2.1. Demographic characteristics of common salamander species following experimental forest harvests in central Appalachian oak forests, 1994-2007. Data were divided into 3 time periods: (1) preharvest, which included sampling years prior to application of silvicultural treatments, (2) early, which included estimates from years 1-6 post-harvest, and (3) late, which included estimates from years 7-13 post-harvest.^a

Species	% Juvenile ^b		% Gravid ^c		Mean Eggs/Female	
	Unharvested	Harvested	Unharvested	Harvested	Unharvested	Harvested
<i>Plethodon cinereus</i>						
Preharvest, Year 0	38 (62/165)	46 (210/453)	65 (22/34)	81 (54/67)	n/a	n/a
Early, Years 1-6	26 (250/978)	29 (231/802)	32 (103/321)	33 (86/261)	6.7	6.9
Late, Years 7-13	28 (242/853) ^d	22 (168/751) ^d	52 (122/235)	55 (125/229)	7.1	7.3
<i>Desmognathus ochrophaeus</i>						
Preharvest, Year 0	38 (203/539)	39 (437/1112)	56 (37/66)	66 (90/137)	n/a	n/a
Early, Years 1-6	35 (74/209) ^d	23 (36/155) ^d	55 (17/31)	57 (17/30)	13.8 ^d	11.3 ^d
Late, Years 7-13	44 (135/310)	45 (66/148)	45 (9/20)	0 (0/3)	12.0	n/a
<i>Plethodon glutinosus</i>						
Preharvest, Year 0	71 (76/107)	74 (211/287)				
Early, Years 1-6	39 (80/121)	55 (84/153)				
Late, Years 7-13	71(102/143)	75 (182/244)				

Plethodon richmondi

Preharvest, Year 0	44 (71/161) ^d	54 (211/391) ^d
Early, Years 1-6	51 (27/53)	40 (23/58)
Late, Years 7-13	64 (55/86)	68 (41/60)

^a Unharvested plots included control and herbicide plots and harvested plots included group selection, shelterwood, leave tree, commercial clearcut and silvicultural clearcut plots.

^b Proportions of juvenile salamanders (number of juveniles/total number of individuals) were calculated by dividing the number of *P. cinereus*, SVL<34 mm, *D. ochrophaeus*, SVL<30 mm, *P. glutinosus* SVL < 58 mm, or *P. richmondi* SVL <38 mm by the total number of that species. Within a time period, the proportion juvenile was compared between harvested and unharvested treatments with a two-tailed binomial proportions test.

^c Gravid females (number of gravid females/total number of females) were totaled from all adult females (*P. cinereus*, SVL \geq 34 mm, *D. ochrophaeus*, SVL \geq 30 mm,) of light-vented species captured on or prior to June 15th of each year. Within a time period, the proportion of gravid females was compared between harvested and unharvested treatments with a two-tailed binomial proportions test. Due to the low samples sizes of female *D. ochrophaeus* during the late period, a statistical comparison was not made for proportion of gravid female *D. ochrophaeus* 7-13 years post-harvest.

^d Statistically different at P<0.05.

<u>Eggs</u>	<u>Juveniles</u>	<u>Adults</u>
0	$\left[\begin{array}{c} \text{probability of juvenile becoming an} \\ \text{adult} \times \text{probability of laying} \times \text{clutch} \\ \text{size} \end{array} \right]$	$\left[\begin{array}{c} \text{adult survival} \times \text{probability of} \\ \text{laying} \times \text{clutch size} \end{array} \right]$
$\left[\begin{array}{c} \text{egg survival} \end{array} \right]$	$\left[\begin{array}{c} \text{probability of remaining a juvenile} \\ (P_i) \end{array} \right]^a$	0
0	$\left[\begin{array}{c} \text{probability of juvenile becoming an} \\ \text{adult} (G_i) \end{array} \right]^b$	$\left[\begin{array}{c} \text{adult survival} \end{array} \right]$

^aWe calculated P_i as $((1-p_i^{d_i-1})/(1-p_i^{d_i})) \cdot p_i$ following Crouse et al. (1987) where p_i is the annual survival estimate of a juvenile and d_i is the number of years spent as a juvenile.

^bWe calculated G_i as $(p_i^{d_i} \cdot (1-p_i)/(1-p_i^{d_i}))$ following Crouse et al. (1987) where p_i is the annual survival estimate of a juvenile and d_i is the number of years spent as a juvenile.

Figure 2.1. Female-based Lefkovich population matrix for eastern red-backed salamanders, *Plethodon cinereus*. Adult and juvenile survival estimates were from Hairston (1981) for *P. jordani* and egg survival was estimated as 0.90.

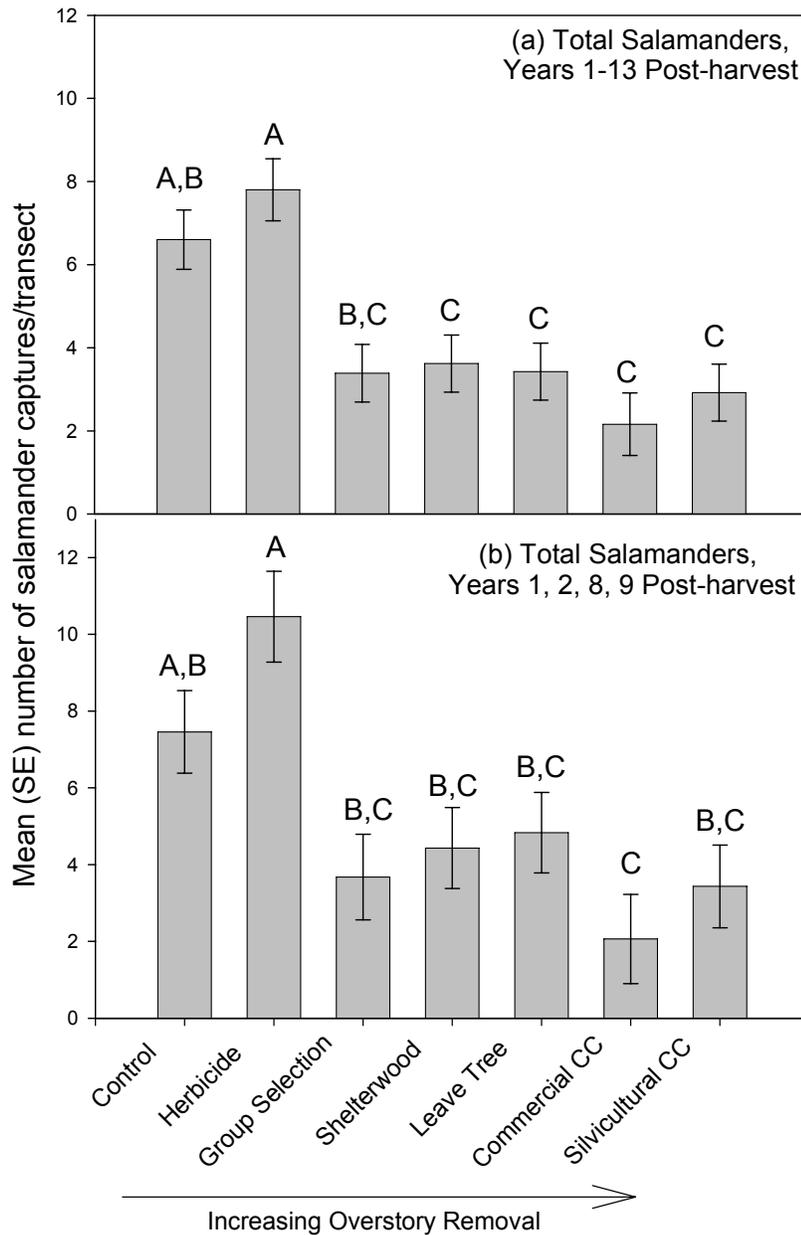


Figure 2.2. Effects of six experimental forest harvests and an untreated control on the relative abundances of (a) total salamander captures from 1-13 years post-harvest on 5 of 6 study sites (b) total salamander captures during years 1, 2, 8, 9 post-harvest on 6 of 6 study sites. Data were analyzed with repeated-measures Analysis of Covariance so that presented means are adjusted by preharvest abundances. Different letters indicate statistical differences among treatments ($P < 0.05$). Non-transformed data are presented, but analyses were conducted on square-root transformed abundances.

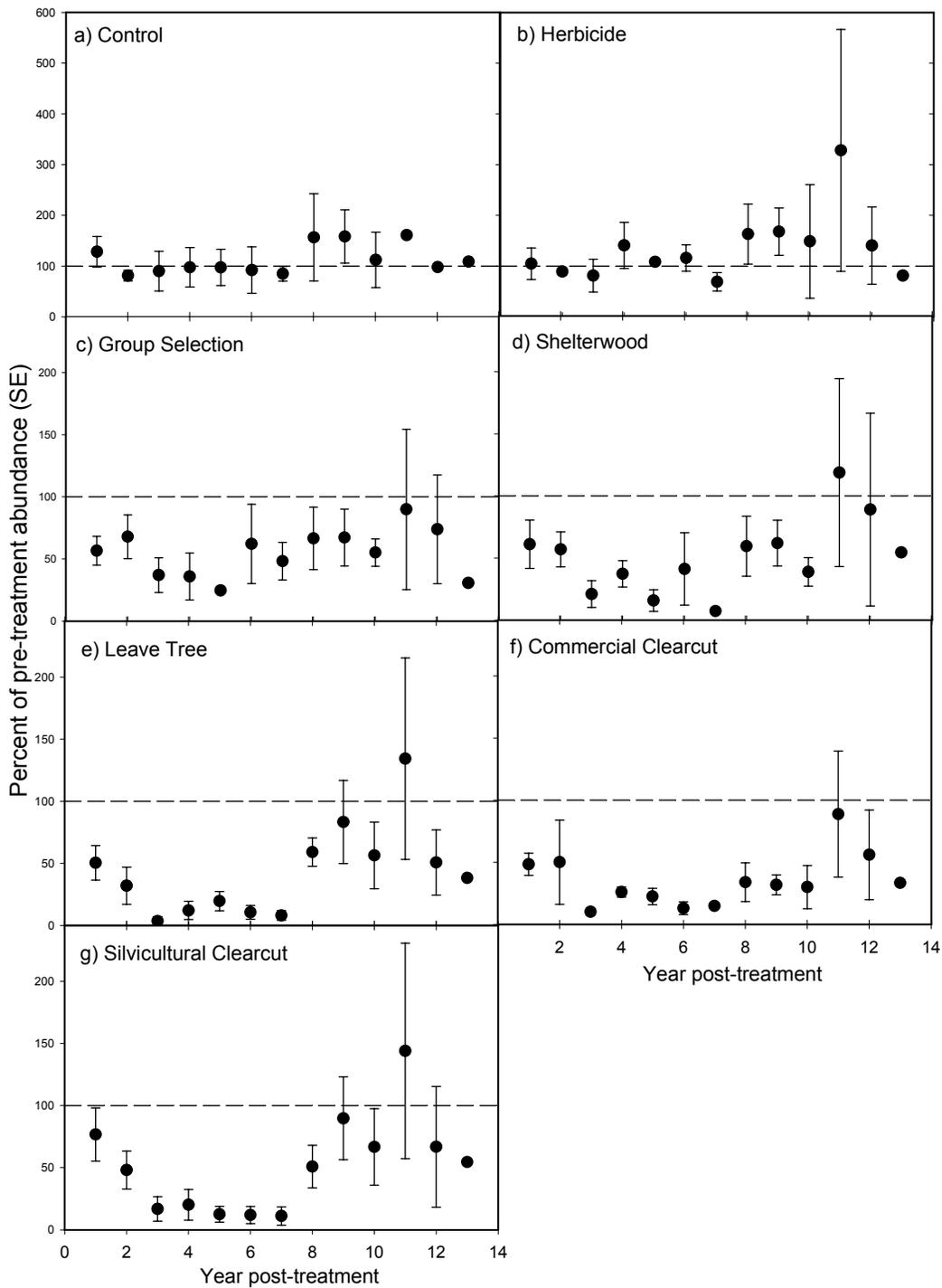


Figure 2.3. Percent of pre-treatment abundance (SE) of terrestrial salamanders across 7 silvicultural treatments in experimentally manipulated forested sites in Virginia (n=4) and West Virginia (n=2), USA to 13-years post-harvest. Sites were harvested in different years, so not every site was sampled yearly or to 13-years post-harvest, which contribute to variation in standard errors across years. Dashed line indicates recovery to pre-treatment abundance (100%).

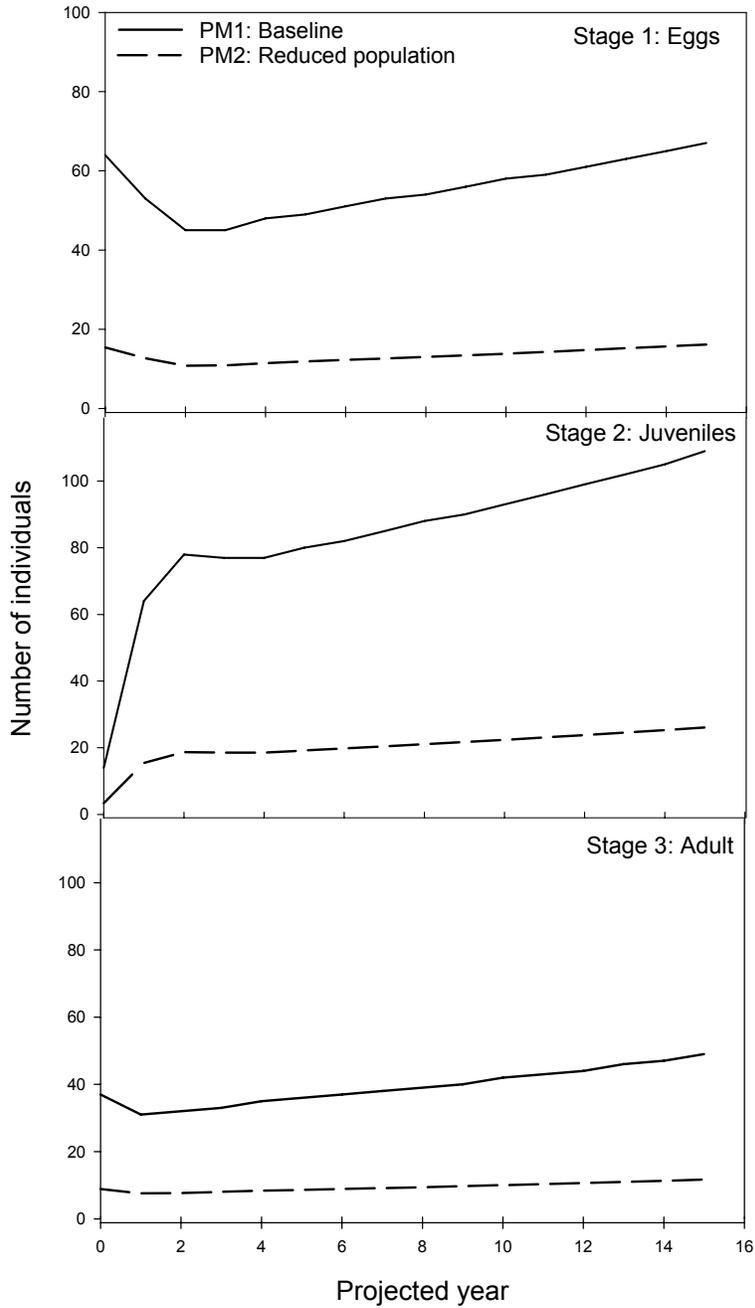


Figure 2.4. Number of individuals from a stage-based population matrix of vital rates of eastern red-backed salamanders (*Plethodon cinereus*) with egg, juvenile, and adult life-stages and projected to 15 years. We used our observed juvenile: adult ratio from years 1-6 post-harvest (14:37) and assumed 50% of females would produce 7 eggs with an equal sex ratio within a year. Two scenarios were projected: (PM1) a baseline projection, where the observed ratio of juveniles: adults from field studies was used, (PM2) where each stage was reduced by 76% to represent observed losses following silvicultural treatments.

CHAPTER 3: EFFECTS OF REPEATED-STAND ENTRIES ON TERRESTRIAL SALAMANDERS AND THEIR HABITAT

Abstract

Throughout eastern North America, silvicultural practices have shifted away from clearcut harvesting towards greater retention of overstory trees through at least a portion of a rotation. However, knowledge of how partial harvesting affects wildlife populations has not kept pace with changes in forest practices. Most studies of effects of partial harvesting on wildlife only have examined short-term impacts after the first stand entry and have not included both pre- and post-harvest estimates of abundance. In this study, I examined the effects of a shelterwood system on terrestrial salamanders both prior to and after an initial harvest and an overstory removal harvest (ORH) 12-13 years later, and compared abundances to similar control plots at two study sites in southwestern Virginia, 1994-2008. I also quantified habitat characteristics known to influence salamander abundances at control and shelterwood plots after the ORH. I detected site-specific differences in the effects of the shelterwood harvest and the ORH on terrestrial salamanders; at one site, abundances of salamanders were lower on shelterwood plots 2-years after the initial harvest and 1-year after the ORH compared to contemporaneous estimates from an unharvested control. At the other site, the same comparisons yielded no significant differences. Although abundance and volume of woody debris were greater in both shelterwood stands, depth of the leaf litter and density of overstory and understory trees were lower in the control plot for the site with fewer post-ORH salamander captures. At both sites, woody debris was more decayed in control plots. The inferences made from this case study of two experimentally manipulated field sites are limited by small sample sizes, but these data

suggest that multiple stand entries may have negative impacts on salamander abundance in some, but not all sites. More long-term monitoring of salamander populations seems justified in silvicultural systems with multiple entries within a rotation.

Introduction

Many jurisdictions within eastern North America have been trending away from intensive harvesting (e.g., clearcutting) and moving towards greater retention of overstory trees through all or part of the rotation (e.g., partial harvesting, where multiple entries often are made during a single rotation) (Siry 2002, Fuller et al. 2004, McWilliams et al. 2005). From the mid-1980s to the mid-1990s, clearcut harvesting made up 21% and 45% of the average annual harvest in the northern and southern U.S., respectively (U.S. Department of Agriculture, Forest Service 2009). In contrast, partial harvesting during the same period accounted for 79 and 55% (U.S. Department of Agriculture, Forest Service 2009). The predominance of non-clearcut harvesting has occurred in part because of the greater emphasis of land managers on retaining forest structure and biodiversity (Gillis 1990, Brunson and Shelby 1992) and the more positive public perception of multi-canopied forests compared to clearcuts (Brunson and Shelby 1992, Sedjo 1999, Bliss 2000). Knowledge regarding the influence of partial cutting, and especially the cumulative effects of multiple stand-entries, on wildlife populations and their habitats is limited (McComb et al. 1993, Fuller et al. 2004, Reichenbach and Sattler 2007, Homyack and Haas 2009). Most research on the effects of silvicultural practices on biodiversity has been short-term and observational, which limits the inferences made from those data (DeStefano 2002). At a landscape scale, partial harvests must be extended over a larger area to produce the same amount of wood fiber per harvest event that a clearcut may produce (Gillis 1990, Hagan 1996, Knapp et al. 2003), which may increase the effects of isolation and fragmentation on wildlife populations

(Saunders et al. 1991, Morrison et al. 1992). At a stand scale, populations of species sensitive to disturbance may not have had adequate time to return to preharvest abundances prior to subsequent harvests in the rotation. Or, by retaining some characteristics of more mature forest, partial harvests may have weaker or more positive effects on wildlife than clearcutting (McComb et al. 1993, Fuller et al. 2004).

Terrestrial salamanders are considered by some to be model organisms for examining the effects of forest harvesting on wildlife because they are physiologically linked to microhabitat and microclimate features by their requirements of cool and moist conditions for cutaneous respiration (Welsh and Droege 2001). In addition, terrestrial salamanders are long-lived, display low inter-annual variation in abundances, and are an apex predator in the leaf litter (Wyman 1998, Welsh and Droege 2001, Walton 2005, Walton and Steckler 2005). Terrestrial salamanders are one of the most abundant vertebrates in forested systems (Burton and Likens 1975) and reach their highest levels of species diversity in the central and southern Appalachians (Petranka 1998). Thus, salamanders have ecological characteristics that make them useful for examining effects of silvicultural practices on forest-interior wildlife.

Research has consistently demonstrated that forest harvesting has negative effects on abundances of terrestrial salamanders across forested systems in North America (deMaynadier and Hunter 1995, Dupuis et al. 1995, Homyack and Haas 2009). In a meta-analysis of 15 studies, untreated control stands had $5.0\times$ greater abundances of plethodontid salamanders than clearcut forest stands (deMaynadier and Hunter 1995). Although a greater focus has been on short-term effects of clearcut harvesting, available information indicates that most forest practices that remove canopy trees negatively affect salamanders (Pough et al. 1987, deMaynadier and Hunter 1995, Harpole and Haas 1999, Knapp et al. 2003, Homyack and Haas

2009), and that declines can be persistent (Petranka et al. 1993, Ash 1997, Homyack and Haas 2009). Despite the fact that multiple entries into a stand within a single rotation are a common component of many silvicultural systems, effects from >1 stand entry on terrestrial salamanders or their habitats have not been well-documented.

The goal of this investigation was to evaluate whether multiple entries in high-leave shelterwood stands have cumulative negative effects on terrestrial salamanders in central Appalachian oak forest. I used a case study approach to examine the effects of experimentally applied harvests on two sites in southwestern Virginia, USA. I predicted that terrestrial salamanders would not have recovered to preharvest abundances prior to the second stand entry and would decline further after a second harvest. Specifically, I examined (1) whether the relative abundances of terrestrial salamanders declined following both an initial and a second overstory removal harvest as compared to untreated control stands, and (2) whether selected within-stand habitat characteristics differed between recently harvested shelterwood stands and untreated control stands. Although inferences from this study are limited by only having two study sites, to my knowledge this research provides the first experimental evidence that evaluates the cumulative effects of multiple stand entries on terrestrial salamanders and their habitat.

Methods

Study Area

Study sites (Blacksburg 1, Blacksburg 2) were located on the Jefferson National Forest, Montgomery County, Virginia. The two sites are part of a long-term investigation of the effects of oak regeneration methods on biodiversity, the Southern Appalachian Silviculture and Biodiversity Project (SASAB) (Harpole and Haas 1999, Knapp et al. 2003, Belote et al. 2008, Homyack and Haas 2009, Chapter 1). Sites were selected to be south-facing (151-153°) with

moderate slopes (16-21%), have no recent history of stand disturbance, and have relatively uniform stocking of merchantable trees (Wender 2000). Dominant overstory trees included oaks (*Quercus spp.*), yellow-poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), and sourwood (*Oxydendron arboretum*) as well as small components of other hardwoods and white pine (*Pinus strobus*). At each site, 2-ha treatment plots (experimental units, EUs) were established and silvicultural treatments were applied randomly so that each site had both a control and a shelterwood EU. Additional details regarding study areas and EUs were provided by Wender (2000), Knapp et al. (2003), and Belote et al. (2008).

The shelterwood EU at the Blacksburg 1 site was harvested during winter 1994-1995 and at the Blacksburg 2 site during winter 1995-1996. With this silvicultural system, the overstory is harvested in two entries, facilitating the development of a cohort of advanced regeneration under the partial canopy after the initial stand entry (Smith et al. 1997). Following the first harvest, 12-14 m²/ha of overstory basal area was retained, which represented an average of 41% reduction (Knapp et al. 2003). Residual stems were dominant or co-dominant trees of preferred species with diameter of breast heights (dbh) of 25-40 cm. During winter 2007-08, residual overstory stems were harvested after EUs had 12-13 years to regenerate. Following the overstory removal harvest (hereafter ORH), residual basal area averaged 6 m²/ha (R.T. Belote, Department of Biological Sciences, Virginia Tech, unpublished data). Commercial loggers conducted harvests with chainsaws and skidders, which is typical of operations in the region. No treatments were applied to control EUs during this study although logging equipment was used and a skid road was accessed near one edge of the control EU at BB1.

Field sampling

My colleagues and I sampled terrestrial salamanders using night-time area-constrained searches on rainy nights spring through fall during 1994-1996 and 2007-2008. Within each EU, a 3×3 grid of 2×15 m sampling transects was established prior to the initial harvest. Each warm rainy night, we randomly selected one transect from the control and one from shelterwood EUs, and 2-3 observers hand-captured terrestrial salamanders active on the surface. We marked each capture location with a uniquely numbered pin flag and placed each salamander in an individually marked resealable plastic bag. Salamanders were brought to the lab where we confirmed species identification and recorded morphological and reproductive data (Knapp et al. 2003). Within 24 hours, salamanders were returned to their exact point of capture and released. Homyack and Haas (2009) provide additional detail regarding the methods used to sample relative abundance of terrestrial salamanders.

I also quantified habitat characteristics during the growing season immediately after the 2007-2008 ORH in the shelterwood and control EUs. I selected habitat characteristics suggested to be important correlates of salamander abundance and that have biological significance for terrestrial salamanders by mediating microclimate, providing foraging habitat, or providing habitat for brooding eggs. These variables included depth of leaf litter, volume of coarse woody debris, abundance of coarse woody debris, decay class of woody debris, abundance of overstory trees (as a surrogate of canopy cover), and abundance of understory stems.

Habitat characteristics were measured on the grid of salamander sampling transects. In 2008, I sampled all nine transects within each of the four EUs. To quantify the amount of coarse woody debris (CWD), I counted the number of root masses (≥ 7.6 cm diameter at the base), stumps (< 2 m height, ≥ 7.6 cm diameter), and logs (≥ 7.6 cm diameter, in contact with ground) within each transect. I quantified the volume of logs within transects by measuring the diameters

at both ends and the length and converted it into a volume by using the formula for the volume of a cone. I calculated the stump volume and root mass volume by measuring height and mid-point diameter of each and calculating it as a cylinder. I evaluated the decomposition class of each piece of CWD and assigned it a value from 1-5 based on the scale described by Maser et al. (1979). I quantified the density of trees (≥ 7.6 cm dbh, ≥ 1.5 m height, standing at $>45^\circ$ from the ground) that occurred within each transect and density of understory woody vegetation by counting the number of woody stems within a plot >0.5 m tall, but <7.6 cm dbh. These data were converted to a per/ha value to facilitate comparisons to other studies. Within a transect, I measured the depth of leaf litter to the Oi horizon at 6 locations (centered along the long axis of the transect at 2.0 m, 3.0 m, 7.0 m, 8.0 m, 12.0 m, 13.0 m) with a ruler held perpendicularly to the surface of the ground. Leaf litter measurements within a transect were averaged into a single value.

Statistical analyses

I wanted to determine whether abundances of salamanders differed between control and shelterwood EUs after both an initial and a second harvest in shelterwood EUs, and to evaluate this trend through time. Thus, I compared ratios of the number of salamander captures that were in the shelterwood EUs to number of captures in control EUs through time with Fisher's Exact Tests conducted separately for each site (Zar 1996). For each site, I compared the number of salamander captures in the shelterwood EUs to control EU for the pretreatment year vs. 1-season after harvest, for 1-season after harvest vs. 2-seasons after harvest, for the pretreatment year vs. 2-seasons after harvest, and for 1-season prior to the ORH vs. the season following the ORH. Secondly, I quantified differences between six selected habitat characteristics between untreated control and shelterwood transects after the ORH, with t-tests for unequal variances (Zar 1996)

and used the Satterthwaite approximation to estimate degrees of freedom (Neter et al. 1996). I considered differences significant at $\alpha=0.10$ because this was a case study approach and my power to detect differences was limited. SAS 9.2 (SAS Institute, Cary, North Carolina, USA) was used for all analyses.

Results

Across the entire study period, I captured 504 terrestrial salamanders on 54 sampling nights. I sampled 2-8 sets of transects/site within a year ($\bar{X}=6$ nights of sampling/site). Most (92%) salamanders were eastern red-backed salamanders (*Plethodon cinereus*), but captures also included white-spotted slimy salamanders (*Plethodon cylindraceus*, 7% of captures) and <1% each of northern dusky salamanders (*Desmognathus fuscus*), two-lined salamanders (*Eurycea bislineata*), and spring salamanders (*Gyrinophilus porphyriticus*) (Table 3.1).

The effects of shelterwood harvesting differed across study sites and between years of post-harvest sampling. At the Blacksburg 1 site, the proportion of terrestrial salamanders captured in the shelterwood EU versus control EU was similar between the pretreatment year and the growing season after treatment (Fisher's Exact Test, $P=0.261$) (Table 3.2), but a lower proportion of salamander captures occurred in the shelterwood EU 2-years after harvest (Fisher's Exact Test, $P=0.002$). I also detected a decline in the proportion of salamanders in the shelterwood EU between years one and two post-harvest (Fisher's Exact Test, $P=0.030$) (Table 3.2). In addition, salamander captures in the shelterwood EU relative to the control EU declined from the year prior to the year following the ORH (Fisher's Exact Test, $P=0.058$). In contrast, for the Blacksburg 2 site, I was unable to detect a difference between the proportion of total salamander captures on the shelterwood EU during the pretreatment versus one year after harvest (Fisher's Exact Test, $P>0.999$), between one and two years after harvest (Fisher's Exact Test,

$P > 0.999$), between the pretreatment year and two years after harvest (Fisher's Exact Test, $P = 0.734$), or between the year prior to and the year after the ORH (Fisher's Exact Test, $P = 0.359$) (Table 3.2).

In general, structural characteristics of shelterwood EUs after the ORH differed from untreated control EUs. The volume (BB1, $t_8 = -2.31$, $P = 0.050$; BB2, $t_9 = -2.88$, $P = 0.019$) and abundance (BB1, $t_{12} = 4.33$, $P < 0.001$; BB2, $t_{10} = -3.95$, $P = 0.003$) of CWD was greater in shelterwood EUs than in control EUs (Figure 3.1a, 3.2b), and CWD was more decomposed in control EUs (BB1, $t_{12} = 2.80$, $P = 0.018$; BB2, $t_{12} = 2.77$, $P = 0.017$) at both study sites (Figure 3.1c). The density of overstory trees was 2.5 and 2.0 \times greater in control EUs at the Blacksburg 1 and Blacksburg 2 sites, but this difference was significant only at Blacksburg 1 (BB1, $t_{13} = 1.93$, $P = 0.076$; BB2, $t_{16} = 1.41$, $P = 0.178$;;) (Figure 3.1d). The control EU had a greater density of understory trees (< 7.6 cm dbh) at Blacksburg 1 ($t_{15} = 1.80$, $P = 0.092$), but did not differ from the shelterwood EU at Blacksburg 2 ($t_{10} = -1.21$, $P = 0.254$) (Figure 3.1e). Lastly, the depth of the leaf litter was 1.7-2.3 \times greater in control EUs (BB1, $t_{12} = 2.36$, $P = 0.04$; BB2, $t_{15} = 5.07$, $P < 0.001$) (Figure 3.1f).

Discussion

In this study of experimentally manipulated oak forest, relative abundances of terrestrial salamanders displayed site-specific differences in the response of salamanders to both the initial harvest and the ORH 12-13-years later. On Blacksburg 1, salamander captures on the shelterwood EU relative to the control declined through two years after treatment, and declined again after the ORH. In contrast, on Blacksburg 2, where the number of salamander captures was only 17% of the total (on the two sites), I did not detect differences in proportions of salamanders at control versus shelterwood EUs between years. The failure to detect differences

between years may have been related to the smaller sample size and range of salamander captures/year during post-harvest sampling (0-14 at Blacksburg 2, vs. 13-68 at Blacksburg 1). In addition, broader studies that included these study sites indicated that differences in salamander abundances between control and harvested treatments were not evident until two years after harvest (Knapp et al. 2003). Thus, additional estimates of salamander captures two or more years after the ORH may lead to consistent declines in the relative abundance of salamanders on both study sites.

Partial harvesting reportedly either negatively affects (Brooks 2001, Grilou et al. 2000, Knapp et al. 2003, Homyack and Haas 2009, this study) or has little effect (Pough et al. 1987, Mitchell et al. 1996, Brooks 1999, Duguay and Wood 2002, Reichenbach and Sattler 2007, Kluber et al. 2008, this study) on the relative abundance of terrestrial salamanders. However, prior research has focused only on effects to salamanders from initial stand entries. In contrast, I quantified relative abundance of salamanders through both the initial and second harvest, and provided evidence that repeated stand entries may negatively affect salamanders. At both study sites, a second harvest caused an additional decline in the numbers of salamanders captured in the shelterwood as compared to the control, but this trend was only statistically significant at Blacksburg 1. At both sites, pre-ORH abundances of salamanders were approximately two-times larger than post-ORH values. Whether this negative effect will be transitory, or will have cumulative long-term impacts to salamander populations currently is unknown.

Some of the discrepancies among studies on the effects of partial harvesting on salamander abundances likely resulted from variation in the amount of basal area retained, the salamander communities affected, or the forest structure resulting after harvest. For example, after the initial harvest, these shelterwood sites retained 12-14 m²/ha of overstory basal area.

Other investigations of effects of partial harvesting on terrestrial salamanders reported residual basal areas of 9.1-18.3 m²/ha (Reichenbach and Sattler 2007), 4-15 m²/ha (Harpole and Haas 1999), 6-14 m²/ha (Knapp et al. 2003), and 48 m²/ha (Grilou et al. 2000), but many other researchers failed to report this characteristic important for interpreting results across investigations and ecosystems.

Besides residual basal area of harvested stands, other aspects of forest structure likely influenced salamander abundances and communities after treatments. In this case study, *a priori* selected habitat characteristics associated with forest-dwelling salamanders differed between untreated control and recently harvested shelterwood EUs. The volume and abundance of coarse woody debris as well as leaf litter depth differed between control and post-ORH shelterwood EUs. Not surprisingly, the ORH caused the density and volume of woody logging slash to be greater than the woody debris in control EUs on both sites (Figure 3.1c, 3.2d). However, coarse woody debris was in a more advanced decomposition stage in control EUs. Additionally, leaf litter depth was 39-57% greater in control EUs, but overstory and understory tree densities only differed on BB1, where salamander abundances were lower after the ORH (Figure 3.1a, 3.2b, 3.2e). It is possible that because the BB2 site retained structural characteristics of more mature forest (e.g., understory and overstory trees were similar to the control) after the ORH, relative abundance of salamanders did not change as much after this treatment.

Changing the structure of mature forest from harvesting generally is perceived to have negative effects on salamander populations. After harvesting, salamanders are hypothesized to emigrate from disturbed areas (evacuation hypothesis), retreat underground until conditions are more amenable (retreat hypothesis), or die, either directly from harvesting equipment or indirectly from changes to habitat and microclimate (deMaynadier and Hunter 1995). Removal

of overstory and understory trees and mechanical disturbance to the forest floor leads to less leaf litter on the ground, thus reducing the available foraging substrate and mediation of microclimate for salamanders. Further, opening of the canopy layer from harvesting often causes increased ground temperatures and decreased soil moisture, which may restrict movements, foraging opportunities, and cutaneous respiration of terrestrial salamanders (Jaeger 1980, Leichty et al. 1992, Chen et al. 1999, Harpole and Haas 1999). Lastly, terrestrial salamanders rely on coarse woody debris for several life history requirements, including maintaining moisture and thermal balances, access to mates and foraging opportunities, and substrates for brooding eggs (deMaynadier and Hunter 1995). Although harvesting produces large inputs of small diameter logging slash, this small woody debris often does not persist through a rotation, and quickly decomposes (Spies et al. 1988, Fraver et al. 2002). The growing season after the ORH, there was more CWD in shelterwood EUs, but because it was less decayed, it likely was not used by salamanders for foraging or brooding eggs. Thus, the large inputs of logging slash after the shelterwood ORH may not have been sufficient to overcome negative changes to microclimate or other life history requirements of terrestrial salamanders.

Management recommendations

Although the conclusions drawn from this case study approach are limited by having only two study sites, this experimental design included both pretreatment estimates of abundance and randomly applied treatments, both of which are uncommon in investigations of forest harvesting on salamanders (deMaynadier and Hunter 1995, Reichenbach and Sattler 2007). These exploratory results indicate that silvicultural regimes that employ multiple entries within a rotation have the potential to negatively affect the relative abundance of terrestrial salamanders. Given that >60 years is expected to be required for salamander populations in Appalachian oak

forest to recover to preharvest levels of abundance from only one stand entry (Homyack and Haas 2009), it is likely that silvicultural regimes such as shelterwood systems that repeatedly reduce salamanders will require much longer for population recovery. During the final year of this study (2008), relative abundances of terrestrial salamanders (mean number of salamanders/transect) were greater in 13-14 year old clearcut EUs compared to the ORH EUs, providing additional evidence that multiple stand entries may increase recovery periods for salamanders. If recovery periods for salamander populations are longer than rotation lengths in shelterwood systems, salamanders could face long-term declines or possibly local extirpation from managed stands. Forest managers, however, will need to weigh the consequences to biodiversity related to partial harvests against the higher costs of partial harvesting, potentially negative effects on soil erosion due to multiple stand entries within a rotation (Hood et al. 2002), and implications for landscape scale effects when applying forest plans. Additional research should consider the long-term effects of multiple stand entries on abundances and demographics of terrestrial salamanders on multiple study sites where both pre- and post-harvest data are quantified.

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Table 3.1. Total number of salamander captures by species and year in mature oak (control) and shelterwood-harvested forest in two field sites (BB1, BB2) in southwestern Virginia, 1994-2008. Sites were harvested in 1994-1996 and residual trees were removed in an overstory removal harvest (ORH) during winter 2007-2008.

	Year	BB1		BB2	
		Control	Shelterwood	Control	Shelterwood
<i>Plethodon cinereus</i>	Pretreatment year	43	39	7	11
	1-year post	59	45	1	0
	2-years post	53	19	10	6
	Pre-ORH	44	24	8	10
	Post-ORH	55	13	15	5
<i>Plethodon cylindraceus</i>	Pretreatment year	1	5	0	0
	1-year post	7	3	0	0
	2-years post	1	0	4	0
	Pre-ORH	4	0	2	2
	Post-ORH	1	0	3	2
<i>Desmognathus ochrophaeus</i>	Pretreatment year	1	0	0	0
	1-year post	0	0	0	0
	2-years post	1	0	0	0
	Pre-ORH	0	0	0	0
	Post-ORH	0	0	0	0
<i>Eurycea bislineata</i>	Pretreatment year	0	0	0	0
	1-year post	1	0	0	0
	2-years post	0	0	0	0
	Pre-ORH	1	0	0	0
	Post-ORH	1	0	0	0
<i>Gyrinophilus porphyriticus</i>	Pretreatment year	0	0	0	0
	1-year post	1	0	0	0
	2-years post	0	0	0	0
	Pre-ORH	0	0	0	0
	Post-ORH	0	0	0	0
Total		274	148	50	36

Table 3.2. Differences in the ratio of total salamander captures in experimentally harvested shelterwood plots in southwestern Virginia. I compared the ratio of salamander captures in shelterwood plots versus unharvested control plots through time with Fisher’s Exact Tests.

Sampling year	<u>Site</u>			
	<u>Blacksburg 1</u>		<u>Blacksburg 2</u>	
	Ratio of captures ^a	Fisher’s Exact Test	Ratio of captures ^a	Fisher’s Exact Test
Pretreatment year	0.98 (44/45)	n/a	0.64 (7/11)	n/a
1-year post	0.71 (48/68)	P=0.261	0 (0/1)	P>0.999
2-years post	0.35 (19/55)	P=0.030	0.43 (6/14)	P>0.999
Pre-ORH ^b	0.49 (24/49)	n/a	1.09 (12/11)	n/a
Post-ORH	0.23 (13/57)	P=0.058	0.54 (7/13)	P=0.359

^a Ratio were calculated as the number of captures in the shelterwood EU in a sampling year divided by the number of captures in the control EU at that site. Between years, the proportion of captures in the shelterwood EU was compared with Fisher’s Exact tests.

^bORH refers to an overstory removal harvest.

Table 3.3. Mean number of salamander captures per transect (SE) in control and shelterwood experimental units in experimentally harvested shelterwood plots in southwestern Virginia.

Sampling year	<u>Site</u>			
	<u>Blacksburg 1</u>		<u>Blacksburg 2</u>	
	<u>Control</u>	<u>Shelterwood</u>	<u>Control</u>	<u>Shelterwood</u>
	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
Pretreatment year	9.0 (2.9)	8.8 (2.1)	2.8 (1.4)	1.8 (0.5)
1-year post	9.7 (2.2)	6.9 (2.6)	0.5 (0.5)	0 (0)
2-years post	7.9 (1.1)	2.7 (0.7)	1.8 (0.7)	0.8 (0.5)
Pre-ORH ^a	9.8 (2.6)	4.8 (1.5)	2.8 (1.0)	3.0 (1.5)
Post-ORH	9.5 (2.1)	2.2 (1.0)	1.9 (0.8)	1.0 (0.6)

^a ORH refers to an overstory removal harvest.

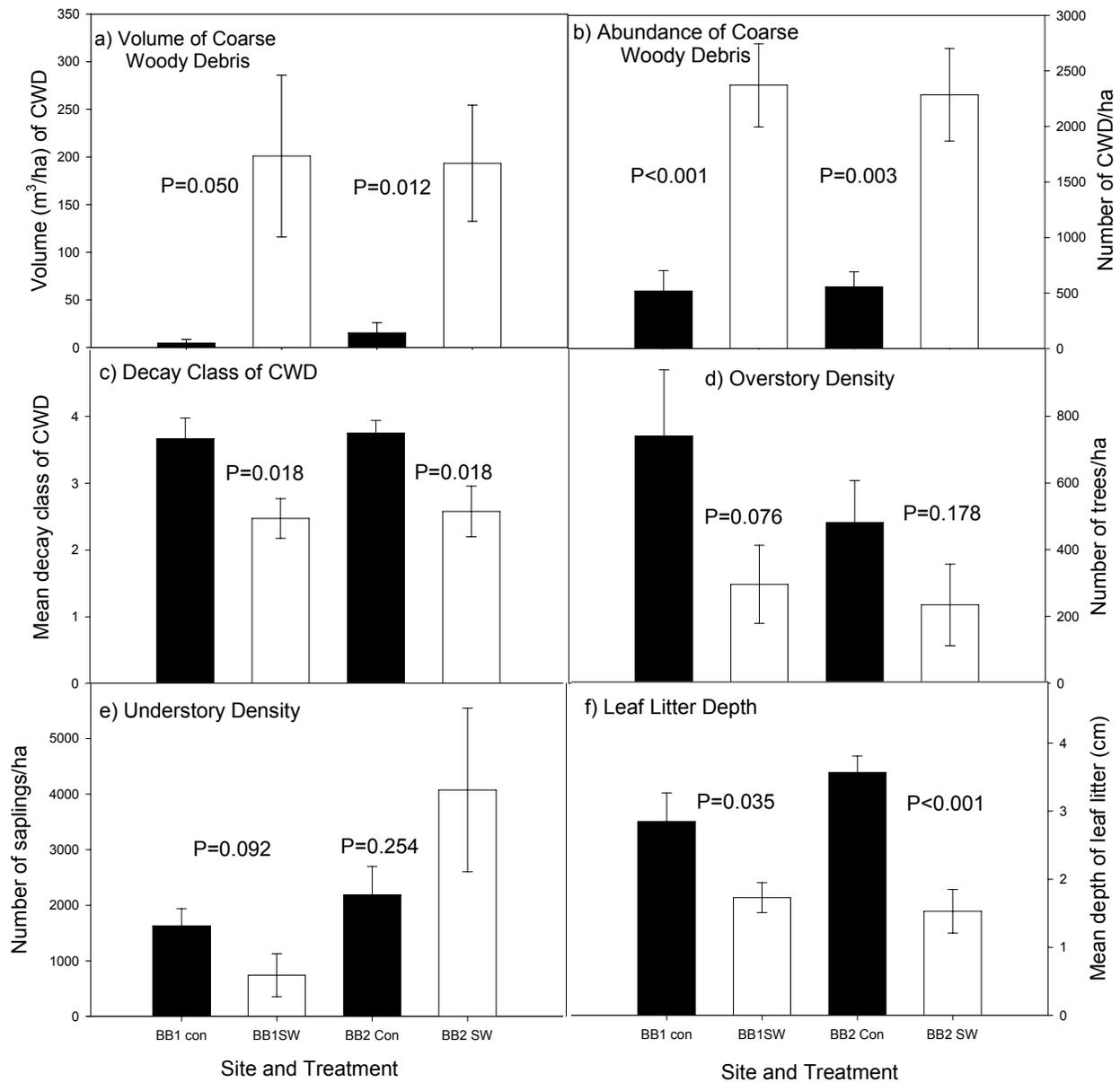


Figure 3.1. Forest structural characteristics for terrestrial salamanders in untreated control experimental units (EUs) (shaded bars) and in shelterwood EUs at two study sites (Blacksburg 1, BB1; Blacksburg 2, BB2) in southwestern Virginia. Forest structure was measured on 9, 2×15 m transects/EU during summer 2008, the growing season following an overstory removal harvest in the shelterwood EUs. Differences between forest structure in control and shelterwood EUs within a site were examined with T-tests for unequal variance.

CHAPTER 4: BIOENERGETICS OF TERRESTRIAL SALAMANDERS ACROSS A DISTURBANCE GRADIENT IN APPALACHIAN HARDWOOD FORESTS

Abstract: Environmental temperatures can affect physiological processes, behavior, and survival of ectotherms. For terrestrial salamanders, energy expenditure increases with temperature; thus, anthropogenic disturbances that alter temperature regimes will affect bioenergetics, possibly leading to changes in demography. I quantified temperature regimes of salamander refugia in a replicated field experiment that included four forest harvest types representing a disturbance gradient in an Appalachian oak forest. Because forest harvesting is known to increase temperatures near the forest floor, I predicted that surface-active salamanders would expend more energy as harvest intensity increased and the amount of residual canopy was reduced. During 2006-2008, I examined the bioenergetics of common salamander species across the disturbance gradient and a temporal component by (1) developing relationships to describe the effect of temperature and body mass on energy expenditure and quantifying the calories required to maintain homeostasis, (2) determining whether available sources of energy (i.e., invertebrate prey) differed, and (3) comparing a body condition index of salamanders. During the growing season following an overstory removal harvest, the mean number of calories required for maintenance costs for eastern red-backed salamanders (*Plethodon cinereus*) was approximately 33% greater ($P < 0.001$), and contrary to my prediction, body condition of red-backed salamanders was higher ($P = 0.011$) (at one of two study sites) compared to unharvested controls. However, metrics of bioenergetics generally were similar ($P > 0.05$) across the disturbance gradient when 8-14 growing seasons had elapsed after forest harvesting. Given that salamanders in recently harvested forest may trade-off growth or reproduction for allocating

energy towards maintenance costs, bioenergetics may contribute to the observed reduction in abundances of salamanders after harvesting across this disturbance gradient.

Introduction

Selection of optimal environmental temperatures by ectotherms is well-documented (Hutchison and Dupré 1992, Tamplin 2006), and individuals, populations, and entire distributions and patterns of diversity of ectotherms are often strongly related to climatic patterns. Within a climate zone, changes in temperature regime can have large impacts on the behavior and physiological functioning of individuals (Fitzpatrick 1973). At the population level, even small changes in environmental temperatures can affect hatching success (Du and Ji 2006), sex ratios (Kamel and Mrosovsky 2006, Azaza et al. 2008), and locomotor performance (Preest and Pough 1989, Stefanski et al. 1989, Jiang and Claussen 1992, Hare et al. 2008) of ectotherms. At the broadest scale, increases in global temperatures because of climate change are predicted to alter distributions of herpetofauna (Kearney and Porter 2004, Araújo et al. 2006, Buckley 2008), change migration patterns of anadromous fish (Welch et al. 1998), or affect global diversity of amphibians (Bernardo and Spotila 2006, Buckley and Jetz 2006). However, effects on ectotherms from anthropogenic alteration of temperature regimes at smaller, but ecologically relevant, scales are less well-understood. Amphibians have limited means to internally regulate body temperatures and the amount of energy expended for metabolism is positively related to temperature (Rome et al. 1992). Thus, increases in temperatures of an amphibian's environment may add to the energy required to sustain life, either from increases in metabolism and/or from behavioral modification (i.e., moving to adjacent habitats or posturing to optimize temperature or to reduce water loss) (Feder 1983).

The effects of changing temperatures on ectotherms is relevant to terrestrial woodland salamanders because microclimate affects their foraging time (Feder 1983, Feder and Londos 1984), selection of microhabitats (Feder and Pough 1975, Keen 1984), respiration (Merchant 1970, Fitzpatrick 1973, Maguire 1981), and assimilation efficiency (Fitzpatrick 1973, Bobka et al. 1981). Salamanders act as nearly perfect poikilotherms with body temperatures closely following the substrate with which they are in contact (Feder 1983). Additionally, plethodontid salamanders are physiologically linked to cool and moist habitats by respiring through their skin. Females of many species lay their eggs in rotting stumps or logs to keep eggs moist through development. Many terrestrial salamanders move only short distances (Petranka 1998), decreasing the likelihood that individuals can adjust to changing temperatures by migrating to less energetically costly habitats. As cutaneous respirators, plethodontid salamanders respond to moisture by altering behavior (Feder 1983), habitat selection (Spotila 1972), distribution (Grover and Wilbur 2002) and metabolic rate (Sherman and Stadlen 1986) of. By potentially influencing bioenergetics, reproduction, and behavior, microclimate may affect survival of salamanders and recruitment of young into the population.

At the scale of a forest stand (i.e., patch), populations of terrestrial salamanders have experienced long-term declines in abundance (Petranka et al. 1993, Ash 1997, Knapp et al. 2003, Homyack and Haas 2009) and changes to demographics (deMaynadier and Hunter 1998, Ash et al. 2003, Homyack and Haas 2009) following timber harvesting. However, little is known about the mechanisms that cause decreased abundances and altered demographics after forest disturbances. Concurrent with declines in salamander populations, soil and surface temperature may increase after harvesting when canopy trees are removed and more light reaches the forest floor (Leichty et al. 1992, Chen et al. 1999, Harpole and Haas 1999, Zheng et al. 2000, Brooks

and Kyker-Snowman 2008). Changes to microclimate have been hypothesized to cause post-harvesting declines in salamanders (Petranka et al. 1993, Harper and Guynn 1999, Brooks and Kyker-Snowman 2008), but few researchers have investigated mechanistically how increasing forest temperatures could result in fewer salamanders (Brooks and Kyker-Snowman 2008).

One explanation for reduced abundances and slow recovery of salamander populations following forest harvesting is changes to energy budgets. Higher temperatures following a disturbance will cause individual salamanders to increase energy expenditure such that either (1) total energy expended remains the same, but less energy is available to allocate into growth, reproduction, or storage because maintenance costs increase (Congdon et al. 1982, Sears 2005, DuRant et al. 2007), (2) salamanders increase total energy expenditure, but maintain the proportions of the energy budget allocated among competing functions (Beaupre 1996), or (3) a combination of both scenarios occur. Under all hypotheses, the absolute amount of energy expended to maintain homeostasis increases with higher temperatures. Coupled with potential decreases to abundance (Willett 2001) or quality of invertebrate prey (Mitchell et al. 1996) and reduced digestive efficiency (Merchant 1970, Bobka et al. 1981) after forest harvesting, salamanders may face energetic challenges from habitat disturbances (Harpole and Haas 1999). Over time, chronic changes to energy budgets could alter dynamics of populations through slower growth, reduced reproduction, or lower survival of individuals (Sears 2005). In fact, 1-13 years after experimental forest harvesting, reproductive demography of some commonly captured plethodontid salamanders was lower on harvested treatments compared to unharvested treatments (Homyack and Haas 2009).

When conditions near the surface are too warm or dry, terrestrial salamanders retreat into the soil or use refugia, such as logs or rocks, to maintain thermal and water balances (Jaeger

1980, Keen 1984), to maintain access to the leaf litter for future foraging attempts (Jaeger et al. 1995a), or to access potential mates during courtship periods (Jaeger et al. 1995b). Therefore, refugia are linked to the life history requirements of salamanders. Whereas numerous studies have documented changes to surface microclimates following harvest (e.g., Johnson et al. 1985, Liechty et al. 1992, Knapp 1999, Rothermel and Luhring 2005, Brooks and Kyker-Snowman 2008), information regarding temperature regimes under refugia and subsequent effects on energy budgets of salamanders across a disturbance gradient is unavailable.

My goal was to examine the energetic response of salamanders to canopy disturbance and to evaluate whether bioenergetics may contribute to observed patterns in abundance and demographics in a long-term field experiment where salamanders were only 18% of pretreatment abundances at three-years after forest harvesting (Homyack and Haas 2009). In this study, I evaluated the bioenergetics of salamanders directly after and 8-14 years after a harvest, when some recovery of vegetation, microclimate, and salamanders would have occurred. I applied a three-point approach. First, I determined the thermal profile of refugia across a disturbance gradient and quantified energy expenditure of the most common species of salamander at the range of field temperatures I observed. From this, I modeled total basic maintenance costs for salamanders within the increasing gradient of disturbance. Second, I determined whether available invertebrate prey varied across the disturbance gradient. Third, I compared indices of body condition for common species of salamanders across the disturbance gradient. I used a weight of evidence approach to evaluate my predictions that changes in microclimate caused by anthropogenic disturbances would alter energy budgets for salamanders by increasing energetic costs, decreasing abundance of prey, and/or decreasing the amount of energy allocated to growth or storage.

Study area

My study area included four sites in Virginia and West Virginia and was part of a larger investigation of the long-term effects of oak regeneration methods on biodiversity, the Southern Appalachian Silviculture and Biodiversity (SASAB) project. Study sites (blocks) were established within the Ridge and Valley and the Cumberland Plateau physiographic provinces in the Jefferson National Forest, Virginia (BB1, BB2), and the Mead-Westvaco Corporation's Wildlife and Ecosystem Research Forest (purchased by Penn-Virginia Corporation in 2007), West Virginia (WV1, WV2) (Belote et al. 2008). Overstories of sites were dominated by oaks (*Quercus spp.*) and included smaller components of red maple (*Acer rubrum*), yellow poplar (*Liriodendron tulipifera*), American beech (*Fagus grandifolia*), and sourwood (*Oxydendron arboretum*) (Wender 2000).

At each of the four sites, I investigated the bioenergetics of terrestrial salamanders within four silvicultural treatments representing a gradient of disturbance. Silvicultural treatments were applied randomly to 2-ha treatment plots (experimental units, or EUs). The silvicultural treatments in order of increasing disturbance included (1) a control where no disturbance was applied, (2) shelterwood harvest where a partial harvest reducing overstory basal area by 41% occurred, (3) leave tree harvest where a partial harvest reducing overstory basal area by 72% occurred, and (4) silvicultural clearcut where all stems >5 cm diameter at breast height (dbh) were felled. Treatments were applied to EUs during 1994-1998. During winter 2007-2008, a second harvest occurred in the shelterwood EUs at BB1 and BB2. During the second entry into the shelterwood EUs, remaining overstory trees were removed to release advanced regeneration of saplings, with approximately 6 m²/ha basal area retained. I intended for the overstory removal harvest (hereafter ORH) to occur at all 4 sites, but changes in land ownership and management

goals prevented the treatment from being applied at WV1 and WV2. This study design also allowed me to examine a temporal gradient, by quantifying bioenergetics of salamanders in EUs directly following a harvest (the ORH) and 8-14 years following a disturbance (all other EUs). Additional details about study sites and silvicultural treatments are provided by Knapp et al. (2003), Belote et al. (2008), and Homyack and Haas (2009).

Methods

Temperature regimes of salamander refugia

I monitored artificial refugia for salamanders by placing five coverboards per EU at each study site (total of 20 boards per site) during March-April 2006. The 20×60×5-cm rough cut yellow-poplar (*Liriodendron tulipifera*) boards were placed approximately 2 m from five of the salamander sampling transects described by Knapp et al. (2003) and Homyack and Haas (2009). I placed coverboards adjacent to the four transects nearest the corners of the salamander sampling grid, and one near the center transect. I used coverboards rather than natural cover objects to standardize the surface area touching the forest floor, moisture content of wood, and decay class, which can vary greatly among natural woody debris (Fraver et al. 2002).

I quantified temperatures with small data loggers (Ibutton DS1921G; Dallas Semiconductor, Sunnyvale, CA) at the interface of refugia and soil surface where salamanders would establish territories. I programmed data loggers to monitor temperatures every 90 minutes from 10 May -15 September 2006, every 120 minutes 1 May-18 October 2007, and every 120 minutes 5 May-9 October 2008. These periods correspond to the majority of the surface-active season for terrestrial salamanders in central West Virginia and southwestern Virginia. Data loggers were programmed to record temperatures simultaneously across EUs and sites. I averaged temperatures across the five subsamples within an EU to develop a seasonal temperature profile for each treatment plot at the four study sites during each of three years. For

the two shelterwood EUs with the ORH (BB1, BB2), I quantified temperature profiles for two years prior to (2006, 2007) and one year after (2008) the second entry.

Quantifying energetic costs to salamanders

To determine whether the amount of energy required for basic maintenance differed for a terrestrial salamander across the disturbance gradient, I translated seasonal temperature profiles into energy output by quantifying the relationship among temperature, body size, and energy expenditure for eastern red-backed salamanders (*Plethodon cinereus*). Red-backed salamanders were an appropriate model of bioenergetics because this species occurred at all four study sites and was the most commonly encountered plethodontid (Homyack and Haas 2009).

I hand-captured red-backed salamanders near my BB1 study site and selected a range of sizes based on snout-vent length (SVL). I captured eight individuals on 16 September 2008 and an additional 8 salamanders on 25 September 2008. I brought them to the lab, weighed salamanders, and ensured I had approximately equal numbers of male and female individuals. Salamanders were fasted for six days at 18° C so individuals were post-absorptive during energetic trials. I placed a post-absorptive salamander, 5 ml of de-chlorinated tap water, and 0.48 g of KimWipe tissue paper (Kimberly-Clark Corporation, Dallas, TX) in individual 50 ml respiratory chambers in a temperature controlled cabinet. Salamanders were housed in darkness in the same cabinet where I quantified respiration.

I estimated energy expenditure across five temperatures, which corresponded with the range of temperatures observed under refugia at my field sites. Oxygen consumption by individual salamanders was quantified with an independent channel on a computer-controlled, closed-circuit, indirect respirometer (MicroOxymax, Columbus Instruments, Columbus, OH) as an indirect measurement of energy consumption (Hopkins et al. 2004). One chamber served as a

blank control and one chamber contained a medical battery that consumed a known amount of O₂/hour. The volume of oxygen consumption (VO₂) for each salamander was monitored at approximately 70 minute intervals for 24 hours at 10°, 15°, 20°, 25°, and 30°C to quantify the energy used at each temperature. I randomized the order of experimental temperatures to which study animals were exposed (with the exception of 30°C) to avoid potential confounding effects of temperature acclimation. The 30°C treatment purposely was run last because this temperature was likely to be the most thermally challenging to salamanders. I ran two complete trials, each with eight salamanders.

From my respirometry trials, I accumulated approximately 20 estimates of VO₂ for each salamander at each temperature. I used these data to estimate the Standard Metabolic Rate (SMR), or the metabolic rate of inactive, post-absorptive, individuals at a pre-determined temperature. I estimated SMR as the lowest quartile of O₂ consumption (mL/hour) for salamanders at each experimental temperature after removing the two first and two last measurements of each trial. Using the lowest quartile value prevented any salamander movement-induced increases in energy output from influencing estimates of SMR (Hopkins et al. 2004). I calculated a multiple linear regression with body mass and temperatures as independent variables to estimate the functional relationship among basic maintenance costs (VO₂), body mass, and temperature. Body mass and VO₂ were log_e-transformed prior to regression analysis. I followed Sprugel (1983) to calculate a correction factor to correct for the known bias in back-transforming log-log regression equations for estimates of VO₂.

Differences in energy expenditure

Salamanders often are inactive, so resting metabolism can account for a large proportion of an overall energy budget (Feder 1983, Gatten et al. 1992, Sears 2005). I converted each

temperature in the seasonal microclimate profiles to an estimate of total number of calories/g by first estimating the corresponding amount of oxygen consumption from my regression.

Therefore, each temperature sample from the coverboards was converted to a measure of basic maintenance costs, creating curves of energy expenditure through time for each treatment by site combination. I calculated the integral under this curve to quantify the total energetic costs to a red-backed salamander for a large component of basic maintenance costs across the disturbance gradient for an active season. This included energy to maintain homeostasis, but excluded energy for digestion, movements, or other behaviors. Lastly, I converted the volume of O₂ to an estimate of calories/g by multiplying by 4.86, the number of calories/ml O₂ consumed (Schmidt-Nielsen 1990).

To examine the effects of the disturbance gradient on the energetic costs for salamanders, I determined whether the estimated required calories differed with a 2-way Analysis of Variance (ANOVA) with silvicultural treatment (control, shelterwood, leave tree, silvicultural clearcut, ORH) and site (BB1, BB2, WV1, WV2) as factors. I conducted ANOVAs separately by year because the shelterwood treatment was harvested between year two and three at two sites, and because the calendar dates of my sampling periods differed slightly from year to year. When significant differences within a year were detected, I compared means with Bonferroni adjusted P-values. I examined normality with normal probability plots and constant variance with modified Levene's tests and transformed any data that failed to conform to the assumptions of ANOVA (Neter et al. 1996).

Effects of forest disturbance on invertebrate prey

Relative abundances of invertebrates were sampled from leaf litter adjacent to coverboards three times per sampling season (two times for coverboards in WV1 and WV2

during 2006). I collected small (<20 g) samples of leaf litter, transported them to the laboratory in individual, sealed plastic bags, weighed samples, and placed litter in Berlese funnels for 48 hours. Litter samples from all treatments at a site were collected within three hours, so samples were subjected to the same climatic conditions at collection. Invertebrates were stored in 70% ethyl alcohol and sorted to group (mites, springtails, spiders, larvae, etc). I converted counts of invertebrates to abundance/g of wet weight of leaf litter and averaged relative abundances within a sampling season.

I compared differences in invertebrate abundances among silvicultural treatments with multivariate analysis of variance (MANOVA) that examined for effects of treatment (control, shelterwood, leave tree, silvicultural clearcut, ORH) and site (BB1, BB2, WV1, WV2) on relative abundance of invertebrates. I used MANOVAs to examine simultaneous differences in invertebrate abundances among treatments and to avoid inflating the rate of Type I error. I included only those invertebrate groups whose abundances made up >2% of the total. MANOVA's were conducted separately by year because the ORH was sampled only at 2/4 sites in 2008. When a MANOVA test was significant, I examined individual variables to determine which invertebrate taxa differed (Johnson 1998). Secondly, I determined whether the total abundances of invertebrates differed among treatments or sites with 2-way ANOVAs conducted separately by year. I examined normality and constant variance of invertebrate abundances with normal probability plots and modified Levene's tests, respectively.

Effects of forest disturbance on body condition of salamanders

Finally, I examined the body condition of commonly captured species of salamanders across the disturbance gradient as an index to the energetic state of populations (deMayanadier and Hunter 1995). Terrestrial salamanders were captured and measured yearly on a grid of

salamander sampling transects at each EU. Details regarding methods to capture and measure salamanders are provided by Knapp et al. (2003) and Homyack and Haas (2009). For each individual salamander capture, I weighed and measured SVL to the posterior edge of the vent and tail length (TL) from the posterior edge of the vent to the tip of the tail. I summed the two values to obtain total length (TOTL) for each salamander. I examined the body condition of eastern red-backed salamanders and slimy salamanders (*Plethodon glutinosus*, *Plethodon cylindraceus*), the three most commonly captured species across my four study sites, but excluded known gravid females.

I used least squares regression of log-transformed mass on log-transformed TOTL as an index to the amount of energy reserves when accounting for body size (Schulte-Hostedde et al. 2005, Welsh et al. 2008). Using this technique, salamanders with a positive residual were considered to be in “good” body condition and individuals with a negative residual were considered to be in “poor” body condition (Welsh et al. 2008). For red-backed salamanders, I pooled data across the 2006-2008 study period, but examined for treatment effects separately for individual sites to reflect potential differences in resource availability across our broad study area. Sample sizes for slimy salamanders were smaller, so I pooled salamanders across years and across the two sites in Virginia and across the two sites in West Virginia. I considered the post-overstory removal shelterwood a fifth treatment for the BB1 and BB2 sites. I used a Kruskal-Wallis test on ranked residuals to determine if body condition of salamanders differed among treatments (Welsh et al. 2008). All analyses were conducted with SAS 9.2 (SAS Institute Inc., Cary, NC, USA).

Results

Effects of forest disturbance on energy budgets of eastern red-backed salamanders

Across the three years of sampling, I logged >484,000 temperatures in EUs. Temperatures at the soil refugia interface rarely (3 of >484,000 temperatures) exceeded the mean critical thermal maximum for red-backed salamanders of 34.6°C (Spotila 1972), but temperature profiles varied among sites and years. In general, temperatures were greatest in the ORH, and temperatures reached their highest values during July-August (Figure 4.1a, Figure 4.1b). Mean temperatures during 2008 were 2.5°C> in ORH EUs than in control EUs at the Blacksburg sites across the entire season.

The mass of salamanders used in the laboratory experiment ranged from 0.06-1.11 g. As predicted, SMR increased significantly with both body size and temperature for red-backed salamanders ($F_{2, 77}=815.59$, $R^2=0.955$, $P<0.001$, Figure 4.2, Figure 4.3). The predictive multiple regression equation was: $\text{Log}_e(\text{VO}_2) = 0.102(\text{temperature}) + 0.681(\text{Log}_e(\text{body mass})) - 4.849$.

Using my temperature data from the field and SMR data from the lab, I estimated the total number of calories required for a 1.0 g red-backed salamander to support basic maintenance across an active season. Across all of my sites and treatments, basic maintenance requirements ranged from 644 - 1070 calories. For all three years, data were normally distributed with homogenous variances ($F_{2,12}<0.50$, $P>0.99$). I detected a treatment effect on the total energy required for maintenance (Figure 4.4) in 2008 ($F_{4, 12}=43.70$, $P<0.001$), which included the ORH at two sites. Approximately 347 more calories were required by salamanders in the ORH EUs, but none of the other silvicultural treatments differed from one another ($P>0.05$) (Figure 4.4). In contrast, I did not detect a treatment effect on the total number of calories expended for basic maintenance costs when just comparing the silvicultural treatments 8-13 years after they were applied in either 2006 ($F_{3, 12}=2.05$, $P=0.178$) or 2007 ($F_{3, 12}=0.51$, $P=0.683$).

Effects of site on the total number of calories expended for basic maintenance costs were consistent across the three years of the study. I detected a significant effect of site in all years (2006, $F_{3, 12}=93.84$, $P<0.001$; 2007, $F_{3, 12}=15.32$, $P<0.007$; 2008, $F_{3, 12}=94.11$, $P<0.001$), with a greater number of calories required by salamanders in the Blacksburg sites compared to the two West Virginia sites. Approximately 127, 123, and 204 more calories were required by a 1.0 g red-backed salamander at the Blacksburg sites compared to the West Virginia sites in 2006, 2007, and 2008, respectively.

Effects of forest disturbance on invertebrate prey

I sorted and identified 13,967 invertebrates to functional groups across the 3-year study. Of those invertebrates, 61.5% were mites, 28.8% were collembola, 3.8% were lepidopteran or coleopteran larvae, 2.6% were ants, 2.1% were spiders, and dipterans, centipedes, proturans, roaches, pseudoscorpians, millipedes, snails, bees, other hymenopterans, moths, crickets, beetles, and unknown invertebrates each accounted for $\leq 1\%$ of the total.

The omnibus test of multivariate comparisons of invertebrates/g was significant in 2006, (Wilks' Lamda=0.002, $F_{18, 12}=4.92$, $P=0.004$), but not 2007 (Wilks' Lamda=0.076, $F_{18, 12}=0.98$, $P=0.532$) or 2008 (Wilks' Lamda=0.015, $F_{18, 9}=1.72$, $P=0.204$). Despite the overall significant MANOVA, I did not detect an effect of silvicultural treatment on multivariate comparisons of invertebrates (i.e., MANOVA) in 2006 ($P>0.05$) or on total numbers of invertebrates in any year (2006, $F_{3, 12}=2.60$, $P=0.117$; 2007, $F_{3, 12}=0.30$, $P=0.822$; 2008, $F_{4, 11}=1.53$, $P=0.283$). Thus, abundances of invertebrates did not differ across the disturbance gradient in any year, including after the ORH.

Although there were no significant effects of site in 2007 or 2008, there was a significant effect of site for the MANOVA in 2006 (Table 4.1). For 2006, I detected a significant effect of

site on the number of collembola ($F_{3,12}=8.23$, $P=0.006$) and larvae ($F_{3,12}=3.48$, $P=0.046$). BB1 had a greater abundance of collembola than the BB2, WV1, or WV2 sites, and BB2 had a greater abundance of larvae than either WV1 or WV2. When I considered the effects of sites on just the total number of invertebrates, I did not detect differences in 2006 or 2007. However, in 2008 the ANOVA was significant, with total number of invertebrates differing among sites ($F_{3,12}=9.74$, $P=0.005$). The WV1 and WV2 had fewer numbers of invertebrates than either the BB1 or BB2 sites in 2008 ($P<0.05$).

Effects of forest disturbance on abundance and body condition of salamanders

I analyzed the body condition of 537 red-backed salamanders and 134 slimy salamanders captured on the 4 study sites from 2006-2008. For red-backed salamanders, 58% of captures were in control EUs, 9% were in shelterwood EUs, 13% captures were in leave tree EUs, 16% were in clearcut EUs, and 3% were in ORH EUs. For slimy salamanders, 45% were in control EUs, 13% were in shelterwood EUs, 26% were in leave tree EUs, 16% were in clearcut EUs, and <1% were in ORH EUs. Based on the distributions of residuals, I detected a difference among silvicultural treatments for BB2 ($F_{4,104}=2.67$, $P=0.036$); post-hoc comparisons indicated that red-backed salamanders from the ORH EU had a greater body condition index than salamanders from the shelterwood EU prior to the second stand entry ($P=0.029$) and greater body condition than salamanders in the control plot ($P=0.049$) (Figure 4.5). In contrast, I did not detect an effect of silvicultural treatment for red-backed salamanders at BB1 ($F_{4,300}=2.24$, $P=0.065$), WV1 ($F_{3,67}=1.06$, $P=0.374$) or WV2 ($F_{3,45}=0.22$, $P=0.885$). Body condition of slimy salamanders did not differ among silvicultural treatments at the combined West Virginia sites ($F_{3,102}=0.37$, $P=0.776$) or at the combined Blacksburg sites ($F_{3,24}=1.28$, $P=0.304$).

Discussion

A recent disturbance that removed overstory trees in the shelterwood EUs in Virginia changed the thermal environment by increasing temperatures near the forest floor. Consequently, red-backed salamanders required a greater number of calories for basic maintenance costs at both sites, but had a higher body condition index at one of two study sites in the ORH EUs. In contrast, energetic requirements, body condition of salamanders, and invertebrate prey populations did not differ across a disturbance gradient when examined 8-14 years past the experimental treatment, suggesting that recovery of important microclimate conditions had occurred. Thus, I detected limited differences in the bioenergetics of terrestrial salamanders across forest stand types during the later post-disturbance period. This is the first research that I am aware of to quantify the potential energetic costs to terrestrial salamanders from chronic changes to microclimate after experimental disturbances.

After forest harvesting, the forest floor microclimate typically becomes hotter as more solar radiation reaches the ground (Johnson et al. 1985, Chen et al. 1999, Harper and Guynn 1999, Zheng et al. 2000). In Massachusetts, a chronosequence study of partially harvested forest reported small ($<1^{\circ}\text{C}$) and short-lived differences in temperature near the forest floor compared to uncut forest stands (Brooks and Kyker-Snowman 2008). Similar to my observations of temperature in the ORH, temperatures rarely exceeded critical maximum temperatures for common amphibians in the area. In South Carolina, mole salamanders (*Ambystoma talpoideum*) experienced increased desiccation and lower survival in clearcut harvests, which had the highest near-ground temperatures of experimental treatments (Rothermel and Luhring 2005). However, as my study suggests, temperature increases at the forest floor from harvesting may have subtle indirect effects on fitness of amphibians in addition to direct mortality.

Assuming other components of an energy budget remained equal, the total amount of calories required for basic maintenance was approximately 33% greater in the ORH EUs than in undisturbed forest. Although most prior research reported $<2^{\circ}\text{C}$ increases in near-ground temperatures following forest disturbances (Chazal and Niewiarowski 1998, Rothermel and Luhring 2005, Brooks and Kyker-Snowman 2008, but see Johnson et al. 1985), these results show how small but chronic increases in temperature could influence the bioenergetics of salamanders. My estimation of seasonal costs of maintenance assumed that salamanders remained at the interface of the soil and refugia for the entire active season and did not account for concurrent changes in moisture. In reality, salamanders move in and out of the soil and leaf litter, and humidity or soil moisture may have differed among treatments and sites, so these values are a simplification. Salamanders at the Blacksburg sites tend to be less active during the warmer summer months, and presumably spend much of this time underground. Further, the calories required for basic maintenance represents only one component of a salamander's energy budget, but variation in maintenance costs can influence rates of growth or reproduction of ectotherms (Sears 2005, DuRant et al. 2007). Across these study sites, I observed differences in reproductive demography of the two most commonly captured plethodontid salamanders, with greater proportions of juvenile salamanders and a greater number of eggs/female salamanders in unharvested plots compared to harvested plots (Homyack and Haas 2009). Changes to energy budgets may help explain these lower reproductive values of salamanders in harvested forest.

Not only could higher environmental temperatures lead to more energy being allocated to basic maintenance, but digestion may be less effective because the assimilation efficiency of red-backed salamanders decreases with increasing temperature from 10-20 $^{\circ}\text{C}$ (Merchant 1970, Bobka et al. 1981). Therefore, terrestrial salamanders may expend more energy to maintain

homeostasis and incorporate less energy from digesting prey, increasing the likelihood of having a negative energy budget during warm periods (Merchant 1970, Bobka et al. 1981). Red-backed salamanders may be in an energy deficit at temperatures as low as 20°C (Merchant 1970), and may need to increase the amount of prey consumed to maintain a positive energy balance. In my study during 2008, the ORH accounted for 48% of the mean temperatures >20°C (averaged across subsamples within EUs). This provides additional evidence that recent disturbance to forested habitats may cause terrestrial salamanders to be in an energy deficit and decrease the amount of energy allocated to growth or reproduction.

When understory herbaceous and woody vegetation had 8-14 growing seasons to recover from disturbance (in 2006 and 2007), microclimate profiles and energetic costs for maintenance were similar. Regrowth of understory and midstory vegetation likely contributed to this recovery (Brooks and Kyker-Snowman 2008). When I sampled temperatures the growing season after a second disturbance to the shelterwood EUs, temperatures of salamander refugia increased. Based upon my estimates of energy required for SMR, I detected a concurrent increase to energetic requirements for basic maintenance costs in the ORH EUs.

Although I did not detect differences across the disturbance gradient in either the total number of detrital invertebrates or in invertebrates separated into broad taxonomic categories, others have reported that invertebrate abundances and diversity vary with forest harvest type (Huhta 1976, Mitchell et al. 1996, Su and Woods 2001, Willett 2001, Bonham et al. 2002). In California redwood (*Sequoia sempervirens*) forest, both spiders and arthropods were negatively correlated with the frequency of logging (Willett 2001). In conifer forest of Maine, abundance and vertical distribution of invertebrates varied among shelterwood, selection, and clearcut harvested stands, with the greatest proportion of near-ground insects occurring in clearcut forest

(Su and Woods 2001). Prey quality of Peaks of Otter salamanders (*Plethodon hubrichti*) was lower in harvested forest in Virginia, as salamander stomachs contained fewer soft-bodied prey items in recently harvested forest (Mitchell et al. 1996). My research suggests that availability of invertebrate prey was not greatly different among silvicultural treatments (but did vary among study sites); however, because I did not quantify consumption of prey by salamanders, it is possible that ingestion rates of particular prey types varied along the disturbance gradient.

Another component of a salamander's energy budget is storage of lipids, and I predicted that salamanders in undisturbed forest (i.e., control EUs) would have larger energy stores than salamanders in disturbed forest, due to either a lower cost of maintenance (Wieser 1991) or due to greater prey availability. In contrast to my prediction, the body condition of red-backed salamanders was greater in the most-disturbed forest at BB2 (Figure 4.4), but not at BB1. The fate of terrestrial salamanders after harvesting is unknown, but reductions in surface abundances are hypothesized to occur because salamanders either (1) die, (2) persist underground using energy stores until habitat conditions improve, or (3) disperse to more suitable habitats (deMaynadier and Hunter 1995, Semlitsch et al. 2008). Abundances of salamanders were reduced by approximately half after the ORH (Chapter 3) and across harvested treatments, were 18% of pre-harvest abundances at 3-years post-treatment (Homyack and Haas 2009). The greater body condition in the ORH EU may have occurred because of decreased intraspecific competition (Welsh et al. 2008), shifts in diet (Mitchell et al. 1996), or because salamanders with the best body condition were able to cope with the more energetically costly habitat conditions and remain active on the surface (Knapp et al. 2003). Other researchers have observed greater sized salamanders in harvested forest and have hypothesized that this may have occurred because surviving salamanders forgo reproduction to increase body size (Ash et al. 2003) or because they

are released from competition in marginal habitats (Welsh et al. 2008). The number of red-backed salamanders I captured in the ORH EUs was small (BB1, n=8; BB2, n=4), so that these results should be viewed cautiously. Future sampling of the ORH EUs to increase sample sizes will provide additional evidence to support or refute the relationship between body condition and level of disturbance.

My results provide evidence that habitat disturbance can increase the energy required for basic maintenance costs and possibly influence body condition of terrestrial salamanders. I focused my research efforts on quantifying the effects of changing environmental temperatures on bioenergetics of salamanders. However, because the cutaneous gas exchange of plethodontids relies on moisture (Feder 1983), potential changes to humidity or soil moisture also may affect fitness through bioenergetics. Initially, soil moisture increases after harvesting due to less evapotranspiration (Johnson et al. 1985, Jutras et al. 2006), but relative humidity reportedly remains high across a range of forest harvest types and range of years (Brooks and Kyker-Snowman 2008). Examining the effects of temperature independent of moisture is a simplification of the complex microclimate that salamanders encounter in the wild, but depicts how environmental conditions affect the trade-offs salamanders face when allocating energy to competing physiological functions.

In addition to the effects of the disturbance gradient I observed differences in invertebrate abundances and caloric requirements across study sites. In general, the two sites in Virginia were warmer, leading to a larger seasonal energetic requirement for SMR. And, invertebrate abundances, including common prey items of red-backed salamanders (e.g., collembola and larvae) (Chapter 4), were greatest in the Virginia sites. The long-term investigation of terrestrial salamanders on these same sites has observed greater abundances of salamanders at the Virginia

sites, but it is currently unclear whether differences in bioenergetics contribute to this observation.

Conclusions

The use of bioenergetics to measure fitness relies on the assumptions that ecological processes are limited by energy and that individuals allocate energy in ways that influence fitness (Pough et al. 1992). I examined multiple metrics describing the bioenergetics of terrestrial salamanders across a disturbance gradient to evaluate whether changes to use (i.e., metabolism, storage) or availability of energy (i.e., prey abundance) after harvesting may have contributed to observed declines in abundance of salamanders, from which populations have yet to fully recover (Homyack and Haas 2009). Although abundances of salamanders remained depressed in harvested treatments for at least 13-years in my study system (Homyack and Haas 2009), microclimate and other habitat characteristics for salamanders in disturbed plots were indistinguishable from controls within this time period. However, *P. cinereus* are estimated to require >60 years for population recovery after forest harvest (Homyack and Haas 2009). The trend of salamander populations recovering from disturbance at a rate slower than habitat conditions recover has been noted in other ecosystems (Dupuis and Bunnell 1999) and after other disturbances (Semlitsch et al. 2007); this pattern could be related to short-term alterations to energy budgets that ultimately may have long-term influences on fitness.

Documenting changes to the use or availability of energy and alterations in growth rates or reproductive output could link bioenergetics to fitness of plethodontid salamanders after experimental forest disturbance. Although Chazal and Niewiarowski (1998) did not detect differences between survival, growth, or lipid content of mole salamanders in recent clearcut harvests compared to intact forest, sagebrush lizards (*Sceloporus graciosus*) from populations

with lower resting metabolic rates had 12.5% more energy available for growth (Sears 2005). Thus, monitoring growth rates or field metabolic rates of plethodontid salamanders through time and among silvicultural treatments should be priorities for future research. Such studies may need to use *in situ* enclosures with caged animals (e.g., Chazal and Niewiarowski 1998, Rothermel and Luhring 2005) because adequate recapture rates are difficult to achieve for terrestrial salamanders.

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Table 4.1. Mean and standard error of the number of collembola and larvae (Lepidopteran and Coleopteran) per gram of leaf litter sampled across a silvicultural disturbance gradient at four mixed-hardwood dominated study sites in Virginia (Blacksburg 1, Blacksburg 2) and West Virginia (West Virginia 1, West Virginia 2), 2006. Statistical differences are presented from univariate Analyses of Variance.

Source	F-Statistic	P-Value	Mean	Standard Error
Collembola				
Treatment	F ₃ =1.54	0.27		
Control			0.19	0.07
Shelterwood			0.31	0.07
Leave Tree			0.36	0.07
Clearcut			0.40	0.07
Site	F ₃ =8.23	0.006		
Blacksburg 1			0.59	0.07
Blacksburg 2			0.35	0.07
West Virginia 1			0.23	0.06
West Virginia 2			0.08	0.08
Larvae				
Treatment	F ₃ =1.10	0.40		
Control			0.11	0.03
Shelterwood			0.17	0.02
Leave Tree			0.14	0.02
Clearcut			0.16	0.02
Site	F ₃ =3.48	0.046		
Blacksburg 1			0.17	0.02
Blacksburg 2			0.21	0.02
West Virginia 1			0.11	0.02
West Virginia 2			0.08	0.08

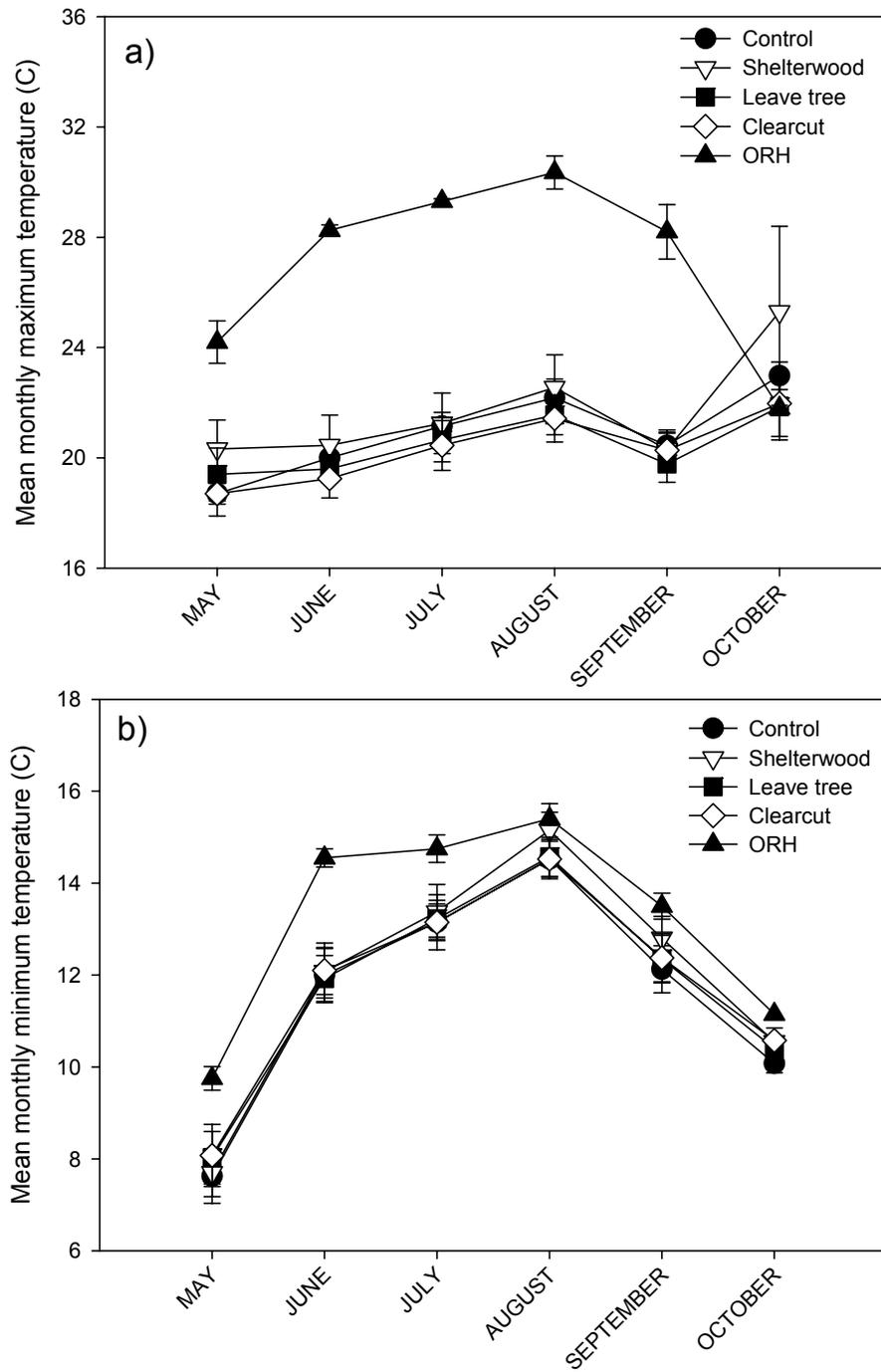


Figure 4.1. Mean maximum (SE) (Figure 4.1a) and mean minimum (SE) (Figure 4.1b) monthly temperatures quantified under coverboards at four study sites in Virginia (n=2) and West Virginia (n=2). Temperatures were quantified with small dataloggers on unharvested control, shelterwood, leave tree, clearcut, and overstory removal harvest (ORH).

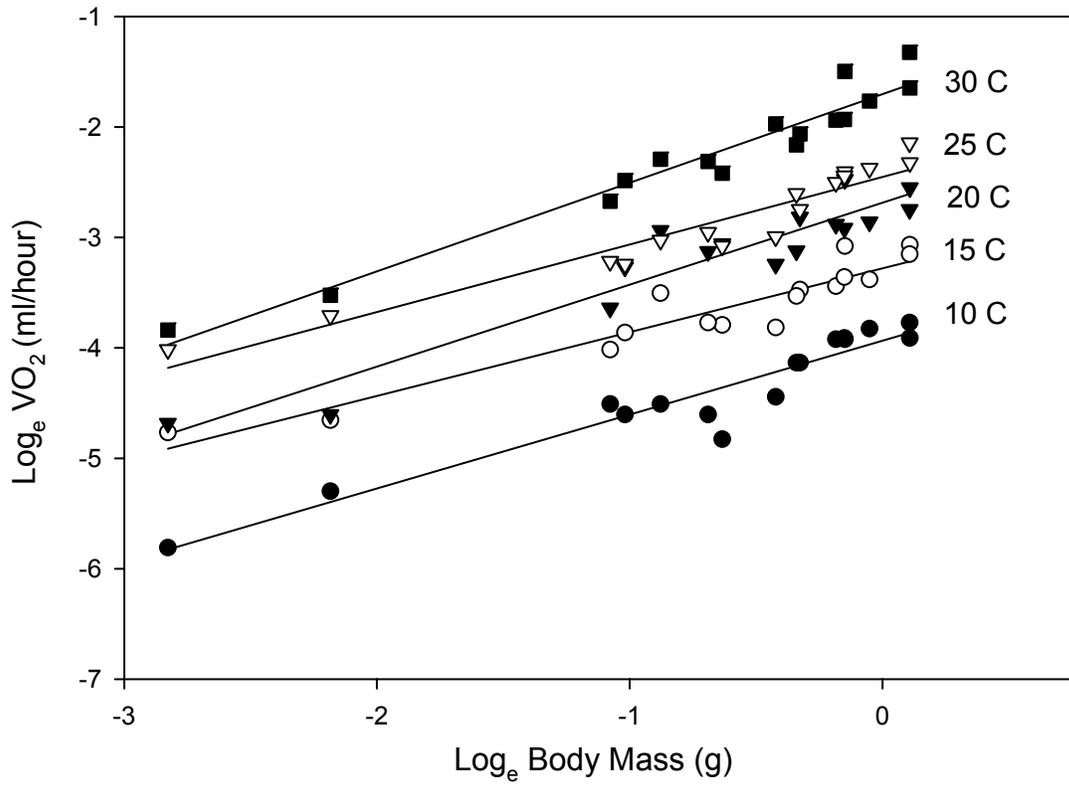


Figure 4.2. Effects of body mass and experimentally manipulated ambient temperatures on oxygen consumption (VO₂) for the standard metabolic rate of *Plethodon cinereus*. Each temperature was significantly related to oxygen consumption ($P < 0.001$, $R^2 = 0.90-0.95$).

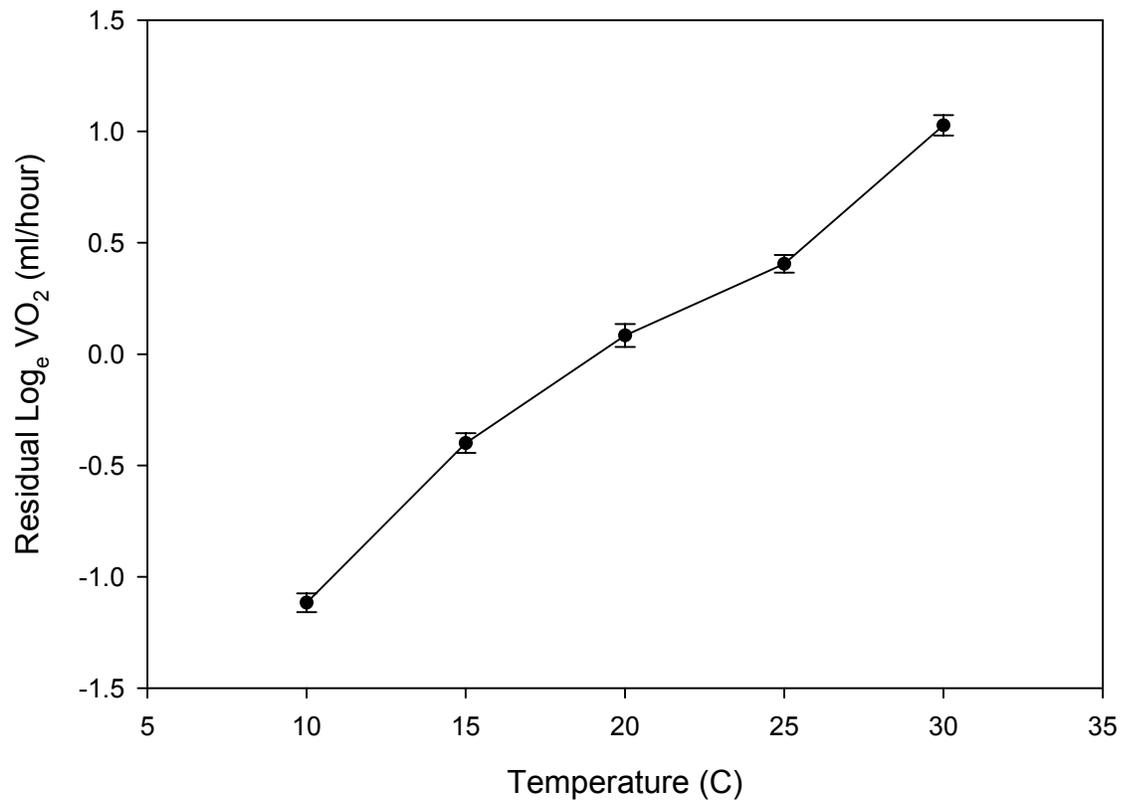


Figure 4.3. Mean (SE) residual $\log_e \text{VO}_2$ of *Plethodon cinereus* after adjusting for body mass across 5 experimentally manipulated temperatures, 10-30°C. I obtained residual values by regressing $\log_e \text{VO}_2$ for estimated standard metabolic rates against \log_e body mass and quantified means and standard errors of individuals for each temperature.

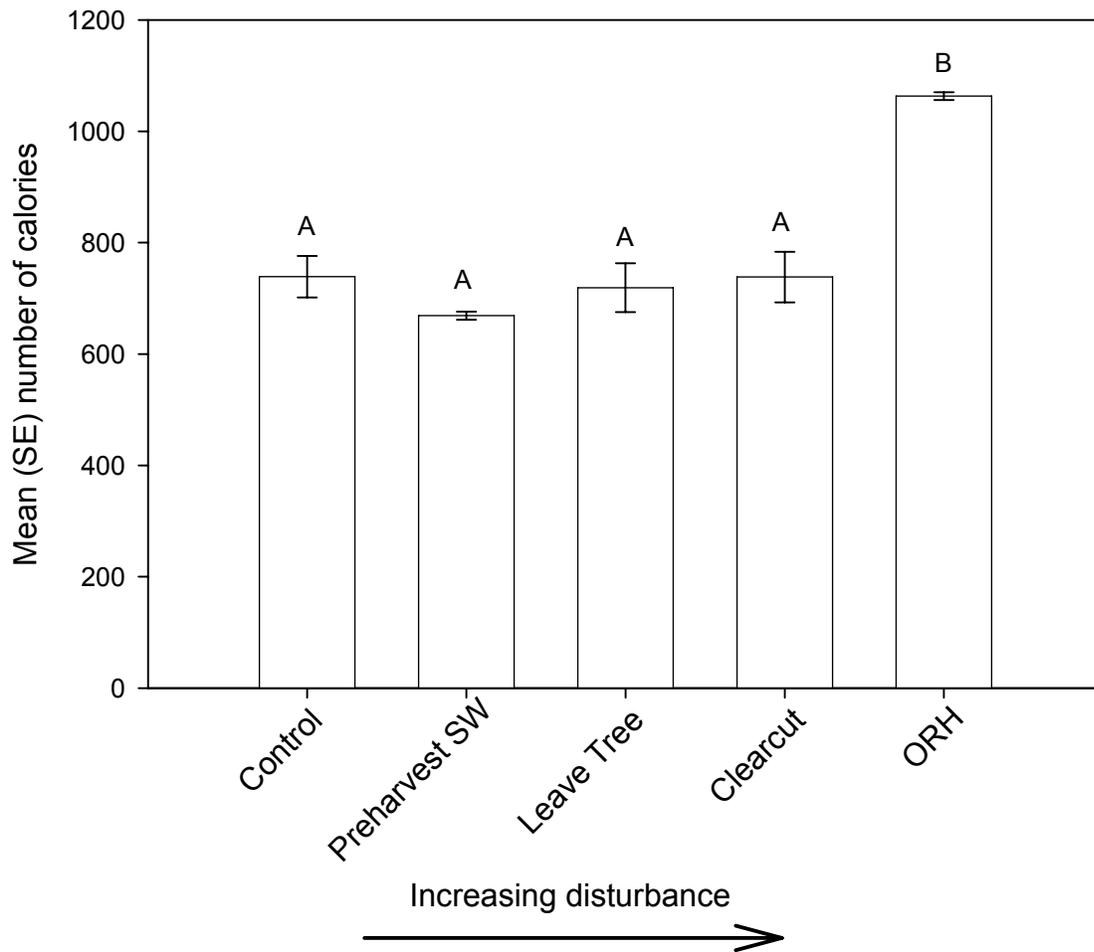


Figure 4.4. Mean (SE) number of calories required for the standard metabolic rate of a 1.0 g *Plethodon cinereus* across a season (May-October) in five silvicultural treatments based on temperature regimes. I evaluated effects on bioenergetics the growing season directly after disturbance (overstory removal harvest, ORH) and 8-14 years after disturbance (control, preharvest shelterwood, leave tree, and clearcut harvest). Different letters indicate statistical differences among treatments ($P < 0.05$).

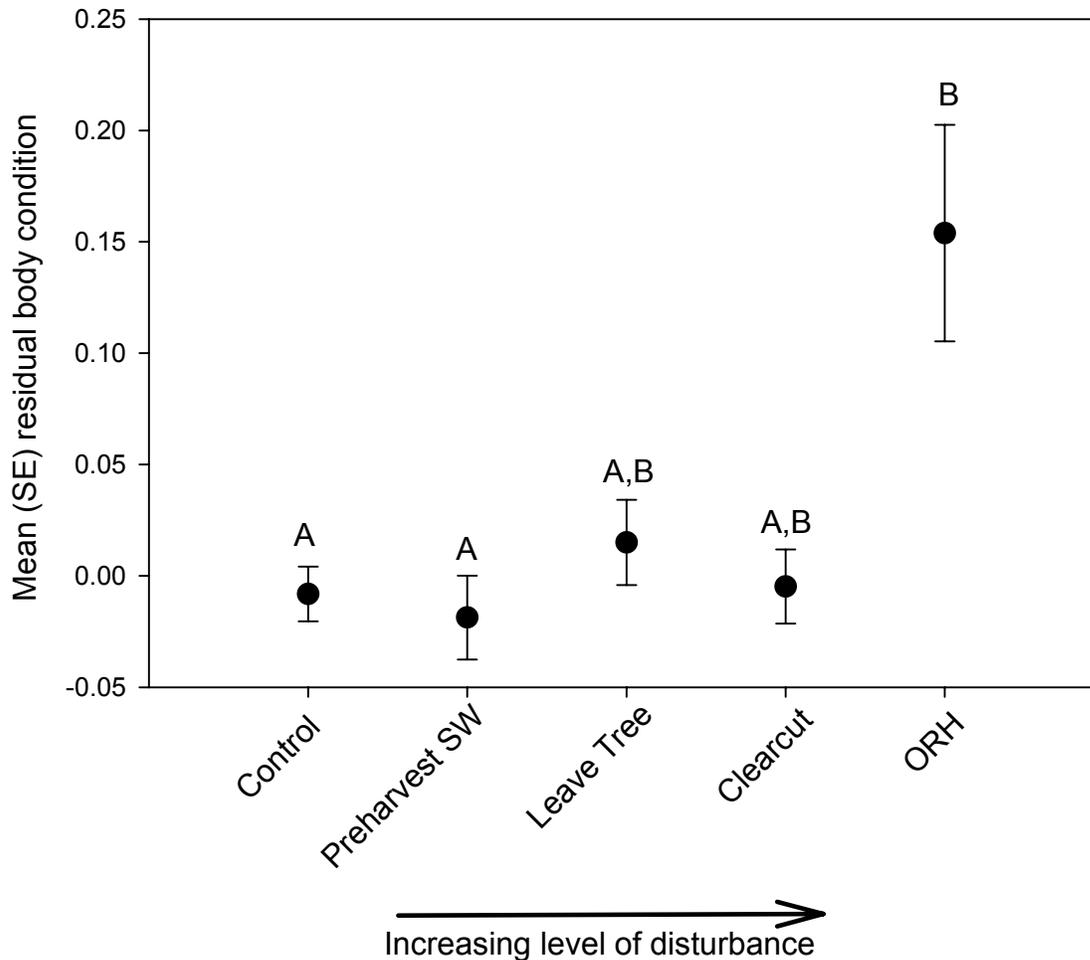


Figure 4.5. Mean (SE) residuals from a regression of log body mass on log body length as a measure of body condition for red-backed salamanders (*Plethodon cinereus*) across a silvicultural disturbance gradient, 2006-2008 at the Blacksburg 2 study site. With this index, salamanders with positive residuals are considered to have a better body condition than those with negative residuals. I evaluated effects on bioenergetics the growing season directly after disturbance (overstory removal harvest, ORH) and 8-14 years after disturbance (control, preharvest shelterwood, leave tree, and clearcut harvest). Different letters indicate statistical differences among treatments ($P < 0.05$).

**CHAPTER 5: DOES *PLETHODON CINEREUS* AFFECT LEAF LITTER
DECOMPOSITION AND INVERTEBRATE ABUNDANCES IN MIXED OAK FOREST?**

Abstract

Ecological interactions among salamanders, invertebrates, and leaf litter decomposition in the detrital ecosystem are poorly understood. Although investigators have determined that some anurans can influence nutrient availability in terrestrial systems, the roles of terrestrial salamanders in providing ecological services are less clear. I examined the effects of the eastern red-backed salamander (*Plethodon cinereus*) on leaf litter decomposition rates and invertebrate populations in the mixed oak forests of southwestern Virginia from May 2006-June 2008. I constructed 12 *in situ* mesocosms with 0, 1.0, or 2.0 *P. cinereus*/m² (4.0 *P. cinereus*/m² in year 2). I quantified decomposition of leaf litter and numbers of invertebrates with litter bags that were removed from mesocosms at monthly intervals throughout the experiment. Further, I assessed what taxa of invertebrates were preyed upon by salamanders with gastric lavage. Across my two-year experiment, I was unable to detect an effect of salamander abundance on rates of leaf litter decomposition, numbers of broad invertebrate taxonomic groupings, or functional guilds of invertebrates. Stomach analysis confirmed that salamanders were euryphagic, but consumed more herbivores than detritivores or predators. Invertebrates were influenced more by season than the presence of salamanders, with their greatest abundances occurring during spring and early summer. Although I am unclear why these results conflict with earlier work indicating that salamanders can influence invertebrates and leaf litter decomposition, variability among tree canopy species or microclimate may have contributed to a

lack of control of invertebrate populations or litter decomposition by salamanders in the complex, mixed-oak forests of Appalachia.

Introduction

Because of the increasing loss of global biodiversity including declines of amphibian populations, the scientific community has emphasized the need to understand how ecosystems will function with diminished species diversity (Wall et al. 2004). In terrestrial forests, organisms in the soil-litter interface provide a myriad of ecosystem services, including the breakdown of organic matter, the return of nutrients to plants to increase primary productivity, and sequestration of carbon (Wall et al. 2004). Allochthonous inputs of leaf litter provide a primary source of nutrients for the detrital system (Gartner and Cardon 2004, van der Putten 2004), and nutrients are returned to the soil via complex community interactions between invertebrates and the microbial community (Wardle 2002, Hattenschwiler et al. 2005). Despite the considerable benefits of soil processes to the global economy and to maintaining ecosystems (van der Putten et al. 2004), little research has examined the roles of individual species in maintaining these functions.

Terrestrial salamanders are one of the most abundant vertebrate taxa in eastern forests (Burton and Likens 1975), and they have been hypothesized to play roles in nutrient cycling through the control of decomposition of leaf litter (Hairston 1987, Wyman 2003, Davic and Welsh 2004). As an apex predator in the forest floor ecosystem, terrestrial salamanders can affect invertebrate populations (Rooney et al. 2000, Walton 2005, Walton and Steckler 2005, Walton et al. 2006), which indirectly may affect forest floor processes (Wyman 1998, but see Walton and Steckler 2005). Most plethodontid salamanders are euryphagic and prey upon numerous guilds of invertebrates (Jaeger 1972, Fraser 1976), and thus have several potential

pathways to influence litter decomposition and nutrient cycling. For example, salamanders have been hypothesized to exert top-down effects on the detrital food web by preying on litter fragmenters, the reduction of which may retard the ability of decomposers to further break down litter, and ultimately increase carbon sequestration (Wyman 1998, Wyman 2003). Alternatively, salamanders could release invertebrate detritivores by consuming their predators and ultimately increasing litter decomposition rates (Rooney et al. 2000). Although other amphibians have been shown to increase the amount of nutrients available in both terrestrial (Beard et al. 2003, Huang et al. 2007) and aquatic systems (Regeister et al. 2006), whether terrestrial salamanders affect the flow of nutrients in the forest floor ecosystem through regulation of invertebrate prey requires broader investigation (Wyman 2003).

To investigate the role of eastern red-backed salamanders (*Plethodon cinereus*) in forest floor processes, researchers have examined the top-down effects of salamander density on the detrital community and decomposition of leaf litter with microcosms or mesocosms. Previous experimental manipulations of salamander densities have documented conflicting effects on invertebrate populations and/or rates of litter decomposition (Wyman 1998, Rooney et al. 2000, Walton and Steckler 2005). It is unclear, however, whether discrepancies among studies were caused by biological variation in ecological communities, differences in experimental methods, or choice of statistical analyses. Wyman (1998) manipulated salamander densities in field enclosures in Albany County, New York and reported that salamanders greatly reduced invertebrate numbers, which indirectly reduced the rate of litter decomposition over 4.5 months. However, he treated individual samples of leaf litter (rather than mesocosms) as independent so that the probability of Type II error may have been inflated. In contrast, no difference in rates of leaf litter decomposition between control and treatment laboratory microcosms using litter

collected from forest in northeastern Ohio over 3 months was detected, despite evaluating densities of salamanders 7.5× higher than Wyman's (1998) treatments (Walton and Steckler 2005). Salamanders were, however, associated with lower densities of macrofaunal (>2.0 mm length) and mesofaunal (0.1-2.0 mm length) detritivores, indicating changes to the soil biota did occur in their presence (Walton and Steckler 2005).

Although previous experiments of effects on terrestrial salamanders on invertebrates and leaf litter decomposition have explored the ecological effects of *Plethodon cinereus*, most were relatively short-term, lasting ≤ 4.5 months. Further, none of the aforementioned investigations described the invertebrate prey actually consumed by study animals, and none examined relationships in environments with the diversity of overstory tree species as the mixed oak forest of central Appalachia. I addressed these issues in our research by manipulating salamander densities in a replicated *in situ* mesocosm experiment to document the potential of top-down influence of red-backed salamanders on invertebrates and rates of litter decomposition for two years. I predicted that salamanders in the mesocosm treatment with the greatest numbers of salamanders would exert top-down effects on invertebrates via predation, thereby releasing detritivores from invertebrate predators, and increasing the rate of leaf litter decomposition. Thus, I expected to observe more rapid rates of litter decomposition, fewer invertebrate predators, and more leaf litter fragmenters/decomposers in treatments with the most salamanders.

Methods

Field methods

Mesocosms can link the reductionist and holistic approaches of laboratory versus field studies (Odum 1984). Further, field experiments can combine a mixture of realism and control of variables to explore relationships among abundances of species and ecosystem processes

(Diamond 1986). I evaluated relationships among terrestrial salamanders, invertebrates, and leaf litter decomposition in closed canopy mixed-oak forest with *in situ* field mesocosms to receive the benefits of both mesocosms and field experiments.

My study site was in the Eastern Divide Ranger District of the Jefferson National Forest, Montgomery County, Virginia. The study site reportedly had no major disturbances to the forest in >70 years (E. Leonard, USDA Forest Service, Eastern Divide Ranger District Silviculturalist, personal communication). The study area had an approximate elevation of 670 m and soils were Clymer series (coarse-loamy, siliceous, active, mesic Typic Hapludult) (Sucre 2008). The selected site was south-facing and had relatively flat topography. Dominant midstory and overstory trees included oaks (*Quercus alba*, *Q. coccinea*, *Q. prinus*), red maple (*Acer rubrum*), white pine (*Pinus strobus*), mockernut hickory (*Carya alba*), and serviceberry (*Amelanchier arborea*). In May 2006, my collaborator and I measured and flagged a 5×5 grid of 20×20 m cells and randomly selected 12 cells from the 25 available to build mesocosms. Field mesocosms were 1.2×2.5 m (area=3 m²) with a rectangular wood frame on the soil surface. The wood frame extended 25 cm above the soil surface, and we attached vinyl flashing perpendicular to the top as a barrier to salamander movements aboveground. Further, we vertically buried vinyl flashing on the sides to approximately 40 cm below the soil surface, attached it to the wood frame with staples, and sealed all the seams with silicone caulking to prevent salamander immigration/emigration belowground. Whereas Wyman (1998) dug into the soil to attach a fiberglass mesh screen below ground, we chose to avoid disturbances to the soil horizons to maintain more natural nutrient flow and soil fauna. Our mesocosm design allowed for allochthonous inputs of leaf litter, natural immigration/emigration of crawling and flying invertebrates, and use by most vertebrates.

To quantify rates of leaf litter decomposition, I added three-sided mesh bags with a predetermined mass of leaf litter to each mesocosm at the beginning of the experiment. I constructed 10×10 cm litter bags from 1 mm fiberglass screening that were open at one end for invertebrates to move freely in and out of them. I uniquely marked leaf litter bags with individually numbered metal tags (Monel 1005-3; National Band and Tag Co., Newport, Kentucky) to aid in random removal of bags. I weighed litter bags with an electronic balance to 0.01 g and filled them with 3.0 g of leaf litter collected adjacent to each mesocosm. Litter was collected on site, so species composition matched that of the dominant overstory trees present at the study site. I placed 60 filled litter bags in each enclosure in June 2006 and removed two bags/mesocosm approximately monthly to calculate the amount of mass lost over time. I did not dry litter prior to addition into mesocosms to avoid biasing litter decomposition rates (Taylor 1998). However, I oven-dried samples of the same litter used to fill litter bags at the beginning of the study period to develop a conversion factor from beginning wet weight to oven-dried ending weight (Beard et al. 2003).

Following construction of experimental units (i.e., mesocosms), I randomly assigned treatments ($n=4$, 0 salamanders, 0 salamanders/m²; $n=4$, 3 salamanders, 1 salamander/m²; $n=4$, 6 salamanders, 2 salamanders/m²) to mesocosms. I chose *Plethodon cinereus* as the study species for our experiment because they are widespread across much of the eastern hardwood forests (Petranka 1998), they were the most abundant plethodontid salamander in my study area (Homyack and Haas 2009) and they were able to meet life history needs (e.g., foraging, reproducing, over-wintering) in a very small area (Petranka 1998). My salamander treatments fell within the range of densities (0.25-2.8 salamanders/ m²) reported for *P. cinereus* in the eastern United States (Petranka 1998). I collected salamanders from the study area and weighed,

sexed using candling (Gillette and Peterson 2001), measured snout-vent length (SVL), and marked them with Visible Implant Elastomer (VIE) (Northwest Marine Technology, Shaw Island, Washington, USA). Each salamander received a unique combination (to that mesocosm) of four ventral VIE marks of orange, red, and/or yellow elastomer, colors that had the greatest readability and retention in *P. cinereus* over time (Heemeyer et al. 2007). Only adult male or non-gravid female salamanders (SVL >34 mm) (Petranka 1998) were selected. I placed four blocks of rough-cut yellow poplar (*Liriodendron tulipifera*) (30 × 20 × 5 cm) in each mesocosm to serve as salamander refugia and to facilitate recapture of study animals throughout the experiment.

The above-ground flashing, buried flashing, and sealed seams were all included to prevent movement of salamanders in and out of mesocosms, but I recognized that some movements would likely occur and that some resident salamanders were present in enclosures. Thus, I used the individual VIE marks on salamanders to distinguish study animals from unmarked salamanders. During each sampling period, I recorded which study animals were encountered. When I encountered unmarked salamanders from June 2006-February 2007, I removed them and placed them >20 m from the nearest mesocosm. Later in the study I batch-marked unmarked individuals with a single VIE injection (March 2007-May 2007) and determined that some translocated salamanders returned to mesocosms. I was unable to ascertain how salamanders re-entered mesocosms, so I transported all unmarked salamanders to the lab and either euthanized them or used them in companion studies. I anticipated this approach would help to manipulate salamander numbers to the desired densities. In May 2007 (12 months into the experiment), I pressed the system further (Bender et al. 1984) by doubling the density of

salamanders in the high salamander treatment to 4 salamanders/m² and continuing to remove unmarked salamanders from all mesocosms.

At approximately 4-week intervals, I randomly selected two litter bags from each enclosure, transported them to the lab in resealable plastic bags, and extracted invertebrates with Berlese funnels. I exposed litter to a 40 w bulb for 48 hours. Invertebrate samples were preserved in 70 % ethyl alcohol, and were sorted to taxonomic category with a binocular dissecting scope. Following extraction of invertebrates from litter, I oven dried leaf litter for >48 hours at 65° C. Any litter that fell into the funnel was included in the sample for drying and weighing.

I quantified food habits of marked salamanders in mesocosms with gastric lavage (Fraser 1976, Mitchell et al. 1996) to increase the scope of inferences regarding the indirect effects of salamanders on litter decomposition. Whereas Wyman (1998) and Walton and Steckler (2005) assumed observed declines in invertebrates were directly related to salamander predation, I quantified which functional groups and how many invertebrates were consumed by *P. cinereus* in mesocosms. Plethodontid salamanders typically forage in leaf litter during and following rain events (Jaeger 1972, Fraser 1976). Thus, I visited mesocosms between 0600 and 1000 hours the morning following a rain event and hand-captured any salamander present under refugia in mesocosms. I used an angiocatheter tube on a 2-cc syringe as a gastric lavage device. The flexible tubing was carefully entered into the esophagus and I injected water until contents were flushed (Fraser 1976). Stomach contents were stored in vials with 70% ethyl alcohol. I sorted invertebrates to functional group, and measured length and anterior and posterior widths with Image Pro Plus 6.1 software (Media Cybernetics, Bethesda, MD) on a dissecting scope relayed

to a computer. I estimated volume for each invertebrate using the formula for a cylinder (Jaeger 1978).

Statistical Analyses

To determine whether rates of litter decomposition differed among salamander treatments, I used linear regression to examine the relationship between the percent of mass lost across time. I conducted separate linear regressions for each treatment (zero, low, and high salamander density) and separately by year because the high salamander treatment was doubled in year two. I examined normality of data with normal probability plots and Kolmogorov-Smirnov goodness of fit tests and equality of variances with modified Levene's tests (Neter et al. 1996). Within a sampling year, I compared slopes of regression lines among treatments with student's t-tests (Zar 1996).

I used repeated-measures one-way multivariate analysis of variance (MANOVA) to detect differences in invertebrate abundances between the zero, low, and high salamander treatments separately by each year. I only used those invertebrate groups that made up >1% of the total number of invertebrates in the leaf litter samples. I was also interested in whether salamanders had variable effects on guilds of invertebrates. Thus, I conducted another analysis that examined the effects of the salamander treatments on functional groups, which I defined as herbivores, detritivores, and predatory invertebrates (Rooney et al. 2000, Willett 2001, Beard et al. 2003). I considered herbivores to include Lepidoptera (moths, butterflies), Gastropoda (snails), and larvae (Coleopteran, Lepidopteran, and Dipteran). I considered members of the orders Collembola (springtails), Acarina (mites), Coleoptera (beetles), Diplopoda (millipedes), Isopoda (sowbugs and pillbugs), Protura (proturans), and Isoptera (termites) as detritivores. Hymenopterans (wasps, bees, ants), Pseudoscorpionidans (pseudoscorpions), Aranaens (spiders),

Dipterans (flies), and Chilopodans (centipedes) were considered predatory invertebrates. There is some diversity of function within these taxonomic groupings, but I generalized here because I did not identify invertebrates to lower levels. I conducted a repeated-measures one-way MANOVA separately for each year with salamander treatment as the factor. I used MANOVAs to examine simultaneous differences in invertebrate abundances among treatments and to avoid inflating the rate of Type I error. Normality and equality of variance was examined separately for each variable and any variable that failed to conform to the parametric assumptions of MANOVA was log-transformed.

Finally, I quantified the abundance and proportions of invertebrate prey consumed by study animals. I compared the average number of prey and average volume of prey consumed by salamanders between the low and high density salamander treatments using two-sample t-tests with unequal variances (Zar 1996) and used the Satterthwaite approximation to estimate associated degrees of freedom (Neter et al. 1996). Prior to analyses, I pooled data across the two years of the study to increase sample sizes. I also conducted a simple use-availability analysis using the stomach contents as my measure of use and matched the most recent sample of invertebrates from leaf litterbags in that mesocosm as my measure of availability. I compared use to availability of invertebrate functional groups (detritivores, herbivores, predators) by ranking use and availability separately for each individual and subtracting the difference in ranked use from availability, so that negative numbers represented preferred prey, positive numbers avoided prey, and numbers near zero represented prey consumed roughly in proportion to availability (Johnson 1980). I averaged the mean difference in ranks across all sampled individuals to determine the order of preference of invertebrate functional groups by

salamanders. All statistical analyses were conducted using SAS 9.1 (SAS Institute, Cary, North Carolina, USA). I considered differences significant at $\alpha=0.05$.

Results

Salamander captures

No species of salamander other than *Plethodon cinereus* was encountered in mesocosms during the entire 25 month period. Most individually marked salamanders (78%) were encountered ≥ 1 time throughout the study. Three marked salamanders were found dead under coverboards, but were replaced with a new individual. Unmarked salamanders were encountered in all treatments; I had 153 captures of unmarked salamanders from June 2006-June 2008. When excluding sampling dates when no salamanders were encountered (during hot and dry summer months or cold winter months), 1.6 \times more marked salamanders were captured in the high density treatment than in the low density treatment in year 1. During the second year, I captured 4.3 \times more marked salamanders in the high density treatment than in the low density treatment. No VIE-marked study animals ever were encountered in the zero salamander treatment. Including captures of unmarked salamanders in addition to VIE-marked study animals indicated that the high density treatment had 1.9 and 1.8 \times more captures than the low and zero density treatments, respectively in year one. In year two, when the numbers of salamanders in the high density treatment was doubled, the high density mesocosms had 3.0 and 2.7 \times more captures than the low and zero density treatments, respectively.

Leaf litter decomposition

I removed litter bags from mesocosms on 22 monthly sampling occasions. During a few winter months, the ground was covered with snow and litterbags were inaccessible. On those occasions, I removed litterbags after the snow melted, or waited until the next scheduled

sampling occasion. Leaf litter lost mass across all mesocosm treatments and across both years (Figure 5.1) and data were normally distributed ($P > 0.05$) with homogeneous variances ($P > 0.05$). Further, time explained between 81-93% of the variability in the percent of litter mass lost in year one and 58-81% of the variability in year 2. However, within both year one and year two of the study, slopes of regression lines for the three salamander treatments did not differ from each another ($P > 0.35$).

Invertebrate abundance

From the 22 sampling occasions for leaf litter, I identified 9,993 invertebrates. Mites (Acarina) and springtails (Collembola) made up the majority of invertebrates at 36 and 48% of the total, respectively. Larvae (Coleoptera, Lepidoptera and Diptera), ants (Hymenoptera), and spiders (Aranaena) each accounted for 7%, 2%, and 2% of the total number of invertebrates and other taxonomic groups each accounted for <1% of the total (Complete list of taxa sampled given in Appendix C). When combined into functional groups, detritivores accounted for 87%, herbivores accounted for 7%, and predators accounted for 6%.

I only included those taxonomic groups that composed >1% of the invertebrate data (Collembola, mites, ants, larvae, and spiders) for that year into analyses. Further, I conducted MANOVA's separately by year because the density of salamanders was doubled between year one and year two. During year one, variances were homogeneous for each invertebrate group ($P > 0.413$) and data were normally distributed. The overall MANOVA examining the effects of salamander treatments, time, and an interaction on invertebrates was not significant (Wilks' Lambda=0.908, $F_{10, 172}=0.85$, $P=0.577$). Individually, neither salamander treatment nor the interaction term was significant for the five taxonomic groups, but spiders, mites, and collembola

all were significantly affected by time ($P < 0.05$) (Table 5.1), with abundances peaking in spring and fall (Figure 5.2).

Results for common taxonomic groups of invertebrates were similar for year two. Data were normally distributed and variances were normal. I was unable to detect a significant omnibus difference with the MANOVA (Wilks' Lambda=0.938, $F_{10, 208}=0.68$, $P=0.740$). Despite no treatment or treatment \times time interaction for each of the invertebrate groups, there was a significant effect of time for collembola, mites, larvae, and spiders (Table 5.1, Figure 5.2). In general, the greatest numbers of invertebrates were encountered during spring and fall, which typically are the wettest months in our study area.

The counts of invertebrates by functional group or guild from year one of the experiment were normally distributed and variances were homogeneous ($P > 0.412$). The MANOVA was not significant (Wilks' Lambda=0.940, $F_{6, 176}=0.93$, $P=0.476$). Among the functional groups, only the detritivores had a significant effect of time ($P < 0.001$) (Figure 5.3). I was unable to detect an effect of either salamander treatment or a salamander \times time interaction for detritivores, herbivores, or predators during year one.

I log-transformed the numbers of detritivores, herbivores, and predators in the second year of sampling because data failed to meet the parametric assumptions of MANOVA. Following transformation, errors were normally distributed and variances were homogeneous ($P > 0.412$). The overall test for this MANOVA (Wilks' Lambda=0.967, $F_{6, 212}=0.59$, $P=0.739$) was not significant. For each comparison of invertebrate functional groups among treatments and times, I detected a significant effect of time ($P < 0.001$), but not of salamander treatment ($P > 0.367$) nor an interaction between treatment and time ($P > 0.238$).

Stomach contents of salamanders. —

I identified and measured 601 invertebrates from the 46 regurgitated stomach contents of salamanders. Stomach contents were collected from at least 29 individual salamanders and included unmarked salamanders captured in the low and high treatments. Of the invertebrates collected, 68% were larvae (Coleopteran, Lepidopteran, and Dipteran), 10% were mites, 9% were Collembola, 4% were ants, 2% were unknown invertebrates, 1% were snails, and 1% were termites. Adult beetles, centipedes, dipterans, bees and wasps, isopods, millipedes, spiders, and earthworms each accounted for <1% of the total. By functional group, 68% of the invertebrates were herbivores, 24% were detritivores, 6% were predators, and 2% were unable to be identified.

After converting each invertebrate to a volume, 38% of the total volume were larvae, 29% were earthworms, 7% were ants, 5% were centipedes, 5% were millipedes, 4% were adult dipterans, 4% were unable to be identified, and 2% were beetles. Wasps and bees, isopods, mites, snails, spiders, and termites each accounted for <1% of the total volume. Detritivorous invertebrates accounted for the greatest volume (40%), followed by herbivores (38%), and lastly by predators (18%) in stomachs. Four percent of the volume was unidentified.

Although the average number of prey consumed by salamanders in the low-density treatment ($\bar{X} = 19.1$ prey items/stomach) was nearly double of that of the high density treatment ($\bar{X} = 11.1$ prey items/stomach), I did not detect a statistical difference between treatments ($t_{13} = 0.53$, $P = 0.603$), due to large variation in samples. I detected the opposite pattern with prey volume; the mean volume of prey in salamander stomachs was greater in the high density treatment ($\bar{X} = 77.5 \text{ mm}^3$) than in the low density treatment ($\bar{X} = 49.9 \text{ mm}^3$). However, the prey volumes were not statistically different from one another ($t_{31} = -0.85$, $P = 0.411$). In addition I could not detect a difference in either the mean number of herbivores ($t_{14} = 0.58$, $P = 0.570$), detritivores ($t_{21} = -0.07$, $P = 0.946$), or predators ($t_{21} = -0.71$, $P = 0.488$) per lavage sample between

the low and high density treatments (Figure 5.4). Based on the use-availability calculations, the order of preference for salamanders starting with most preferred was herbivores (-0.57), predators (-0.22) and, detritivores (0.57) ($F_{2,68}=9.94$, $P<0.001$).

Discussion

Although salamanders have been predicted to influence community interactions and ecosystem processes, the results of my two-year experiment indicated that *P. cinereus* did not have detectable effects on rates of leaf litter decomposition or on abundances of common detrital invertebrates in natural conditions. Instead, abiotic factors such as seasonal changes in climate appeared to have a greater influence on invertebrate numbers. Further, the mixed deciduous leaf litter in the study system decomposed independent of the number of salamanders present in mesocosms. Because food preferences of terrestrial salamanders may have had the greatest influence on the decomposition pathway (Huang et al. 2007), my mechanistic approach of examining stomach contents was imperative to linking salamanders directly to the detrital food web and exploring the pathways that may have been affected by an apex predator in the leaf litter.

Contrary to my predictions and in contrast to Wyman (1998), decomposition rates of leaf litter in mixed oak forest did not differ among mesocosms even with a 3-fold difference in total salamander numbers. Although I cannot determine definitively the causes of these discrepancies, several key factors may have contributed to whether *P. cinereus* altered the rate of litter decomposition among studies. First, I experimentally manipulated salamanders in an area with a diversity of overstory and understory tree species. Because I collected leaf litter adjacent to our mesocosms, our samples contained a mixture of species, but litter was primarily from recalcitrant and slow-decomposing oaks. Wyman's (1998) study site was strongly dominated by beech

(*Fagus spp.*), which has an even slower decay rate than oak litter (Jonard et al. 2008).

Decomposition rates of mixtures of leaf litter differ in unpredictable ways from litter of single species (Gartner and Cardon 2004). I tracked decomposition of mixed species samples of leaf litter in our mesocosms for approximately two years, which was enough time to track significant mass loss from the mixed composition litter through time. Indeed, after two years in litterbags, leaf litter from my experiment had lost 45% of its original dry mass. It is possible that the composition of leaf litter added variation to decomposition rates, and made it difficult to detect differences among salamander treatments.

Secondly, mine was the first investigation into the effects of red-backed salamanders on leaf litter that confirmed treatments by monitoring use of experimental enclosures with individually marked salamanders. By monitoring salamander use of mesocosms through time, I determined that exact treatment densities were difficult to maintain. However, based on my index to surface-active salamanders among treatments, I am confident that there were differences in salamander use between the zero and high treatments. I chose to leave soil layers intact and to leave mesocosms open to allow for more natural nutrient, water, and invertebrate dynamics rather than enclose study animals inside sealed mesocosms. The trade-off was that my experimental units began with an unknown number of salamanders in them, but given the propensity for red-backed salamanders to escape from captive or semi-captive conditions (Heemeyer et al. 2007), I doubt that any changes to mesocosm design would have completely resolved this problem. In short, prior field mesocosm experiments without marked study animals likely faced similar, but unrecognized, difficulties with maintaining salamander treatments. My index to abundance of surface-active salamanders showed that the high treatment was greater than the zero salamander treatment, and prior research has shown abundances of surface-active

salamanders to be linearly related to the true population size (Welsh and Droege 2001, Williams and Berkson 2004, Reichenbach and Sattler 2008). It is possible, however, that my mesocosm design was more permeable to salamander movement than that of Wyman (1998). If this is the case and there was more dispersal out of the high density treatments, then observing the effects of salamanders would have been more difficult.

Instead of salamanders, the effects of time, or seasonality, had a greater effect on the relative abundance of common invertebrates. Across both years of the study, invertebrates, and especially detritivores, were highest during spring and fall, coinciding with the periods of cool temperatures, high rainfall, and lower evapotranspiration in southwestern Virginia. Seasonal dynamics of invertebrate abundances or species diversity is typical (McBrayer et al. 1977, Bird et al. 2000, Rooney et al. 2000). Walton (2005) determined that environmental conditions greatly influenced invertebrates in open field plots. I noted that the mean abundance of detritivores/sampling date tended to decline as the experiment progressed through time (Pearson's $r=-0.23$, $df=21$, $P<0.001$), suggesting that invertebrates may have emigrated outside of litterbags into freshly fallen leaf litter. As litter decomposed, the proportion of lignin would have increased. Thus, after natural inputs of litter in fall 2007, some detritivores may have relocated outside of litterbags to use more nutritious freshly fallen leaves, accounting for declines. Similar declines in invertebrate abundances outside of litterbags through time also were observed in Ohio (Walton 2005).

My results indicated that *Plethodon cinereus* preyed less on predators or litter fragmenters and more on herbivorous larvae than suggested by previous investigators (Wyman 1998, Rooney et al. 2000, Walton and Steckler 2005). In my study, salamanders rarely preyed upon predatory invertebrates (only 36 of 601 consumed invertebrates), which may explain why I

did not detect differences in rates of leaf litter decomposition among salamander treatments. I predicted that salamanders would exert top-down effects on the detrital food web, and by consuming predatory invertebrates, would release and enhance detritivore populations. In my study, the greatest abundance and volume of prey items in salamander stomachs were larvae, suggesting that salamanders preferentially fed on larger soft-bodied invertebrates and avoided more abundant but smaller Acari and Collembola. Based on a simple analysis of preference for invertebrate functional groups, salamanders consumed herbivores (primarily larvae) in a greater proportion than their availability. Across our 528 litterbags sampled (22 months \times 2 litterbags \times 12 mesocosms) and nearly 10,000 invertebrates identified, I detected only 680 larvae (6.8% of total invertebrates) and 0 earthworms, indicating they were uncommon in leaf litter, yet were commonly consumed. Larvae were primarily from fungus gnats, which feed on plant tissue in the top layers of the soil. Red-backed salamanders may feed on herbivores, such as larvae, when they forage on herbaceous plants rather than on leaf litter (Jaeger 1978). Larvae were reported as important food sources for *Plethodon* salamanders in Virginia (Jaeger 1972, Fraser 1976) and Tennessee (Maglia 1996). Thus, salamanders may be important for influencing plant-herbivore relationships outside of the detrital ecosystem and affect above or below-ground herbivory.

Even though I did not detect effects of salamanders on litter decomposition in this study, salamanders could have influenced nutrient availability through pathways other than leaf litter. For example, carcasses and waste products from terrestrial frogs (*Eleutherodactylus coqui*) in Puerto Rico altered nutrient availability in the leaf litter (Beard et al. 2002). Phosphorus concentrations were increased by the presence of Taiwan common toads (*Bufo bankorensis*), but the direct source of the nutrient was not elucidated (Huang et al. 2007). Results from a companion study on the effects of *P. cinereus* on below-ground nutrient processes suggest that

salamanders may have influenced nitrate concentrations below the soil surface (Sucre 2008). Despite not detecting strong influences of terrestrial salamanders on litter decomposition via changes to the invertebrate community, salamanders may still be significant contributors to ecosystem services in forested systems.

Conclusions

The potential cascading effects of human alterations to biological systems on salamanders, invertebrates, and ultimately nutrient cycling are important to understand the consequences of resource extraction on ecosystem services. Elucidating relationships among species within an ecosystem is necessary to establish baselines and to determine whether anthropogenic effects on ecosystem services are occurring and to evaluate potential costs. Because systems are typically a mixture of top-down and bottom-up effects (Ponsard et al. 2000), discerning relationships can be a difficult task. My research suggests that red-backed salamanders are not controlling leaf litter decomposition through the invertebrate food web at least for the species composition of leaf litter that I examined, yet additional investigations into salamander contributions of nitrogen as well as comparisons to more-controlled experiments is necessary to confirm these results. Future work should also examine effects of salamanders on herbivory and herbivore communities and consider that salamander may feed more underground than previously thought.

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Table 5.1. Comparison of invertebrate abundances sampled from leaf litter by treatment (zero, low, or high densities of eastern red-backed salamanders (*Plethodon cinereus*)) or year (year 1, June 2006-May 2007; year 2, June 2007-June 2008) in field mesocosms. Mesocosms were located on the Jefferson National Forest in Montgomery County, Virginia. I conducted a separate Multivariate Analysis of Variance (MANOVA) for each year and only included those taxonomic groups that accounted for >1% of the total invertebrates.

Sampling Year	Source	Degrees of freedom	F-Statistic	P-Value
Year 1	Wilks' Lambda = 0.908	10, 172	0.85	0.577
	Collembola			
	Treatment	2	1.04	0.359
	Time	9	22.32	<0.001
	Treatment X Time	18	0.50	0.954
	Mites			
	Treatment	2	1.12	0.330
	Time	9	4.17	<0.001
	Treatment X Time	18	1.11	0.361
	Ants			
	Treatment	2	0.83	0.437
	Time	9	1.11	0.364
	Treatment X Time	18	1.17	0.301
	Larvae			
	Treatment	2	0.85	0.430
	Time	9	1.90	0.061
	Treatment X Time	18	0.72	0.781
	Spiders			
Treatment	2	0.82	0.445	
Time	9	4.03	<0.001	
Treatment X Time	18	0.73	0.776	
Year 2	Wilks' Lambda=0.938	10, 208	0.68	0.741
	Collembola			
	Treatment	2	1.65	0.197
	Time	11	5.70	<0.001
	Treatment X Time	22	0.78	0.741
	Mites			
	Treatment	2	0.90	0.408
	Time	11	2.00	0.035
	Treatment X Time	22	0.78	0.741
	Ants			
	Treatment	2	0.68	0.509
	Time	11	0.88	0.562
	Treatment X Time	22	1.03	0.432
	Larvae			
	Treatment	2	0.32	0.724
	Time	11	2.87	0.002

Treatment X Time	22	0.85	0.653
Spiders			
Treatment	2	0.02	0.983
Time	11	3.42	<0.001
Treatment X Time	22	0.82	0.699

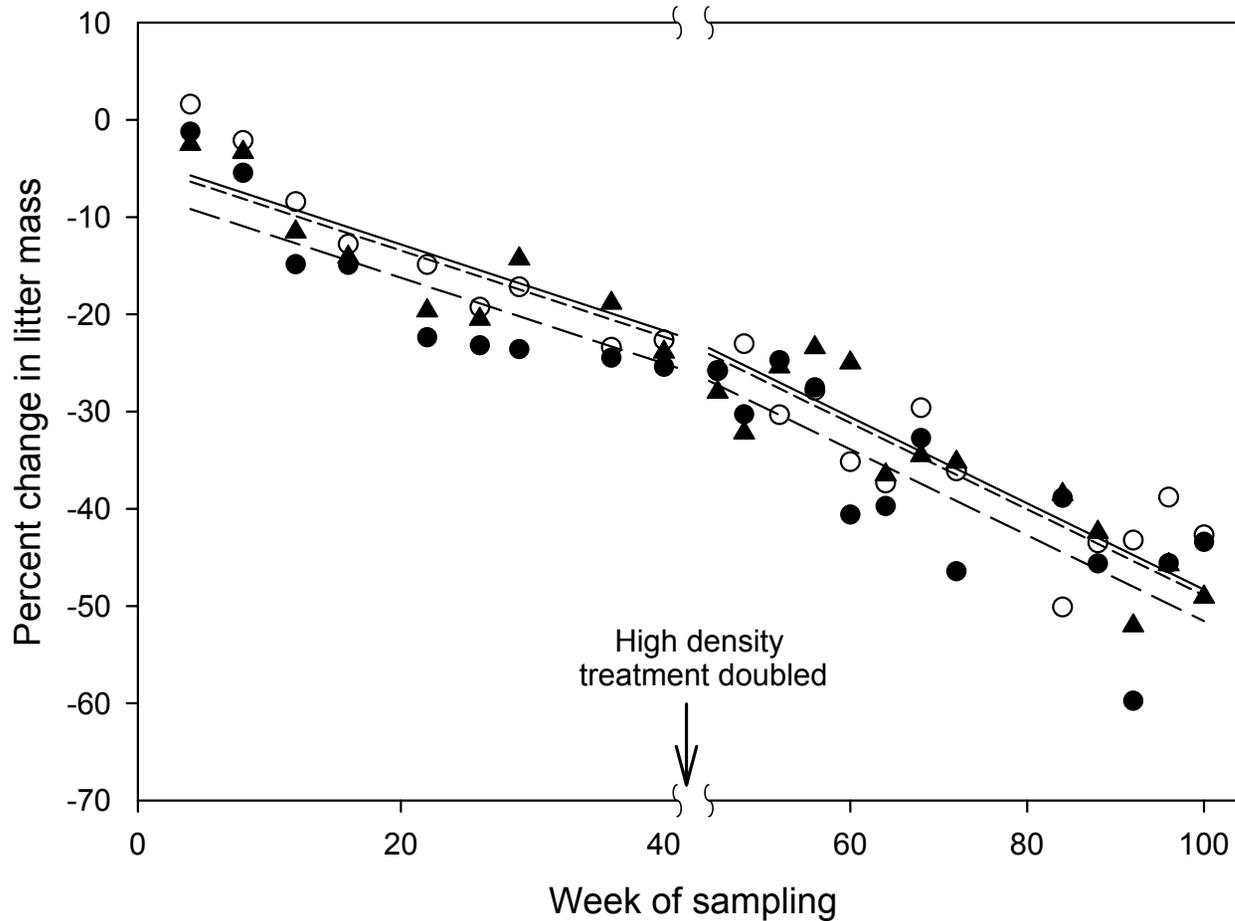


Figure 5.1. Percent change in mass of litter from leaf litterbags in field mesocosms with densities of eastern red-backed salamanders (*Plethodon cinereus*) in 2006-2008. Mesocosms were located on the Jefferson National Forest in Montgomery County, Virginia. During Year 1, the zero density treatment had no salamanders added to mesocosms (○), the low density treatment had 1.0 salamander/m² (●), and the high density treatment had 2.0 salamanders/m² (▲). During the second year of sampling, the number of salamanders in the high density treatment was doubled to 4.0 salamanders/m².

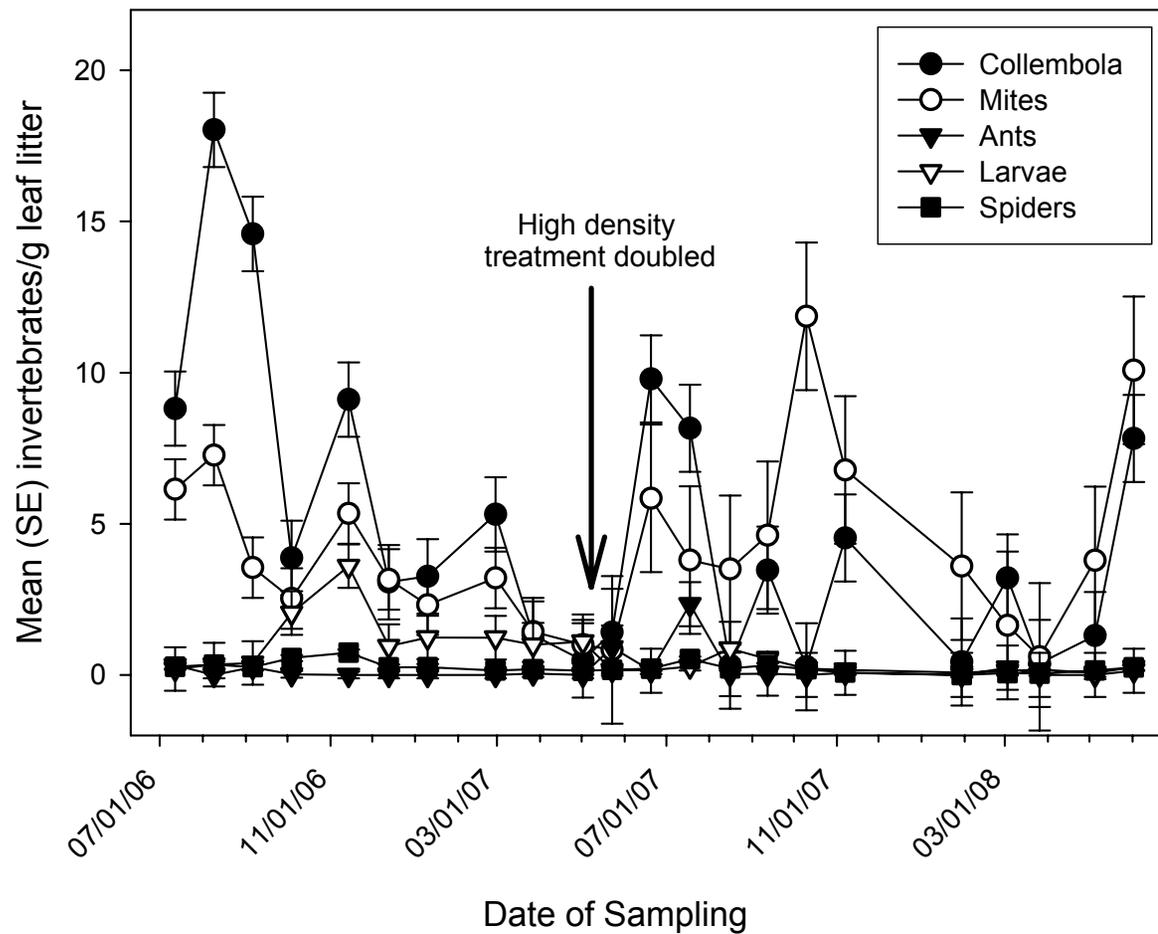


Figure 5.2. Effects of sampling period (time) on mean abundances (SE) of invertebrates/g of leaf litter through time in mesocosms in mixed-oak forest, Montgomery County, Virginia. Means are averaged across salamander treatments, which included densities of 0, 1.0, 2.0 salamanders/m² in year 1 and densities of 0, 1.0, 4.0 salamanders/m² in year 2.

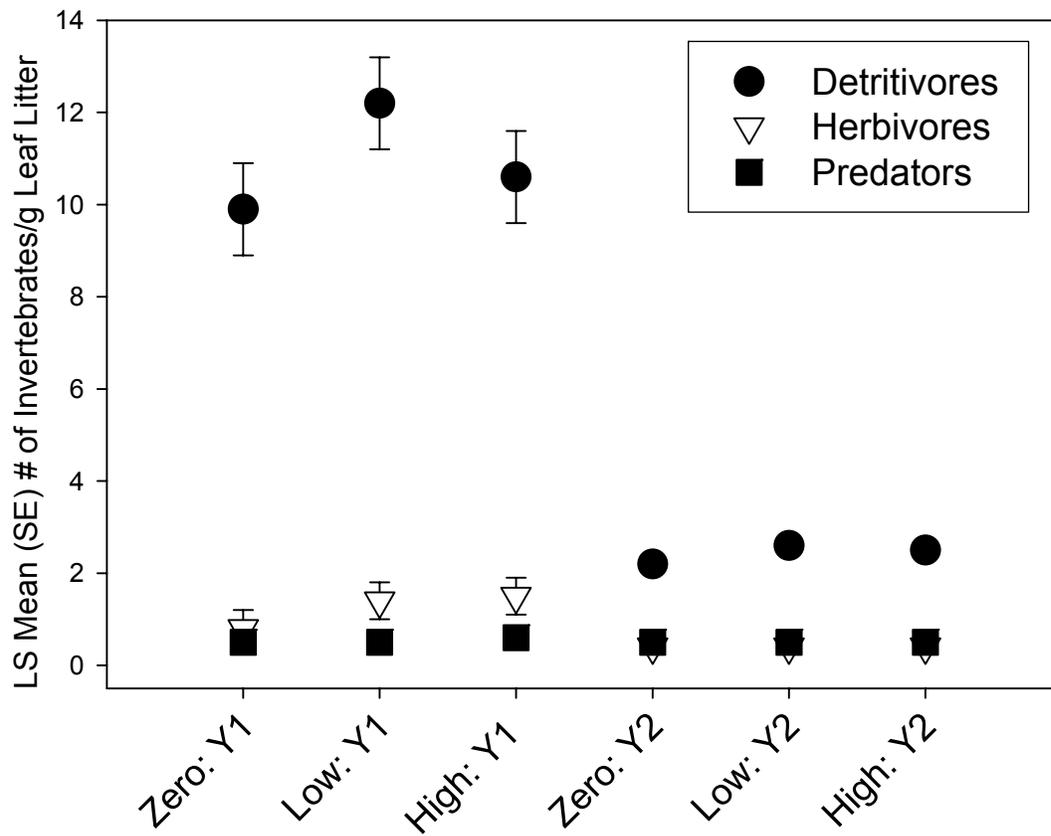


Figure 5.3. Effects of salamander abundance on functional groups of invertebrates in leaf litter in a mesocosm field experiment in southwestern Virginia, June 2006-June 2008. Abundances of detritivores, herbivores, or predators did not differ across salamander treatments (zero, low, or high densities), but the number of detritivores was greater during year 1 of the experiment.

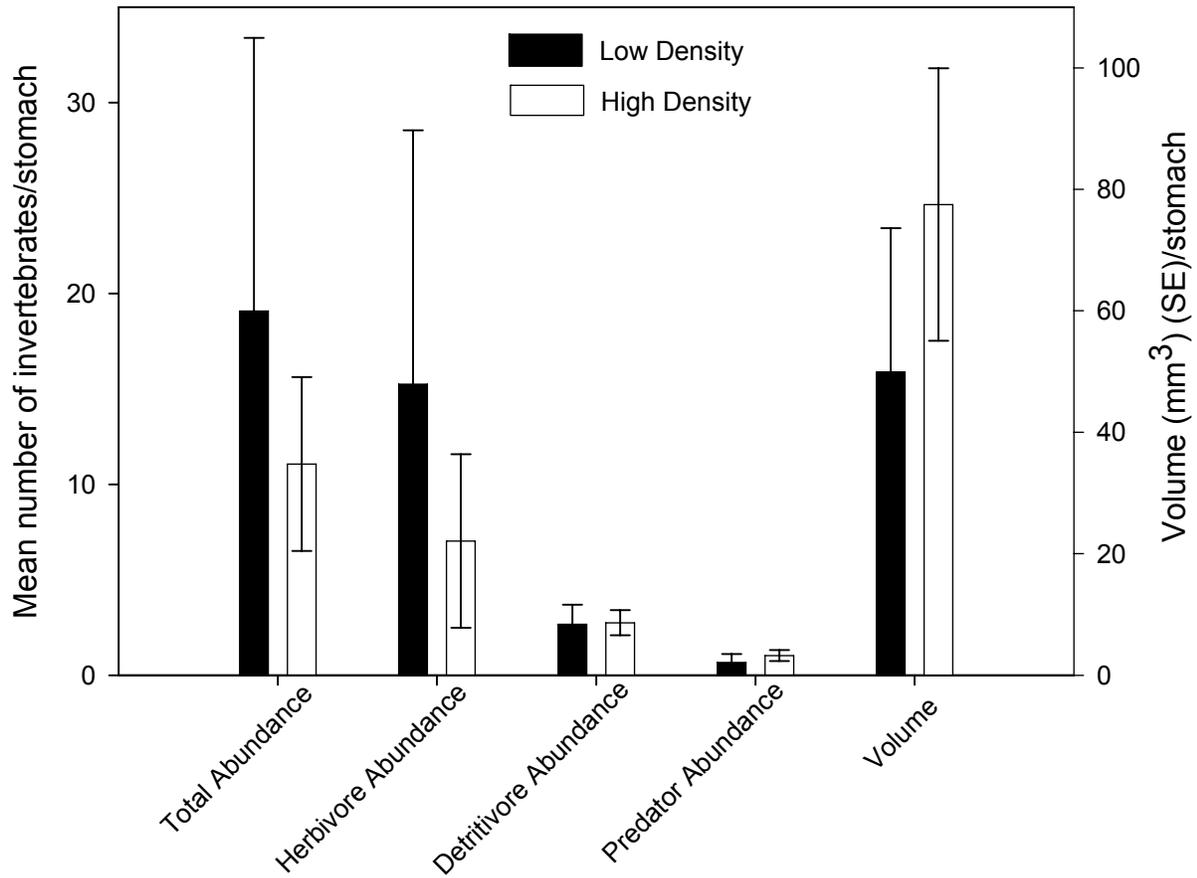


Figure 5.4. Mean numbers of invertebrates (SE)/stomach and volume of invertebrates (SE)/stomach consumed by eastern red-backed salamanders (*Plethodon cinereus*) (n=46 samples from ≥ 29 salamanders) in field mesocosms, in southwestern Virginia, June 2006-June 2008. High density mesocosms had 2 (June 2006-May 2007) or 4 (June 2007-June 2008) times more salamanders experimentally added than low density mesocosms.

CHAPTER 6: HABITAT CHARACTERISTICS OF TERRESTRIAL SALAMANDERS AT MULTIPLE SPATIAL SCALES

Abstract

Terrestrial salamanders have significant ecological roles as predators and prey in forested ecosystems and are known to decline after application of a wide range of forest harvesting techniques. Understanding the habitat relationships of salamanders across spatial scales may identify those forest structural characteristics important to mitigating losses of salamanders or to hastening their recovery after disturbance. I developed a set of candidate models representing biological or environmental hypotheses relating abundances of salamanders to forest structure and evaluated the relative evidence for each with an information-theoretic approach. I quantified the relative abundance of terrestrial salamanders and measured a suite of habitat characteristics at two spatial scales across six study sites in southwestern Virginia and north-central West Virginia, 2007. Study sites included treatment plots that received a range of experimental disturbance, from no treatment through silvicultural clearcut harvesting. Across both of the sub-stand scales examined, the most parsimonious models ($\Delta AIC < 2$) included positive relationships with the numbers of salamanders and amount of basal area of the surrounding stand as well as woody and herbaceous vegetation in the understory. Based on these analyses, terrestrial salamanders in central Appalachian forest responded more to broader-scale habitat conditions, and less to sub-stand-scale metrics. Retaining canopy cover and providing understory vegetation for foraging habitat may be necessary to maintain abundances of salamanders on managed forest landscapes.

Introduction

Given that habitat degradation is considered the primary threat to global biodiversity (Wilcove et al. 1998, Wilson 1999, Cockrem 2005), extensive knowledge of habitat relationships has significant implications for conserving wildlife populations. The study of wildlife habitat relationships developed from researchers qualitatively describing the habitat a species uses to modeling relationships at multiple spatial scales with the goal of predicting abundances (Stauffer 2002). Habitat selection at multiple spatial scales results in the temporal and spatial distribution of species (Tonkovich and Stauffer 1993), so that examining habitat relationships across more than one scale may be useful for understanding effects of anthropogenic activities on wildlife populations. This multi-scale approach is necessary to detect patterns describing how species select habitats, and to increase the value of interpretations of habitat associations (Orians and Wittenberger 1991).

Habitat relationships of wildlife in central Appalachian oak (*Quercus* spp.) forest have received additional attention as of late, in part due to the numerous ecological threats faced by oaks, which serve as a foundation genus in this region (Ellison et al. 2005, McShea et al. 2007). Oaks are the primary mast producers in eastern forests, and provide food and habitat for hundreds of wildlife species, as well as stabilize ecological processes (Ellison et al. 2005, McShea et al. 2007, Belote and Jones 2009). Regeneration of this group of trees is declining from diverse causes such as introduced pathogens and pests, changes to silvicultural practices, fire suppression, and herbivory from white-tailed deer (*Odocoileus virginianus*).

Forests of the central and southern Appalachians, whose overstories often are dominated by oaks, also contain some of the highest diversity of terrestrial salamanders (Petranka 1998). In forested ecosystems, terrestrial salamanders may make up more biomass than other vertebrate groups (Burton and Likens 1975), provide prey for a variety of avian and mammalian predators

(Petranka 1998), and reportedly alter leaf litter dynamics by acting as apex predators of invertebrates (Wyman 1998, Walton 2005, Walton and Steckler 2005, but see Chapter 5). The abundance of most terrestrial salamanders is positively related to components of mature, closed-canopy forest such as abundance of woody debris, a deep layer of leaf litter, and a shaded, cool forest floor (Pough et al. 1987, deMaynadier and Hunter 1995, Ash 1997). Thus, forest practices (e.g., clearcut harvesting) that alter forest structure by opening the canopy and increasing forest floor temperatures typically reduce abundances of salamanders (Petranka et al. 1993, deMaynadier and Hunter 1995, Harpole and Haas 1999, Knapp et al. 2003, Homyack and Haas 2009).

Numerous studies have compared abundances of terrestrial salamanders among forest stands subjected to various silvicultural regimes and documented corresponding changes in stand structure (Pough et al. 1987, Brooks 1999, Harpole and Haas 1999), but fewer have modeled salamander abundances across a range of silvicultural disturbances (but see Mosely et al. 2006). Additionally, little information is available on habitat relationships of salamanders at spatial scales smaller than the forest stand although most plethodontid salamanders maintain home-ranges orders of magnitude smaller than this (home range of *Plethodon cinereus*, 0.2-25.0 m²; *Desmognathus fuscus*, 1.4-114.0 m²; *D. ochrophaeus*, <1 m²) (Kleeberger and Werner 1982, Petranka 1998). From the perspective of terrestrial salamanders, the scale of a forest stand may be perceived as a landscape filled with overlapping territories whereas an area <30 m² would be representative of an average to large-sized home-range. Detecting specific forest structural characteristics associated with salamanders could identify attributes that forest managers could use to mitigate losses or speed recovery of salamander populations and maintain ecosystem processes after forest harvesting. Identifying fine-scaled habitat associations also could be used

to corroborate inferences made from larger spatial scales and recognize those features associated with maintaining salamander populations.

The few predictive models that have related the relative abundance of terrestrial salamanders to habitat and climate variables on a sub-stand scale (e.g., scale of individual home-ranges) described <35% of the variation in abundances (e.g., DeGraaf and Yamasaki 2002, Williams 2003, Kelly 2005). Variation in both the predictor (i.e., habitat variables) and response (i.e., abundances of salamanders) variables likely contributed to relatively low model fit in prior studies. Many researchers have related abundances of animals only to a few habitat characteristics, which may limit the detection of habitat metrics selected for by species (Orians and Wittenberger 1991, DeGraaf and Yamasaki 2002). In addition, methods used to estimate salamander abundances were not always limited to certain times or climatic conditions. Plethodontid salamanders are known to vary activity with climate, season, and time of day (Brooks 1999, Hyde and Simons 2001) so that sampling methods should be standardized as much as possible to reduce variation (DeGraaf and Yamasaki 2002).

To better understand both the spatial scales and specific habitat characteristics to which terrestrial salamanders respond in central Appalachian oak forest, I quantified fine-scaled habitat metrics and relative abundance of terrestrial salamanders across six sites in Virginia and West Virginia. My objective was to consider a suite of hypotheses describing biological features to which salamanders may respond positively, and to evaluate these hypothesized relationships across multiple spatial scales and across a wide range of silvicultural disturbance. I predicted that abundances of terrestrial salamanders would be positively related to metrics describing foraging habitat and salamander refugia.

Study Area

I investigated habitat relationships of terrestrial salamanders on six study sites located either on the Jefferson National Forest, Virginia (n=4) or Mead-Westvaco Corporation's Wildlife and Ecosystem Research Forest (MWERF), West Virginia (n=2). Sites were dominated by moderately productive, mixed-hardwoods and ranged in age from approximately 62-100 years (Hammond 1997). Oak species dominated the overstory of study sites, but sites also contained red maple (*Acer rubrum*), yellow-poplar (*Liriodendron tulipifera*), American beech (*Fagus grandifolia*), Fraser magnolia (*Magnolia fraseri*), sourwood (*Oxydendron arboretum*) and small components of other overstory trees (Wender 2000).

These study sites were part of a larger research project examining the effects of oak regeneration on biodiversity in central Appalachian forest, the Southern Appalachian Silviculture and Biodiversity (SASAB) Project (Chapter 1). The broad goal of SASAB was to evaluate a suite of potential methods to regenerate oak in Appalachian forest. A range of silvicultural systems, ranging from no management, to silvicultural clearcut, was applied randomly to the seven, 2-hectare treatment plots located at each site during 1994-1998. In order of increasing overstory removal, treatments included a control, a midstory removal with herbicide, group selection, high-leave shelterwood, leave-tree harvest, commercial clearcut, and silvicultural clearcut. Additional details about study sites and silvicultural treatments are provided by Knapp et al. (2003), Belote et al. (2008), and Homyack and Haas (2009).

Methods

Salamander abundances

During this study, I quantified habitat characteristics and relative abundances of terrestrial salamanders on sampling grids of 2×15 m transects established within each treatment plot at each study site (Figure 6.1). Each transect was divided into 3, 2×5 m sub-transects. I

quantified relative abundance of salamanders using night-time, area-constrained searches on warm rainy nights, April through August, 2007. For each sampling occasion, I randomly selected one transect from each silvicultural treatment at a site and captured salamanders. Night-time searches were standardized by sampling only during and following rain events when the leaf litter remained moist and when the temperature exceeded 4°C. On nights that met these conditions, two to three observers crawled along transects and hand-captured salamanders active on the surface. Observers placed captured salamanders in individually-marked resealable bags and marked the point of capture for each salamander with an individually-numbered pin-flag. Salamanders were transported to the lab where I identified them to species. Salamanders were returned to their point of capture within 24 hours after processing. When returning salamanders to transects, I recorded which individual salamanders were captured in each sub-transect by counting the individually-numbered pin-flags.

Habitat characteristics

I quantified habitat characteristics on the night-sampling transects at two spatial scales: (1) at the scale of the entire 30 m² transect, and (2) at a smaller, sub-transect scale of 10 m² (Figure 6.1). The 2×15 m transects were spaced >30 m apart, which is > the average daily movement distances (0.43 m) or home ranges of *P. cinereus* (<25 m²) (Kleeberger and Werner 1982). For the smaller nested sub-transect, I randomly selected one of the three available 2×5 m segments as a sampling unit. I considered either transects or sub-transects as independent samples and the unit of replication because it was unlikely that salamanders captured on one transect were observed on another. Because the area of transects was small and approximated the size of a home range for plethodontids, I considered habitat variables quantified within

transects to be at a “sub-stand” scale. Habitat variables quantified at the treatment plot scale were considered to be representative of the surrounding forest matrix, or landscape.

I selected habitat variables to quantify during this study that other investigators have reported as important correlates or predictors of salamander abundance (Pough et al. 1987, deMaynadier and Hunter 1998, Williams 2003, Kelly 2005) or that contribute to the life history of common plethodontid species, such as herbaceous vegetation for foraging (Jaeger 1978). Because my objective was to be able to predict salamander abundances across a wide range of silvicultural disturbance, I included metrics known to be altered by forest harvesting. I quantified depth of the leaf litter, number, volume, and decomposition class of coarse woody debris (CWD), densities of trees and shrubs, and percent cover of leaf litter, vegetation, rocks, moss, bare soil and CWD. Basal area quantified at the larger scale of the 2-ha treatment plot was used as a measure of salamander habitat of the surrounding matrix and the number of overstory trees within transects or subtransects was considered a measure of canopy at a micro-scale. I combined these variables into models representing biological or environmental hypotheses of structural attributes that may be related to abundances of terrestrial salamanders (Table 6.1).

During spring-summer 2007, I measured variables within each 2×5 m sub-transect sub-transect, and summed across them to estimate values within a transect. With the exception of visual estimates of ground cover, I quantified habitat characteristics on transects that were recently sampled for salamanders (generally <30 days after). I visually estimated ground cover <1 month prior to night-sampling because field personnel would have disturbed herbaceous vegetation and leaf litter by crawling across the transects to capture salamanders. I visually estimated the percent cover of leaf litter, herbaceous vegetation, rocks, moss, bare soil, and CWD using the Daubenmire cover classes (i.e., <5%, 5-25%, 25-50%, 50-75%, 75-95%, 95-

100%) and used midpoints for analysis (Daubenmire 1959). I quantified the density of trees (≥ 7.6 cm diameter at breast height, ≥ 1.5 m height, $>45^\circ$ from the ground) within plots. I measured the depth of leaf litter to the Oi horizon at 0.5 m from the center of each sub-transect in each direction (total of 6 measurements for entire transect) with a ruler held perpendicularly to the surface of the ground. To reduce confounding effects of moisture conditions compacting leaf litter, I measured leaf litter when >3 days had passed since the last rainfall (Marsh and Beckman 2004). To quantify coarse woody debris, I counted the number of root masses (≥ 7.6 cm diameter), stumps (<2 m height, ≥ 7.6 cm diameter), and logs (≥ 7.6 cm diameter, in contact with ground) within each plot and noted their decomposition class (classes 1-5 as described by Maser et al. 1979). I quantified the volume of logs by measuring diameters at both ends and the length of the log and converted it into a volume by using the formula for the volume of a cone. I measured the volume of logs within a transect and excluded portion of the logs outside of transect boundaries. I calculated the volume of stumps and root masses by measuring height and the mid-point diameter and used the formula for a cylinder. I quantified understory woody vegetation by counting the number of woody stems (>0.5 m height, <7.6 cm dbh) within a plot. Basal area was measured in three 24 m by 24 m tree plots within each treatment plot by C. Atwood, Department of Forestry, Virginia Tech (Atwood 2008).

Analyses and modeling

I developed a suite of a priori models to describe abundances of salamanders with fine-scaled habitat measurements (Table 6.1). The candidate model set contained habitat metrics that described forest structure related to foraging, refugia and nest sites, retention of ground-level moisture, and combinations of the three factors (Table 6.1). I also included a global model and a model that related salamander abundances to the basal area of the surrounding matrix (i.e., 2-ha

treatment plot). The basal area model represented the hypothesis that salamanders responded to large-scale habitat characteristics rather than the micro-scale metrics that I measured.

I considered each model a competing hypothesis (Chamberlain 1897) and evaluated the relative strength of each hypothesis (model) given the observed data. I used an information-theoretic approach and Akaike's Information Criteria (AIC) to evaluate which model had the best balance between goodness-of-fit and statistical parsimony (Burnham and Anderson 2002). I used simple and multiple linear regression with number of salamanders per transect or sub-transect as the response variable and habitat characteristics as predictors. I applied my suite of models to abundances and habitat quantified separately at the scale of the 30 m² transect and the 10 m² nested sub-transect to assess whether salamanders responded to different metrics at the two spatial scales. For sub-transects, I randomly selected one of the three available for each transect to develop my dataset. I examined normality of residuals with normal probability plots. I compared the relative strength of each model with AIC, model weights (w_i), and R^2 values. I used SAS 9.2 (SAS Institute, Cary, North Carolina, USA) for all analyses.

Results

During spring-fall 2007 I quantified both habitat and abundances of salamanders on 155 transects across the 6 study sites. Abundances of salamanders ranged from 0-22 per transect and I captured a total of 653 salamanders across the 155 transects. Fourteen percent of transects had zero captures. Salamander captures were dominated by eastern red-backed salamanders (*Plethodon cinereus*) (35%), Allegheny mountain dusky salamanders (*Desmognathus ochrophaeus*) (26%), slimy salamanders (*Plethodon cylindraceus*, *Plethodon glutinosus*) (21%), and ravine salamanders (*Plethodon richmondi*) (14%) (Table 6.2). At the smaller scale, abundances ranged from 0-10 per sub-transect, and I captured 243 salamanders across the 155

sub-transects. Forty-five percent of sub-transects had zero captures of salamanders. Similar to the transect-scale, eastern red-backed salamanders (35%), Allegheny mountain dusky salamanders (25%), and slimy salamanders (21%) were the three most dominant species at this scale (Table 6.2).

Of the a priori developed candidate model set, OVERHEAD CANOPY CONDITIONS + FORAGING best described abundances of terrestrial salamanders at the scale of the 30 m² transect ($\Delta AIC=0$, $w_i=0.58$) (Table 6.4). This model positively associated abundances of salamanders with basal area and the percent of herbaceous cover and negatively associated salamander abundances with the depth of leaf litter (Table 6.5). In addition, the second best model, LARGE-SCALE HABITAT CONDITIONS, also received support ($\Delta AIC=1.40$, $w_i=0.29$), but the weight of evidence was strongly in favor of OVERHEAD CANOPY CONDITIONS + FORAGING ($w_{\text{OVERHEAD CANOPY CONDITIONS + FORAGING}}/w_{\text{LARGE-SCALE HABITAT CONDITIONS}}=2.0$). Finally, OVERHEAD CANOPY CONDITIONS did receive some empirical support ($w_i=0.11$), but all other models had $\Delta AIC>7$, indicating that these combinations of parameters were poor predictors of salamander abundances in this study system (Table 6.4).

For sub-transects, the model with the greatest weight of evidence for predicting salamander abundances was LARGE-SCALE HABITAT CONDITIONS ($\Delta AIC=0$, $w_i=0.59$), which indicated that increasing basal area was positively associated with increasing abundances of salamanders at the sub-transect scale (Table 6.7). Other models receiving support included OVERHEAD CANOPY CONDITIONS ($\Delta AIC=1.98$, $w_i=0.22$) and OVERHEAD CANOPY CONDITIONS + FORAGING ($\Delta AIC=2.38$, $w_i=0.18$) (Table 6.6). The OVERHEAD CANOPY CONDITIONS model indicated that salamander abundances at the 10 m² scale were positively associated with both basal area and density of woody understory vegetation. Based on the

OVERHEAD CANOPY CONDITIONS + FORAGING model, salamanders increased abundances with increasing levels of basal area, density of woody understory vegetation, and amount of herbaceous vegetation, and with decreasing leaf litter depth.

Discussion

Modeling of salamander abundances with habitat variables at two spatial scales suggested that characteristics describing the forest overstory and foraging structure had the best balance between predictive power and parsimony. At both spatial scales, my modeling efforts indicated that as the amount of basal area increased, abundances of salamanders increased. Habitat relationships generally were consistent between the 30 m² and 10 m² plots, suggesting that terrestrial salamanders may respond similarly to canopy disturbances at multiple spatial scales.

Consistent with prior modeling efforts of salamander habitat relationships in West Virginia and New England (DeGraaf and Yamasaki 2002, Lowe and Bolger 2002, Williams 2003, Moseley et al. 2008), up to 30% of the variation in salamander abundances was described by habitat characteristics (Table 6.4, Table 6.6). Based on the R² values, my suite of *a priori* developed models performed better at the larger spatial scale (0.02-0.30 vs. 0.02-0.22), yet both modeling efforts fell within the range of variation explained by other researchers. In another multi-scale study in West Virginia, greater variation in abundance of *Desmognathus* salamanders was explained at the larger scale (forest stand, 27%; stream reach, 12%), suggesting that despite limited movement capabilities, plethodontid salamanders may respond to broader habitat structure (Moseley et al. 2008). Abundance and distribution of salamanders in Great Smoky Mountains National Park also were better described by large-scale habitat characteristics (e.g., disturbance history, elevation) than by microhabitat variables (Hyde and Simons 2001).

The most parsimonious models describing salamanders at both spatial scales included basal area as a variable, and in all cases the relationship between salamander abundances and basal area was positive. Thus, a dense, closed canopy was one of the most important variables for salamanders across our broad study area and across two fine-scales. Certainly canopy trees themselves were not what salamanders responded to, but rather were a surrogate for another metric, or were a general descriptor of mature forest. A developed canopy layer mediates changes to microclimate, helps to retain moisture of the forest floor, and provides shade and litter for foraging habitats (Rothermel and Luhring 2005, Reichenbach and Sattler 2007), all of which may contribute to positive energy balance or increased survival of salamanders (Harpole and Haas 1999, Rothermel and Luhring 2005, Chapter 4).

In addition to a dense canopy, I detected positive relationships between salamanders and density of understory woody stems, which I hypothesized to be an important component of foraging habitat. During nights when moisture is great enough to support above-ground movements, salamanders forage in the leaf litter and climb understory vegetation where foraging success may be higher (Jaeger 1978). A structurally diverse understory layer also may support a greater abundance or diversity of invertebrate prey above the ground, so that understory vegetation may contribute to greater foraging success, more salamanders in a positive energy balance and, ultimately greater abundances of salamanders (see Chapter 4 for discussion). In a related mesocosm experiment, salamanders preyed mostly upon herbivorous larvae, which may have been more abundant or accessible on understory vegetation (Jaeger 1978, Chapter 5). In hardwood forest in New England (Brooks 1999) and New York (Pough et al. 1987), red-backed salamanders were positively associated with woody or herbaceous understory vegetation. In contrast, Kelly (2005) who quantified habitat structure near the West Virginia 1 and West

Virginia 2 SASAB sites, reported a negative relationship between terrestrial salamander abundances and woody understory stems, but acknowledged that across her sites, high cover from understory stems tended to occur in recently harvested stands. Thus, negative effects from forest harvesting likely obscured other habitat relationships in that study.

Deep, high quality leaf litter is thought to be an integral part of salamander habitat, and renewal of the litter layer after forest harvesting is considered necessary for recovery of salamander populations (Pough et al. 1987, deMaynadier and Hunter 1995, Ash 1997). A well-developed layer of leaf litter on the forest floor provides invertebrate prey and moisture; therefore, I hypothesized that leaf litter would be an important predictor, and like prior research, would have a positive relationship with salamander abundances (reviewed by deMaynadier and Hunter 1995, Kelly 2005). Contrary to my prediction and for reasons that remain unclear, I detected a negative association of salamanders with the depth of the leaf litter (Table 6.4, 6.6). I speculate that a negative relationship was observed because 9-13 years had elapsed since study sites were harvested when litter depth was sampled. The mean litter depth of transects in clearcut EUs (\bar{X} =4.6 cm) was slightly greater than litter depth in the control EUs (\bar{X} =3.8 cm) (Table 6.8), suggesting that the litter layer had recovered in silvicultural treatments at the time of this study.

Modeling habitat relationships of salamanders, like most studies of free-ranging animals, is made more difficult by the variation in estimating abundances, the response variable (Zar 1996, Stauffer 2002). I attempted to increase precision of abundances estimates of salamander abundances by standardizing when I sampled by weather conditions and time of year, which may affect the proportion of salamanders active on the surface (Hyde and Simons 2001, Bailey et al. 2004a). I anticipated that using relative abundances of salamanders quantified by night-time,

area-constrained searches as my response variable would improve the overall fit of habitat models as compared to past modeling attempts, but based on R^2 values, this did not occur. However, the precision of these estimates of abundance may have been better as compared to searching cover objects with no weather restrictions, which prior studies have done (DeGraaf and Yamasaki 2002, Williams 2003, Kelly 2005, Moseley et al. 2008). In addition, I anticipated that quantifying habitat characteristics across the wide range of silvicultural treatments on the SASAB study sites would aid in detecting habitat relationships. For this habitat modeling, I assumed that sites with greater abundances of salamanders reflected sites with greater habitat quality (Cline et al 1991, Morris 2003) and I assumed that surface counts of salamanders were linearly and positively related to total population sizes (surface + subsurface individuals) (Welsh and Droege 2001, Bailey et al. 2004b, Reichenbach and Sattler 2007).

Conclusions

Maintenance of wildlife populations, including terrestrial salamanders, can be compatible with forest harvesting with some alteration (deMaynadier and Hunter 1995, Brooks 1999). However, understanding the specific structural attributes associated with abundances is necessary to ensure that forest harvesting does not have detrimental effects on salamanders. This research suggests retention of canopy trees and a structurally diverse understory may be important attributes influencing abundances of salamanders at small spatial scales in central Appalachian oak forest. Other research on the SASAB study sites indicates that even small disturbances to the canopy have negative impacts on salamander abundances (Knapp et al. 2003, Homyack and Haas 2009), but that salamanders in less intensively managed stands (e.g., group selection harvests) may experience shorter-term negative effects (Homyack and Haas 2009). At first thought, this would seem to suggest that forest managers should minimize disturbances and

retain canopy trees throughout a rotation (Brooks 1999). In practice, however, less-intensive forest management typically entails multiple entries within a rotation, which may have cumulative negative effects to salamanders (Knapp et al., 2003, Chapter 3), increased soil erosion (Hood et al. 2002), and less regeneration of oaks (Atwood et al. 2009), all of which must be considered by forest managers.

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Table. 6.1. Candidate model set developed to evaluate biological and environmental hypotheses regarding habitat characteristics to which terrestrial salamanders respond at multiple spatial scales.

Hypothesis	Variables included in model
FORAGING	Leaf litter depth, density of woody understory stems, percent cover of herbaceous vegetation
REFUGIA	Volume of woody debris, number of highly decayed logs (decay class 3-5 ^a), percent cover of rock
FORAGING + REFUGIA	Leaf litter depth, density of understory stems, volume of woody debris, number of highly decayed logs (decay class 3-5 ^a), percent rock
SURROUNDING GROUND COVER	Percent cover of leaf litter, rock, bare ground, moss, herbaceous vegetation, coarse woody debris
OVERHEAD CANOPY CONDITIONS	Basal area of matrix surrounding transect (2-ha plot), density of woody understory stems
OVERHEAD CANOPY CONDITIONS + FORAGING	Basal area of matrix surrounding transect (2-ha plot), density of woody understory stems, leaf litter depth, percent cover of herbaceous vegetation
LOCAL-SCALE CANOPY	Abundance of trees (>7.6 cm dbh)
LARGE-SCALE HABITAT CONDITIONS	Basal area of matrix surrounding transect (2-ha plot)
GLOBAL MODEL	All variables

^aDecay classes as described by Maser et al. 1979,

Table 6.2. Salamander captures by species in 2×15 m salamander sampling transects and 2×5 m sub-transects. Salamanders were sampled with night-time area-constrained searches at 6 study sites in southwestern Virginia and north-central West Virginia, April-August, 2007.

Species	Percent of total (number of captures)	
	Entire transect scale	Sub-transect scale
Eastern red-backed salamander (<i>Plethodon cinereus</i>)	34.9 (228)	35.4 (86)
Allegheny mountain dusky salamander (<i>Desmognathus ochrophaeus</i>)	26.4 (172)	24.7 (55)
Slimy salamander (<i>Plethodon glutinosus</i> , <i>Plethodon cylindraceus</i>)	20.7 (135)	20.6 (50)
Ravine salamander (<i>Plethodon richmondi</i>)	13.9 (91)	14.4 (35)
Northern dusky salamander (<i>Desmognathus fuscus</i>)	1.7 (11)	2.5 (6)
Southern two-lined salamander (<i>Eurycea cirrigera</i>)	1.1 (7)	1.65 (4)
Wehrle's salamander (<i>Plethodon wehrlei</i>)	0.8 (5)	0.8 (2)
Northern spring salamander (<i>Gyrinophilus porphyriticus</i>)	0.3 (2)	0 (0)
Green salamander (<i>Aneides aeneus</i>)	0.2 (1)	0 (0)
Four-toed salamander (<i>Hemidactylium scutatum</i>)	0.2 (1)	0 (0)

Table 6.3. Means and range of habitat variables measured on 155 salamander sampling transects at two spatial scales and across a range of silvicultural treatments in southwestern Virginia and north-central West Virginia, 2007. Occupied transects had captures of terrestrial salamanders during night-time area-constrained searches and unoccupied transects did not.

Variable	Scale of sampling							
	<u>2×15 m transect</u>				<u>2×5 m sub-transect</u>			
	Occupied (n=134)		Unoccupied (n=21)		Occupied (n=89)		Unoccupied (n=66)	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Litter depth (cm)	4.0	0.7-11.5	5.4	1.8-12.4	3.6	0.1-17.4	5.1	0.25-19.3
Number of woody understory stems/plot	31.3	0-144	45.1	2-114	9.9	0-50	12.7	0-51
Number of trees >7.6 cm dbh/plot	1.4	0-5	1.1	0-6	0.4	0-2	0.5	0-5
Number of pieces of woody debris/plot	6.2	0-24	7.1	1-13	2.3	0-9	1.9	0-8
Number of logs/plot in decay class 3-5 ^a	5.2	0-24	5.5	0-10	2.0	0-9	1.7	0-7
Volume of woody debris/plot (m ³)	2.7	0-73.0	7.3	0.0-43.7	0.6	0-10.9	1.5	0-24.2
Basal area (m ² /ha)	18.5	0-43.1	10.3	0-43.1	20.6	0-43.1	12.8	0-43.1
% herbaceous cover	9.8	2.5-54.2	5.8	2.5-38.3	10.2	2.5-62.5	7.2	2.5-62.5
% litter cover	72.9	22.5-97.5	75.8	22.5-89.17	73.1	15.0-97.5	74.1	15.0-97.5
% rock	6.0	2.5-54.2	6.8	2.5-77.5	4.8	2.5-37.5	7.1	2.5-85.0
% moss	2.8	2.5-10.8	2.7	2.5-6.67	2.6	2.5-15.0	2.7	2.5-15.0
% bare ground	5.3	2.5-54.2	5.5	2.5-22.5	6.3	2.5-62.5	5.6	2.5-37.5
% woody debris	10.4	2.5-45.8	9.1	2.5-25.8	10.2	2.5-37.5	9.3	2.5-62.5

^aDecay classes as described by Maser et al. 1979.

Table 6.4. Relative strength of evidence to support hypothesized relationships between abundances of terrestrial salamanders and forest structural characteristics at the scale of the 2 × 15 m salamander sampling transect (n=155). Salamanders and forest structure were sampled at 6 study sites in southwestern Virginia and north-central West Virginia, 2007.

Model	Number of Parameters	R ²	AIC	ΔAIC	Model Weight (w_i)
OVERHEAD CANOPY CONDITIONS + FORAGING	6	0.29	188.86	0	0.58
LARGE-SCALE HABITAT CONDITIONS	3	0.20	190.26	1.40	0.29
OVERHEAD CANOPY CONDITIONS	4	0.20	192.18	3.32	0.11
FORAGING	5	0.05	196.55	7.79	0.01
LOCAL-SCALE CANOPY	3	0.02	199.18	10.32	0.00
GLOBAL MODEL	13	0.30	201.18	12.32	0.00
FORAGING+REFUGIA	8	0.18	201.93	13.07	0.00
REFUGIA	5	0.04	206.66	17.94	0.00
SURROUNDING GROUND COVER	8	0.12	215.61	26.75	0.00

Table 6.5. Parameter estimates from linear regression models relating abundances of terrestrial salamanders to forest structural characteristics at a 30 m² scale (n=155) with the best empirical support given the data (Akaike's Information Criteria <2). Abundances of salamanders and habitat characteristics were quantified in mixed-oak forest on 6 study sites in southwestern Virginia and north-central West Virginia, April-August 2007.

Model	β	S.E.	R ²	Relationship
OVERHEAD CANOPY CONDITIONS + FORAGING			0.29	
Intercept	2.724	1.039		
Basal area	0.146	0.030		+
Understory density	0.003	0.014		+
Leaf litter depth	-0.410	0.147		-
Percent herbaceous Cover	0.061	0.029		+
LARGE-SCALE HABITAT CONDITIONS			0.20	
Intercept	1.435	0.536		
Basal area	0.158	0.025		+

Table 6.6. Relative strength of evidence to support hypothesized relationships between abundances of terrestrial salamanders and forest structural characteristics on randomly selected 2 × 5 m subplots on salamander sampling transects (n=155). Salamanders and forest structure were sampled at 6 study sites in southwestern Virginia and north-central West Virginia, 2007.

Model	Number of Parameters	R ²	AIC	ΔAIC	Model Weight (w_i)
LARGE-SCALE HABITAT CONDITIONS	3	0.15	84.51	0.00	0.59
OVERHEAD CANOPY CONDITIONS	4	0.15	86.49	1.98	0.22
OVERHEAD CANOPY CONDITIONS + FORAGING	6	0.19	86.89	2.38	0.18
FORAGING	5	0.06	94.75	10.24	0.00
REFUGIA	5	0.02	97.70	13.19	0.00
FORAGING+REFUGIA	8	0.07	99.84	15.32	0.00
SURROUNDING GROUND COVER	8	0.03	103.00	18.49	0.00
GLOBAL MODEL	13	0.22	104.51	20.00	0.00

Table 6.7. Parameter estimates from linear regression models relating abundances of terrestrial salamanders to forest structural characteristics at a 10 m² scale (n=155) with the best empirical support given the data (Akaike's Information Criteria <2). Abundances of salamanders and habitat characteristics were quantified in mixed-oak forest on 6 study sites in southwestern Virginia and north-central West Virginia, April-August 2007.

Model	β	S.E.	R ²	Relationship
LARGE-SCALE HABITAT CONDITIONS			0.15	
Intercept	0.421	0.246		
Basal area	0.059	0.011		+
OVERHEAD CANOPY CONDITIONS			0.15	
Intercept	0.371	0.359		
Basal area	0.060	0.013		+
Understory density	0.003	0.015		+

Table 6.8. Mean (SE) values of forest structural characteristics were sampled across 7 silvicultural treatments at 6 study sites in southwestern Virginia and north-central West Virginia, 2007. Forest structure was sampled at the scale of the 2 by 15 m transect.

Variable	<u>Silvicultural treatment</u>						
	Control	Midstory removal	Group selection	Shelterwood	Leave tree	Commercial clearcut	Silvicultural clearcut
Litter depth (cm)	3.8 (0.3)	3.8 (0.3)	4.7 (0.5)	4.2 (0.5)	4.3 (0.3)	4.2 (0.8)	4.6 (0.5)
Number of woody understory stems/plot	8.8 (1.4)	10.9 (2.6)	26.2 (4.5)	43.9 (4.4)	52.0 (6.7)	49.6 (8.1)	42.8 (3.8)
Number of trees >7.6 cm dbh/plot	1.7 (0.3)	1.6 (0.3)	1.3 (0.3)	1.0 (0.2)	1.0 (0.3)	1.1 (0.2)	1.6 (0.3)
Number of pieces of woody debris/plot	3.3 (0.4)	3.8 (0.6)	6.3 (0.7)	8.2 (1.1)	6.6 (0.6)	7.8 (1.0)	8.4 (0.9)
Number of logs/plot in decay class 3-5 ^a	2.8 (0.4)	3.1 (0.6)	5.1 (0.7)	6.6 (1.1)	5.6 (0.6)	6.2 (0.9)	7.3 (0.8)
Volume of woody debris/plot	1.7 (1.0)	2.1 (1.0)	3.3 (1.9)	5.9 (3.6)	3.1 (1.4)	3.3 (1.7)	4.3 (1.9)
Basal area (m ² /ha)	31.7 (1.5)	33.6 (0.9)	20.2 (1.1)	15.4 (1.7)	9.8 (1.8)	9.7 (1.0)	1.9 (0.4)
% herbaceous cover	8.9 (2.3)	10.7 (2.7)	10.2 (2.4)	8.6 (2.6)	11.5 (2.8)	9.7 (2.1)	5.6 (1.1)
% litter cover	78.2 (2.9)	81.7 (2.6)	75.7 (2.3)	69.8 (2.9)	72.9 (3.6)	67.1 (3.6)	68.0 (3.8)
% rock	7.1 (1.9)	2.8 (0.2)	3.4 (0.6)	8.3 (2.8)	5.0 (1.0)	5.0 (1.9)	10.3 (3.6)
% moss	2.7 (0.2)	3.2 (0.4)	2.5 (0)	2.9 (0.3)	2.5 (0)	2.9 (0.4)	2.9 (0.2)
% bare ground	4.9 (1.2)	4.0 (0.7)	5.0 (0.9)	4.4 (0.7)	5.4 (0.8)	5.9 (1.5)	7.7 (2.3)
% woody debris	6.3 (0.8)	7.4 (0.9)	9.3 (1.0)	12.7 (2.2)	11.4 (1.1)	12.0 (2.0)	12.6 (1.6)

^aDecay classes as described by Maser et al. 1979.

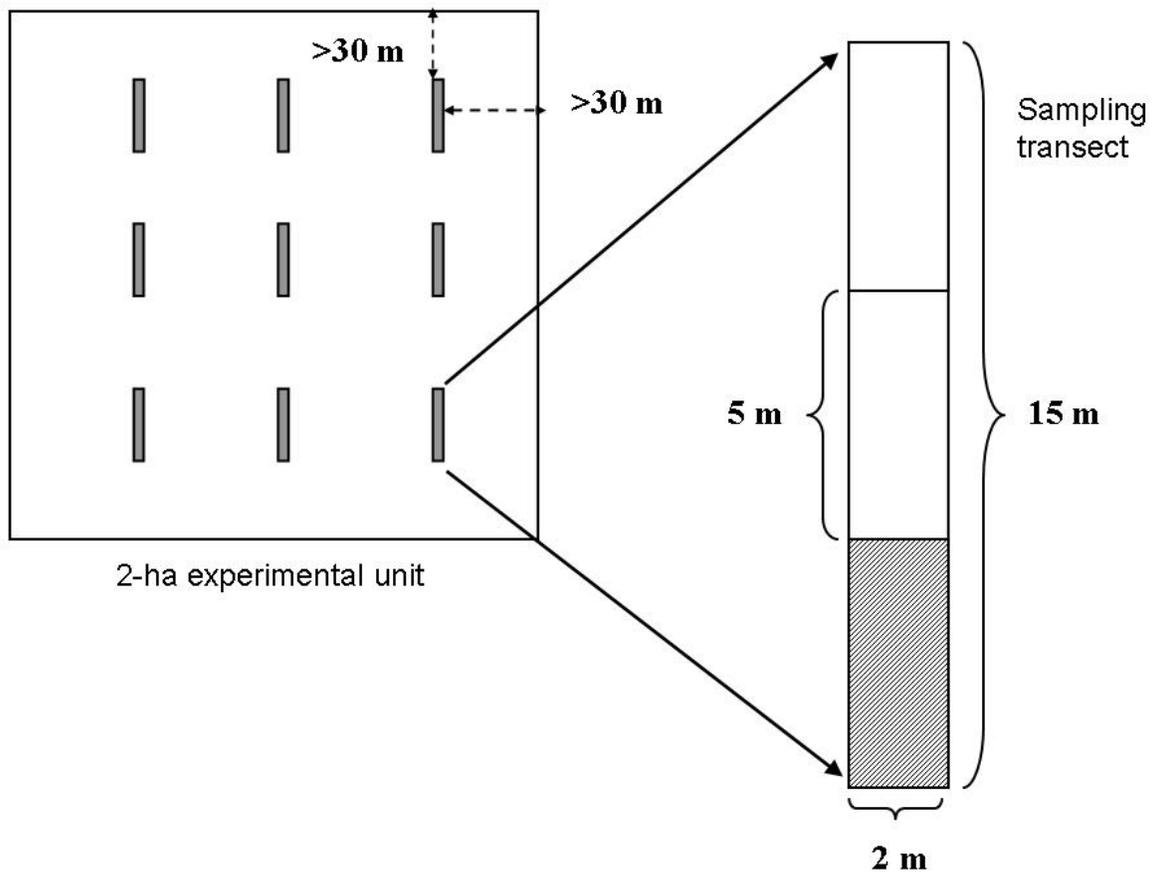


Figure 6.1. Habitat relationships of terrestrial salamanders were modeled at 2 spatial scales in the central Appalachian oak forests of Virginia and West Virginia. Both habitat characteristics and relative abundances of salamanders were quantified at (1) the scale of a $2 \times 15\text{ m}$ transect (entire area shown), and (2) within a nested $2 \times 5\text{ m}$ sub-transect (hatched area).

CHAPTER 7: CONCLUSIONS AND FUTURE DIRECTIONS

In agreement with Leopold's Group B mentality (Leopold 1949), managers of our nation's forests must consider the multiple and often conflicting goals of ensuring actions are economically, socially and environmentally sustainable. To provide information relevant to natural resource managers regarding how oak regeneration treatments influence biodiversity and sustainability in central Appalachia, Virginia Tech and other cooperators developed the Southern Appalachian Silviculture and Biodiversity (SASAB) project.

Although terrestrial salamanders have been studied extensively in eastern forests, many questions regarding long-term effects of silvicultural disturbances on population dynamics and habitat relationships remain. With this dissertation, I documented the long-term effects of a wide gradient of silvicultural practices on terrestrial salamanders in central Appalachian hardwood forest. In Chapter 2, I investigated the effects of forest harvesting on salamanders to 13-years after treatment and used population modeling to estimate a recovery period for eastern red-backed salamanders (*Plethodon cinereus*) after silvicultural disturbance. Relative abundances of terrestrial salamanders in treatments with canopy disturbance (group selection through silvicultural clearcut) remained depressed relative to control experimental units (EUs) through 13-years of post-harvest sampling. At years 8-9 post-harvest, those treatments with canopy disturbance had 33-70% of the pre-harvest salamander abundances, but the control and herbicide EUs had salamander abundances >during the pretreatment period. Forest harvesting affected habitat quality for at least some species of salamanders based on estimates of the number of eggs/gravid female and the proportion of juvenile salamanders. Finally, population recovery of all stage classes of red-backed salamanders may require at least 60 years to grow to preharvest

abundances. For this species, adult survival had the greatest influence on the population growth rate.

Next, I investigated whether a second harvest in the shelterwood EUs (see Chapter 1 for a description) would have cumulative negative effects on terrestrial salamanders and described the resulting habitat conditions (Chapter 3). Both the Blacksburg 1 and Blacksburg 2 study sites were harvested in 1995 and 1996, respectively. During the winter of 2007-2008, the remaining overstory trees were felled to release the advanced regeneration after 12-13 growing seasons. At the Blacksburg 1 site, salamander numbers in the shelterwood EUs declined after both the first stand entry and the second overstory removal. At Blacksburg 2, I was unable to detect a difference in salamander numbers in the shelterwood EUs after either harvest. Forest structure in the shelterwood EUs after the overstory removal differed from structure in the control EUs, with abundance and volume of woody debris greater in shelterwood EUs and depth of the leaf litter greater in control EUs. To my knowledge, no other researcher has evaluated effects of multiple stand entries on salamander populations. Although limited by only having two experimentally manipulated study sites, these results suggest that shelterwood systems may have cumulative negative effects on terrestrial salamanders.

The negative effects of forest harvesting have been well-described and correlated with changes to habitat, but specific mechanisms of both the initial decline and slow recovery period of plethodontid salamanders have not been elucidated. In Chapter 4, I quantified changes to bioenergetics of plethodontid salamanders during the growing season following and 11-13 years after forest harvesting at four of the SASAB study sites. With a concurrent laboratory study, I estimated the standard metabolic rate of red-backed salamanders across the range of temperatures I observed in the field. Across three active seasons for salamanders (May-

October), I quantified temperature regimes at the forest floor, estimated available invertebrate prey, and compared body condition of salamanders across a silvicultural disturbance gradient. Red-backed salamanders required 33% more total energy for basic maintenance directly after silvicultural disturbance, but at 8-14 years after forest harvest there was no difference in energetic requirements across the disturbance gradient. Invertebrate abundances did not differ across the disturbance gradient even after a recent disturbance. Thus, the additional energy required by salamanders for basic maintenance may have caused salamanders to allocate a smaller portion of their energy budgets to either growth or reproduction, and could help explain the initial decline of salamander populations after harvesting or lower reproductive demography values in harvested forest.

Given that forest harvesting has negative effects on abundances of salamanders, there is a need to understand how forested systems may function with fewer salamanders. In Chapter 5, I describe a field experiment where I manipulated densities of eastern red-backed salamanders in 12 *in situ* mesocosms. From June 2006-June 2008, I quantified invertebrate abundances, decomposition of leaf litter, and the stomach contents of salamanders across a zero salamander, low salamander (1.0 salamander/m²), or high salamander (2.0 salamanders/m² in 2006-2007, 4.0 salamanders/m² in 2006-2007) treatments. Abundances of salamanders did not have a detectable effect on any of these metrics, and invertebrate abundances were related more to seasonality than salamanders. In contrast with my prediction that salamanders would influence the detrital food web by consuming predatory invertebrates, they more commonly preyed upon herbivores, particularly dipteran larvae. Thus, in the ecologically diverse forests of central Appalachia, salamanders did not appear to be controlling litter decomposition, but additional studies could be

used to confirm these results and determine if they may be having important indirect influences on plant growth and species composition.

Finally, in Chapter 6, I modeled the habitat relationships of terrestrial salamanders at the scale of the salamander sampling transect (30 m²) and at a smaller scale of the sub-transect (15 m²). I developed a suite of biological hypotheses describing features to which salamanders may respond (e.g., foraging habitat, refugia, etc). On six of the SASAB study sites I measured a group of habitat characteristics that were correlated to abundances of salamanders in other studies and related them to estimates of salamander abundance from night-time searches (as described in Chapter 2) at both spatial scales. Using multiple linear regression and with an information-theoretic framework, I evaluated which groupings of forest structural variables best described salamander abundances at the two scales with Akaike's Information Criteria. The basal area of the surrounding EUs, understory herbaceous vegetation, and understory woody vegetation were included in the most parsimonious models at both scales. Thus, maintaining some canopy cover and a structurally complex understory for foraging habitat may help to mitigate losses of salamanders after disturbance.

As a whole, this dissertation suggests that silvicultural regimes that retain some portion of the canopy through the rotation may have less of an effect on terrestrial salamanders than complete overstory removal on a short-term time scale. Forested stands with some canopy trees retained through the rotation may experience a more rapid recovery of salamander populations after an initial decline (Chapter 2) and may have only transient effects on microclimate and subsequently bioenergetics (Chapter 4). However, as described in Chapters 2 and 3, partial harvesting may have cumulative negative effects on terrestrial salamanders when taking into account all of the stand entries within a rotation. Forest managers will also need to consider the

potentially longer rotation times, lower economic return, less vigorous stump sprouting of oaks (Atwood et al. 2009), increased soil erosion (Hood et al. 2002), and effects on other wildlife populations when implementing shelterwood harvests.

From an ecological perspective, these data suggest that salamander populations were most stable on the control EUs across the 13-year study period. If salamanders exhibit greater inter-annual variability following a disturbance, it suggests that populations may have a lower capacity to withstand stochastic events. With this scenario, stochastic events on disturbed sites could cause local extinctions of rare or imperiled salamanders. In addition, projections of salamander populations through time suggested that vital rates may limit population recovery, and that habitat conditions may become suitable within 10-15 years after disturbance. Thus, translocations of rare salamanders could be successful in regenerating forest, which many would consider marginal habitats.

Future research on the SASAB study sites should continue to track abundances and demography of terrestrial salamanders across the disturbance gradient, particularly focusing on obtaining additional data from the shelterwood EUs. Population models for terrestrial salamanders could be refined or expanded to include other species if researchers acquired age-specific estimates of survival on different treatments. In addition, quantifying field metabolic rates and prey use of terrestrial salamanders across a range of silvicultural disturbance could be important to providing more detailed energy budgets and understanding the consequences of forest harvesting on fitness. The relationship among temperature, moisture, and energy use by salamanders in field studies also should receive further attention. Additional investigations of the role of salamanders in ecosystem functioning with field enclosures should use individually marked animals to help determine actual treatment densities, should quantify the nutrient inputs

from salamander waste and carcasses to below-ground processes, and confirm whether salamanders feed belowground on larvae more often than previously thought. And finally, modeling habitat relationships of terrestrial salamanders may benefit from refining estimates of salamander abundance by sampling transects multiple times.

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APPENDIX A: LATITUDE AND LONGITUDE OF SALAMANDER SAMPLING

TRANSECTS

Table A.1. Estimated latitude and longitude of salamander sampling transects on the six study sites of the Southern Appalachian Silviculture and Biodiversity Project

Transect Identification	Latitude	Longitude
1-1BB1	37.2917031	-80.45417419
1-2BB1	37.291771	-80.45390965
1-3BB1	37.2919733	-80.45340783
1-4BB1	37.2918047	-80.45417804
1-5BB1	37.2919679	-80.45390094
1-6BB1	37.2921905	-80.45343013
1-7BB1	37.292065	-80.4545243
1-8BB1	37.2921381	-80.45416572
1-9BB1	37.292317	-80.4538172
2-1BB1	37.2926301	-80.45483166
2-2BB1	37.2928089	-80.45448239
2-3BB1	37.2929779	-80.45402256
2-4BB1	37.2930348	-80.45503199
2-5BB1	37.2931735	-80.45471264
2-6BB1	37.2932975	-80.45428835
2-7BB1	37.293231	-80.45521011
2-8BB1	37.2934578	-80.45488682
2-9BB1	37.2935313	-80.45437401
3-1BB1	37.2921791	-80.45631752
3-2BB1	37.2923095	-80.45587454
3-3BB1	37.2925245	-80.45539392
3-4BB1	37.2923898	-80.45638525
3-5BB1	37.2925569	-80.4561581
3-6BB1	37.2928079	-80.45564764
3-7BB1	37.2926305	-80.45660662
3-8BB1	37.2929192	-80.45625256
3-9BB1	37.2930687	-80.45573473
4-1BB1	37.2915747	-80.4574407
4-2BB1	37.2917023	-80.45740977
4-3BB1	37.2917511	-80.45694952
4-4BB1	37.2918731	-80.45794495
4-5BB1	37.2918201	-80.45764714
4-6BB1	37.2921735	-80.45703837
4-7BB1	37.292195	-80.45813271
4-8BB1	37.2922486	-80.45761236
4-9BB1	37.2925383	-80.45741924
5-1BB1	37.2938767	-80.45559308
5-2BB1	37.2940397	-80.45516702

5-3BB1	37.2941123	-80.45485438
5-4BB1	37.2941696	-80.45582861
5-5BB1	37.294325	-80.45542058
5-6BB1	37.2944203	-80.45512855
5-7BB1	37.2944075	-80.45594788
5-8BB1	37.2943283	-80.45549853
5-9BB1	37.2946779	-80.45513727
6-1BB1	37.2933027	-80.45704239
6-2BB1	37.2934519	-80.45660402
6-3BB1	37.2936127	-80.4560716
6-4BB1	37.2935761	-80.45718061
6-5BB1	37.2937257	-80.45671348
6-6BB1	37.2938392	-80.45631342
6-7BB1	37.2938406	-80.45740181
6-8BB1	37.2939846	-80.45712252
6-9BB1	37.2941882	-80.45664098
7-1BB1	37.2928711	-80.45838199
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7-3WV2	38.6984871	-80.09708617
7-4WV2	38.6978212	-80.09768313
7-5WV2	38.6981274	-80.0974595
7-6WV2	38.6985417	-80.09751406
7-7WV2	38.6980032	-80.09764927
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APPENDIX B: EXPERIMENTAL LAYOUT OF TREATMENTS AND SALAMANDER SAMPLING TRANSECTS

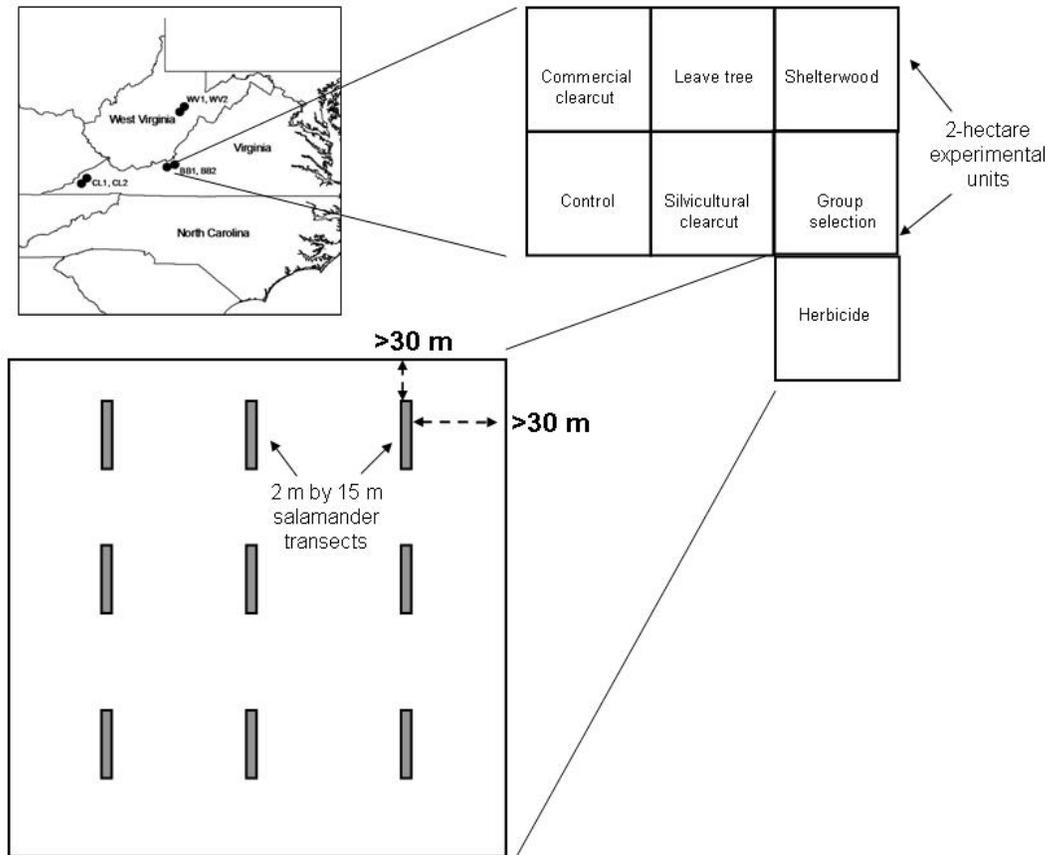


Figure B1. Typical layout of silvicultural treatments and salamander sampling transects at each of six study sites on the Southern Appalachian Silviculture and Biodiversity Project.

**APPENDIX C. RECOVERY OF SALAMANDER POPULATIONS THROUGH TIME
ON THE BLACKSBURG 1 AND BLACKSBURG 2 SITES, VIRGINIA, USA**

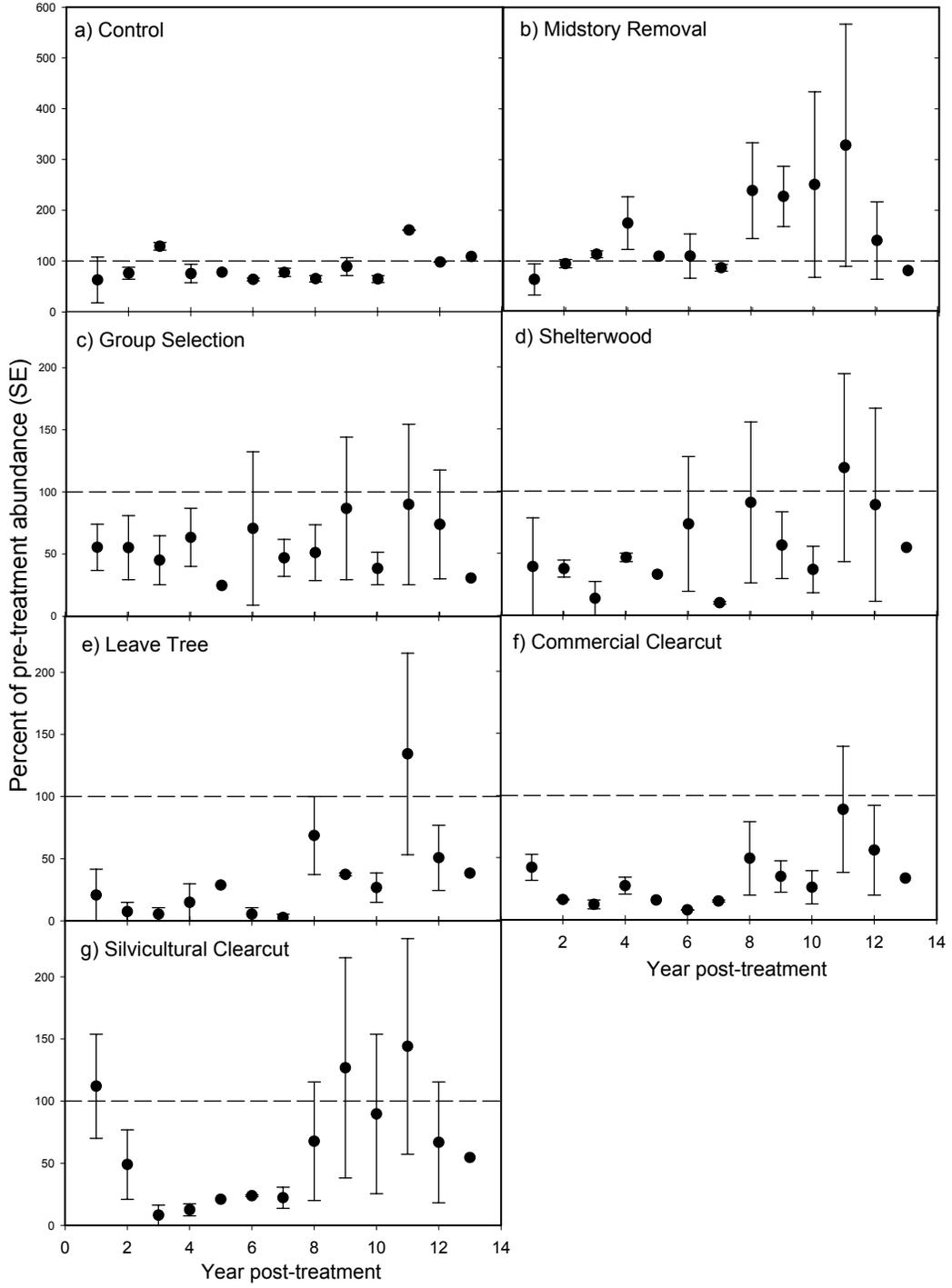


Figure C.1. Percent of pre-treatment abundance (SE) of terrestrial salamanders across 7 silvicultural treatments in experimentally manipulated forested sties in Virginia (n=2), USA to 13-years post-harvest. Years 5 and 13 post-harvest only include estimates from the Blacksburg 1 site. Dashed line indicates recovery to pre-treatment abundance (100%).

**APPENDIX D. PROJECTIONS OF EASTERN RED-BACKED SALAMANDER
POPULATIONS ACROSS POTENTIAL SCENARIOS OF DISTURBANCE**

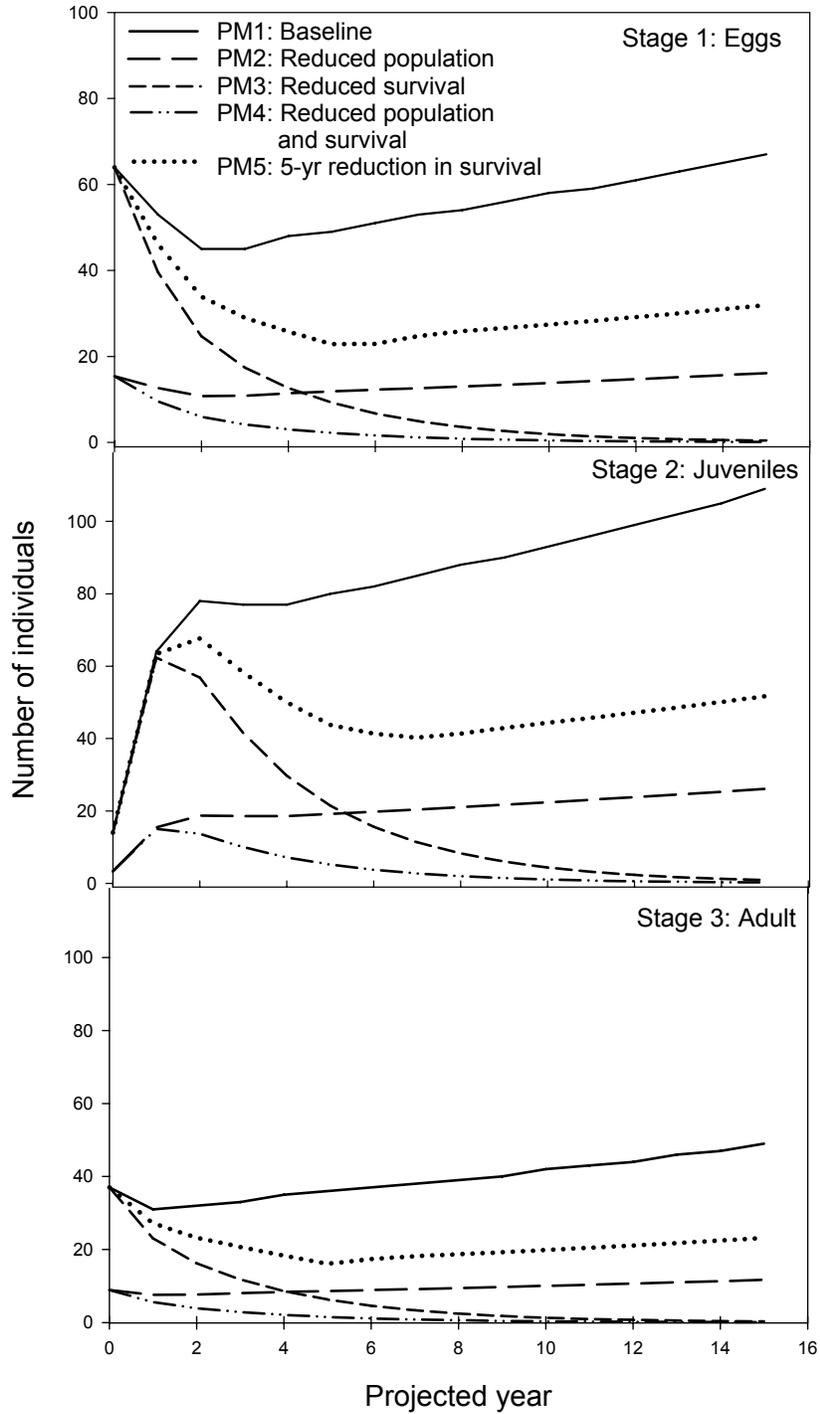


Figure D.1. Number of individuals from a stage-based population matrix of vital rates of eastern red-backed salamanders (*Plethodon cinereus*) with egg, juvenile, and adult life-stages and

projected to 15 years. We used our observed juvenile: adult ratio from years 1-6 post-harvest (14:37) and assumed 50% of females would produce 7 eggs with an equal sex ratio within a year. Four scenarios were projected: (PM1) a baseline projection, where the observed ratio of juveniles: adults from field studies was used, (PM2) where each stage was reduced by 76% to represent observed losses following silvicultural treatments, (PM3) where juvenile and adult survival was reduced by 20% to represent potential changes in vital rates from silvicultural treatments, (PM4) where the population was reduced by 76% and survival of juveniles and adults was reduced by 20%, and (PM5) where juvenile and adult survival was reduced by 10% for 5-years and then returned to baseline levels. PM1 and PM2 are the same curves as in Figure 2.4.

APPENDIX E: HABITAT CHARACTERISTICS OF OVERSTORY REMOVAL

HARVEST AND CONTROL EXPERIMENTAL UNITS

Table E1. Mean (range) values of salamander habitat characteristics quantified at the Blacksburg 1 and Blacksburg 2 sites in Montgomery County, Virginia, 2008. Habitat metrics were measured on grid of 2 m by 15 m salamander sampling transects on control and overstory removal harvest plots at both sites.

	<u>Blacksburg 1</u>		<u>Blacksburg 2</u>	
	Control	Overstory removal harvest	Control	Overstory removal harvest
Volume of coarse woody debris (m ³ /ha)	4.67 (0-35.08)	201.04 (3.00-769.85)	15.27 (0-92.00)	555.56 (0-1333.33)
Abundance of coarse woody debris (#/ha)	518 (0-1667)	2370 (667-4667)	193.43 (0-474.06)	2283.95 (1000.00-4666.67)
Average decay class of coarse woody debris ^a	3.67 (3-5)	2.47 (1.39-4.00)	3.8 (3.0-4.5)	2.6 (1.0-4.0)
Overstory density (#/ha)	741 (0-1667)	296 (0-1000)	482 (0-1333)	235 (0-1000)
Understory density (#/ha)	1630 (667-3667)	741 (0-3333)	2185 (1000-5667)	4074 (0-13667)
Depth of leaf litter (cm)	2.9 (1.0-5.4)	1.7 (0.8-2.9)	3.6 (2.8-4.8)	1.5 (0.5-3.5)

^aDecay classes as described by Maser et al. 1979

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APPENDIX F. INVERTEBRATE TAXA SAMPLED FROM MESOCOSMS

Table F.1. Occurrence (marked with “X”) of invertebrate taxa in samples of leaf litter and lavaged from the stomach of study salamanders during a field-mesocosm experiment in southwestern Virginia, 2006-2008.

Invertebrate taxa	Source	
	Leaf litter bags	Lavage samples
Collembola	X	X
Acarina	X	X
Coleoptera (adult)	X	X
Diplopoda	X	X
Isopoda	X	X
Protura	X	
Isoptera	X	X
Lepidoptera (Adult)	X	
Gastropoda	X	X
Diptera	X	X
Hymenoptera	X	X
Pseudoscorpia	X	
Aranea	X	X
Chilopoda	X	X
Larvae (Coleopteran, Dipteran, and Lepidopteran)	X	X