
Initial Effects of Clearcutting and Alternative Silvicultural Practices on Terrestrial Salamander Abundance

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Abstract: *Several studies have demonstrated the negative effects of clearcutting on terrestrial plethodontid salamander populations. However, none has experimentally compared clearcutting with multiple alternative timber-harvest methods. Using a randomized, replicated design, we compared the short-term effects (1–4 years after harvest) of clearcutting to effects of leavetree, group selection, and two shelterwood cuts on terrestrial salamanders in the southern Appalachian Mountains of Virginia and West Virginia (U.S.A.). Treatment plots were 2 ha each. We also compared salamander age class (percent juvenile), fecundity (percentage of females carrying eggs and average number of eggs per gravid female), size of gravid females, and species composition and diversity between treatments with canopy removal (cut) and those without canopy removal (uncut). All treatments with canopy removal had significantly fewer salamanders than the control treatment, but salamander abundances on alternative treatments with canopy removal did not differ significantly from salamander abundances on the clearcuts. There were no significant differences between cut and uncut treatments in the proportion of females that were gravid or in the average number of eggs in gravid females; however, gravid *Plethodon cinereus* females weighed more on the cut treatments and gravid *Desmognathus ochrophaeus* females weighed more on uncut treatments. There were no significant differences between cut and uncut treatments in the proportion of the sample that was juvenile, except in the largest species tested, *P. glutinosus*, which had a significantly higher proportion of juveniles in the uncut treatments. We conclude that initial declines in terrestrial plethodontid abundance caused by timber harvesting may be minimized across the landscape by concentrating high-intensity timber harvesting (clearcutting) in small areas (a few hectares in size).*

Efectos Iniciales de la Tala Rasa y de Prácticas Silvícolas Alternativas sobre la Abundancia de Salamandras Terrestres

Resumen: *Varios estudios han demostrado los impactos negativos de la tala rasa sobre poblaciones de salamandras pletodóntidas terrestres. Sin embargo, ninguno ha comparado experimentalmente la tala rasa con múltiples métodos alternativos de cosecha de madera. Utilizando un diseño aleatorio, replicado, comparamos los efectos a corto plazo (1–4 años postcosecha) de la tala rasa con los efectos de prácticas silvícolas alternativas sobre salamandras terrestres en el sur de las montañas Apalaches en Virginia y Virginia del Oeste (E.U.A.). Las parcelas de tratamiento eran de 2 ha cada una. También comparamos la clase de edad de salamandras (porcentaje de juveniles), fecundidad (porcentaje de hembras con huevos y promedio de huevos por hembra grávida), tamaño de hembras grávidas y composición de especies y diversidad entre tratamientos con remoción de dosel (corte) y sin remoción de dosel (sin corte). Todos los tratamientos con remoción de dosel tuvieron un número significativamente menor de salamandras que el control; sin embargo, las*

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abundancias de salamandras en tratamientos alternativos con remoción de dosel no difirieron significativamente de las abundancias de salamandras en las zonas taladas. No hubo diferencias significativas entre tratamientos con y sin corte en cuanto a la proporción de hembras grávidas, ni en cuanto al promedio de huevos en las hembras grávidas; sin embargo, las hembras grávidas de Plethodon cinereus pesaron más en los tratamientos con corte y las hembras grávidas de Desmognathus ochrophaeus pesaron más en los tratamientos sin corte. No hubo diferencias significativas entre tratamientos con y sin corte en cuanto a la proporción juvenil de la muestra, excepto en la especie estudiada de mayor tamaño, P. glutinosus, que tuvo una proporción significativamente mayor de juveniles en los tratamientos sin corte. Concluimos que las disminuciones iniciales en la abundancia de plelodóntidos terrestres debido a la cosecha de madera pueden minimizarse en el paisaje al concentrar la cosecha intensiva de madera (tala) en áreas pequeñas (de unas pocas hectáreas de extensión).

Introduction

Plethodontid salamanders are an important component of forest ecosystems in the eastern United States. Burton and Likens (1975) estimated that the biomass of salamanders is roughly equal that of small mammals and twice that of birds in a New Hampshire forest. These species help cycle nutrients in detritus back into higher levels of the food web by feeding on invertebrate detritivores (Burton 1976; Petranka 1998) and in turn serving as prey for larger forest species such as snakes and birds (Petranka 1998). It has even been suggested that salamanders may alter carbon dynamics in forest ecosystems (Wyman 1998). Welsh and Droege (2001) suggest that terrestrial plethodontid salamanders would be ideal indicator species with which to monitor the biodiversity and ecosystem integrity of North American forests because of their abundance; their sensitivity to environmental stresses such as temperature (Spotila 1972; Feder & Pough 1975), moisture (Spotila 1972; Jaeger 1978; Grover 1998), and pH (Mushinsky & Brodie 1975; Wyman & Hawksley-Lescault 1987; Frisbie & Wyman 1991, 1992); and their population stability (Hairston & Wiley 1993).

Several studies have documented reduced abundances of terrestrial salamanders following timber harvests (Pough et al. 1987; Petranka et al. 1993, 1994; deMaynadier & Hunter 1995, 1998; Ash 1997; Sattler & Reichenbach 1998; Herbeck & Larsen 1999; Grialou et al. 2000). Many of these dealt only with clearcutting, but some studies included alternative silvicultural practices such as shelterwoods (Mitchell et al. 1996; Sattler & Reichenbach 1998) and single-tree selection or thinning (Pough et al. 1987; Messere & Ducey 1998; Grialou et al. 2000). Of these studies, only Sattler and Reichenbach (1998) and Grialou et al. (2000) applied treatments randomly. To effectively manage a forested landscape for salamanders or any group of species, it is necessary to assess the relative effects of alternative management techniques.

We focused on terrestrial, lungless salamanders of the

family Plethodontidae, including the genus *Plethodon*, the woodland salamanders, which lay eggs on land and produce fully terrestrial young, and the genus *Desmognathus*, the dusky salamanders, which lay eggs in streams and produce aquatic larvae. Although we occasionally encountered some species of *Desmognathus* or *Gyrinophilus* that were primarily aquatic (even as adults), all the numerically dominant species in our study were strongly terrestrial as adults.

Because they are lungless, respiration in plethodontids is primarily cutaneous, making them particularly prone to desiccation. There is no physiological control over water loss, and because smaller salamanders have more evaporative water surface area in relation to body volume, they desiccate at a faster rate than larger salamanders (Spotila 1972). These salamanders are primarily limited to foraging when conditions are cool and wet, and they seek refuge under cover objects or in underground burrows when conditions are not favorable. Lunglessness coupled with ectothermy, however, gives the plethodontids lower rates of metabolism than other small vertebrates, including other ectotherms (Merchant 1970; Fitzpatrick 1973; Feder 1983), and they have been known to survive in captivity for several months with no food (Stebbins 1954; Feder 1983). For small species, these plethodontids have relatively long lives (typically 5–10 years; Hairston 1987) and low reproductive rates, requiring 3–6 years to become sexually mature (Hairston 1987). Clutch sizes range between 6 and 20 eggs, which are laid annually or biennially, depending on the species (Petranka 1998).

Timber harvesting may affect the salamanders' environment in a number of ways. Although some prey may be available under cover objects (Gabor 1995), salamanders forage far less effectively under dry conditions (Fraser 1976; Jaeger 1980). With a decrease in leaf litter production and moisture and an increase in temperatures, the biomass of the salamanders' leaf-litter and soil invertebrate prey may decrease (Huhta 1976; Burke & Nol 1998) or the relative quality of the prey may decrease via a shift in the invertebrate community to more

chitinous species (Mitchell et al. 1996). Additionally, with less insulating canopy, leaf litter dries faster (Johnson et al. 1985; Harpole & Haas 1999), reducing the amount of time suitable for salamanders to forage. Because of the long lifespan and low metabolism of these salamanders, however, the effects of timber harvesting on salamander abundance may be substantially delayed. Thus, we examined reproductive parameters in addition to abundance and analyzed data from later years separately, wherever possible. We built on the results of Harpole and Haas (1999) and examined the effects of several silvicultural practices on terrestrial salamanders in a randomized, replicated design.

Methods

Study Sites and Treatments

Commercially harvested forest sites in the southern Appalachians typically are relatively dry, medium-quality for timber production, and oak-dominated areas on slopes with southern and western aspects (Smith 1994). We chose sites typical of southern Appalachian forests and did not specifically select areas with above-average salamander densities. Our results are applicable to the majority of areas in this region that are commercially harvested, but our results might differ from those from cooler, moister environments that represent better habitat for terrestrial salamanders.

We established five sites (Blacksburg 1, Blacksburg 2, West Virginia 1, West Virginia 2, and Clinch) in the Appalachian Mountains of southwestern Virginia and West Virginia. Blacksburg 1 was the site used by Harpole and Haas (1999); our results include data used by them and an additional year of post-harvest data from that site. Sites were moderately sloped (16–38%) with predominately southern aspects (108–270°). Site elevations ranged from 710 to 1040 m. Pretreatment stand ages ranged from 73 to 100 years. Site indices, SI_{50} white oak (the average height a white oak, *Quercus alba*, is expected to grow in 50 years under stand conditions), ranged from 20 to 23 m. Dominant canopy species included oaks (*Quercus* spp.), hickories (*Carya* spp.), and maples (*Acer* spp.). Each site consisted of seven 2-ha treatment plots to which one of seven silvicultural treatments was randomly assigned. An exception was West Virginia 1, which consisted of only five 2-ha plots.

The seven treatments are referred to as (1) control, (2) herbicide, (3) group selection, (4) shelterwood 1, (5) leavetree, (6) shelterwood 2, and (7) clearcut. These treatments are described briefly here; further description is available in Harpole and Haas (1999) and especially in Hood (2001).

- (1) No silvicultural activities were conducted in control plots. The average residual basal area was 30 m²/ha, with an average reduction in basal area of 3% from preharvest levels.
- (2) Streamline basal application of Garlon⁴ was carried out on the herbicide plots to reduce competition from economically undesirable woody species in the shrub layer. No canopy was removed. This treatment was not conducted on the West Virginia 1 site. The average residual basal area was 32 m²/ha, with an average increase of 7% from preharvest levels.
- (3) Group selection plots contained two or three circular or elliptical group cuts. Between these cuts, trees were selectively felled and left on site, reducing the density of canopy trees. The harvests were designed as five age-class stands with entries every 20 years. The average residual basal area was 18 m²/ha, with an average reduction of 41% from preharvest levels.
- (4) The shelterwood 1 treatment was a high-leave shelterwood, with residual trees being dominant (canopy) or codominant stems. In shelterwood cuts, individual trees are removed uniformly over the plot to produce a stand of the desired density. The average residual basal area for the shelterwood 1 treatment was 14 m²/ha, with an average reduction of 41% from preharvest levels. Plans are to remove residual stems within 5–10 years after harvest.
- (5) The leavetree treatment was designed to retain up to 50 trees/ha, with residual trees being dominant or codominant stems uniformly distributed across the plot. The average residual basal area was 8 m²/ha, with an average reduction of 72% from preharvest levels.
- (6) The shelterwood 2 treatment was a low-leave shelterwood, equivalent to a commercial clearcut. Residual stems were small-diameter trees (5–25 cm diameter at breast height [dbh]). This treatment was not conducted on the West Virginia 1 site. The average residual basal area was 6 m²/ha, with an average reduction of 81% from preharvest levels.
- (7) In the clearcut treatment, all merchantable stems >5 cm dbh were harvested. Stems that were not merchantable were felled and left on site, with the exception of up to 12 wildlife trees or snags per 2-ha plot. The average residual basal area was 1 m²/ha, with an average reduction of 96% from preharvest levels.

Although plans call for additional activity in some plots, stand reentry did not occur within the course of this study. Tree tops and branches were left on site. Basal areas were measured the second year after harvest on three 576-m² plots per treatment plot (Wender 2000). Percent change in basal area was calculated from preharvest measurements on the same plots.

Sampling Methodology

We used nighttime, area-constrained searches to estimate relative salamander abundance. Although the salamanders captured on the surface represent only a small portion (<10%, Fraser 1976; 3–10%, Kramer et al. 1993) of the total population, the abundance of salamanders on the surface is a commonly used index of relative abundance for salamanders (e.g., Petranka et al. 1993; Petranka 1994; Grover 1998; Welsh & Droege 2001).

A grid of 9–15 sampling subplots or “transects” was established on each treatment plot, each transect measuring 2 × 15 m. No transects were located within 30 m of the edge of the treatment plot. On rainy nights from April to October we sampled one transect on each treatment plot within a given site. All treatments within a site were sampled on the same night so that any weather- or season-related changes in salamander activity would not bias results. Transects were chosen randomly, without replacement so that any transect was sampled only once per year. We hand-captured all salamanders seen on the surface and did not disturb potential cover objects or leaf litter. Although our sampling was not time-constrained, we typically spent 20–30 minutes on a transect. We spent more time on transects with many salamanders as a consequence of the additional time it took to handle and record each salamander. Additional details about sampling protocols and transect layout are given by Knapp (1999).

All captured salamanders were brought to the lab for species identification and measurement. We measured snout-vent length (SVL) and tail length to the nearest 0.1 mm with dial calipers. We measured mass to the

nearest 0.01 g with an electronic balance. For salamanders that have light-colored venters, we determined sex and the presence and number of eggs by holding them up to a fiber-optic light. We identified mature males by the presence of pigmented testes. Numbered flags were placed at the location of capture so that all salamanders could be returned to the exact location of capture on the following day.

We collected 1 year of preharvest data on the two Blacksburg sites and the West Virginia 1 site and 2 years of preharvest data on the Clinch and West Virginia 2 sites. Because of a lack of direct control over when the sites were harvested, the season of timber harvesting on each site varied, as did the number of post-harvest years sampled. Harvest dates for the five sites were November 1994 to March 1995 (Blacksburg 1), November 1995 to June 1996 (Blacksburg 2), May to September 1997 (West Virginia 1), April to August 1998 (West Virginia 2), and August 1997 to March 1998 (Clinch). We were able to collect 4 years of post-harvest data on Blacksburg 1 (1995–1998), 3 years on Blacksburg 2 (1996–1998), 2 years on West Virginia 1 (1998–1999), and 1 year each on West Virginia 2 (1999) and Clinch (1998). At all sites, the earliest year listed is the first year after the timber harvest.

Salamander species present at each site and their preharvest relative abundances are given in Table 1. Highton et al. (1989) genetically distinguished the slimy salamander (*Plethodon glutinosus*) into 13 species, including the northern slimy salamander (*P. glutinosus*) found at Clinch and West Virginia 1 and 2 and the white-spotted slimy salamander (*P. cylindraceus*) found at

Table 1. Average (± 1 SE) preharvest abundance of each salamander species on five sites in the Appalachian Mountains of Virginia and West Virginia: Blacksburg 1 (BB1), Blacksburg 2 (BB2), Clinch (CL), West Virginia 1 (WV1), and West Virginia 2 (WV2).^a

Scientific name (common name)	Site ^b				
	BB1	BB2	CL	WV1	WV2
<i>Aneides aeneus</i> (green)			*		
<i>Desmognathus fuscus</i> (northern dusky)	0.3 \pm 0.1	0.3 \pm 0.2	0.1 \pm 0.1		
<i>D. monticola</i> (seal)	*	*	*		*
<i>D. ochrophaeus</i> (mountain dusky)			7.9 \pm 0.8	0.9 \pm 0.3	3.3 \pm 0.5
<i>D. quadramaculatus</i> (blackbellied)			*		
<i>D. welteri</i> (Black Mountain)			*		
<i>Eurycea bislineata</i> (northern two-lined)				*	*
<i>E. cirrigera</i> (southern two-lined)	*	*	*		
<i>Gyrinophilus porphyriticus</i> (spring)	*		*		
<i>Plethodon cinereus</i> (redback)	7.9 \pm 0.9	1.7 \pm 0.2		0.1 \pm 0.1	1.7 \pm 0.2
<i>P. cylindraceus</i> (white-spotted slimy)	0.5 \pm 0.1	0.1 \pm 0.0			
<i>P. glutinosus</i> (northern slimy)			1.1 \pm 0.2	1.3 \pm 0.2	1.2 \pm 0.1
<i>P. kentucki</i> (Cumberland Plateau)			0.2 \pm 0.1		
<i>P. richmondi</i> (ravine)			3.7 \pm 0.3		
<i>P. wehrlei</i> (Wehrle's)				*	0.2 \pm 0.1
<i>Pseudotriton ruber</i> (northern red)	*		*		

^aValues are the average number of salamanders active on the surface of a 30-m² transect in one sample night. Sample sizes (plots × nights) are 49, 56, 70, 25, and 91 for BB1, BB2, CL, WV1, and WV2, respectively.

^bAn asterisk indicates that the species was present but in densities of <0.1 salamander/30 m²/sample preharvest.

Blacksburg 1 and 2. These are members of a semispecies complex that is poorly resolved and taxonomically controversial. We followed Petranka (1998) and refer to both as *P. glutinosus*.

Relative Abundance

To summarize the effect of each treatment on salamander relative abundance for all sites, we used the SAS procedure GLM to conduct an analysis of covariance (ANCOVA). We ran two sets of analyses, one with only the first year after harvest and one with all years. For both analyses, we averaged all samples taken from within the same site, treatment, and year. We used treatment as the main effect, site as a blocking factor, and preharvest abundance at the plot as a covariate; the latter allowed us to correct for possible differences in microhabitat quality between plots. Because the control was always sampled under the same conditions and by the same personnel as the treatment plots, year-to-year and night-to-night variation due to factors such as weather or the experience of personnel were accounted for. For the analysis incorporating all years, post-harvest year was also included as a blocking factor. We used the pdiff option in GLM to perform a multiple-range test.

Although the raw data were based on counts that often have a Poisson distribution and have to be normalized by square-root transformation (Sokal & Rohlf 1995), we used average counts within a year for the ANCOVA and tested for normality with the Kolmogorov-Smirnov test in the SAS procedure univariate normal. For both sets of analyses, the data were normally distributed ($p > 0.15$).

Demography

To determine whether timber harvest had an effect on demography, we looked at the percentage of juveniles captured for the four most abundant species (*Plethodon cinereus*, *P. glutinosus*, *P. richmondi*, and *Desmognathus ochrophaeus*) and the percentage of gravid females for two of these species that have light-colored venters (*P. cinereus* and *D. ochrophaeus*). Because post-harvest salamander abundances were low for treatments with canopy removal, we lumped treatments into two categories to increase sample size. The uncut category included the control and herbicide treatments, and the cut category included both shelterwoods, the leave-tree, and the clearcut. The group-selection treatment was excluded because it included both areas that were completely open and areas with nearly intact canopy and therefore was considered an intermediate category. For both of these analyses, we pooled all post-harvest years. We tested differences between uncut and cut categories using a two-tailed binomial proportions test (Ott 1993). Adult or juvenile age class was assigned by SVL.

Maximum SVLs for the juvenile class were 34 mm for *P. cinereus*, 58 mm for *P. glutinosus*, 38 mm for *P. richmondi*, and 30 mm for *D. ochrophaeus* (Petranka 1998). For analysis of percent gravid we used only adult females and only data collected before 15 June each year. After 15 June, most gravid females would be expected to be brooding eggs and therefore unavailable for sampling of the surface population (Petranka 1998). With this cut-off date, only three gravid *D. ochrophaeus* were excluded from the analysis, and no gravid *P. cinereus* were excluded.

We also compared the average number of eggs per gravid female and the average SVL, mass, and mass/SVL of gravid females with a two-tailed *t* test. For these analyses, we used gravid females from any collection date and of any SVL. Only females with yolked eggs that would be laid that year were counted as "gravid" for both these analyses. Because of the relatively long lives of these species and the likelihood that a winter harvest would have little effect on the reproductive condition of animals as they emerge the following spring, there may be a lag in the population response to timber harvesting in demographic data. Therefore, where possible, we also analyzed the same data sets with year-1 data excluded.

Species Composition

We tested whether timber harvesting affected all salamander species evenly or whether there was a greater impact on some species than on others. Based on the results of previous studies of a number of salamander species (e.g., Pough et al. 1987; Petranka et al. 1993, 1994; deMaynadier & Hunter 1995; Ash 1997; Sattler & Reichenbach 1998; Harpole & Haas 1999; Herbeck & Larsen 1999), we assumed that no species would actually benefit from timber harvesting, although the proportional abundance of one or more species might increase. To test for a change in species composition, we again lumped treatments into two categories, cut or uncut, as in the demography analysis. This was done both to increase sample sizes and reduce the dimensionality of the comparison, thus increasing the power of the test.

Using Whittaker's (1952) index of association (D_0 , Legendre & Legendre 1998), we tested for differences in proportional species composition due to timber harvest. This index is suited to an analysis of species composition because numbers of each species are transformed into proportional abundances so that the index equals zero when all the species are found in the same proportions, regardless of the total number of individuals at each site (Legendre & Legendre 1998).

If proportional abundance of the species is affected by timber harvest, there should be some ecological distance ($D_0 > 0$) between cut and uncut treatment plots as well as between the cut treatment plots before and after harvest. In theory, there would be no distance ($D_0 = 0$) be-

tween cut and uncut sites before the harvest, and there would be no difference in the uncut treatment between years. However, temporal variation (e.g., weather differences between years), spatial variation (e.g., differences in microhabitat quality between plots), and sampling error can result in a distance coefficient greater than zero even when no treatment has been applied. Comparisons between cut and uncut treatments before harvest (spatial), between uncut treatments before and after harvest (temporal), and between cut treatments before harvest and uncut treatments after harvest (spatial*temporal) were not expected to differ in species composition ($D_0 = 0$). These comparisons served as a baseline for mean and variance in ecological distance and are referred to as “same” comparisons. Comparisons between cut and uncut treatments post-harvest (spatial), between cut treatments pre- and post-harvest (temporal), and between cut treatments post-harvest and uncut treatments preharvest (spatial*temporal) are all expected to exhibit some differences in D_0 if there is a significant difference in salamander species composition due to timber harvest. These comparisons are referred to as “different” comparisons. If timber harvesting resulted in changes in species composition greater than would be produced by spatial and temporal variation and sampling error, the mean different distance will be significantly greater than the mean same distance.

Using a *t* test on the first-year post-harvest data, we compared the mean distance coefficients for the three same comparisons and the three different comparisons on each of the five sites using only the first-year post-harvest data ($n = 30$). To take advantage of what would hypothetically be the largest ecological distances, we used post-harvest year 4 from Blacksburg 1 and post-harvest year 3 from Blacksburg 2 ($n = 12$) in an unpaired *t* test of the three same comparisons and the three different comparisons.

In an effort to further characterize species composition, we calculated Simpson’s diversity index (D ; Simpson 1949) and Shannon’s index (H' ; Magurran 1988) for cut and uncut treatments at each site in each year. We used a paired *t* test to compare the mean diversity of the two treatments in the first year after harvest ($n = 5$ cut vs. 5 uncut). Comparisons of later years were not possible because of small sample size.

Results

Relative Abundance

Using only first-year post-harvest data we found a significant treatment effect on abundance ($p = 0.05$; Table 2). Treatments with canopy removal all had similar average abundances, which ranged from 14% to 46% less than the control, with the exception of the shelterwood 1

Table 2. Analysis of covariance for the treatment effect on salamander abundance.*

Source	First year post-harvest				All post-harvest years			
	df	MS	F	p	df	MS	F	p
Treatment	6	10.6	2.5	0.0544	6	45.8	10.8	<0.0001
Site	4	10.2	2.4	0.0805	4	6.2	1.5	0.2279
Year					3	5.6	1.3	0.2802
Preharvest abundance	1	110.0	26.2	<0.0001	1	116.9	27.5	<0.0001
Error	21	4.2			58	4.3		

*Site and year were blocking factors, and preharvest salamander abundance was the covariate.

treatment, which was 34–59% higher than the other treatments with canopy removal (Fig. 1).

When all years were included, there was a significant treatment effect on abundance ($p < 0.0001$; Table 2). Average salamander abundance generally declined with increasing canopy removal (Fig. 2). Average abundance on treatments with canopy removal ranged from 58% (shelterwood 1) to 24% (shelterwood 2) of average abundance on the control treatment. All treatments with canopy removal had significantly fewer salamanders than the control and herbicide treatments. The herbicide treatment had the highest abundance, with an average of 29% more salamanders than the control, but this was not highly significant ($p = 0.08$).

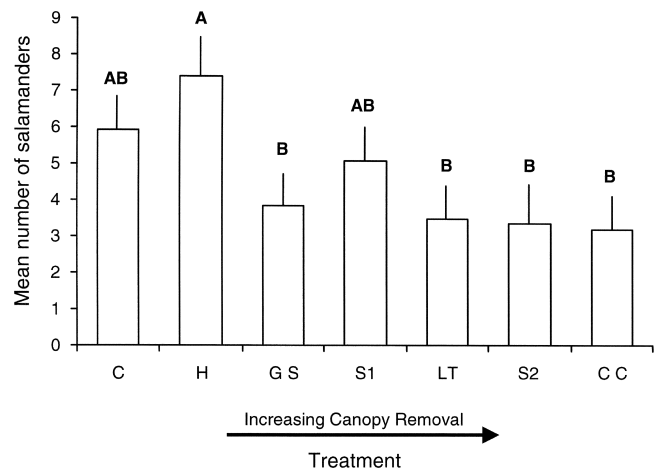


Figure 1. Number of salamanders per treatment during the first year after harvest (mean number collected per 30-m² transect + SE). Values include all species and all sites and are adjusted for preharvest abundances. Letters above the bars indicate significant difference at $p = 0.05$. Treatments in order of increasing canopy removal are control (C), herbicide (H), group selection (GS), shelterwood 1 (S1), leave-tree (LT), shelterwood 2 (S2), and clearcut (CC).

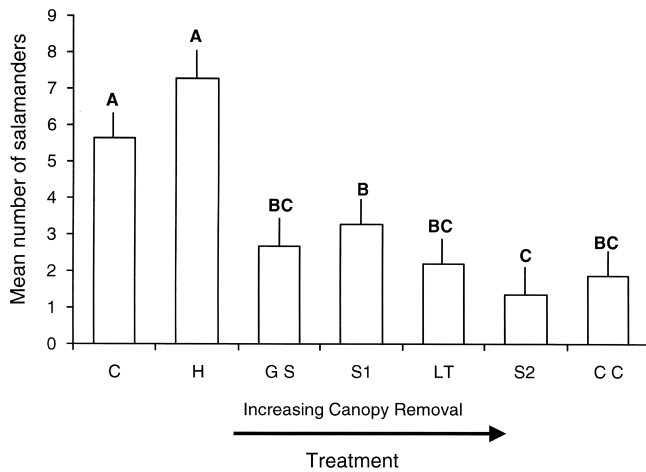


Figure 2. Number of salamanders per treatment for all years (mean number collected per 30-m² transect + SE). Values include all species and all sites and are adjusted for preharvest abundances. Letters above the bars indicate significant difference at $p = 0.05$. Treatments in order of increasing canopy removal are control (C), herbicide (H), group selection (GS), shelterwood 1 (S1), leavetree (LT), shelterwood 2 (S2), and clearcut (CC).

Demography

When data from all years were used, three of the four most abundant species showed no significant difference ($p > 0.3$) in the proportion of juveniles between uncut and cut treatment categories (Table 3). Only the largest species, *P. glutinosus*, had a significantly larger proportion of juveniles in the uncut category than the cut category ($p = 0.03$). There was no significant difference in

either the proportion of adult females that were gravid ($p > 0.8$) or the average number of eggs per gravid female ($p > 0.3$) for either *P. cinereus* or *D. ochrophaeus* (Table 4). There was no significant difference in average SVL of gravid females between uncut and cut treatments in either *P. cinereus* ($p = 0.30$) or *D. ochrophaeus* ($p = 0.19$). However, gravid *P. cinereus* weighed significantly less on the uncut treatments than the cut treatments ($p = 0.05$), and gravid *D. ochrophaeus* weighed significantly more on the uncut treatments than on the cut treatments ($p = 0.04$). Using mass adjusted for length (mass/SVL), gravid *D. ochrophaeus* still weighed significantly more on the uncut treatments than on the cut treatments ($p = 0.02$). Gravid *P. cinereus* were slightly lighter on the uncut treatments than the cut treatments, but this difference was not highly significant ($p = 0.08$).

Demographic analyses excluding the first year after harvest could only be done for *P. cinereus* and *P. glutinosus*. Although *D. ochrophaeus* was present on a site with more than first-year post-harvest data (West Virginia 1), sample sizes were too small for meaningful analysis. When only post-harvest years 2–4 were used in the analysis, *P. cinereus* did not differ in the proportion of gravid females ($p = 0.82$), the proportion of juveniles ($p = 0.68$), the average number of eggs ($p = 0.85$), or the SVL of gravid females ($p = 0.62$) between the two treatments (Tables 3 & 4). However, significant differences did emerge in the mass of gravid *P. cinereus* ($p = 0.01$) and the mass/SVL of gravid *P. cinereus* ($p = 0.005$; Table 4). When first-year post-harvest data were excluded, there was a greater difference in the proportion of juvenile *P. glutinosus* on uncut versus cut plots ($p = 0.05$) than when first-year post-harvest data were included (Table 3).

Table 3. Demographic data on the four most abundant salamander species, including the percentage of juveniles for each species and the percentage of sexually mature females that were gravid before 15 June.^a

Species	Juvenile (%) ^b		Gravid (%) ^c	
	uncut	cut	uncut	cut
<i>Desmognathus ochrophaeus</i>				
all years	30 (34/112)	24 (20/83)	57 (12/21)	55 (11/20)
<i>Plethodon cinereus</i>				
all years	28 (204/722)	28 (110/387)	31 (81/258)	32 (47/147)
years 2–4	27 (147/539)	29 (59/205)	27 (53/195)	26 (18/70)
<i>Plethodon glutinosus</i>				
all years	70 ^d (53/75)	53 ^d (37/70)		
years 2–4	73 ^d (30/41)	38 ^d (3/8)		
<i>Plethodon richmondi</i>	50 (15/30)	41 (14/34)		

^aThe category uncut includes the control and herbicide treatments; the category cut includes both shelterwoods, leavetree, and clearcut treatments.

^bThe fraction in parentheses is the number of juvenile salamanders in that category over the total number of salamanders in that category.

^cThe fraction in parentheses is the number of gravid female salamanders in that category over the total number of female salamanders in that category.

^dTwo-tailed binomial proportions test, $p \leq 0.05$.

Table 4. Mean number of eggs, snout-vent-length (SVL), mass, and mass/SVL (± 1 SD) of gravid female *Desmognathus ochropbaeus* and *Plethodon cinereus*.^a

Species	n		eggs		SVL (mm)		mass (g)		mass/SVL (g/mm)	
	uncut	cut	uncut	cut	uncut	cut	uncut	cut	uncut	cut
<i>Desmognathus ochropbaeus</i>										
all years	13	13	13.1 ± 2.8	12.2 ± 2.0	37.7 ± 3.0	36.3 ± 2.1	0.98 ^b ± 0.21	0.82 ^b ± 0.17	0.026 ^b ± 0.003	0.022 ^b ± 0.004
<i>Plethodon cinereus</i>										
all years	81	47	6.7 ± 1.2	6.9 ± 1.1	43.2 ± 2.2	43.7 ± 3.0	1.14 ^b ± 0.16	1.21 ^b ± 0.23	0.026 ± 0.003	0.027 ± 0.004
years 2–4	18	53	6.7 ± 1.2	6.8 ± 0.9	43.1 ± 2.4	43.5 ± 3.5	1.12 ^b ± 0.17	1.26 ^b ± 0.26	0.026 ^b ± 0.003	0.029 ^b ± 0.004

^aThe category uncut includes the control and herbicide treatments; the category cut includes both shelterwoods, leavetree, and clearcut treatments.

^bTwo-tailed t test, $p \leq 0.05$.

Species Composition

Changes in species composition due to timber harvesting were limited. Generally, species composition at each site was strongly dominated by the same one to three species before and after harvest.

During the first year after harvest, there was no greater ecological distance ($p = 0.34$) between samples that were expected to have only random differences in species composition (i.e., “same” comparisons; e.g., pre- and post-harvest samples on uncut treatments; mean $D_{\text{same}} = 0.16$) than between samples that could have differences in species composition resulting from canopy removal (i.e., “different” comparisons; e.g., pre- and post-harvest samples on cut treatments; mean $D_{\text{different}} = 0.21$). However, the latest post-harvest data (post-harvest year 4 at Blacksburg 1 and post-harvest year 3 at Blacksburg 2) yielded some difference between same and different comparisons ($p = 0.01$). Same comparisons had a mean distance of 0.03, whereas different comparisons had a mean distance of 0.20, indicating that timber harvest altered species composition.

There was no significant difference between uncut and cut treatments during the first year based on either Simpson’s index (1.89 ± 0.93 SD vs. 1.96 ± 0.66 SD; $p = 0.87$) or Shannon’s index (0.65 ± 0.51 SD vs. 0.78 ± 0.37 SD; $p = 0.50$). Examining the latest possible data (year 4 at Blacksburg 1 and year 3 at Blacksburg 2), we found that both indices show somewhat higher diversity in the cut treatment than the uncut treatment; at all sites, however, both diversity indices were higher for the cut plots before harvest.

Discussion

The absence of a treatment effect on age class, reproduction, and species composition, and the only marginal

decrease in abundance in the first year after harvest, may be artifacts of small sample size (five sites) or a reflection of a lag in response to timber harvesting. Terrestrial salamanders are generally long-lived, not reaching sexual maturity for 3–6 years (Hairston 1987). They also have very low metabolisms: *P. cinereus* uses only 8.3 calories/g/day at 15° C (Merchant 1970) and has been known to survive in captivity without eating for several months (Stebbins 1954; Feder 1983). First-year post-harvest samples typically comprise salamanders recently emerged from winter estivation, when they have not been exposed to the effects of habitat alteration for a significant length of time. In addition, many salamanders should be able to survive even with no food through a full season under the altered habitat conditions (Stebbins 1954; Feder 1983). Declines in abundance from preharvest levels reflected in the first year of observation may be due primarily to isolated incidents in which salamanders were killed directly by timber-harvesting operations (e.g., crushed by a skidder). Increased mortality due to starvation or dehydration is not likely to occur until late in the first year after harvest or later, but the season of the harvest may be a factor. Much of our demographic and species-composition analysis was highly influenced by first-year post-harvest data. This is an unfortunate but inevitable consequence of the drastically reduced salamander abundances on sites 2–4 years after harvest. Because of these potential lag effects, the results of studies that found no effect of timber harvesting on salamanders when sampling was not conducted beyond the first full year after harvest (e.g., Messere & Ducey 1998; Sattler & Reichenbach 1998) should be treated with caution.

Although sites were dominated by the same few species before and after harvest, there was some evidence that species composition changed with timber harvesting. The change in species composition based on data from 3–4 years after harvest may either be due to the

result of some species declining disproportionately to the other species or to the less common species simply dropping below the level of detection on harvested sites. For example, before harvest on the Blacksburg 1 site, all species other than *P. cinereus* and *P. glutinosus* made up only 15 of 1782 captures (0.8%). By the fourth year after harvest, only 99 salamanders were captured on the four cut treatments, so the expected number of salamanders other than *P. cinereus* and *P. glutinosus* is <1.0 . In this case, however, 10% of the salamanders captured were not the two dominant species; nine were *D. fuscus* and one was a *G. porphyriticus*. Additionally, both diversity indices were slightly higher on cut treatments than on uncut treatments, but this may be an artifact of the cut treatment encompassing twice the area of the uncut treatment (four 2-ha plots vs. two 2-ha plots per site). The patterns of change in species composition are not clear.

Although there was some indication that timber harvesting may cause measurable differences in the species composition of salamanders, for the most part these silvicultural practices appear to act on the salamander populations evenly without disproportionately affecting any one species, any one age class, or reproductive potential. Large salamanders may be expected to persist longer in more severe habitats because they are less prone to desiccation (Spotila 1972) and are more likely to be able to defend high-quality burrows and cover objects (Mathis 1990; Jaeger & Forester 1993; Gabor 1995). Alternatively, larger salamanders near the edges of harvested forest may be able to displace smaller conspecifics from closed-canopy forest into the harvested habitat (deMaynadier & Hunter 1998). A size advantage was apparent only in *P. glutinosus*, however, which attains an adult body size nearly twice that of the other three most abundant species. The cut-off SVL for juvenile *P. glutinosus* was larger than that of the largest adults of the other three species. Size advantage may be manifested only in the larger species. This hypothesis is supported by A. Ash (personal communication), who observed that most salamanders on young clearcuts (4–12 years old) were primarily large adult *P. jordani* and *P. teyabalee*, similar in size to *P. glutinosus*. Our data showed no obvious indication of increased persistence of *P. glutinosus* over the other species, but our sites were younger in age (1–4 years old).

The only other demographic parameter that differed between uncut and cut treatments was the mass and size-corrected mass (mass/SVL) of gravid female *P. cinereus* and *D. ochrophaeus*. Gravid *P. cinereus* weighed more on cut plots than uncut plots, suggesting that females must be in better physiological condition to reproduce on the cut plots or that reproductive maturity is delayed until a larger body size is achieved, which would indicate that the intrinsic population growth rate has decreased. The trend for gravid *D. ochrophaeus* was the

opposite of that in *P. cinereus*, however, so effects on reproduction remain inconclusive.

None of the alternatives to clearcutting we tested that entailed canopy removal resulted in salamander abundances significantly different from those in the clearcut treatment. These alternatives to clearcutting carry less of a negative connotation and may be more acceptable to the public than clearcutting, but they may be more detrimental to salamander populations on a landscape scale because a larger area must be disturbed to obtain the same amount of timber. For example, the group-selection cut would require disturbing 2.4 times the land to produce the same amount of wood as the clearcut (based on removal of only 41% of the canopy for the group-selection cut, compared with nearly 100% removal for the clearcut). With no significant difference in the impact on salamander abundance per unit area, salamander population abundance would be reduced 2.4 times as much across the landscape for initial group-selection cuts than for clearcuts. Reduction in salamander abundance across the landscape relative to clearcutting would be 1.9 times more for the shelterwood 1, 1.4 times more for the leavetree, and 1.2 times more for the shelterwood 2 treatments.

Even if there was a real difference in the impact on salamander abundance between clearcutting and alternative timber-harvest methods that could not be detected because of low power (five sites), clearcuts would still have the lowest impact, although the difference would not be as stark. Using the difference between the average salamander abundance on the control and the average salamander abundance on each of the treatments as a “real” measure of the impact of each silvicultural practice, we can recalculate their relative landscape-level effects in the following manner. The group-selection cut removes 51% of the salamander population per unit area, and the clearcut removes 66%. Furthermore, the group-selection cut requires 2.4 units of land to yield equivalent amounts of timber as 1 unit of land for a clearcut. Therefore, the landscape-level impact of an initial group-selection harvest is 1.8 times that of a clearcut (group selection removes 51% of the salamander population \times 2.4 units of land = 122; clearcut removes 66% of the salamander population \times 1 unit of land = 66; $122/66 = 1.8$). Reduction in salamander abundance across the landscape relative to clearcutting would be 1.2 times more for the shelterwood 1, 1.3 times more for the leavetree, and 1.4 times more for the shelterwood 2 treatments.

Other trade-offs between clearcuts and alternative silvicultural practices involve the frequency of re-entry into the stand. A clearcut involves a single entry into the stand to remove all or most of the timber, after which the stand is left to regenerate for several decades. Methods such as group selection and shelterwood involve several entries into the stand. The percent basal area re-

moved that is reported in the methods section is valid only for the first entry. Typically, these methods involve returning for the remaining trees after 10–20 years. This not only exposes the salamander community to a re-opening of the canopy and the associated drying of the environment, but it also results in recompaction or disturbance of the soil and leaf litter from tree felling and logging traffic.

Temporal comparison of the effects of clearcutting to alternative silvicultural practices is problematic, however. First, the recovery rate on treatments such as the group-selection and shelterwood cuts are unknown. It is unlikely that full population recovery would occur within the 10–20 years before re-entry and harvest occurred, based on estimates that population recovery from clearcutting requires 50–70 years (Petranka et al. 1993) or even more than 120 years (Petranka et al. 1994), although one longitudinal study of 15 years predicts population recovery by 20 years (Ash 1997). The rate of population recovery on a less intensively harvested treatment should be no less than that on the clearcut. Second, it is unknown whether the second and any subsequent reentries within a full 80- to 100-year harvest rotation would have the same relative impact on the population as the initial harvest (e.g., for a group-selection cut, approximately a 50% reduction in population size) or whether there is an additive effect of additional entries as a result of such factors as soil compaction, soil or leaf-litter loss, or edge effects from additional logging roads and skid trails. Even if we assume that group-selection or shelterwood cuts have a higher rate of population recovery and the effect of each successive harvest does not cause population declines that are higher than the initial harvest, if full population recovery is not reached before the next harvest, population levels will never reach preharvest levels and may continually decline over time.

In addition, our treatment plots were only 2 ha. Our results from a 2-ha clearcut may differ from results on clearcuts that can typically encompass several dozen hectares. The decrease in the edge-to-area ratio as the size of a clearcut increases suggests that the rate of recolonization could be significantly reduced. Although public pressure to limit clearcut size is growing, a study examining the effect of clearcut size on the decline and recovery of terrestrial salamanders would be important to our understanding of the landscape-level effects of clearcutting on salamander populations.

With the currently increasing rate of harvest in southern Appalachian hardwood forests, understanding the effects of alternative forest-management practices is critical. Our results suggest that on sites typical of the southern Appalachians, where forests are commercially harvested, initial declines in terrestrial salamander abundance because of timber harvesting may be minimized across the landscape where high-intensity timber harvest-

ing (clearcutting) is concentrated in small areas (a few hectares in size) rather than where low-intensity harvests are spread across a greater portion of the landscape.

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