EFFECTS OF TIMBER HARVESTING ON TERRESTRIAL SALAMANDER ABUNDANCE AND BEHAVIOR

by

Shannon M. Knapp

Thesis submitted to the Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE
IN
FISHERIES AND WILDLIFE SCIENCES
APPROVED:

Carola A. Haas, Chair	Roy L. Kirkpatrick, Co-Chair
Dean F. Stauffer	Jackson R. Webster

May 1999
Blacksburg, Virginia

Keywords: salamander, timber harvest, clearcut, surface activity, sampling bias, risk-sensitive foraging

EFFECTS OF TIMBER HARVESTING ON TERRESTRIAL SALAMANDER ABUNDANCE AND BEHAVIOR

by

Shannon M. Knapp

Carola A. Haas, Chair

Fisheries and Wildlife Science

(ABSTRACT)

We examined the short-term (1 - 4 years postharvest) effects of 7 silvicultural treatments on terrestrial salamander populations at 4 sites in southwest Virginia and West Virginia. The 3 silvicultural treatments with the most canopy removal (4-7 m^2 basal area Shelterwood, Leavetree, Clearcut) had significantly fewer salamanders than the control ($p < 0.10$) postharvest. No differences were found among treatments in age class distribution, the percent of females that were gravid, or average clutch size.

We tested the nighttime, surface-count census method for visibility and behavior-induced bias among silviculture treatments and estimated the proportion of a salamander population that is active on the surface in harvested and control habitats. Instantaneous rates of salamander activity ranged from 1.3 to 11.7% of the population for redback *(Plethodon cinereus*) and slimy salamanders (*P. glutinosus*). Timber harvest caused up to a 2-fold increase or decrease in activity rates. There was evidence for bias in the night census method, but differences were not consistent enough to suggest general bias corrections.

We also tested whether poorly fed salamanders exhibited risk-sensitive foraging in a dry environment in a laboratory experiment. Poorly fed salamanders were observed out of their simulated burrows less than well fed salamanders suggesting salamanders, particularly females and small adults, are risk-averse.

ACKNOWLEDGEMENTS

I would like to thank my advisor, Dr. Carola Haas, for giving me the opportunity to work on this project as well as her support over the past 2 years. I would also like to thank her and Doug Harpole for establishing this study, its protocols, much of the data I present here, and continued advice and assistance on this project. Dr. David Wm. Smith, David Wright, and Bryan Wender established the sites for Chapter 2, provided data on the effects of timber harvesting on the plant community on those sites, and provided advice and general information on forestry practices. Jesse Overcash, USFS, helped me locate sites for Chapter 3 and provided additional information and advice. My co-advisor, Dr. Roy Kirkpatrick was instrumental in the initial brain-storming and final design refining that lead to Chapters 2 and 3. The remainder of my committee, Dr. Jack Webster and Dr. Dean Stauffer, provided valuable advice and made themselves available (often at the last minute).

This project would not have been possible without extensive assistance in the field. I would particularly like to thank my technicians: Lynne Tomovick, Rachel Hurt, Kacie Miller, Camille Darby, Jessica McGlothlin, Jean Lorber, Lawrence "LJ" Johnson, Kelly Rinker, Jessica Dorr, Eric Wolfe, Nathaniel Hamilton, Robin Rossmanith, and Angela Burkhart and especially Don Mackler who not only provided assistance in the field but took care of many of the day-to-day details, organization, and supervision for me. I also would like to thank the countless volunteers that came out at the last minute and helped sample in the rain and cold and made this project possible. Mihn Lu and Eric Canady also provided assistance in the lab.

And finally, I would like to thank my parents, friends, and fellow grad students for their support and the occasional distractions from work. I would especially like to thank Christy, Ria, Sue, Rebekah, the Brainiacs, Jeff and Kristen and the WVUSG, Marilyn, and Alison. I would also like to thank the teachers who inspired and guided me along the way, especially Gretchen Taylor, Dan Fong, and Dave Culver.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1 - INTRODUCTION

There has recently been an interest in the apparent global decline of amphibians (Blaustein and Wake 1990, Wake 1991, Blaustein 1994). One facet of interest is the effects of timber harvesting on salamanders. Studies have indicated that older forest stands have larger salamander populations than younger and recently clearcut stands. Comparing salamander populations in recently harvested stands or plantations to old growth or 50+ year second growth stands showed reductions on the order of 80% (review by deMaynadier and Hunter 1995) in relative abundance and changes in species composition in such diverse habitats from Florida longleaf pine savanna (Means *et al.* 1996) to the California Redwoods (Bury 1983) and east to the Appalachians (Petranka *et al*. 1993, Petranka *et al*. 1994, Ash 1997) and New York deciduous forests (Pough *et al.* 1987). Although the impacts of clearcutting have been well documented, the effects of alternative methods of timber harvesting have not been well examined. Alternative methods such as shelterwood and group selection cuts, which leave part of the canopy intact or create smaller canopy gaps, could cause a lesser impact or no impact on the population or could hasten the population's recovery.

The Appalachians are unique in that they hold some of the world's highest salamander diversity (Cohn 1994). The Appalachian mountain streams are also the evolutionary birthplace of the family Plethodontidae, the lungless salamanders (Dunn 1972, Hairston 1986). The terrestrial plethodontids of the Appalachians are the focus of this study.

In terrestrial plethodontids, lunglessness means that respiration is primarily cutaneous, and therefore these animals are prone to desiccation. Salamanders have no control over water loss. Smaller salamanders have more evaporative surface area in relation to volume of body and, therefore, desiccate at a faster rate than larger salamanders (Spotila 1972). Their foraging time is limited by both temperature and moisture (Feder 1983). Feder (1983) provided an equation for salamander foraging time in which foraging time decreases with decreasing percent relative humidity, increasing temperature, increasing wind speed, and decreasing body size. By manipulating the insects available and the moisture level of an enclosure in a laboratory experiment, Fraser (1976) tested the

hypothesis that the abundant invertebrate prey of *Plethodon spp*. may not always be available to the salamanders. He concluded that it was the reduced mobility of the salamanders, not a lack of prey, that resulted in weight loss in salamanders tested in dry conditions. Jaeger (1980a) supported this with field data. Analysis of stomach contents showed that both the volume and number of prey per unit salamander length increased with increasing amount of rainfall over the previous 3 days and the number of salamanders with empty stomachs decreased over the same period.

Taub (1961) demonstrated that leaf litter was but a small part of the habitat of these salamanders. During the winter they burrow underground to hibernate in warmer, insulated layers (Vernberg 1953). In dry periods of the summer and during the day they may move vertically, burrowing into more cool and moist layers of soil (Heatwole 1960, Taub 1961) or horizontally, taking shelter under cover objects such as rocks and fallen logs (Heatwole 1962, Jaeger 1972, Jaeger 1980b).

Although many studies have demonstrated that terrestrial salamander populations were lower on plots previously subjected to timber harvesting than on unharvested plots, there is debate about the degree of impact, the time required for recovery, and the validity of sampling methods (Ash and Bruce 1994, Petranka 1994, Ash 1997). Two commonly used sampling methods are night searches during rainy periods when salamanders are likely to be active on the surface (the primary method used in Chapter 2) and day searches in which cover objects such as rocks and logs are turned. Nishikawa (1985) reviewed several mark-recapture studies and found those that used night searches had higher recapture success. Alternatively, Petranka *et al*. (1994) claimed that numbers of salamanders caught on night searches can vary by as much as ten-fold from night to night, whereas day searches yielded far more consistent numbers even during periods of drought. Ash and Bruce (1994) contended that studies using day searches of cover objects can effectively sample as little as 1% or less of a population. Petranka (1994) countered that only a small percentage of a salamander population may be on the surface at any one time to be sampled by night searches. I evaluate the night search method in Chapter 3 and compare it to day sampling (coverboards) in Chapter 2.

Timber harvesting has several impacts on salamander habitat. Air and soil temperatures increase (Kittredge 1948, Johnson *et al*. 1985, Liechy *et al*. 1992), leaf litter drying rate increases (Harpole and Haas 1999), insect biomass may either increase (Huhta 1976, Harper and Guynn 1999) or decrease (Seastedt and Crossley 1981), and there are indications that the nutritional quality of the insect prey decreases (Mitchell *et al*. 1996).

In Chapter 2, I compare the short term effects these changes have on the abundance and demographics of terrestrial salamanders in clearcuts and 5 alternative silvicultural treatments to controls. I also test the night sampling method for biases due to differences in salamander observability, by comparing results from night sampling to results from coverboard sampling. In Chapter 3, I test the night sampling method for biases due to differences in salamander activity levels under favorable, wet conditions in harvested plots compared to controls using mark-recapture techniques. In Chapter 4, I use a controlled laboratory experiment to test for differences in activity under unfavorable, dry conditions between well-fed and poorly-fed salamanders. Finally, In Chapter 5, I summarize results from Chapters 2, 3, and 4 and give suggestions for management and further study.

OBJECTIVES

1. Compare the short-term effects of clearcutting and alternative silviculture methods to controls on salamander abundance, age-class/size-class distribution, and reproduction.
2. Test the night sampling method
   a. for biases in salamander observability due to timber harvesting and
   b. for biases in salamander activity due to timber harvesting.
3. Estimate what percent of a salamander population is active and available for capture in the night sampling method.
4. Test for difference in activity between well-fed and poorly-fed salamanders under unfavorable, dry conditions.

CHAPTER 2 - EFFECTS OF 7 SILVICULTURAL METHODS ON TERRESTRIAL SALAMANDERS

INTRODUCTION

This project was initiated in 1994 by Dr. Carola Haas and Doug Harpole of the Virginia Tech Department of Fisheries and Wildlife in cooperation with Dr. David Smith, Muffy Brown, and Jesse Thompson of the Virginia Tech Department of Forestry to examine the effect of various silvicultural methods on biodiversity, specifically, the effects on terrestrial salamanders and on the forest herbaceous and shrub layers. Over the years, several technicians and countless volunteers conducted the salamander sampling. Other graduate students from the Department of Forestry involved with this project have included David Wright, Dan Hammond, Bryan Wender, and Sharon Hood. I became involved in the project in 1997. In 1994, preharvest data were taken on the 4 original sites. Harpole (1996) reported preharvest data taken on the 4 original sites and the first year postharvest results from the Blacksburg 1 site. Harpole and Haas (1999) reported the first 3 years of postharvest data from Blacksburg 1. Four additional sites were added during 1995 and 1996. Due to litigation and other delays in harvesting, only 5 sites were harvested by the summer of 1998. One of those 5 sites (Newcastle) had excessively low salamander abundances even before harvest and so is not including in this analysis. Here I present results from the 4 sites with postharvest data: Blacksburg 1, Blacksburg 2, Clinch 2, and West Virginia 1.

The terrestrial plethodontid salamander species that are the focus of this study occupy basically the same niche. All eat small invertebrates on the forest floor. All are limited to foraging when conditions are cool and wet and use underground burrows or cover objects when conditions are not favorable. All have low metabolic rates. At 15˚C, the mountain dusky salamander (*Desmognathus ochrophaeus*) uses only 3.8 calories per gram per day (Fitzpatrick 1973a) and the redback salamander uses only 8.3 calories per gram per day (Merchant 1970) and have been known to survive in captivity without eating for several months (Stebbins 1954, Feder 1983). For small species, they have relatively long lives typically living 5 to 10 years (Hairston 1987) and low reproductive

rates, requiring 3 to 6 years to become sexually mature (Hairston 1987) and clutch sizes of 6 to 20 eggs annually or biennially, depending on species (Petranka 1998).

Foraging times are limited by environmental conditions (temperature, humidity, and wind speed) and by the mass of the salamander (Feder 1983). Limitations due to size are largely a function of surface area to volume ratio, so larger salamanders dehydrate at a slower rate and are able to forage longer (Spotila 1972). Although salamanders are generally similar in form, there are slight interspecific differences in shape that affect the surface to volume ratio. Species also can differ in rehydration rates (Spotila 1972).

Habitat alterations such as timber harvesting can potentially affect any of several population characteristics including population size, reproductive rate, and age distribution. Because terrestrial salamanders are fairly long lived, changes in population size may not be evident until several years after a harvest, but reproductive rates may be reduced in the short term. I addressed this by looking for treatment effects in fertility and fecundity rates. I also examined the effects of the treatments on average body size and the proportion of juveniles in the population. Because smaller salamanders have larger surface area to volume ratios and, therefore, are more vulnerable to dry conditions, there may be an effect of timber harvesting on juvenile survival, which would be evident in the proportion juvenile or in the mean snout-vent length (SVL). An effect on smaller salamanders may also occur across species, where the survival of juveniles and of smaller species is reduced, which would be evident in overall average SVL differences.

In addition to examining the effects of the treatments on the salamander populations, I looked at the effects of the treatments on microhabitat and compared two commonly used sampling methods. Harpole (1996) and Harpole and Haas (1999) examined several microhabitat variables at the Blacksburg 1 site in the first year postharvest. I repeated some of these microhabitat measurements at the same site in the fourth year postharvest to examine whether the response of microhabitat variables to the timber harvesting treatments followed similar trends as did the response of salamander abundance to these treatments. Night searches were used as the primary count method, but there was

concern that reductions in salamander numbers could be due to an artifact of our ability to see and capture salamanders. Immediately after harvest, dense slash (limbs and tops of trees left on site by logging operations) covers the ground through which it is difficult to see or capture salamanders. Within 3 years after harvest, dense growth of vegetation begins to cause the same problem. To address this possibility I compared results from night samples to those from coverboard samples on 2 sites.

METHODS

STUDY SITES

All 8 sites were located in the Appalachian Mountains of southwest Virginia and West Virginia. Virginia sites (6) were located in the George Washington and Jefferson National Forest. West Virginia sites (2) were located in the Westvaco Wildlife and Ecosystem Research Forest. Each site consisted of 7 2-ha treatment plots with one of the silvicultural treatments randomly assigned to each. Details on the location and dates of harvest of the 4 sites with postharvest data are listed in Table 2. 1. Sites were moderately sloped (10 to 40%) with predominantly southern aspects. Forest stand compositions were typical of mid-elevation (600-1050 m) Southern Appalachian forests, dominated by oaks, hickories, and maples with canopy tree ages ranging from 50 to 150 years (Dr. David Wm. Smith, Virginia Tech Department of Forestry, pers. comm.).

TREATMENTS

The silvicultural treatments are listed below in order of increasing canopy removal.

1. Control – unmanipulated.
2. Herbicide – direct application of herbicide to reduce economically undesirable species in the shrub layer (1 to 5 m in height), but no canopy was removed.
3. Group Selection – 2 to 3 circular or elliptical cut areas totaling approximately approximately one-fourth of the total plot (0.5 ha) with thinning of trees on the remainder of the plot; approximately 30% of the total basal area was removed.
4. 12-14 Shelterwood – a thinning of trees with 12-14 m^2/ha basal area remaining including many large canopy trees (approximately 40% of the original basal area was removed).

5. 4-7 Shelterwood – a thinning of trees with 4-7 m^2/ha basal area remaining (approximately 70% of the original basal area was removed). All merchantable timber was removed and the remaining basal area was primarily small trees.
6. Leavetree – a thinning of trees with 3-4 m^2/ha basal area remaining (approximately 85% of the original basal area was removed). Only large canopy trees were left.
7. Clearcut – all merchantable timber was removed with the exception of up to 12 trees per 2-ha treatment plot, left for wildlife.

(See Appendix 1 for actual remaining basal areas for each treatment on 3 sites.)

SAMPLING

Night Sampling

Night-time, area-constrained searches were the primary sampling method. We sampled from April to October on rainy nights when temperatures were > 4˚C. Because we sampled only when we believed salamanders were likely to be found on the surface, nights in which no salamanders were collected on any plot in a site were excluded from the analysis. Sampling subplots or "transects" were located in a grid on each treatment plot (Figure 2. 1). Transects were 2-m x 15-m and were no less than ≥ 30 meters from the edge of the treatment plot. The original grid included locations for 9 transects. This number was later increased to 15 on Blacksburg 1 and 2 in 1997 because these sites were intensively sampled that year. The sampling transect was chosen randomly without replacement so a different transect was sampled each night of sampling. On occasion, transects were accidentally repeated within a sampling season. One transect on each plot was sampled each night. To avoid effects of the time of night, treatment plots were sampled in a fixed order with the starting plot systematically rotated. Two to 3 people working side by side crawled the transect along its longest dimension, spending roughly 20 minutes per transect. All salamanders encountered were captured by hand and placed in numbered plastic bags with wet leaf litter. A numbered flag was placed at the location of capture. Salamanders that escaped capture were recorded and included in abundance analysis. Captured salamanders were brought to the lab for species identification and measurement. Snout-vent-length (SVL), and tail length were taken with dial calipers and recorded to the nearest 0.1 mm. Mass was measured using an electronic balance and

recorded to the nearest 0.01 g. For most species, sex was determined by shining a fiber optic light through the salamander and looking for the presence of pigmented testes. For the dark-bodied slimy salamanders, adult males were determined by the presence of an englarged mental gland under the chin. We were not able to determine sex for other dark-bellied species. Viewing with the fiber optic light also allowed us to determine the presence and number of eggs in gravid females. Salamanders were returned to the exact location of capture the next day. Red-spotted newt (*Notophthalmus viridescens*) efts were occasionally encountered, but were not collected or used in analyses.

Microhabitat Variables

Harpole (1996) collected data on leaf litter biomass, soil temperature, and leaf litter drying rate on the Blacksburg 1 site in the first-year postharvest (1995). To determine how these variables changed by the fourth-year postharvest, these measurements were taken at the same site in August 1998.

Leaf Litter Biomass

Using a 0.25 m x 0.25m PVC frame, 5 samples of leaf litter were taken at approximately 3-m intervals at each of 8 transects on each treatment plot, for a total of 40 samples per treatment. The transects used were the same ones used in 1995. Samples were dried for at least 48 h at 65˚C and weighed to the nearest 0.1 g.

Soil Temperature

Soil temperatures were taken on 4 days between 1000 and 1600 EDT. Each day, temperatures were recorded at 2 locations on the 8 transects used for leaf litter biomass. At each location, temperatures were recorded at depths of 2.5 cm and 10 cm. Temperatures were recorded to the nearest 1˚C using Weksler brand soil thermometers.

Leaf Litter Drying Rate

To determine the drying rate of leaf litter of each treatment, leaf litter samples were taken on 3 consecutive days following a day of at least 2.5 cm of rain. Each day, samples were taken at 10 locations on each plot. Locations were based on transect locations, but

because some of the treatments had very little leaf litter, leaf litter was taken from the surrounding area until roughly a handful of litter was collected. Leaf litter was weighed wet, dried at 65˚C for 48 h, and reweighed.

Coverboard Sampling

We installed a coverboard array on Blackburg 1 and 2. The coverboard array consisted of 5 groups of 10 boards. Groups were placed approximately 5 m into the center of the plot from each of the corner transects and approximately 5 m to one side of the center transect (Figure 2. 1). The boards were 5 x 20 x 60-cm rough cut yellow-poplar (*Liriodendron tulipifera*). The 10 boards for each group were laid roughly a meter apart spanning the 15-m length of the adjacent transect. Coverboards were sampled during daylight hours, 1-3 d after a rain. We recorded species and measured SVL to the nearest 0.1 mm with dial calipers in the field and immediately returned the salamanders to their coverboard. Coverboards were sampled in the fall of 1997 and in the summer and fall of 1998 on Blacksburg 1 and in the summer and fall of 1998 on Blacksburg 2. Data within a site were lumped and compared with night data taken within the same months.

STATISTICAL ANALYSIS

Because of their ecological similarities, I treated the salamanders in this study as an ecologically homogeneous group and analyzed the effects of the timber harvest treatments on them as a collective group. Where sample sizes permitted, I also analyzed species separately. Differences between species could arise as a result of differences in competitive ability for food or underground retreats, particularly as an the environment becomes more limiting, and because species differ in average size, which is an important ecological variable in this group.

For all analyses, I used 0.10 for the level of significance.

Abundance

Within Sites

Within each site, I tested for differences in salamander abundance among treatments within years, and among years within treatments using a Kruskal-Wallis test computed using the SAS procedure NONP1WAY and the option ANOVA. For this test, all species were lumped, data were not transformed, and data from all years were used.

All Sites Analysis of Covariance (ANCOVA)

To summarize the effect of each treatment for all sites and all years, I analyzed postharvest salamander abundances as an analysis of variance (ANCOVA) using the SAS procedure GLM. I averaged all samples taken within the same site-treatment-year. For the 2 sites with more than 1 year of postharvest data (Blacksburg 1 and 2), I took the average of each year's average. Because my dependent variable was count data, I used a square-root transformation of the abundance data for all abundance analyses. However, in graphs, I give the squared adjusted means to give more realistic numbers for the reader. In discussion of relative abundance I have translated the squared adjusted means for each treatment into a percent of the control. I do not intend to imply that any treatment differs from the control *significantly* by that particular percentage. I report values relative to the control instead of the squared adjusted mean because I consider this to be a more meaningful value. The ANCOVA included treatment as the main effect, site as a blocking factor, and preharvest abundances as a covariate. Because average preharvest abundances varied up to three-fold within a site, I treated the average number of salamanders caught per night preharvest as an index of habitat quality for the plot and used it as a covariate in the model. At one site, Clinch 2, I had preharvest data from 2 years available. In this case I averaged the two year's values to obtain the covariate. To determine which treatments differed significantly I performed a multiple range test using the pdiff option in SAS procedure GLM. See Appendix 2 for the parallel analysis run on salamander biomass.

I also ran the above ANCOVA on two subsets of the data. The first subset used only data from the first-year postharvest for all salamander species combined at each of the four

sites. For the second subset, instead of lumping all species, I ran one ANCOVA for each of the numerically dominant, or "main" species, using only those sites on which that species occurred and all available years. Main species over these 4 sites were the redback salamander (*Plethodon cinereus*), the slimy salamander (*P. glutinosus*), the ravine salamander (*P. richmondi*), and the mountain dusky salamander (*Desmognathus ochrophaeus*).

Population Characteristics

Snout-Vent-Length

I analyzed treatment effects on salamander length over all sites with an ANOVA, again using the SAS procedure GLM. As in the abundance analysis, I used only postharvest data and took the average SVL within each site-treatment-year and then averaged this value among years when there was more than one year of postharvest data. I used treatment as the main effect and blocked by site but used no preharvest covariate. I ran this analysis lumping all species and on each of the main species individually. The analysis lumping all species is susceptible to differences in the abundance of species and in effect is a combination of the effects on sizes of each species and abundances on each species, but it provides a combined picture of the effect of the silvicultural treatments on the average size of the terrestrial salamander guild. I have analyzed the effects of these treatments on individual species size and abundance elsewhere in this paper.

I constructed size distribution box-and-whisker plots lumping salamanders from all sites and postharvest years and provide 5^{th}, 10^{th}, 25^{th}, 75^{th}, 90^{th}, and 95^{th} percentiles, medians, and means. Means given in box-and-whisker plots differ from those given by the ANOVA analysis above due to differences in weighting of the sites. In the ANOVA analysis, each site is weighted equally reqardless of the number of samples taken at the site, number of postharvest years, or average salamander abundance. In the box-and-whisker plots, each salamander is weighed equally, so sites with more salamander captures have more impact on the mean. I constructed plots for all species combined and for each of the main species individually.

Proportion Juvenile

Changes in population size distribution can also be manifested as changes in the proportion of the population that is juvenile or adult. For this analysis, I used only the main species and pooled all postharvest years. Because sample sizes decreased with harvesting, I lumped treatments into two categories to get reasonable sample sizes for proportion tests. Treatments were classed as either "uncut" (Control and Herbicide) or "cut" (Shelterwoods, Leavetree, and Clearcut). Because the Group Selection may have been an intermediate between these two categories, it was not included in this analysis. The purpose here was to look for any effect of timber harvesting on salamander age-distribution. Differences between uncut and cut treatments were tested using a simple binomial proportions test (Ott 1993). Age class (juvenile or adult) was determined by length. Maximum SVLs for the juvenile class were 30 mm for the mountain dusky salamander, 34 mm for the redback salamander, 58 mm for the slimy salamander, and 38 for the ravine salamander. These lengths were based on Petranka (1998).

Proportion Gravid

I also analyzed the effect of harvesting on the proportion of adult females that were gravid. This analysis was only run on the mountain dusky salamander and the redback salamander. The other 2 main species were dark-bellied, so gravidity could not be reliably determined. As with the analysis of the proportion juvenile, I lumped treatments into either uncut or cut, used only data from postharvest years, and used a test of binomial proportions (Ott 1993) to determine statistical differences between treatment groups. Only females with yolked eggs which would be laid that year were counted as "gravid". Additionally, I only used adult females (adult age-class determined as in analysis of proportion juvenile) and only used data collected before June 15 each year. After June 15, most gravid females would be expected to be brooding eggs and unavailable for sampling of the surface active population (Petranka 1998). I also calculated average number of eggs per gravid female. For this calculation, I used gravid females from any collection date and regardless of female SVL. Only yolked eggs were included in this analysis.

RESULTS

ABUNDANCE

Within Sites

Blacksburg 1

Average salamander abundances did not differ significantly among treatment plots in the preharvest year at Blacksburg 1 ($p = 0.95$) (Table 2. 2). Abundances differed significantly among treatments in all 4 postharvest years ($p = 0.02$ for year 1, $p < 0.01$ for all subsequent years). Looking at change within a treatment plot among years, there was no significant difference among years in the Control plot ($p = 0.68$). Abundances on the Herbicide plot appeared to increase, although this is not significant ($p = 0.64$). Abundance on all treatments with canopy removal differed significantly among years, and average salamander abundances were less than the preharvest year in all postharvest years. In the first year postharvest, abundances on the Group Selection, 12-14 Shelterwood, and Clearcut treatments all showed slight drops (Figure 2. 2a). Abundances on the 4-7 Shelterwood and the Leavetree treatments had more drastic declines, with roughly 50% reductions in average abundance among years. By the second year postharvest, treatments with canopy removal all had low average abundances, ranging from 3.5 to 1.0 salamanders caught per transect per night. In these treatments, although abundances on all but the 12-14 Shelterwood declined, there was little difference from the second to third year postharvest. Third year postharvest averages for this treatment ranged from 2.8 to 0.7. Abundances on these 5 treatments all increased between the third and fourth years postharvest, ranging from a 39% increase in the Clearcut to a 280% increase in the Leavetree. However, even with the fourth year increases, average numbers of salamanders were far lower than preharvest numbers, ranging from 55% of the preharvest average for the Group Selection to 21% for the Clearcut.

Blacksburg 2

At Blacksburg 2, abundances did differ significantly among treatment plots in the preharvest year ($p = 0.01$) (Table 2. 3). Abundances also differed significantly among treatment plots in the second year postharvest ($p < .01$), but not in the first ($p = 0.49$) or third ($p = 0.19$) years postharvest . At Blacksburg 2, year-to-year changes in abundance

within a treatment did not follow a clear pattern as seen at Blacksburg 1, and only two treatments showed a significant difference in abundance among years (4-7 Shelterwood, $p = 0.03$; and Leavetree, $p = 0.06$). On the 4-7 Shelterwood, changes in abundance followed a similar pattern to that seen at Blacksburg 1, with a slight decrease in the first year, followed by a more substantial decline in the second year and little change from the second to third year (Figure 2. 2b). Abundances on the Leavetree dropped to zero in the first year postharvest and remained at zero in the second and third years. Abundances did not differ significantly among years on the remainder of treatments at this site. Abundances on the Control fluctuated with up to a 3-fold change between consecutive years. Abundances on the Group Selection dropped over 50% in the first year postharvest, then returned to near preharvest levels in the second year. Abundances on the 12-14 Shelterwood dropped to zero in the first year, increased to 49% of preharvest numbers in the second year postharvest, and returned to zero in the third year postharvest. In the first year postharvest, abundances on the Clearcut increased 60% over preharvest levels, then dropped to only 71% of preharvest numbers in the second year. Abundances on the Clearcut dropped to zero in the third year postharvest. The dramatic differences in second year abundance relative to all other years may be largely attributable to sampling error, as this site was only sampled twice in the first postharvest year.

Clinch 2

At Clinch 2, average salamander abundances differed significantly among treatments in the postharvest year and in both preharvest years (1994, $p = 0.07$; 1996, $p = 0.02$) as well as when both preharvest years were combined ($p = 0.08$) (Table 2. 4). Within treatments, differences in abundance among years were highly significant ($p < 0.01$) for all treatments except the 12-14 Shelterwood ($p = 0.23$). However, this difference may be attributed to the overall higher averages in 1994 than in 1996. Comparing the combined preharvest years to the postharvest year, there is no significant difference in abundance on the Control, Herbicide, or 12-14 Shelterwood, although abundance on all three declined by 16% (Herbicide) to 30% (12-14 Shelterwood) from the preharvest average (Figure 2. 2c). Abundances on the remaining treatments differed significantly from pre- to postharvest years (Group Selection, $p = 0.05$; 4-7 Shelterwood, $p = 0.06$; Leavetree, p

= 0.01; and Clearcut, p < .01). Numbers of salamanders on these treatments declined by 59% (4-7 Shelterwood) to 88% (Clearcut) from their preharvest averages.

West Virginia 1

At West Virginia 1, abundances did not differ significantly among treatments in either the preharvest (p = 0.53) or postharvest year (year 1) (p = 0.66) (Table 2. 5). There were no significant differences between pre- and postharvest salamander abundances for any of the 5 treatments (Control, p = 0.20; Group Selection; p = 0.82; 12-14 Shelterwood, p = 0.31; Leavetree, p = 0.89; and Clearcut, p = 0.85). The Group Selection, Leavetree, and Clearcut treatments changed very little between years (Figure 2. 2d), ranging from a 9% decrease on the Group Selection to a 6% increase in average abundance on the Clearcut. Only the 12-14 Shelterwood showed a notable, though nonsignificant, decline of 41% of the preharvest average. The Control, however, increased 82% from the preharvest year. Again this large difference in the means was not significant.

All Sites ANCOVA

All Postharvest Years

Combining data from all sites, all years, and adjusting for preharvest abundances, I found a significant treatment effect (p = 0.04) on abundance. The Herbicide treatment had the highest abundance, 25% higher than the control and significantly higher than all treatments with canopy removal (Figure 2. 3). The Control had the second highest abundance overall and had significantly more salamanders than the 4-7 Shelterwood, Leavetree, and Clearcut. Treatments with canopy removal had from 60% (Group Selection) to 35% (Clearcut) of Control abundances. Percent difference from the control are given only to indicate the range of mean values; I do not intend to imply the treatments differed significantly from the control or that I tested that they differed from the control by that specific margin.

First Year Postharvest

Only including first year postharvest data, I found no significant treatment effect ($p = 0.50$). Relative abundances ranged from 23% higher than the Control on the Herbicide treatment to only 53% of Control abundances on the Leavetree (Figure 2. 4).

Main Species

Four species dominated our sites, the mountain dusky, the redback, the slimy, and the ravine salamander (Table 2. 6). Of all captures over all years and all four sites, the mountain dusky salamander made up 26%, the redback salamander made up 55%, the slimy salamander made up 9%, and the ravine salamander made up 10%.

Miscellaneous species (Table 2. 7) combined made up only 4% of all captures. Of preharvest captures at the four sites they made up 4% at Blacksburg 1, 14% at Blacksburg 2, 3% at Clinch 2, and 8% at West Virginia 1. Although this value appears high on Blacksburg 2, these species were found only on one of the treatments (Group Selection) at this site.

The mountain dusky salamander was found at 2 sites, each of which had only 1 year of postharvest data. This species composed 60% of preharvest captures at Clinch 2 and 35% of preharvest captures on West Virginia 1. There was no significant treatment effect in this species ($p = 0.26$); however, relative abundances varied from 137% higher than the Control on the Herbicide treatment to only 13% of Control abundance on the Clearcut (Figure 2. 5).

The redback salamander, the most dominant species numerically, was found at 3 sites. It made up 91% of preharvest captures on Blacksburg 1, 81% of preharvest captures on Blacksburg 2, and 6% of preharvest captures on West Virginia 1. The treatment effect was significant in this species ($p = 0.04$). The Control and Herbicide treatments had significantly higher abundances than all treatments with canopy removal except the Group Selection (Figure 2. 6). With 73% of Control treatment numbers, the Group

Selection had significantly higher abundances than the Leavetree which had the lowest abundance (16% of Control numbers).

The slimy salamander was the only species found at all four sites. It made up 5% of preharvest captures on both Blacksburg 1 and on Blacksburg 2, 9% of preharvest captures on Clinch 2, and 51% of preharvest captures on West Virginia 1. The treatment effect was not significant in this species. Relative abundances ranged from the Group Selection, with 13% more slimy salamanders than the Control, to the Leavetree, with only 32% as many slimy salamanders as the Control (Figure 2. 7). Based on Conant and Collins (1991), slimy salamanders at Blacksburg 1 and Blacksburg 2 are the white-spotted slimy (*Plethodon cylindraceus*) and those at Clinch 2 and West Virginia 1 are the northern slimy salamander (*P. glutinosus*); however, I have followed Petranka (1998) and recognized only one species of slimy salamander.

The ravine salamander was found only at Clinch 2 where it made up 28% of preharvest captures. In this species, the Control had the highest postharvest abundance (Figure 2. 8), followed by the 4-7 Shelterwood and Herbicide with 58% and 54% of Control treatment abundances respectively. The Group Selection and Clearcut treatments had the lowest abundance of the ravine salamander, each with only 13% of Control abundances. Because this species was found only at one site, statistical analysis was not done.

POPULATION CHARACTERISTICS

Snout-Vent-Length

There was no significant effect of treatment on average SVLs using all species ($p = 0.82$), only redback salamanders ($p = 0.19$), or only slimy salamanders ($p = 0.55$). There was a marginally significant treatment effect in the mountain dusky salamander average SVLs ($p = 0.09$). I could not run statistical analysis on the ravine salamander SVLs because of lack of replication.

All Species

Over all species, average SVLs varied from 43.0 mm on the Leavetree to 37.2 mm on the Control. Distributions of the data were similar among treatments except that the distributions of the 4-7 Shelterwood, Leavetree, and Clearcut treatments were somewhat more skewed towards larger SVLs (Figure 2. 9). Again, this analysis is influenced by the relative abundances of large versus small species on each treatment. Analyses for individual species follow.

Main Species

In mountain dusky salamanders, the highest average SVL of 38.7 mm on the Leavetree was significantly longer than the smallest average SVL of 32.2 mm on the 12-14 Shelterwood. Sample sizes were generally low in this species with only 2 mountain dusky salamanders included in the Clearcut, and only 6 and for the 4-7 Shelterwood and Group Selection respectively. Low sample sizes partially contributed to the heterogeneity of SVL distributions. SVL distributions for the Control, Herbicide, and, to some extent, the 12-14 Shelterwood were skewed towards smaller SVLs, but there was no apparent pattern of increasing SVL or skewness with increasing or decreasing canopy removal (Figure 2. 10).

In redback salamanders, average SVLs ranged from 37.4 mm on the Control to 33.3 mm on the Clearcut. The distributions of SVLs were similar among treatments and were all slightly skewed towards smaller SVLs (Figure 2. 11).

Average slimy salamander SVLs ranged from 51.4 mm on the 12-14 Shelterwood to 34.0 mm on the Clearcut. The distributions were generally similar and skewed towards larger SVLs except on the Leavetree and Clearcut treatments where the distributions were skewed towards smaller SVLs (Figure 2. 12).

In ravine salamanders, average SVLs ranged from 42.5 mm on the 4-7 Shelterwood to 29.1 mm on the 12-14 Shelterwood. Distributions of the data were very different among treatments. This difference is in part due to the very low sample sizes in this species

ranging from 2 for the Clearcut to 19 for the Control. Some treatments have positively skewed distributions, others have negatively skewed distributions (Figure 2. 13). There is no apparent pattern in the direction of skewness.

Proportion Juvenile

Three of the 4 main species showed no significant difference in the proportion of juveniles between "uncut" treatments and "cut" treatments. Of mountain dusky salamanders, 27% (26/98) in uncut treatments were juvenile versus 26% (18/70) in cut treatments. Of redback salamanders, 26% were juvenile in both uncut (180/685) and cut (96/365) treatments. Of ravine salamanders, 50% (15/30) in uncut treatments were juvenile versus 41% (14/34) in cut treatments. However, in the slimy salamander, the uncut treatments had significantly larger proportion of juveniles in the sample than cut treatments ($p = 0.01$), with 79% (50/63) juveniles in uncut treatments and 57% (32/56) juveniles in cut treatments.

Proportion Gravid

I found no significant difference between cut and uncut treatments in the proportion of adult females that were gravid in either the mountain dusky salamander or the redback salamander. In the mountain dusky salamander, 58% (11/19) of adult females on uncut treatments were gravid versus 61% (11/18) of adult females on cut treatments. Average numbers of eggs per gravid female was 12.7 in uncut treatments and 12.2 in cut treatments. In the the redback salamander, 31% (81/258) of adult females were gravid on uncut treatments versus 32% (46/146) of adult females on cut treatments. Average number of eggs per gravid female was 6.7 on uncut treatments and 6.9 on cut treatments.

MICROHABITAT VARIABLES

Four years after harvest at Blacksburg 1, average leaf litter biomass was not directly related to amount of canopy removal or salamander abundance (Figure 2. 14). The Control and both Shelterwood treatments had the greatest leaf litter biomass with averages of 805 to 858 g/m^2. The Clearcut had the lowest leaf litter biomass with an average of only 419 g/m^2, followed by the Herbicide with 574 g/m^2. Variation was

highest in the 4-7 Shelterwood and Leavetree. Average soil temperature at 2.5 cm depth was lowest on the Control and Herbicide treatments and highest on the Clearcut (Figure 2. 15). Average soil temperature at 10 cm depth was lowest on the Herbicide and highest on the Clearcut. There was little clear difference among treatments in leaf litter drying rate (Figure 2. 16). All treatments had roughly the same average leaf litter moisture by the third day. Average moisture on the first day was highest on the Control and 4-7 Shelterwood. Variation appeared to increase with increasing canopy removal.

COVERBOARDS

Figure 2. 17 shows how coverboard counts compared with nighttime surface counts taken in the same seasons for the two Blacksburg sites. At Blacksburg 1, average numbers were similar among methods for most treatments in absolute as well as relative numbers with the exception of the Herbicide treatment where coverboard counts found twice as many salamanders as night counts. At Blacksburg 2, night counts of salamander abundance were several times higher than coverboard counts on the Control, but variance on that night count estimate was large. At this site, coverboard counts gave higher estimates than night counts for all treatments with canopy removal (with the exception of the 12-14 Shelterwood on which no salamanders were collected that season), including detecting some salamanders on the Leavetree and Clearcut where none were detected using night counts.

DISCUSSION

The major finding of my study was that any type of canopy removal reduced salamander numbers. Although reductions were not seen on all treatments or all sites (Within Site Analysis), the average effect of canopy removal was a 40% to 65% reduction in salamander numbers by treatment with reductions typically higher on treatments with greater canopy removal (All Sites ANCOVA). Age class distribution, fertility (percent of adult females that were gravid), and fecundity (mean clutch size per gravid female) were unaffected.

PROBLEMS WITH WITHIN-SITE ANALYSIS

I used two categories of analysis on the abundance data in this study: within-site and an ANCOVA combining all sites. Within sites, I looked for a treatment effect within years and for differences among years within a treatment following Harpole (1996) and Harpole and Haas (1999). The ANCOVA combining all sites had few replicates (4 sites), but was free of pseudoreplication, and accounted for variation among sites and for preharvest differences in abundance among plots. I argue here that the within site analysis is problematic and the latter analysis or a similar form should be used in studies such as this one that look at the effects of some type of habitat alteration.

First, finding variation among treatments can be misleading if variation existed preharvest. This was not a problem for Harpole (1996) who dealt with the first year of postharvest data on the Blacksburg 1 site or Harpole and Haas (1999) who dealt with the first 3 years of postharvest data on the Blacksburg 1 site. However, even controlled ecological experiments are rarely entirely homogeneous. Both Blacksburg 2 and Clinch 2 showed significant variation among plots preharvest (Table 2. 3 and Table 2. 4).

Second, variation among years within a treatment can also be misleading. The Clinch 2 site had two years of preharvest data available. When testing for differences among all 3 years, I found significant differences in 6 of the 7 treatment plots, including the Control (Table 2. 4). This difference can be attributed to the differences in abundances between the two preharvest years; consistently more salamanders were found in 1994 than in 1996. Differences between preharvest years do not negate the validity of this sampling method, assuming relative abundances among plots remain similar year-to-year without habitat alteration. Sources of the difference among years can include differences in average sampling effort or average salamander activity among years. A variety of technicians and volunteers sampled over the years for this project. The ability of different individuals to observe salamanders may vary. Even if the same sampling crews were used from year to year, there could be differences among years due to increased experience. Also, there are differences in salamander activity among nights. Even within our protocols, some nights are wetter, closer to optimal temperatures, or earlier in

the season (when females are not yet brooding eggs) than others. Because sampling nights are dependent upon the weather, we are not able to sample either randomly or on a fixed schedule, and the average quality of sampling nights for finding salamanders could vary among years. At the West Virginia 1 site, there was no significant change between years in any of the treatments, and 3 of the 4 treatments with canopy removal either decreased by less than 10% or increased from the preharvest year to the first year postharvest (Table 2. 5). However, the Control increased 82% in the same time period. Because all treatments were always sampled during the same night by the same people, if there was that large of an increase in the Control, one would expect the other plots to have increased as well, had they not been harvested. Accounting for this expected increase, the apparent lack of change in those 3 harvested plots would translate into declines of 40 to 50%.

Finally, the advantage of this study is that it compares several silvicultural methods simultaneously, allowing the assesment of the relative costs or advantages of one method over another. The most useful management implications to be gained from this type of study are the impacts of one option on salamanders versus the impacts of another option. Relative impacts are obfuscated by separate analysis. Differences in preharvest abundances and changes in the Control plots must both be taken into account. In addition, there will be at least some differences in response site-to-site due to observational and experimental error. With 6 non-Control treatments and 4 sites, this quickly becomes too much information to determine by eye. Combining all information allows a clearer picture to form.

COMPARISON OF RESULTS WITH SIMILAR STUDIES

Ash (1997) found that plethodontid salamanders, primarily Jordan's salamander (*Plethodon jordani*), declined by 30 to 50% within the first year on clearcut plots and declined to near zero by the second year. This first year decline is comparable to that seen on our clearcut plots. The clearcut on Blacksburg 2 did drop to zero by the third year postharvest, but average abundance on the clearcut was never below 1 salamander per transect on Blacksburg 1. Petranka *et al*. (1993), whose primary species were

Jordan's salamander and the mountain dusky salamander, found declines of 75 to 80% due to clearcutting. However, clearcuts up to 10 years old were used in that study and so are not directly comparable to the short term effects dealt with here. In their review, deMaynadier and Hunter (1995) also found reductions of 80% due to clearcutting; but again this included studies with clearcuts less than 1 year old up to 40 years old.

Some studies also examined the effects of shelterwoods; selective cuts, such as thinning for firewood; and the effect of gaps. Sattler and Reichenbach (1998) looked at the effects of clearcuts and shelterwoods on the Peaks of Otter salamander (*Plethodon hubrichti*) within the first two years postharvest. Their shelterwood treatments removed from 33 to 64% of the original basal area, which is comparable to the 12-14 Shelterwood in this study, which removed about 40%. The Peaks of Otter salamander declined 70% in the clearcut, comparable to the results in this study, but there was no change in numbers in the shelterwood treatment. Although the 12-14 Shelterwood in this study had only 54% of the salamander abundance as the Control, this was not significantly different from the Control. Mitchell *et al*. (1996) examined the effects of 4-5 year old clearcuts and 2-4 year old shelterwoods on the Peaks of Otter salamander. They found 10 to 66% reductions on shelterwoods and 45 to 47% reductions on clearcuts, neither of which was statistically significant. Messere and Ducey (1998) found no effects of selective logging on redbacked salamanders in the first year postharvest. However, at 22 to 94 m^2, the forest gaps they studied were only 1 to 6% as large as the average Group Selection cut used in this study. Pough *et al*. (1987) also examined the effects of selective cuts for firewood one year postharvest and found it had no effect on redback salamanders. Both of these studies examined treatments with far less canopy disturbance than any treatment with canopy removal in this study.

Current estimates of time for a salamander population to recover to preharvest levels from clearcutting are as little as 20 to 24 years (Ash 1997) to as long as 50 to 70 years (Petranka 1993 *et al*). This study examined only the immediate postharvest effects of the 7 silviculture methods. There was little or no replication of postharvest years 2 through 4, so year effects were not analyzed here. However, differences in recovery rates among

the treatments will potentially have greater management implications. Following these sites for several years postharvest will not only allow for the comparison of recovery times of different treatments but will also contribute to the understanding of recovery times for clearcuts by avoiding difficulties due to chronosequence techniques (Petranka *et al*. 1993) or due to pseudoreplication (Ash 1997, see also Petranka 1999).

ABUNDANCE INCREASES ON HERBICIDE TREATMENT

The Herbicide treatment had abundances 24% higher than those on the Control. Our sample size was low (4 sites) and the difference was not statistically significant, so the question remains whether the trend is real and will be supported with further replication. The Herbicide treatment in this study may have resulted in a slight (10-15%) increase in herbaceous plants which would insulate the ground and lead to a slight (10-15%) increase relative humidity (Dr. David W. Smith, Virginia Tech Department of Forestry, pers. comm.). This should increase the amount of time a salamander is able to forage. Jaeger (1978) found that redback salamanders foraging on plants ingested a significantly larger volume of food than those that remained on the forest floor to forage. The increased herbaceous layer could also provide higher quality foraging opportunities. It is unclear whether increases in salamander counts on this treatment are a result of increases in population size or in activity rates (see Chapter 3) due to the increased humidity.

IMPACTS ON AGE CLASS DISTRIBUTION AND REPRODUCTION

Results from SVL distributions, proportion gravid, and proportion juvenile (except in the slimy salamanders) all suggest that timber harvesting affected the entire salamander population without targeting any age class or species more than another.

The percent gravid and percent juvenile differed less than 3% between treatment classes for the redback and mountain dusky salamander. However, although mean SVL did not differ significantly among treatments, the treatments with the least canopy removal and highest salamander abundances (Control, Herbicide, and Group Selection) had the smallest SVLs. Further replication and longer periods after harvest may provide evidence of a relationship between timber harvest and size distributions in terrestrial salamanders. Larger salamanders may be expected to persist longer in more severe

habitats because they are less prone to dessication (Spotila 1972) and more likely to be able to defend high quality burrows and cover objects (Mathis 1990, Jaeger and Forester 1993, Gabor 1995).

Fertility and fecundity estimates were somewhat lower in this study than what has been reported previously for these species. Fertility rates of adult (> 30 mm SVL) female mountain dusky salamanders were approximately 60% in this study with average clutch size between 12 and 13 eggs, compared to annual reproduction (100%) and mean clutch sizes of 16 to 20 eggs in Pennsylvania and Virginia respectively (Petranka 1998). In this study, fertility rates of adult (> 34 mm SVL) female redback salamanders were approximately 30% with mean clutch size of just under 7 eggs. The mean clutch size is similar to with previous studies that found mean clutch sizes of 6 to 9 eggs from studies in Massachusetts, New York, Connecticut, Michigan, Tennesee, and Virginia; however, reproduction in this species is generally thought to be annual to biennial (Petranka 1998) (50 to 100%). Fecundity in salamanders can be measured by clutch volume (egg number times egg volume). Size of eggs could not be measured here because it would require sacrificing gravid females, thereby affecting results of later years. Reduced egg volume could reduce juvenile survivorship (Kaplan 1980, Travis 1983, Kaplan 1985) but the lack of a treatment effect in the proportion juvenile in these species suggests there was no reduced juvenile survivorship.

BIAS IN SAMPLING METHOD

Results from the Blacksburg 1 site indicate the night sampling method was not biased due to reduced ability to see salamanders in harvested plots (Figure 2. 17). However, results from the Blacksburg 2 sites seem to contradict results from Blacksburg 1. At Blacksburg 2, counts on the treatments relative to the Control were all higher with coverboards than with night counts. However, on Blacksburg 2, the night sample Control mean had a large variation. The high mean is due to one anomolously high night sample. Removing that sample night, the Control mean is only 0.25 salamanders per night, less than the mean for the coverboard sample. Without that sample, counts on the treatments relative to the controls are very close with both methods. They are higher with night counts than

coverboards on the Herbicide and Group Selection, identical between methods on the both Shelterwoods, and higher with coverboards on the Leavetree and Clearcut on which no salamanders were detected during that time period in night samples.

Table 2. 1. Locations, harvest dates, and years sampled (Pre- and Postharvest) for the four sites used in this study. Aspect, Slope, Site Index, and Stand Age from Bryan Wender, Virginia Tech Department of Forestry (unpublished).

	Blacksburg 1	Blacksburg 2	Clinch 2	West Virginia 1
Location	Montgomery Co., Viginia	Montgomery Co., Virginia	Wise Co., Virginia	Randolph Co., West Virginia
Harvest Dates	11/94 - 5/95	11/95 - 6/96	5/97 - 3/98	5/97 - 8/97
Preharvest Sampling Years	1994	1995	1994, 1996	1996
Postharvest Sampling Years[a]	(1) 1995 (2) 1996 (3) 1997 (4) 1998	(1) 1996 (2) 1997 (3) 1998	(1) 1998	(1) 1998
Elevation	710 m	730 m	1040 m	880 m
Aspect	153˚	151˚	108˚	270˚
Slope	16%	21%	16%	38%
Site $Index_{50}$ White Oak	23 m	22 m	20 m	23 m
Stand Age	100 yrs	99 yrs	76 yrs	73 yrs

[a] Number in parentheses represents the year postharvest.

Table 2. 2. Average salamander abundance per 2 m x 15 m transect per sampling night for Blacksburg 1 site, showing results of Kruskal-Wallis nonparametric test across years within treatments and across treatments within years. Standard errors are shown in Figure 2. 2.

		Treatment							
Year	n	Control	Herbicide	Group	12-14 Shelter.	4-7 Shelter.	Leavetree	Clearcut	p
0 (1994)	7	8.00	8.14	10.86	7.43	9.86	7.14	9.00	0.95
1 (1995)	9	9.22	9.78	9.44	5.56	3.56	3.67	6.33	0.02
2 (1996)	10	6.90	10.00	3.50	2.00	1.60	1.00	1.80	< 0.01
3 (1997)	11	10.64	9.82	2.82	2.00	0.91	0.73	1.36	< 0.01
4 (1998)	9	8.44	13.00	6.00	3.78	2.56	2.78	1.89	< 0.01
	p	0.68	0.64	0.01	0.04	< 0.01	< 0.01	< 0.01	

Table 2. 3. Average salamander abundance per 2 m x 15 m transect per sampling night for Blacksburg 2 site, showing results of Kruskal-Wallis nonparametric test across years within treatments and across treatments within years. Standard errors are shown in Figure 2. 2.

		Treatment							
Year	n	Control	Herbicide	Group	12-14 Shelter.	4-7 Shelter.	Leavetree	Clearcut	p
0 (1995)	8	1.63	1.00	5.38	1.38	2.75	1.63	1.25	0.01
1 (1996)	2	0.50	0.50	2.50	0.00	2.00	0.00	2.00	0.49
2 (1997)	9	1.56	1.22	5.11	0.67	0.56	0.00	0.89	< 0.01
3 (1998)	5	3.40	1.80	4.40	0.00	0.60	0.00	0.00	0.19
	p	0.74	0.76	0.84	0.10	0.03	0.06	0.19	

Table 2. 4. Average salamander abundance per 2 m x 15 m transect per sampling night for Clinch 2 site, showing results of Kruskal-Wallis nonparametric test across years within treatments and across treatments within years. Standard errors are shown in Figure 2. 2.

		Treatment							
Year	n	Control	Herbicide	Group	12-14 Shelter.	4-7 Shelter.	Leavetree	Clearcut	p
0 (1994)	5	25.00	21.40	14.60	18.00	13.80	15.80	19.60	0.07
0 (1996)	5	10.80	5.20	3.00	12.80	5.60	8.60	9.40	0.02
0 (both)	10	17.90	13.30	8.80	15.40	9.70	12.20	14.50	0.08
1 (1998)	6	14.67	11.17	2.00	10.83	4.00	4.83	1.67	< 0.01
	p[a]	< 0.01	0.01	< 0.01	0.25	0.01	< 0.01	< 0.01	
	p[b]	0.41	0.67	0.05	0.23	0.06	0.01	< 0.01	

[a] This test compared each calendar year separately.

[b] This test compared the combined preharvest years (1994 and 1996) with the postharvest year (1998).

Table 2. 5. Average salamander abundance per 2 m x 15 m transect per sampling night for West Virginia 1 site, showing results of Kruskal-Wallis nonparametric test across years within treatments and across treatments within years. This site lacked the Herbicide and 4-7 Shelterwood treatments. Standard errors are shown in Figure 2. 2.

		Treatment							
Year	n	Control	Herbicide	Group	12-14 Shelter.	4-7 Shelter.	Leavetree	Clearcut	p
0 (1996)	5	1.40	n/a	3.40	3.00	n/a	2.60	2.20	0.53
1 (1998)	9	2.56	n/a	3.11	1.78	n/a	2.44	2.33	0.66
	p	0.20	n/a	0.82	0.31	n/a	0.89	0.85	

Table 2. 6. Relative abundance of main species at each site. Values given are the percent of total captures each species comprised over all sampling years at each site.

	Mountain Dusky	Redback	Slimy	Ravine
Blacksburg 1	-	93% (1654/1782)	5% (84/1782)	-
Blacksburg 2	-	75% (207/276)	12% (32/276)	-
Clinch 2	62% (749/1213)	-	8% (102/1213)	28% (337/1213)
West Virginia 1	19% (33/173)	12% (20/173)	60% (103/173)	-
All Sites	23% (782/3444)	55% (1881/3444)	9% (321/3444)	10% (337/3444)

Table 2. 7. Number of salamanders of miscellaneous species captured from 1994 to 1998 at each site.

Species	Blacksburg 1	Blacksburg 2	Clinch 2	West Virginia 1
Green (*Aneides aeneus*)			2	
N. dusky (*Desmognathus fuscus*)	35	27		
Seal (*D. monticola*)		2		
N. two-lined (*Eurycea bislineata*)				2
S. two-lined (*Eurycea cirrigera*)	2	8		
Spring (*Gyrinophilus porphyriticus*)	5			
Wehrle's (*Plethodon wehrlei*)				15
Cumberland Plateau (*P. kentucki*)			4	
N. red (*Pseudotriton ruber*)	2			

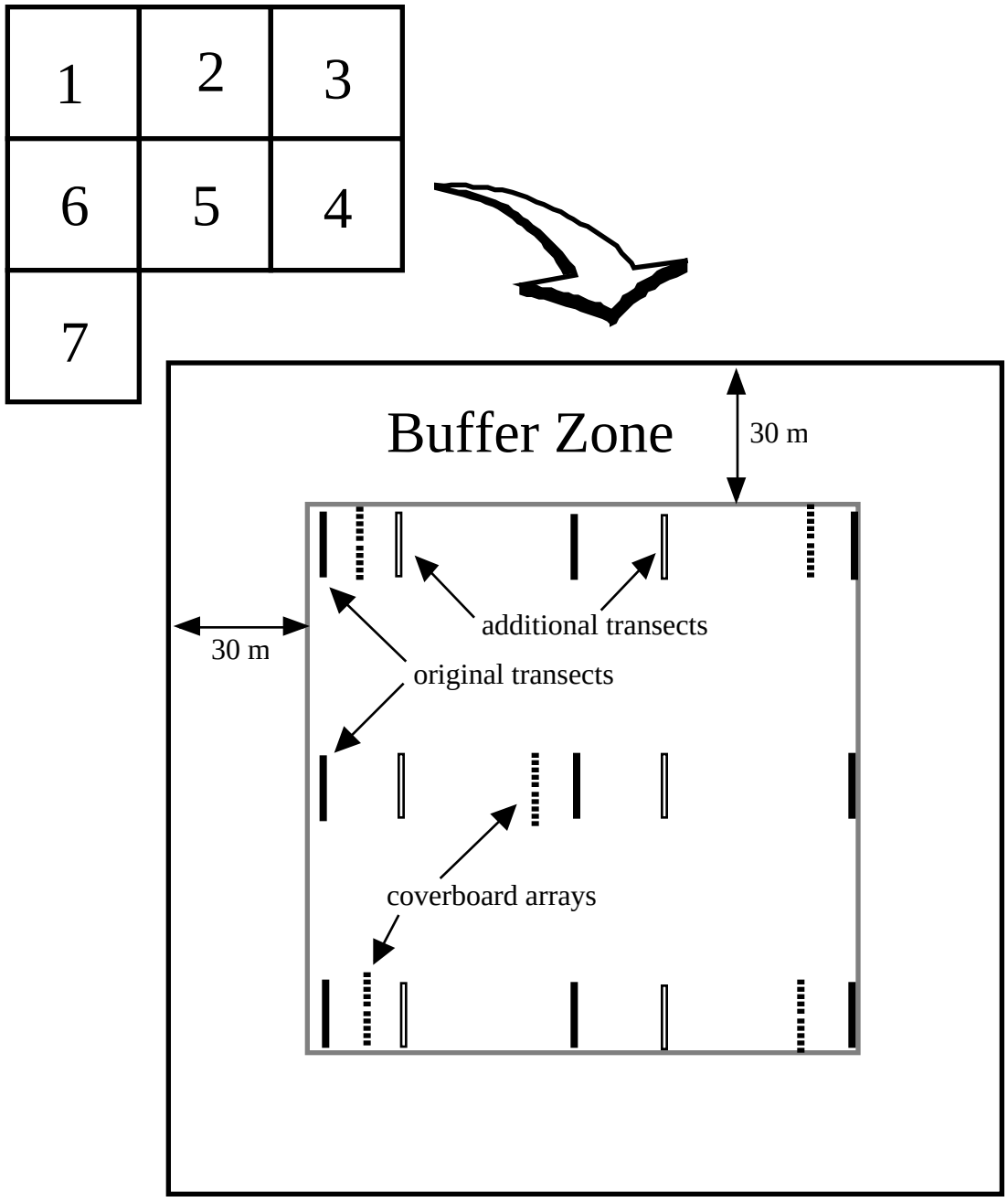

Figure 2. 1. Diagram of site and treatment layout. Scale is approximate. Nine transects of orginial grid shown as long black rectangles. Six additional transects shown as long white rectangles.

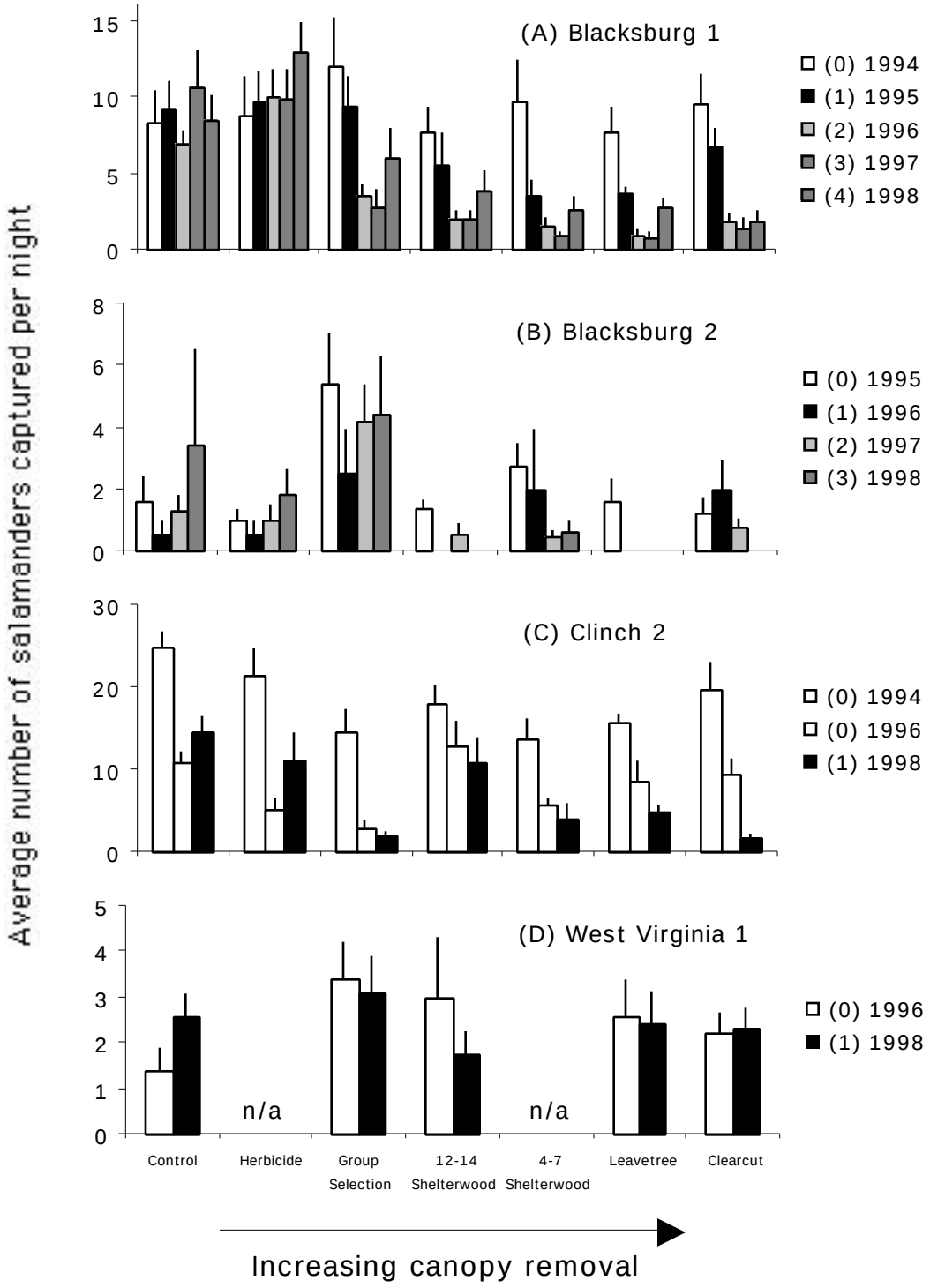

Figure 2. 2. Average number of salamanders captured per night per transect (mean + SE) for (A) Blacksburg 1, (B) Blacksburg 2, (C) Clinch 2, and (D) West Virginia 1.

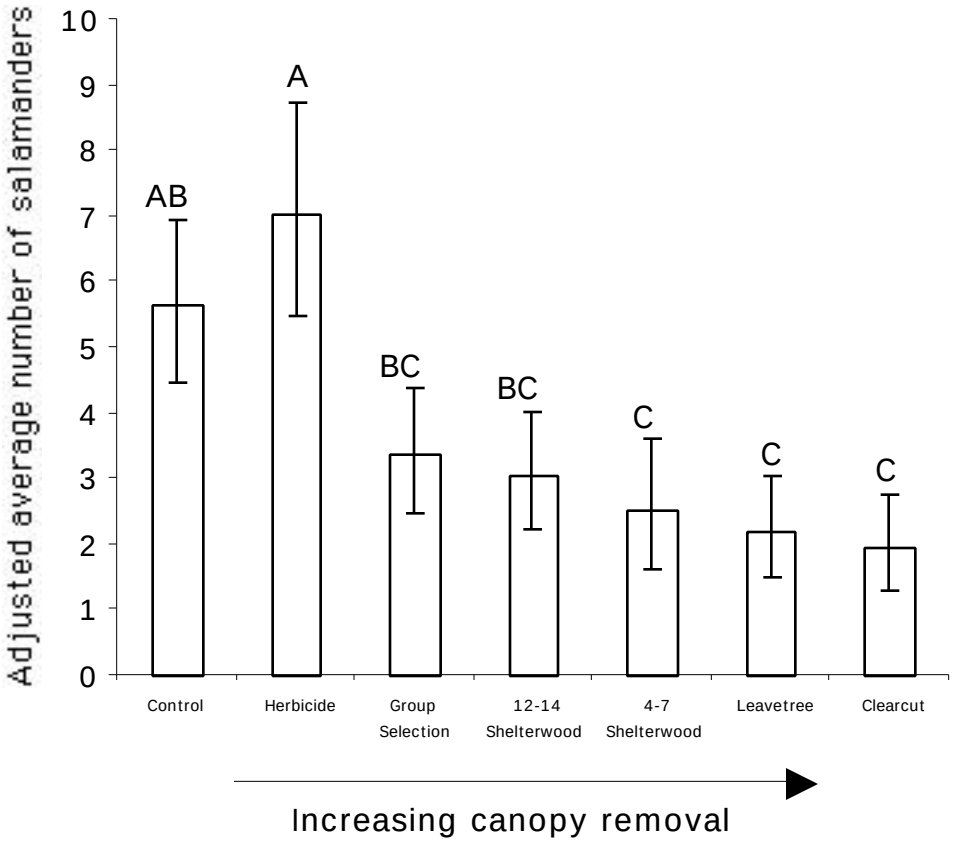

Figure 2. 3. Number of salamanders per treatment (mean + SE). Values given include all species, all sites, and all years and are adjusted for preharvest abundances. Letters above the bars indicate significant difference at p = 0.10.

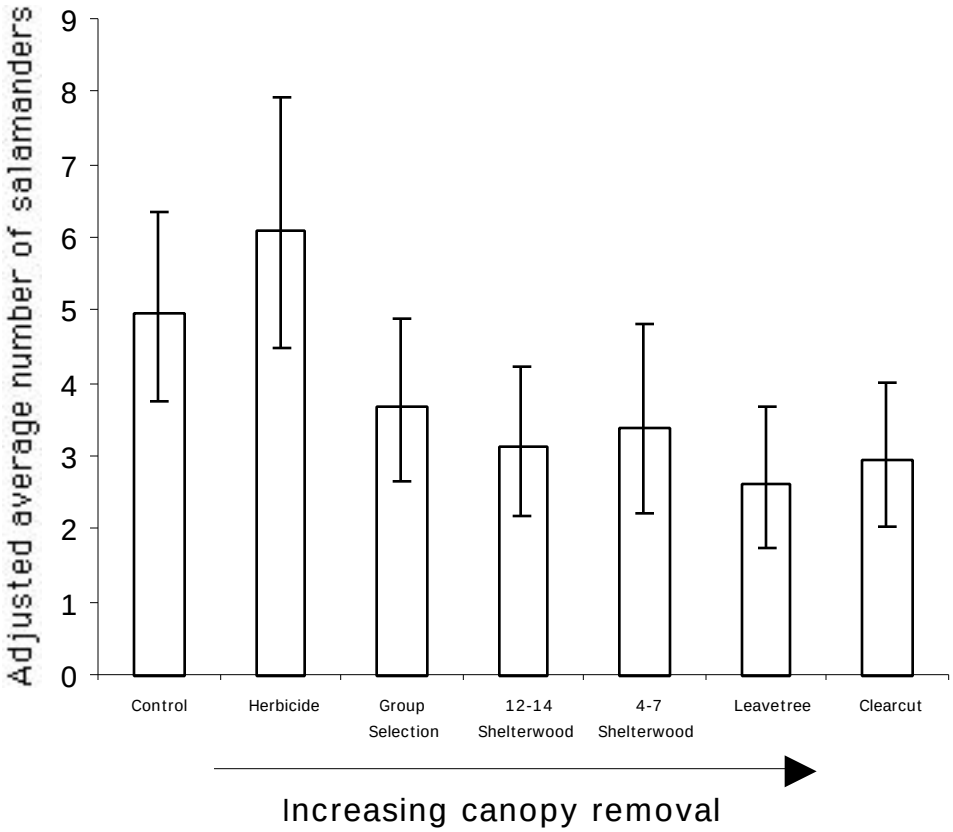

Figure 2. 4. Number of salamanders per treatment (mean + SE). Values given are adjusted for preharvest abundances and include all species and all sites, but only data from the first-year postharvest. Treatments did not differ at p = 0.10.

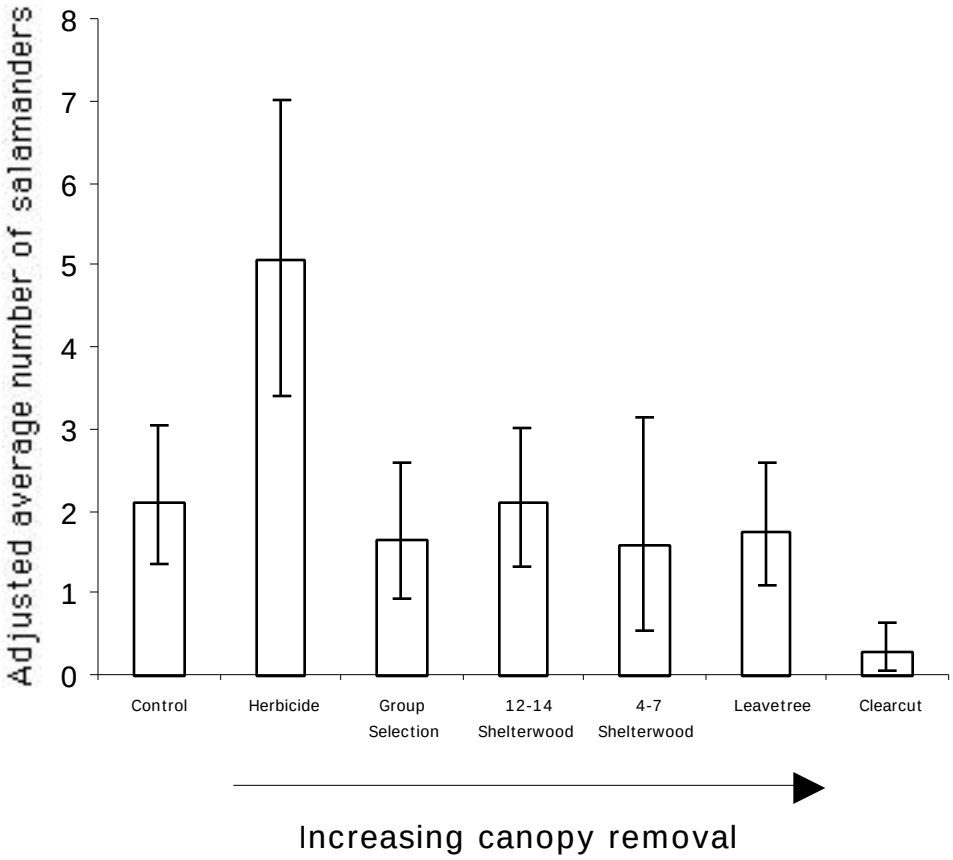

Figure 2. 5. Number of mountain dusky salamanders (*Desmognathus ochrophaeus*) per treatment (mean + SE). Values are adjusted for preharvest abundances and include first-year postharvest data from Clinch 2 and West Virginia 1. Treatments did not differ at p = 0.10.

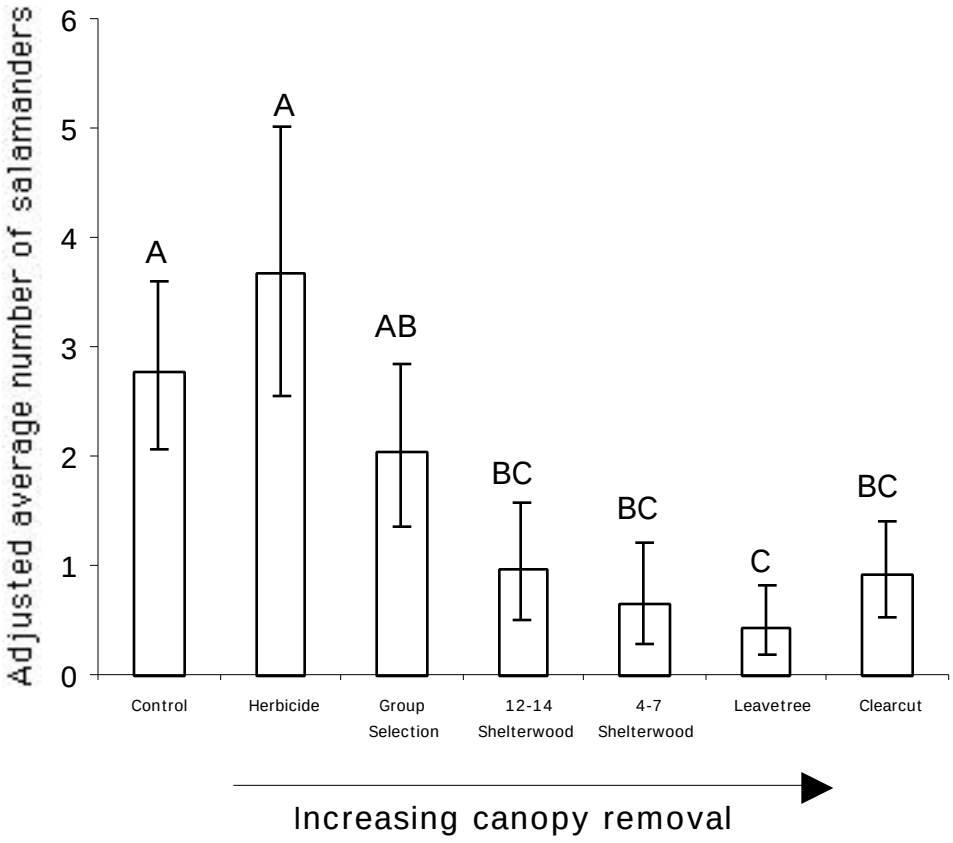

Figure 2. 6. Number of redback salamanders (*Plethodon cinereus*) per treatment (mean + SE). Values are adjusted for preharvest abundances and include all years from Blacksburg 1, Blacksburg 2, and West Virginia 1. Letters above the bars indicate significant differences at p = 0.10.

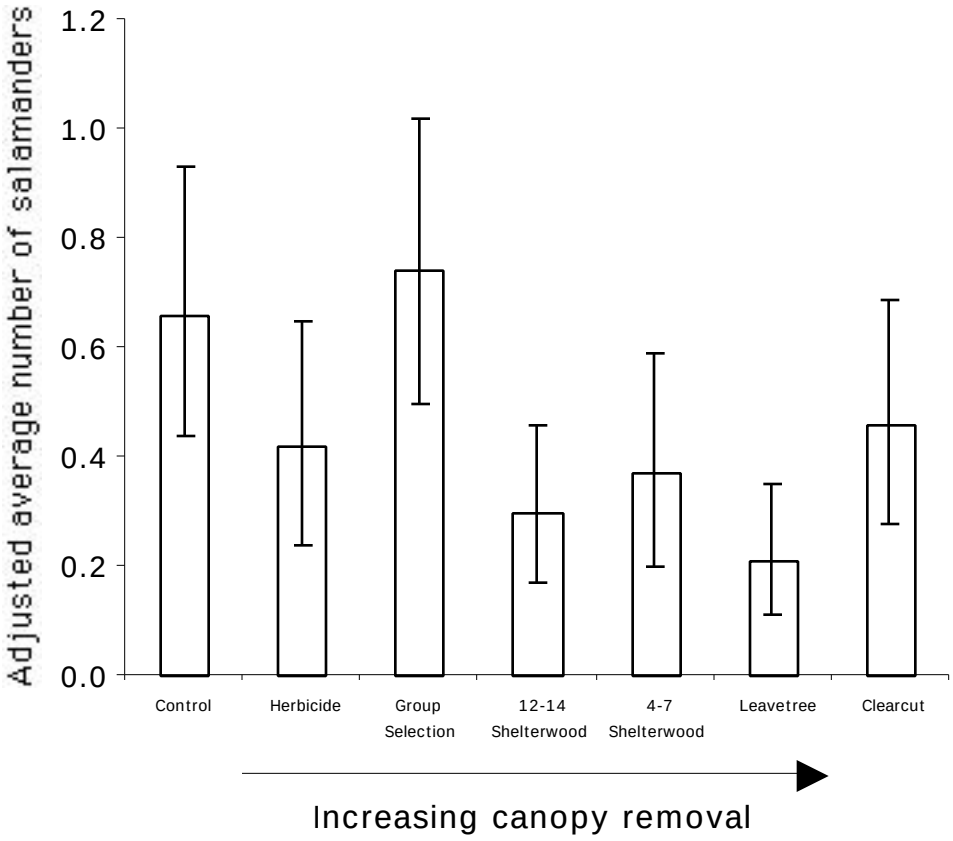

Figure 2. 7. Number of slimy salamanders *(Plethodon glutinosus*) per treatment (mean + SE). Values are adjusted for preharvest abundances and include all years and all sites. Treatments did not differ at p = 0.10.

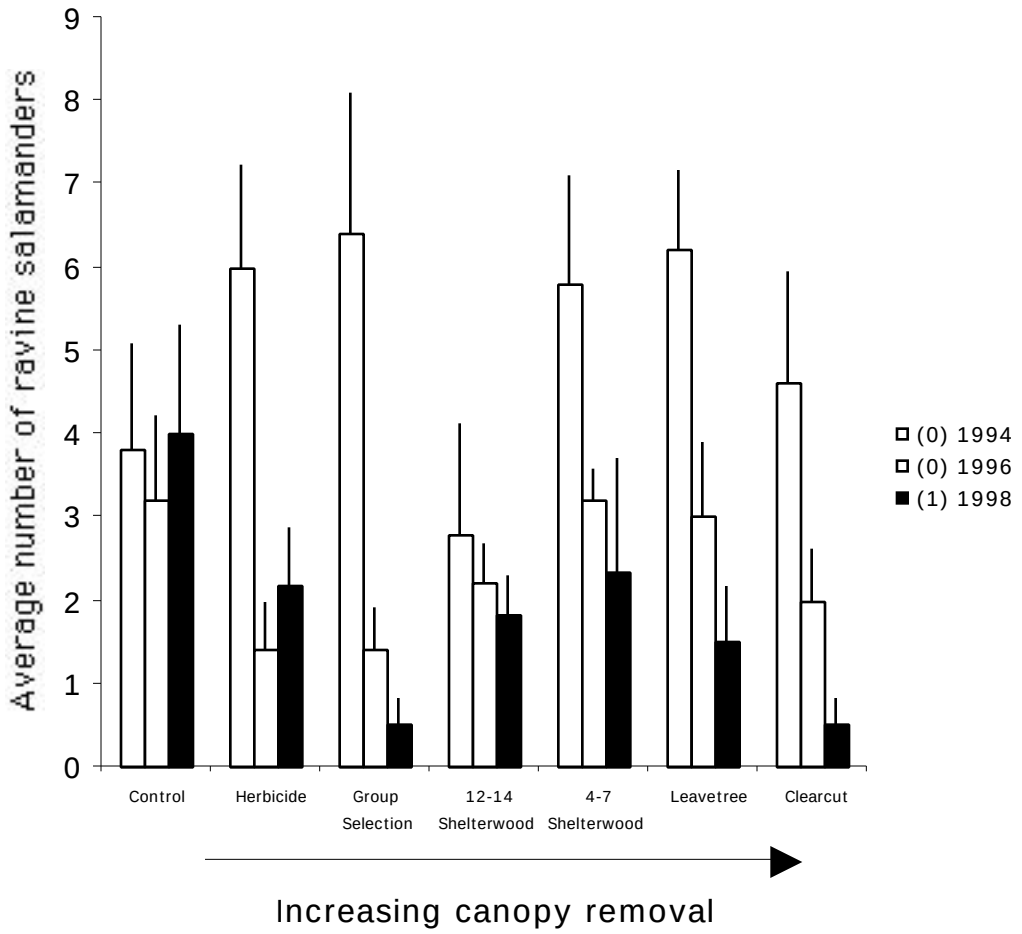

Figure 2. 8. Number of ravine salamanders (*Plethodon richmondi*) (mean + SE) per treatment plot per year.

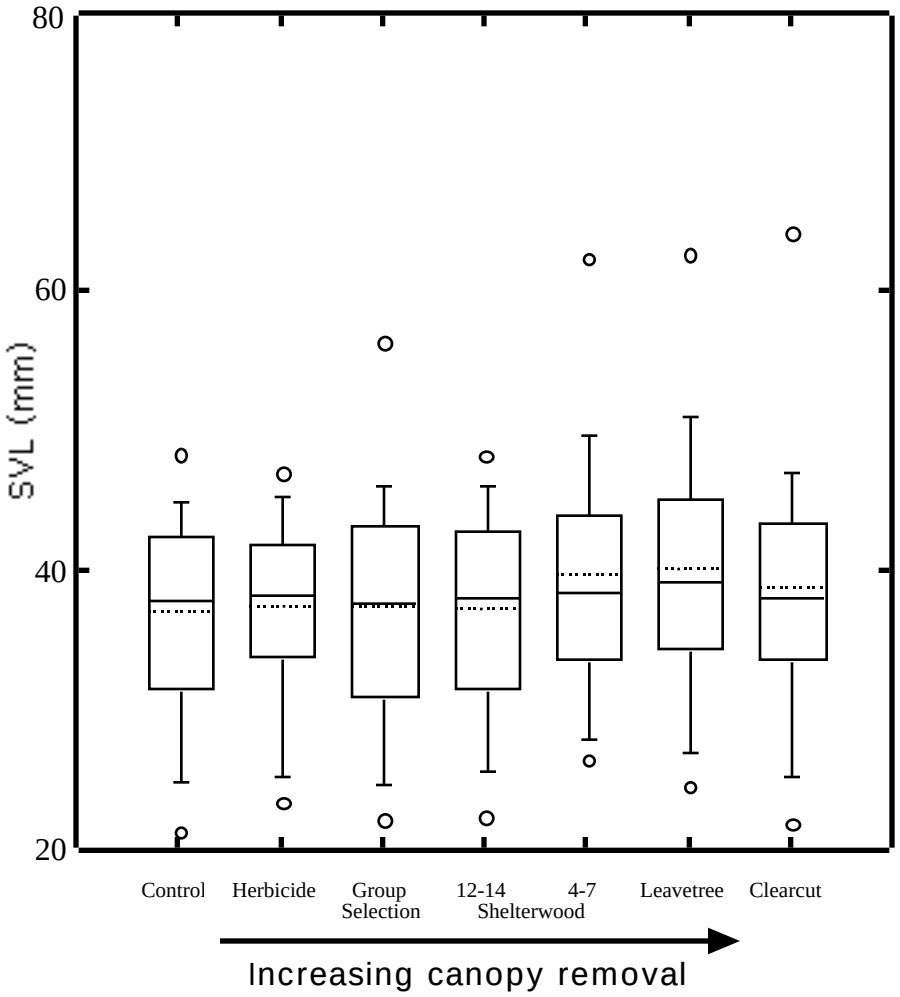

Figure 2. 9. Snout-Vent Length (SVL) distributions by treatment for all species combined. Boxes represent the 25th and 75th percentiles. Vertical bars represent the 10th and 90th percentiles. Fifth and 95th percentiles are represented by circles. Medians are represented by solid lines within boxes. Means are represented by dotted lines. Values given here lump all sites and postharvest years. Means presented in the text are the averages of the within-site averages.

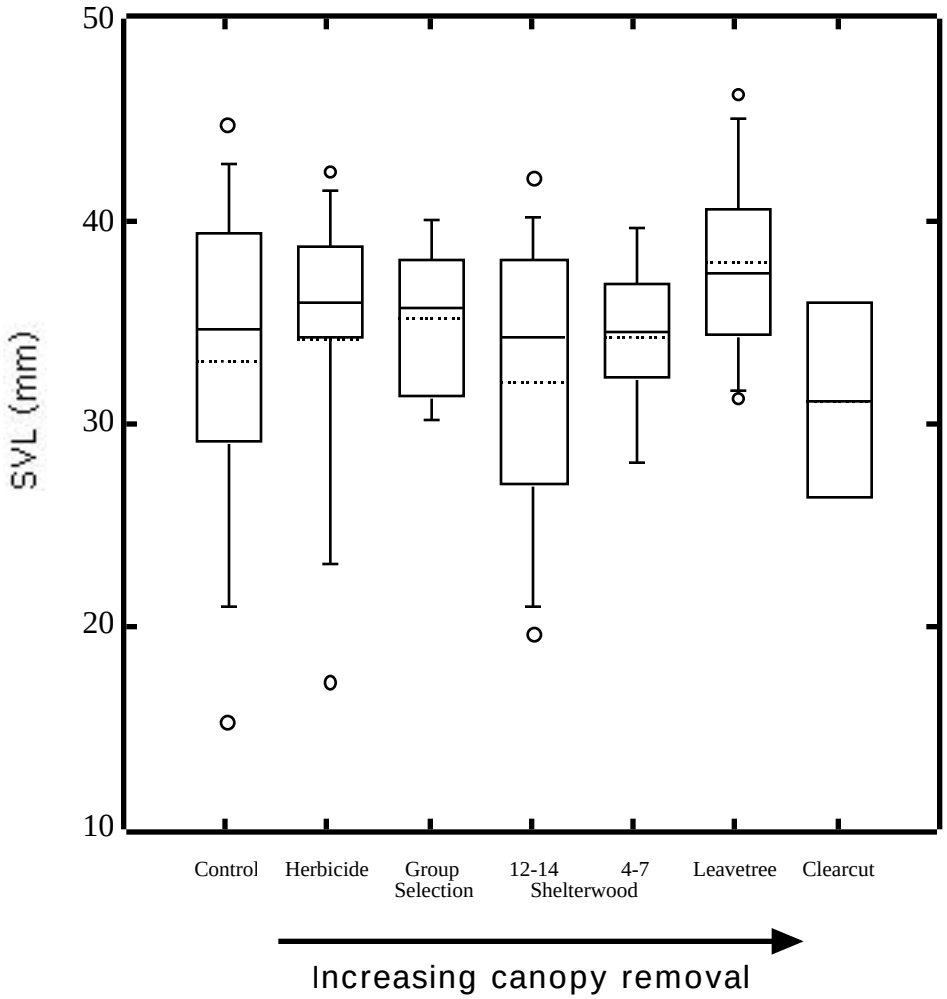

Figure 2. 10 . Snout-Vent Length (SVL) distributions by treatment for mountain dusky salamanders *(Desmognathus ochrophaeus*) from the Clinch 2 and West Virginia 1 sites. Boxes represent the 25th and 75th percentiles. Vertical bars represent the 10th and 90th percentiles. Fifth and 95th percentiles are represented by circles. Medians are represented by solid lines within boxes. Means are represented by dotted lines. The box for the Clearcut represents only 2 salamanders, so mean and median are both the middle bar. Values given here lump all sites and postharvest years. Means presented in the text are the averages of the within-site averages.

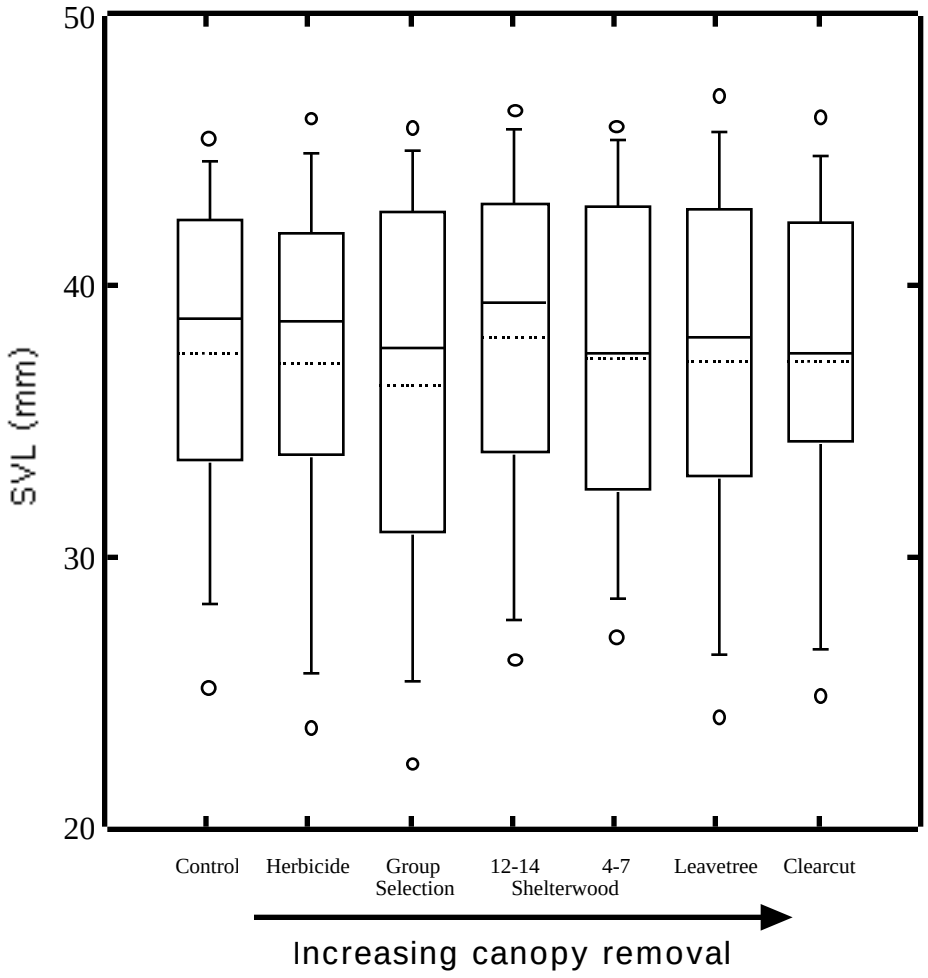

Figure 2. 11 Snout-Vent Length (SVL) distributions by treatment for redback salamanders (*Plethodon cinereus*) from the Blacksburg 1, Blacksburg 2, and West Virginia 1 sites. Boxes represent the 25th and 75th percentiles. Vertical bars represent the 10th and 90th percentiles. Fifth and 95th percentiles are represented by circles. Medians are represented by solid lines within boxes. Means are represented by dotted lines. Values given here lump all sites and postharvest years. Means presented in the text are the averages of the within-site averages.

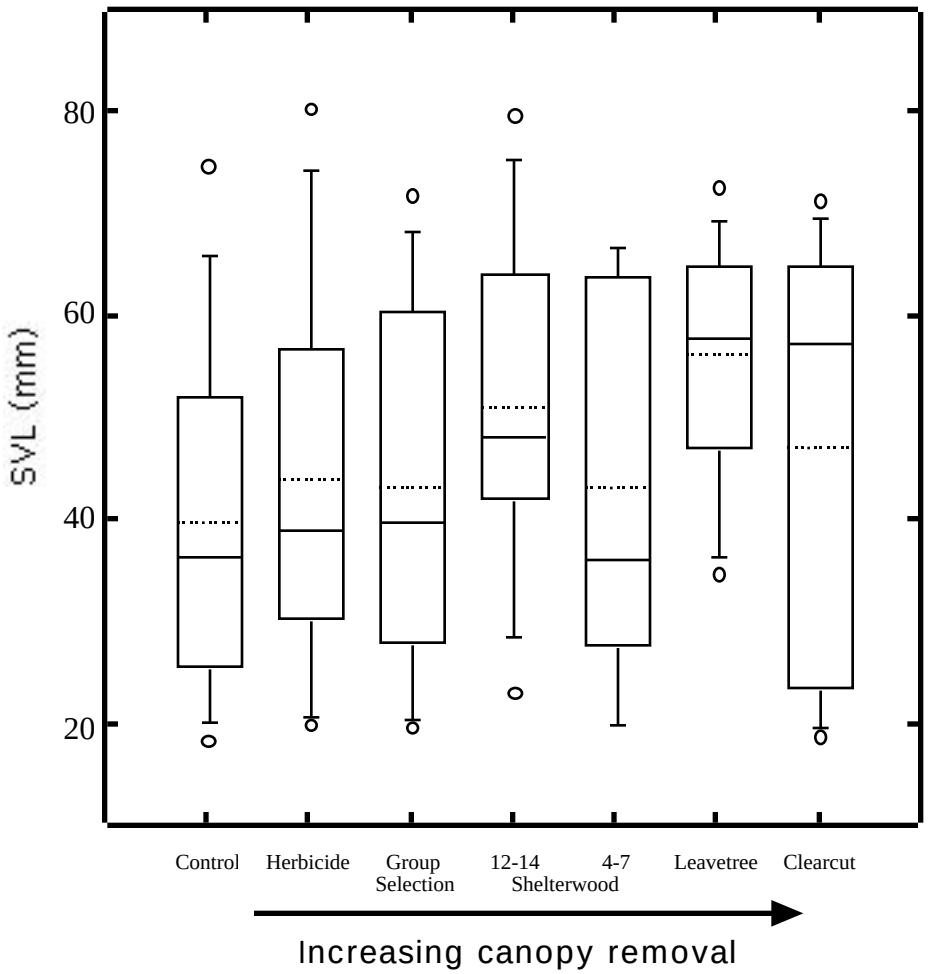

Figure 2. 12. Snout-Vent Length (SVL) distributions by treatment for slimy salamanders (*Plethodon glutinosus*) from all sites. Boxes represent the 25th and 75th percentiles. Vertical bars represent the 10th and 90th percentiles. Fifth and 95th percentiles are represented by circles. Medians are represented by solid lines within boxes. Means are represented by dotted lines. Values given here lump all sites and postharvest years. Means presented in the text are the averages of the within-site averages.

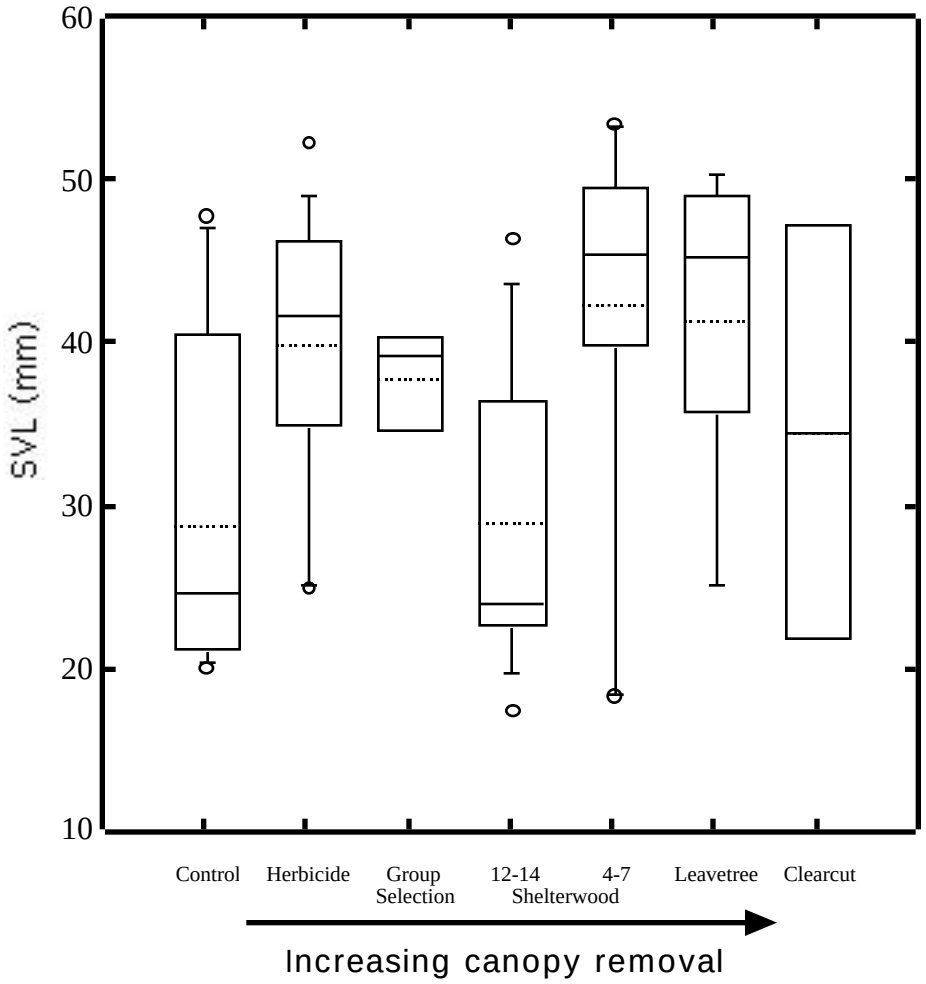

Figure 2. 13. Snout-Vent Length (SVL) distributions by treatment for ravine salamanders (*Plethodon richmondi*) from the Clinch 2 site. Boxes represent the 25th and 75th percentiles. Vertical bars represent the 10th and 90th percentiles. Fifth and 95th percentiles are represented by circles. Medians are represented by solid lines within boxes. Means are represented by dotted lines. The box for the Clearcut treatment is derived from only 2 salamanders so the mean and median are both the middle bar. Additionally, the box for the Group Selection treatment is derived from only 3 salamanders and, therefore, lacks vertical bars. Values given here lump all sites and postharvest years. Means presented in the text are the averages of the within-site averages.

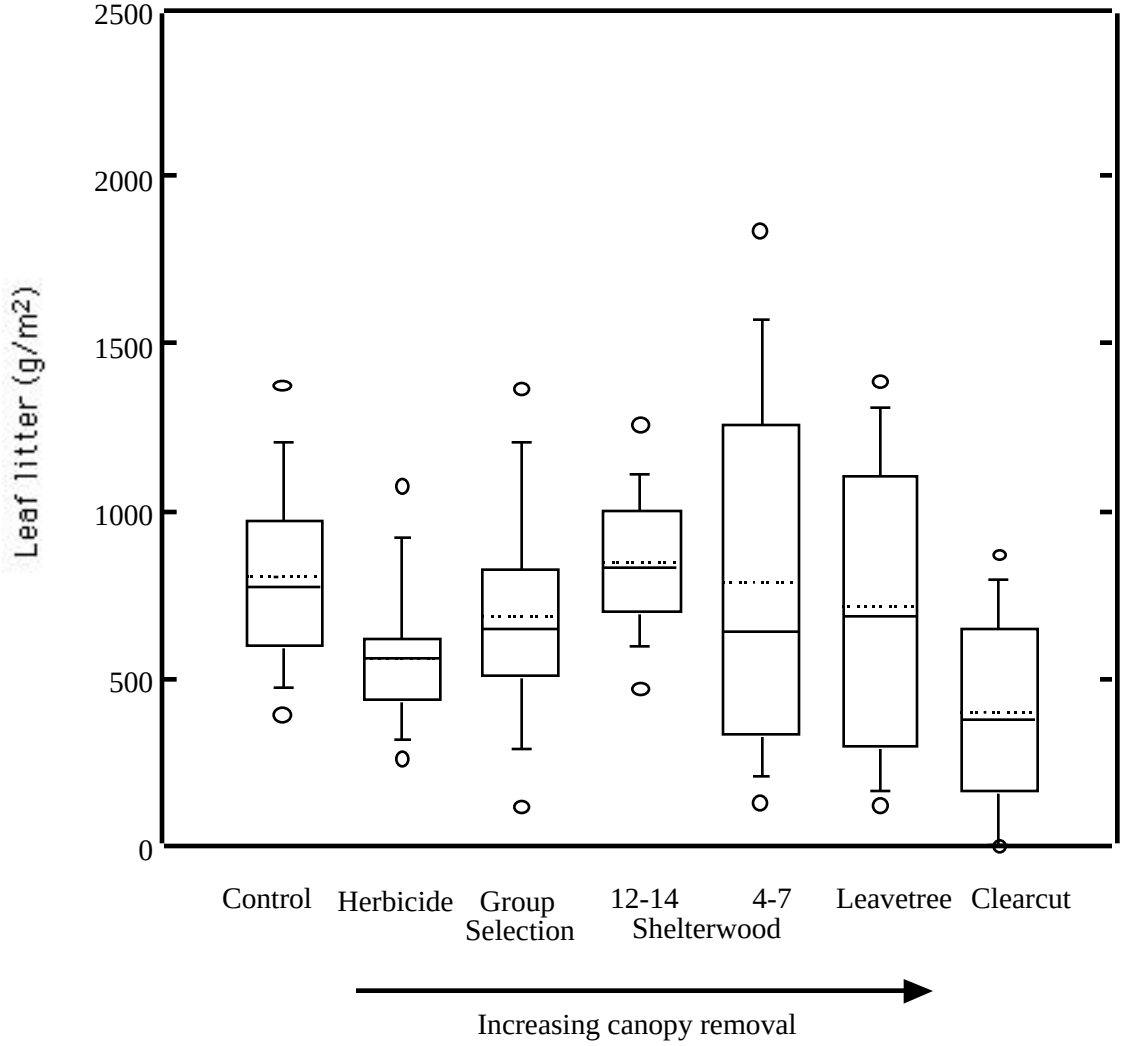

Figure 2. 14. Leaf litter biomass taken at Blacksburg 1 in August 1998 (4th year postharvest). Boxes represent the 25th and 75th percentiles. Vertical bars represent the 10th and 90th percentiles. Fifth and 95th percentiles are represented by circles. Medians are represented by solid lines within boxes. Means are represented by dotted lines.

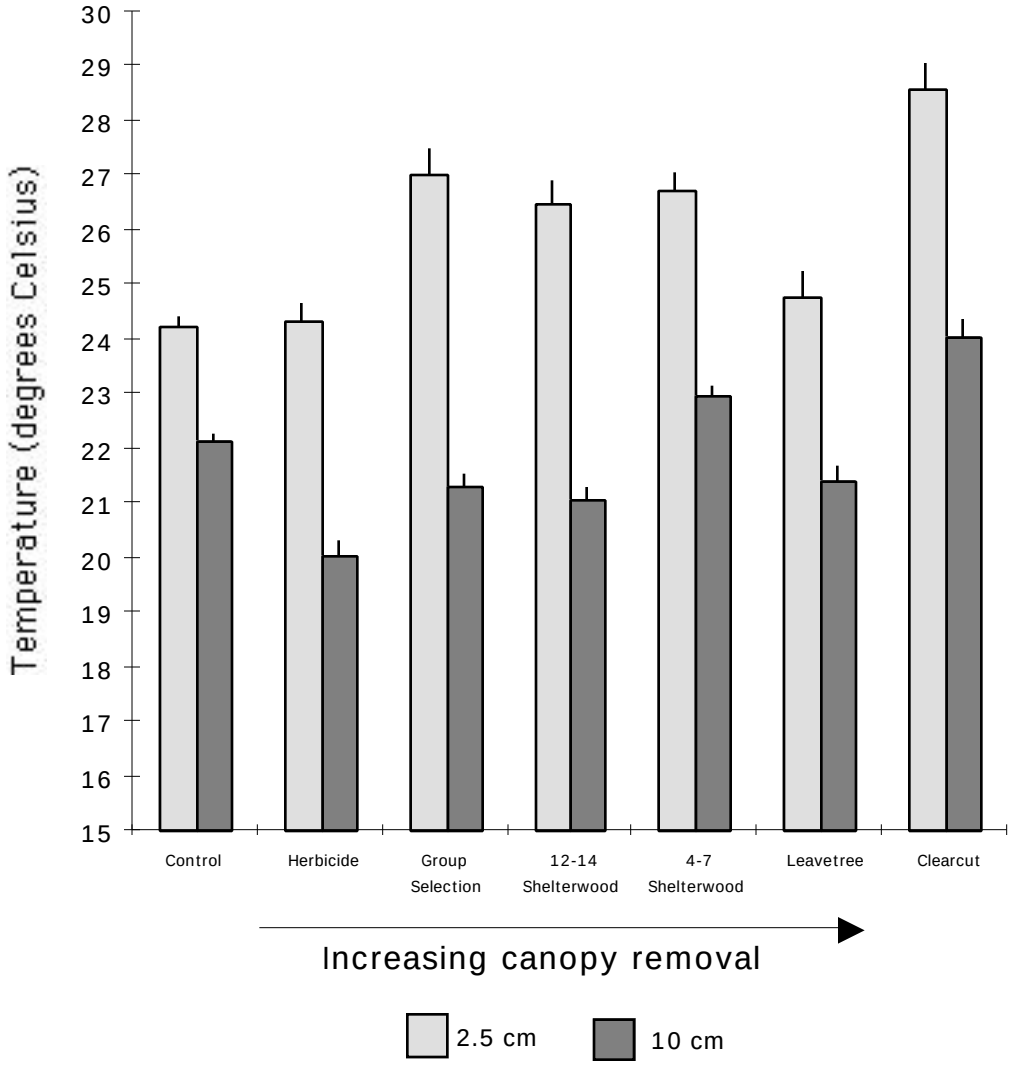

Figure 2. 15. Average daytime soil temperatures (mean + SE) at two depths taken at Blacksburg 1 in August 1998 (4th year postharvest).

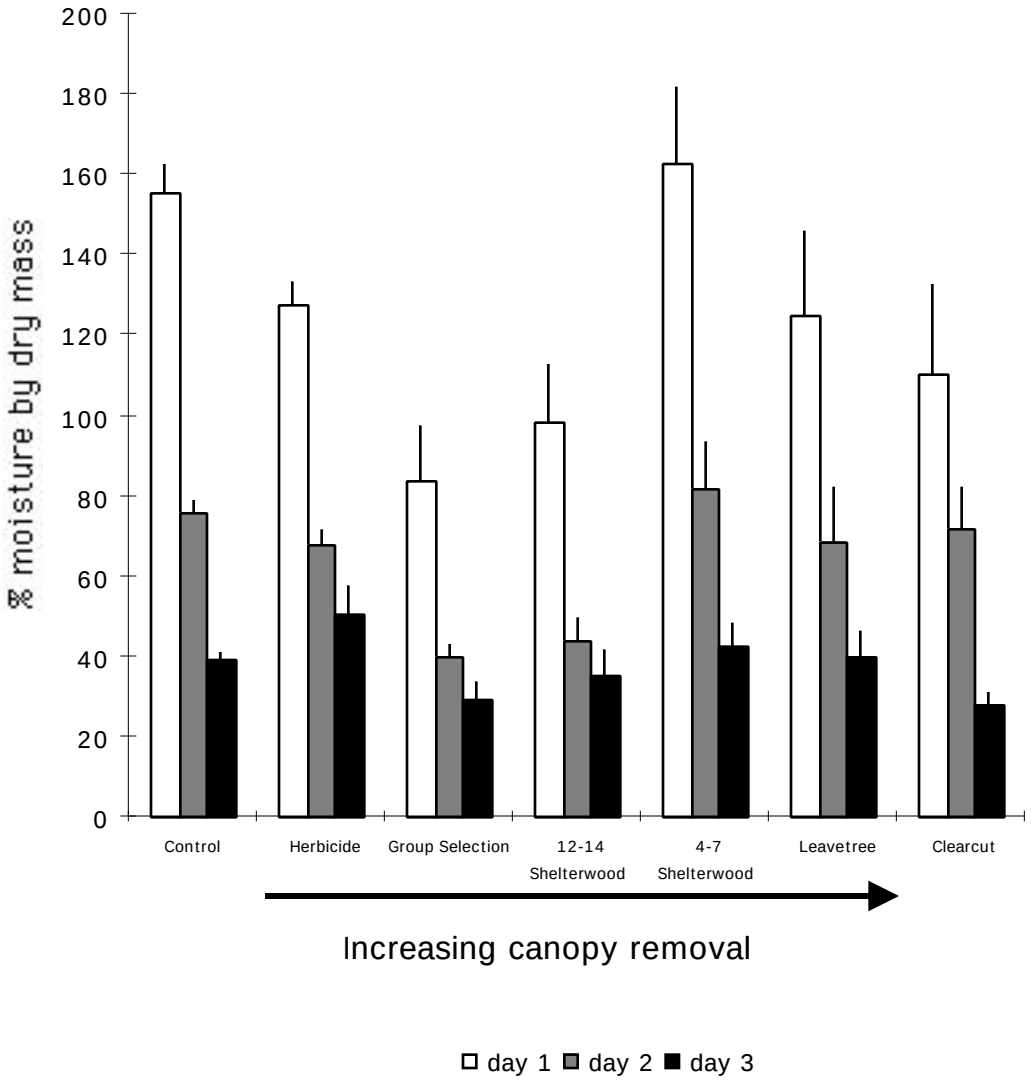

Figure 2. 16. Leaf litter drying rate for Blacksburg 1 taken in August 1998 (4th year postharvest). Values given are the percent moisture (mean + SE) by dry mass over three consecutive days following > 2.5 cm rain.

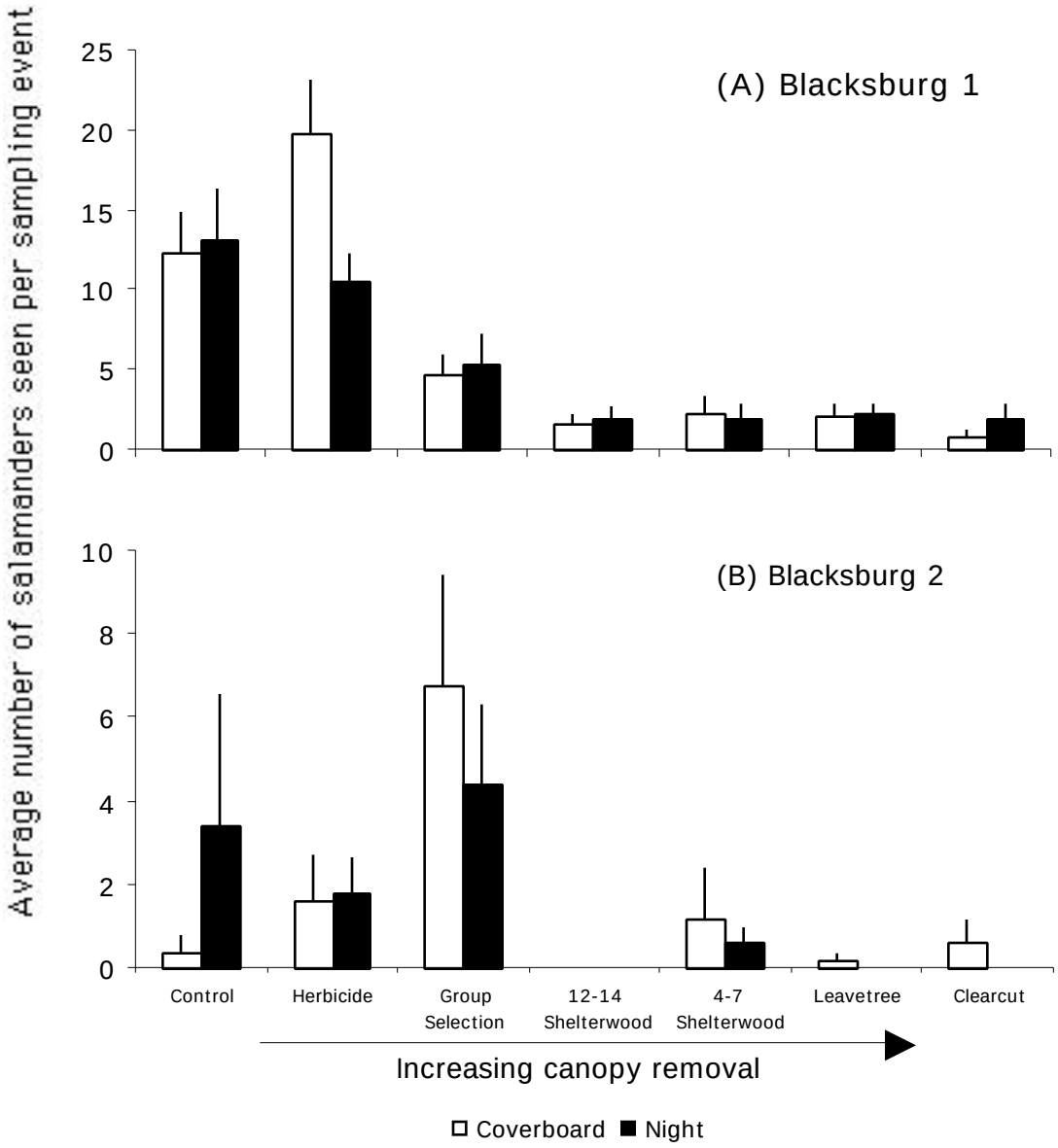

Figure 2. 17. Comparison of salamander relative abundance between night sampling and coverboard sampling methods from (A) Blacksburg 1 (8 samples for each method) and (B) Blacksburg 2 (5 samples for each method). For night sampling, a sampling event involved searching a 30 m^2 plot. For coverboard sampling, a sampling event involved searching under 50 5 x 20 x 60-cm coverboards.

CHAPTER 3 - EFFECTS OF TIMBER HARVESTING ON SURFACE ACTIVITY IN TERRESTRIAL SALAMANDERS

INTRODUCTION

In the previous chapter, I compared night sampling with coverboard sampling to address whether there is a treatment-induced bias in the night sampling method in assessing impacts of timber harvesting on salamander abundance due to differences in salamander observability among treatments. In this chapter, I address whether there is such a bias due to differences in surface activity levels of salamanders in different silvicultural treatments.

Relatively few studies have assessed what percent of a salamander population is on the surface on the rainy nights when they are commonly found. Fraser (1976) estimated that less than 10% of a population of the Valley and Ridge salamander (*Plethodon hoffmani*) was on the surface at any one time. Nishikawa (1985) estimated with marked populations that individual slimy salamanders (*P. glutinosus*) were active on 24.3% of all nights sampled and Jordan's salamander (*P. jordani*) were active on 17.9% of all nights sampled. Hairston (1987) estimated via casual removal observations that 25% of individual Jordan's salamanders were present on the surface each night sampled. Kramer *et al*. (1993) found that 3-10% of a marked population of the Peak's of Otter salamander (*P. hubrichti*) was active at any one time. All of these studies were done on intact forest sites. Petranka (1994) has made the assumption (for cover-object, day searches of salamanders, but equally applicable to night searches) that "a significant correlation exists between the number of animals on the ground surface and absolute population size" citing Hairston (1980, 1986) who showed that with the experimental removal of salamanders, the surface active portion of the population declined in response to the reduction in the total population. However, this only means that these searches yield valid relative abundance figures within the same habitat conditions.

A decrease in quantity and/or quality of food could force individuals to spend more time on the surface to gain sufficient energy. This would effectively increase the proportion of

the population active on a given sampling night. Alternatively, if salamanders are not being selective and are eating the lower quality food as was found by Mitchell *et al*. (1996) this may reduce the proportion active per night. The low quality prey are low quality because of their high chitin to volume ratio. Chitin is partially digestible, but it lengthens the digestion time (Bobka *et al*. 1981). Salamanders on high chitin diets may not be able to empty their stomachs to forage again as fast as salamanders in unaltered forests living on a lower chitin diet. This could reduce the proportion of the population active on the surface. An increase in temperature on the forest floor leads to the leaf litter drying at a faster rate (Johnson *et al*. 1985, Harpole 1996), decreasing the amount of time when it is suitable for a salamander to forage. In turn, this could force more salamanders to forage at once, increasing the proportion of the population active on sampling nights.

If a larger proportion of the population is active on an altered site, it would lead to an overestimate of relative abundance and an underestimate of the impact of timber-harvesting or other habitat alteration on salamander populations. Sampling the salamanders active on the surface during night searches or salamanders under cover objects during day searches is intended to measure relative abundance between habitats or treatments. There is the implicit assumption that equal proportions of the population are being sampled in each habitat. Therefore if sampling counts yield half as many salamanders on a treated site versus a control or pretreatment count, this could be interpreted as showing that the treatment reduced the salamander population by half or that one habitat has 50% the population size as the other habitat. However, if twice the proportion of the population is active at once on the treatment as on the control and sampling yields 50% of the control numbers on the treatment, the actual impact would be a 75% reduction in the population size due to the treatment. Alternatively, the effect of the treatment may be to reduce the proportion of the population that is active on the surface. The population size of the treatment site will then be underestimated and the impact of the treatment will be seriously overestimated. Taken to extremes, apparent substantial impacts of timber harvesting on salamander numbers could in reality be only artifacts of the sampling methods.

I conducted field observations to determine if there is a difference in the proportion of surface active salamanders between altered and unaltered habitats using mark-recapture population estimates on set plots. By limiting comparisons to pairs of matched plots sampled the same night, I avoided differences due to moisture level, temperature, and seasonal behavior.

METHODS

PLOT DESIGN AND STUDY SITES

This study was not conducted on any of the 8 sites used to study the effects of the 7 silvicultural methods from Chapter 2. Different study sites were required for 2 reasons. First, I was employing a mark-recapture technique, and marking may reduce survival. Even small declines in survivorship would be detrimental in a long-term study on abundance. Second, mark-recapture requires many repeated visits to the same plot, as does any measure of variation in surface counts over time. For the study sites in the previous chapter, the emphasis was on sampling as many transects as possible, and, preferably, not resampling the same transect within a year.

I compared unharvested, control sites to group selection cuts, harvested within 1 year prior to sampling. This silvicultural method was used because recently harvested sites were available locally, it allowed replication within a relatively small area, and the impact on total abundance should have been small enough to have a sufficiently large salamander population to study. The group selection cuts consisted of small (< 1 ha) clearcuts within a larger thinned area. Sampling plots on harvested areas (harvested plots) were located at the edge of the group selection cut, and up to 2 or 3 meters into the edge of the cut to buffer the effects of the harvest and ensure there would be a large enough salamander population to analyze. I paired harvested plots with a control in the same forest stand or an adjacent stand with similar preharvest age and site index (Figure 3. 1, Figure 3. 2, and Figure 3. 3). The exact locations of the plots were somewhat subjective. I avoided areas of dense slash and skid trails. I believed that skidders could have compressed the ground, removed leaf litter and top soil, and killed vegetation enough to make the habitat particularly inhospitable for salamanders. Dense slash is

virtually impossible for observers to maneuver through and would make accurate counts difficult or impossible. My technicians and I would be less able to see and capture those salamanders that were active on the surface but beneath slash piles. Because of these requirements and the tendency for slash to fall downslope, plots were always located at the upslope edge of the cut. I chose control plots for slope and aspect similar to the paired harvested plot and for subjectively "good salamander habitat" such as a full hardwood canopy and high percent cover of leaf litter. This subjective plot location is justified because I am not testing for the effects of the group-selection alteration on the population. I assumed *a priori* that there will be a negative effect. My purpose is to observe salamander activity rates in "good" habitat versus "poor" habitat.

There was a total of 3 sites located in the Blacksburg Ranger District of the George Washington and Jefferson National Forest in Southwest Virginia (Figure 3. 4). Each site contained 1 or 2 harvested-control pairs of plots. Site elevations ranged from 600 to 1040 m with either southeast or northwest aspects (Table 3. 1). The dominant forest type was White Oak (*Quercus alba*) - Northern Red Oak (*Quercus rubra*) – Hickory (*Carya spp.*) with the exception of one plot (Harvested 2) which was White Oak – Northern Red Oak – Yellow Poplar (*Liriodendron tulipifera*). Sampling was initiated from a few months to a full year after harvest. Sites 1 and 3 each had 2 pairs of 10 m x 10 m plots (Pairs 1a, 1b, 3a, and 3b). Site 2 had 1 pair of 20 m x 20 m plots (Pair 2). Plots were divided into 1-m wide strips. Each strip was marked off into 1-m increments, resulting in a grid of 1-m^2 sections. Redback salamanders (*Plethodon cinereus*) were the dominant species at all sites, followed by the slimy salamander (*P. glutinosus*). According to Conant and Collins (1991), slimy salamanders on Site 1 are white-spotted slimy salamanders (*P. cylindraeceus*) and on Sites 2 and 3 are northern slimy salamanders (*P. glutinosus*); however, as in Chapter 2, I considered these to be a single species following Petranka (1998). Only the redback and slimy salamanders were used in analyses.

SAMPLING

My technicians and I began sampling at dusk, during or shortly after rain. Because of a low number of sufficiently wet nights, we occasionally sampled when one or more plots

was dry at Sites 2 and 3. We sampled Site 1 and 3 plots in a randomized-rotated order, so that within a site each plot was sampled first, second, third, and fourth over time. We always sampled treatment-control pairs consecutively. At Site 2, we alternated the starting plot. Working in pairs, we crawled adjacent 1-m strips and hand captured all salamanders active on the surface. After a pair of strips was sampled, we skipped the next pair of strips to avoid sampling areas where salamanders had recently been disturbed. The first pair of strips to be sampled was chosen randomly. For the 10-m x 10-m plots, all strips were sampled each night. In the larger 20-m x 20-m plots, only every other pair of strips was sampled each night, for a total of 200 m^2. We alternated which set of strips to sample, so that all 400 m^2 was sampled after 2 nights.

Salamanders seen on the surface were captured, and time and location to the nearest 1-m^2 quadrant was recorded. Any salamanders observed but not captured (escaped) were recorded and included in the surface counts. Unmarked salamanders were placed in plastic bags and processed after all strips were sampled. They were then toe-clipped with individual 3-4 toe identification numbers (Appendix Figure A1). No more than 2 toes were cut on any one foot. We used cosmetic cuticle nippers for toe clipping. Between each salamander, we sterilized the nippers in 70% EtOH. To help prevent infection, we treated the cut feet with Bactine® (Martin and Hong 1991). We also checked for gravidity, recorded snout-vent length (SVL), species, and any identifying characteristics and returned them to the quadrant of capture within 1-2 h of capture. Recaptured salamanders were processed immediately at the location of capture. For recaptures, we recorded the identification number, snout-vent length (SVL), species, and any other identifying characteristics such as regenerating tails or color phase, and immediately released the salamander. SVL was taken for the purpose of confirming recaptures and was measured only approximately with a small ruler marked into mm increments.

Leaf litter samples were taken each sampling night at each plot beginning in June 1997, and percent leaf litter moisture was determined gravimetrically. At Sites 2 and 3, 2 transects were set up on either side of each plot, 5 m from the plot, and ran the length of the plot. On the harvested plots, one transect was laid on the side of the plot nearest the

edge of the harvested area; the other was on the opposite side. On control plots, the transects were laid with the same orientation as the paired harvested plot. Transects were divided into 20 sections and leaf litter was taken at one randomly selected section of both transects each night. At Site 1, these measurements were only taken on the last 3 sampling nights. At this site, samples were taken several paces from a randomly selected strip on both sides of the plot.

ANALYSIS

Test of Binomial Proportions

To test for a statistical difference in proportions active between paired plots, I used only the proportion recaptured of those marked, totaled for the plot. The proportion active (*p*) was calculated as

$$p = \frac{\sum R_t}{\sum M_t}$$

where

M_t = the number of marked animals immediately before taking sample *t*, i.e. the number of marks at risk on night *t*; and

R_t = the number of previously marked animals in sample *t*; i.e. the number of recaptures on night *t*.

I used a test of binomial proportions (Ott 1993) to test for differences in proportions. I used a 2-tailed test and considered a test significant at p = 0.10. Only data from nights when both plots in a pair were wet were included in this analysis. Because only half of the plot was sampled within a given night at Site 2, I divided M_t in half to estimate the proportion active.

Population Estimates

A more conceptually direct way of looking at the data is to compare the relative abundance of salamanders between treatments that we see in surface counts to what we see in population estimates. Population size was estimated using the closed-population

procedure in Program MARK (White 1998), and a null population model (no behavioral, heterogeneity, or time response in capture probability) and used only data from wet nights. I used the null model because recapture rates were very low, which may make the model selection procedures unreliable (Dr. Thomas R. Stanely, USGS BRD, pers. comm.). For the purposes of comparison among sites, all population estimates were standardized to salamanders per 100 m^2.

Closed population models assume no birth, death, or migration within the sampling period. I believe these assumptions are approximately met for the maximum 2-month sampling periods. In the redback salamander, egg laying occurs in June, with hatching in mid to late August. Further, if young-of-the-year are encountered, they are easily excluded from the sample by size. These species are relatively long lived and survival is high, especially for such short sampling periods. The redback salamander and the slimy salamander do not attain maturity until the second and fifth year of life respectively (Sayler 1966, Semlitsch 1980), and survivorship is Type III (low in juveniles and relatively constant in adults) (Semlitsch 1980, Hairston 1983). These species are territorial, occupying fixed home ranges (Mathis 1991, Thurow 1976), so migration should be limited.

RESULTS

Because of variation in the frequency of rain, the number of wet sampling nights differed among sites and occasionally between treatments within a pair when it began to rain midway through an otherwise dry sampling night. For Pairs 1a and 1b, all sample nights were wet for all plots so I used 13 nights for both population estimates and the test of proportions. For Pair 2, I used 7 nights for both calculations. An additional 5 nights were dry for both plots of Pair 2 so were not used in analysis. For Pair 3a, there were 7 nights when both plots were wet. In addition to those 7 nights each plot of Pair 3a was wet 1 additional night, but on different dates; therefore I used 7 nights for the test of proportions and 8 nights for population estimates. For Pair 3b, there were 9 nights when both plots were wet and 1 additional night when only the control was wet so 9 nights

were used for the test of proportions and for the population estimate of the harvested plot, but 10 nights were used for the population estimate on the control.

PROPORTION ACTIVE

Redback Salamanders

I found significant differences in the proportion of redback salamanders active in 3 of the 5 pairs of plots (Table 3. 2). Of these, two had higher activity on the harvested plots (Pairs 1a and 1b) and one had higher activity on the control (Pair 2). In all three cases, the plot with higher activity had more than twice the proportion active as the plot with lower activity. The remaining two plots were both located at the same site, but one had higher activity on the harvested plot (Pair 3a), while the other had higher activity on the control (Pair 3b). The proportions active on Pair 3a closely matched those on Pairs 1a and 1b, again with twice the activity on the harvested plot. However the difference between treatments on Pair 3b was much smaller. Overall, activity was low, ranging from under 2% on the controls in Pairs 1a, 1b, and 3a, to a high of 9.2% on the control of Pair 2.

Slimy Salamanders

Numbers of slimy salamanders were too low for valid statistical tests with the exception of 2 cases; Pair 2 had higher activity on the control ($p = 0.09$) and Pair 3b showed no significant differences between treatments ($p = 0.80$). On Pairs 1a, 1b, and 2, the control plot had 40 to over 200% higher activity than the harvested plot (Table 3. 3). On Pairs 3a and 3b, the harvested plot had 15 to 70% higher activity than the control. Activity in the slimy salamanders was generally slightly higher than in the redback salamanders on the same plots, with estimates ranging from 3.6 to 11.7%.

Program MARK

Program MARK also provides estimates of the proportion of the population active (the capture probability). Although the absolute values and relative differences between them differed from the above estimates of the proportion active, the treatment having higher activity within a pair did not differ from the above results (Appendix 4).

SURFACE COUNTS VS. POPULATION ESTIMATES

Redback Salamanders

Comparing average nightly surface counts to population estimates, I found that the ratio of redback salamanders on harvested plots to controls was higher in surface counts than in population estimates on 3 of the 5 pairs (Pairs 1a, 1b, and 3a) (Figure 3. 5), thus surface counts overestimated the relative abundance of salamanders on the harvested plots in these 3 cases. In these pairs, surface counts indicated there were 10 to 63% more redback salamanders on harvested plots than on controls, while population estimates indicated there were only 37 to 59% as many redback salamanders on harvested plots as on controls.

On the remaining 2 pairs (Pairs 2 and 3b), the ratio of redback salamanders on harvested plots to controls was lower in surface counts than in population estimates, so surface counts underestimated the relative abundance of salamanders on these 2 harvested plots. On Pair 2, surface counts indicated the harvested plot had only 45% of the salamanders as the control, while population estimates indicate the harvested plot had a marginally higher (8%) number of redback salamanders than the control. On Pair 3b, surface counts indicated there were 35% more redback salamanders on the harvested plot than the control and population estimates indicated there were 51% more redbacks on the harvested plot than the control.

Slimy Salamanders

I found the ratio of slimy salamanders on harvested plots to controls was lower in surface counts than population estimates on 3 of the 5 pairs (Pairs 1a, 1b, and 2) (Figure 3. 6), thus surface counts underestimated the relative abundance of salamanders on the harvested plots in these 3 cases. On Pair 1a, surface counts indicated there were 15% more slimy salamanders on the harvested plot than the control, while population estimates indicated there were 72% more slimy salamanders on the harvested plot than the control. On Pair 1b, surface counts indicated there were only 86% as many slimy salamanders on the harvested plot as the control, while population estimates indicated

there were 70% more slimy salamanders on the harvested plot than the control. On Pair 2, surface counts indicated the harvested plot had only 32% as many slimy salamanders as the control, while population estimates indicated there were 80% as many on the harvested plot as the control.

In both pairs of plots at Site 3 (Pairs 3a and 3b), I found that the ratio of slimy salamanders on the harvested plots to controls was higher in surface counts than in population estimates, and, thus, surface counts overestimated the relative abundance of slimy salamanders on harvested plots at this site. On Pair 3a, surface counts indicated the harvested plot had 35% as many slimy salamanders as the control, while population estimates indicated there were only 18% as many on the harvested plot as the control. On Pair 3b, surface counts indicated the harvested plot had 25% more slimy salamanders than the control, while population estimates indicated there were roughly as many slimy salamanders on the harvested plot as the control (25 on the harvested plot versus 26 on the control).

TRENDS IN ACTIVITY

Within Pair

Figure 3. 7, Figure 3. 8, and Figure 3. 9 illustrate the surface counts of each species on each plot each sampling night. Overall, there is a good deal of variability in the number seen each night. In Pair 2 (Figure 3. 8) the control always had more salamanders than the harvested plot for both species. With the exception of that pair, there was no consistency in which treatment has more salamanders among nights or which treatment has more salamanders between species within a night. There was also a general lack of tracking between species; peak nights in redback salamander counts do not appear to correlate with peak nights in slimy salamander counts.

Within Site

To compare the tracking of the harvest-control relationship among nights within a site, I plotted the surface count of redback salamanders on the harvested plot as a percent of the surface count on the control each night for both pairs in a site (Figure 3. 10). There is

some evidence of between-Pair tracking in both Site 1 and Site 3. However, there is a notable breakdown in this relationship in sampling night 11 and 12 in Site 1. Because there was no replicate within site 2, comparisons cannot be made with that pair, although values each night are shown (Figure 3. 10b). The number of slimy salamanders was too low to make comparable graphs for this species; in particular there were a number of nights when no slimy salamanders were found on the control plots.

Activity vs. Leaf Litter Moisture

I also plotted the proportion active each night versus leaf litter moisture and calculated a regression line for each treatment. In order to get a nightly value for the proportion active, I divided the number seen each night (including escapes) by the population estimate. There was a positive relationship between leaf litter moisture and activity (Figure 3. 11) as expected. The slope of the relationship was slightly steeper for the harvested plots than controls, suggesting salamanders may be more active on a harvested plot than a control with the same amount of leaf litter moisture. However, the trend was very weak for both treatments (R^2 = 0.19 and 0.15 for harvested and control respectively). There was also an apparent tendency for the controls to have higher leaf litter moisture, which may explain the differences in the slope.

DISCUSSION

INTERPRETING STUDIES OF TIMBER HARVESTING ON SALAMANDERS

Studies examining salamander relative abundance on a harvested plot relative to a control are interested in gauging the impacts of the harvest on salamander population size. Generally, if the relative abundance of salamanders on the harvested plot is overestimated, the severity of the harvest on the salamander population is underestimated and, conversely, underestimating the relative abundance of salamanders on the harvested plot results in overestimation of the severity of the harvest. In this study, the problem became more complex. Contrary to expectations, harvested plots frequently had higher salamander numbers than their paired controls both in surface counts (4 of 5 pairs in redback salamanders, and 2 of 5 pairs in slimy salamanders) and in population estimates (2 of 5 pairs in redback salamanders, and 2 of 5 pairs in slimy salamanders). More

interestingly, pairs showing higher abundances with one method were not necessarily those with higher abundances in the other method. These "trend reversals," where one method indicated harvesting leads to a decline in salamander numbers and the other indicated harvesting leads to an increase, occurred in 4 of the 5 pairs in redback salamanders and in at least 1 of the 5 pairs in slimy salamanders. In an additional pair, surface counts of slimy salamanders indicated increases in salamander numbers following harvesting and population estimates indicated there was no effect of the harvest on salamander numbers. There is a great deal of error inherent in these comparisons because they rely on compounded estimates; an estimate of surface counts on the harvested plot divided by an estimate of surface counts in the control is compared to an estimate of population size on the harvested plot divided by an estimate of population size on the control. However, with the magnitude of some of these differences, there is the potential to have significant effects on the results and interpretations of studies on the effects of timber harvests on salamanders. Surface counts that overestimated salamander relative abundance on harvested plots did so by factors of 1.3 to 3.0. Surface counts that underestimated salamander relative abundance on harvested plots did so by factors of 1.1 to 2.5. Applying the largest overestimate (3.0X) and largest underestimate (2.5X) as corrections to the average 80% reduction in salamander populations following timber harvesting (deMaynadier and Hunter 1995), actual reductions may range from as little as 50% to as much as 93% of the population.

Although a reduction of 93% or 50% versus 80% is not as dramatic as the differences seen in this study, with apparent increases that were actually decreases, differences in salamander surface activity levels between treatments may explain the lack of significant results in the first year data in Chapter 2. Site 1 in this study was within a mile of the Blacksburg 2 site. These two sites were similar in surface count densities. Both were relatively low elevation, southeastern aspects, generally very dry, and can be considered poor quality sites for salamanders. Although geographically distant from these sites, the West Virginia 1 site also had very low surface count densities. Surface count densities at Blacksburg 2 and West Virginia 1 either increased, or remained the same in the first year postharvest (Figure 2. 2), which is equivalent to the time period studied at Site 1. It may

be that the sharp increase in activity observed at Site 1 is indicative of the response at already poor quality sites, where salamanders in unharvested forest are already existing at the brink of starvation. If these salamanders were unable to maintain a positive energy budget with any increase in metabolism due to increased temperatures, with no energy reserves, they would be forced to forage longer than they would under unharvested, control conditions. Similarly, if prey densities were at a minimum for maintenance and were then reduced because of the harvest, salamanders would be forced to increase activity levels to avoid starvation. At higher quality sites where salamanders normally exist on a large, positive energy budget, changes in temperature or food supply may not be enough to put individuals on a negative energy budget with the same activity levels. Studies on the response of salamanders to timber harvesting, and the general ecology of salamanders (Appendix 5), are typically done at high elevation, wet sites, where salamander densities are high, similar to Site 2, Site 3, and Clinch 2 in this study. Study sites may be specifically chosen based on high densities of the target species (e.g. Hairston 1980, Semlitsch 1980, Sattler and Reichenbach 1998).

TRENDS AND PREDICTABILITY

I found no consistency in surface activity rates within treatments, within sites, within pairs, or between species. In both redback and slimy salamanders there was no consistency in whether the control or harvested plot had the higher average activity, even within a site. In the redback salamanders, there was one site where one pair had higher activity on the harvested plot (Pair 3a) and one that had higher activity on the control (Pair 3b). I did, however, see within-site consistency with the slimy salamanders. The treatment with higher activity does not appear consistent between species either night-by-night (Figure 3. 7, Figure 3. 8, and Figure 3. 9) or on average. Average surface activity on the harvested plot was higher than the control plot in redback salamanders but lower in slimy salamanders in Pairs 1a and 1b, lower in both species in Pair 2, higher in both species in Pair 3a, and lower than the control in redback salamanders but higher in slimy salamanders in Pair 3b (Table 3. 2 and Table 3. 3). There was some consistency within a night (Figure 3. 10), but even this was not entirely consistent.

Differences in relative activity rates at Site 2 compared to the other sites may be attributable to differences between an immediate response and a longer-term response. Site 2 was sampled only months after the harvest was completed and before the salamanders had spent a full season living in a degraded or hostile habitat. There was little difference in population estimates between these two treatments, and it is logical that population sizes had not yet declined. This was the only pair in which both redback and slimy salamander surface counts were much lower on the harvested plot than the control and the only pair in which redback surface counts were lower on the harvested plot than the control. Salamanders typically spend days between rains (Jaeger 1972, Fraser 1976) to months overwinter (Keen 1979) not foraging until conditions are favorable to surface. It may be that the immediate response to timber harvesting is to avoid foraging until such time as conditions improve, but after a full year, strategies change.

Differences in activity and activity response between age-classes may also exist. Unfortunately, my data set was too small to split juveniles and adults, but I observed some notable differences in activity and recapture rates between adult and juvenile slimy salamanders, particularly on the Control of Site 2, which had the highest average surface counts of slimy salamanders (Figure 3. 6) and which had numerous holes and rocks used by adult slimy salamanders. On this plot, large adult slimy salamanders were frequently observed with only their heads protruding out of their burrows, and, therefore, could not be captured. The smallest juvenile slimy salamanders were quite active - several were captured after they jumped onto my hand - and on this plot, all 10 slimy salamanders recaptured more than once were between 16 and 32 mm SVL, including the 2 (SVL 16 and 25 mm) recaptured 3 times (4 total captures) in the 12 sampling nights. The different foraging strategies (sit-and-wait adults and actively foraging juveniles) may affect observed age ratios between treatments.

ESTIMATES OF SURFACE ACTIVITY

Published estimates of < 10% activity in the Valley and Ridge salamander (*P. hoffmani*) (Fraser 1976) and 3 to 10% activity for the Peaks of Otter salamander (*P. hubrichti*)

(Kramer *et al.* 1993) are very close to activity rates found in this study. Both studies used night surveys with apparently only one search of the plot per night and used marked animals and, therefore, are comparable in both methods and results to the present study. Fraser's (1976) estimate is derived from finding 7 marked salamanders on one night and 3 on another when 54 and 58 marked salamanders were known to be on the plot respectively. Fraser (1976) acknowledged that the total population in that area was thought to be much higher, so his estimate of 10% is an overestimate. Kramer *et al*. (1993) found only 3 to 5% of the population was surface active during the months corresponding to the sample period in the present study.

Estimates of activity from Nishikawa (1985) and Hairston (1987) are much higher than those obtained in this study, ranging from 17.9 to 25% for Jordan's salamander (*P. jordani*) and the slimy salamander. Nishikawa (1985) used salamanders captured and marked during night searches, but searched plots up to 3 times per night. Her estimate represents the fraction of nights an individual salamander is likely to be on the surface. Hairston's (1987) estimate was obtained by removing all specimens seen on a single search and repeating the removal each successive night for 10 nights. The number removed declined steadily by 25% (Dr. Nelson G. Hairston, Sr., University of North Carolina at Chapel Hill, Department of Biology, pers. comm.). Because this estimate resulted from a single search within a night, and is, therefore, methodologically comparable to the estimates from this study, it may represent a true deviation from results here and in similar studies. However, results may have also been affected by differences in soil and leaf litter moisture over the sampling period, with each successive night being drier than the previous.

Estimates of percent active in this study ranged from 1.3 to 9.2% for redback salamanders and 3.6 to 11.7% for the larger slimy salamanders. These numbers represent the instantaneous activity rate, a snapshot of what fraction of the population is active at that point in time. This instantaneous rate is the value relevant in studies of the effects of timber harvesting (see Chapter 2) that count salamanders active on the surface. These numbers do not represent the fraction of the population that is active over the course of

the entire night nor the fraction of nights any one individual is active. These latter two estimates of activity should be equivalent and could be independent of the instantaneous activity rate. Even if same fraction of individuals is active over the course of a night, if on one treatment they are active less at any one time then, on average, individuals of that treatment spend less time foraging than individuals of the other treatment. This difference could be due to better foraging opportunities in the first treatment, so less time is required for foraging resulting in no difference in nutritional conditions between treatments, or it could be due to more hostile conditions (warmer, drier, more windy) in the first treatment, which would have a negative impact on the nutritional condition of salamanders in that treatment.

The estimate of proportion active in this study is actually a capture rate as from a mark-recapture study; it is dependent on both the actual activity rates of salamanders and on the ability of observers to see and catch salamanders. Although I did not measure vegetation or percent cover in this study, in hindsight, differences in vegetation may have contributed to differences in response. Sites 1 and 3 were both sampled a year after harvest. However, on the harvested plots at Site 1, there was negligible vegetation, while at Site 3, both harvested plots had relatively dense vegetation, including trees regenerating from stumps and shrubs such as mountain laurel (*Kalmia latifolia*) and blueberry (*Vaccinium spp.)*. The controls on Site 1 had little low-level vegetation, as did the control of Pair 3b, but the control of Pair 3a had much more low level vegetation, primarily mountain laurel and blueberry. This could explain differences in the results of redback salamander activity. Pairs with roughly equal forest floor visibility (Pairs 1a, 1b, and 3a) had higher activity on the harvested plot. Pair 3b, which had higher relative forest floor visibility on the control, had higher activity on the control. Results of the study are not negated even though differences in "activity" may be solely due to differences in observability between treatments. Differences in salamander observability among timber harvest treatments would bias results in exactly the same manner as would differences in salamander activity rates. Furthermore, in Chapter 2, I found no apparent differences in captures due to observability between controls (with forest floor visibility

much higher than any plot on Site 3) and harvested treatments, based on comparisons of night sampling with coverboard sampling.

BIASES IN MARK-RECAPTURE ASSUMPTIONS

Both the actual population estimates and the estimate of the proportion active (*p*) are based on the null, closed-population model. This model assumes no births, deaths, or migration during the study period, as well as assuming no difference in capture probabilities among nights, among individuals, or between marked and unmarked individuals. Differences in capture probabilities between plots, which were the focus of this study, do not violate any of these assumptions.

One possible violation is migration. Although the species used in this study are territorial, Mathis (1991) found that up to 49% of a high density (2.8/m^2) redback salamander population at Mountain Lake Biological Station in Giles County, Virginia, were nonterritorial floaters, based on the percent of salamanders that were never recaptured in 51 censuses of 5 9 m^2 plots. Floaters may be either sedentary, occupying fixed home ranges, or wandering, with no fixed home range. The estimate by Mathis (1991) implies this is a wandering floater population. If this is the case, higher proportions of floaters would result in lower recapture rates and, therefore, lower estimates of the proportion active. If populations in both treatments have the same proportion of floaters, the proportion active is biased by the same factor between treatments. Using the Mathis (1991) estimate of 49%, actual proportions active are twice that given in this study. Estimates for redback salamanders would range from 2.6 to 18.4% and estimates for slimy salamanders would range from 7.2 to 23.4%. The magnitude of differences between treatments, however, would not be affected. However, if there is a difference in the proportion of floaters in a population between treatments, that could contribute to the difference in the estimates of activity. If differences in the estimated proportion active were due to differences in the proportions of floaters, this would mean that for the redback salamanders there was a higher proportion of floaters in the controls of Pair 1a, 1b, and 3a and in the harvested plots of Pairs 2 and 3b. For the slimy salamanders, this would mean a higher proportion of floaters in the controls of

Pairs 3a and 3b and in the harvested plots of Pairs 1a, 1b, and 2. It is not clear, however, whether higher or lower quality habitat is likely to have the higher proportion of floaters. In several bird species, higher proportions of floaters are expected on higher quality habitats (Smith 1978, Zack and Stutchbury 1992, Kokko and Sutherland 1998) or with higher total population densities (Smith and Arcese 1989),either because floaters select high quality territories to increase the likelihood of eventually obtaining a high quality territory (Smith 1978, Zack and Stutchbury 1992) or because more young were previously produced on high quality territories (Kokko and Sutherland 1998). It is not clear to me whether this trend would also apply to salamander populations or this study in particular. Because low-quality, harvested plots were near the edge of the forest, it is possible there may be more floaters on these plots that have been forced onto lower quality habitat, perhaps, in part, by larger salamanders invading from the harvested area. Differences in proportions of floaters between treatments due to differences in reproductive success would not have been manifested by the time of the sampling period.

However, in most bird species where nonbreeder tactics have been closely examined, floaters did maintain limited home ranges (Zack and Stutchbury 1992); this tendency may be reinforced by long breeding seasons or the maintenance of year-round territories (Smith 1978). If the floaters in a terrestrial salamander population, which is clearly resident year-round, also maintain fixed home ranges, absolute or relative proportions of floaters between treatments would have no effect on the data presented here.

BIASES IN NIGHT SAMPLING

I examined the utility of the night sampling method in assessing relative abundances of salamanders in different silviculture treatments. In this chapter, I found that surface counts are biased by differences in surface activity between treatments and, in Chapter 2, found this method may also be biased due to differences in observability among treatments (Blacksburg 2). However, this does not mean that night sampling is an inferior method to coverboard or other day sampling methods. Cover objects may dry faster on harvested sites than unharvested sites and salamanders will be less likely to be found under a dried-out cover object than one that is still moist. This may not have as

serious an effect on exceptionally good salamander sites, where the leaf litter is never fully dry, except in the first year or two after harvest. Day sampling methods that use natural cover objects rather than standardized coverboards are subject to differences in quantity (Grover 1998) and quality (i.e. size and material) of available cover objects. Harpole (unpublished data) found differences in relative species composition and percent juvenile between day sampling and night sampling methods in the same unharvested sites. A variety of relative abundance counts are used for a host of species (e.g. drumming and gobbler counts, scat counts) to compare habitats or one habitat over time. And these counts, in turn, are intended to indicate the relative quality of the habitat. Many of these can be biased by the habitat they seek to assess. Visibility bias may be a substantial source of error in wildlife surveys (Samuel *et al.* 1992). Habitat related biases in visibility have been found in aerial or spotlight counts of feral livestock (Bayliss and Yeomans 1989), kangaroos (Short and Bayliss 1985), and crocodiles (Bayliss *et al.* 1986). In addition, biases in age ratio estimates due to differences in breeding grounds and flyways have been found in Canada Geese (*Branta canadensis*) (Krohn and Bizeau 1989). In general, we must be careful about what conclusions we draw from counts. In Chapter 2, salamander numbers were used as a measure of relative habitat quality for salamanders of each treatment, but high numbers, even when real, are not always indicative of better habitat quality (Van Horne 1983).

Table 3. 1. Locations and descriptions of sampling sites.

	Site 1	Site 2	Site 3
Location	Sinking Creek Mtn., Montgomery Co., VA	Big Mtn., Giles Co., VA	Fork Mtn., Giles Co., VA
Elevation	600 m	1040 m	980 m
Aspect	SE	NW	NW
Forest Type	White Oak - Northern Red Oak - Hickory	White Oak - Northern Red Oak - Hickory (Control); White Oak - Northern Red Oak - Yellow Poplar (Harvested)	White Oak - Northern Red Oak - Hickory
Harvested	Spring 1996	Spring 1997	Spring 1997
Sampled	13 May - 26 June 1997	1 July - 12 August 1997	25 May - 7 July 1998
Plot Pairs	1a and 1b	2	3a and 3b
Plot Dimensions	10 m x 10 m	20 m x 20 m	10 m x 10 m

Table 3. 2. Average percent of redback salamanders active per night. Calculated as the sum of the number of salamanders recaptured each night divided by the sum of the number of marks at risk each night ($\Sigma R_t / \Sigma M_t$) times 100.

Pair	Control	Harvest	Higher Activity on	Z	p-value
1a	1.6	4.2	Harvest	1.84	0.07
1b	1.3	3.9	Harvest	1.74	0.08
2	9.2	4.0	Control	2.29	0.02
3a	1.7	4.5	Harvest	1.58	0.11
3b	4.3	2.9	Control	0.98	0.33

Table 3. 3. Average percent of slimy salamanders active per night. Calculated as the sum of the number of salamanders recaptured each night divided by the sum of the number of marks at risk each night ($\Sigma R_t / \Sigma M_t$) times 100.

Pair	Control	Harvest	Higher Activity on	Z	p-value[a]
1a	5.1	3.6	Control	n/a	n/a
1b	10.0	5.5	Control	n/a	n/a
2	11.7	3.8	Control	1.69	0.09
3a	4.4	7.5	Harvest	n/a	n/a
3b	6.0	6.9	Harvest	0.25	0.80

[a] No statistical test could be performed where sample sizes were too low. determined by *p* times M_t (for the smaller of the two treatments) < 5.

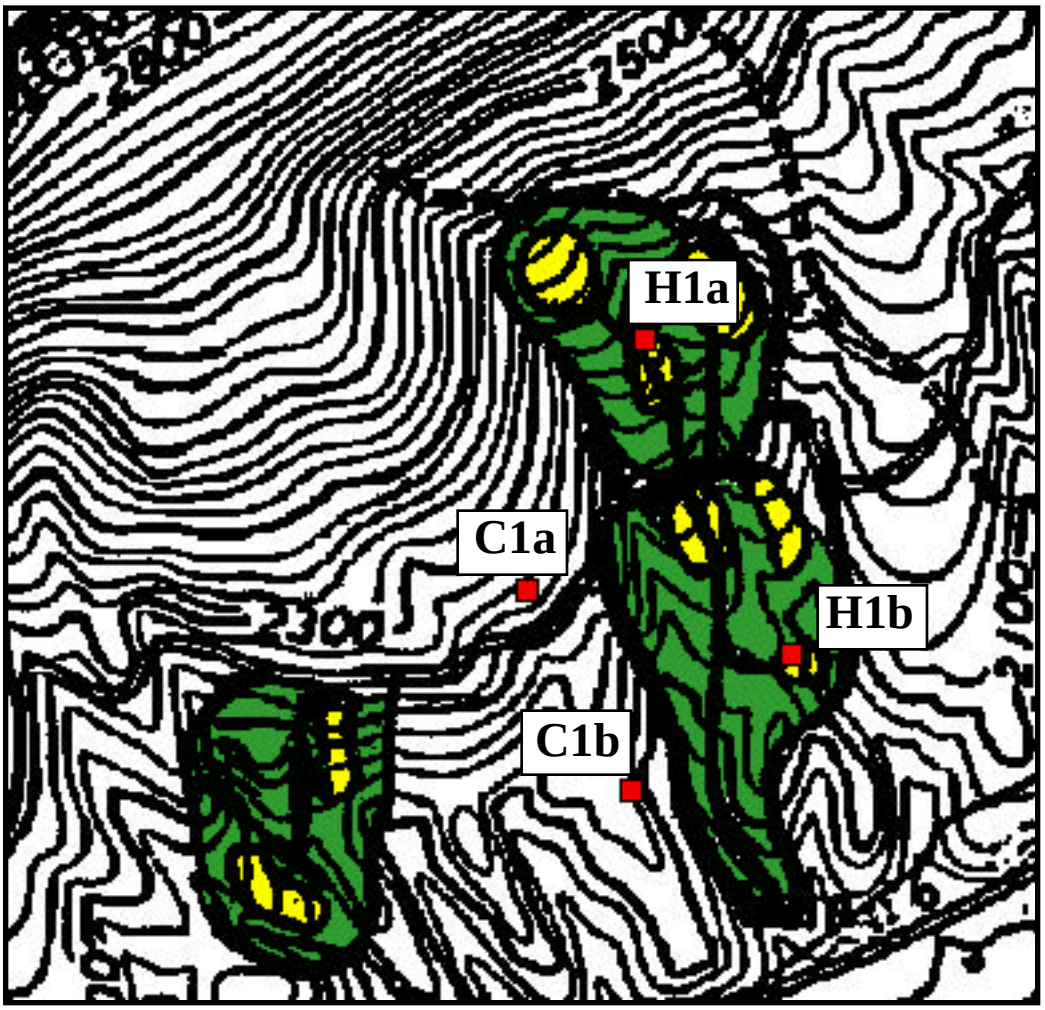

Figure 3. 1. Overview of Site 1. Yellow areas are group selection cuts. Green areas are where thinning occurred. Red squares are sampling plots. H indicates a harvested plot; C indicates a control plot. Plots H1a and H1b are approximately 0.3 km apart.

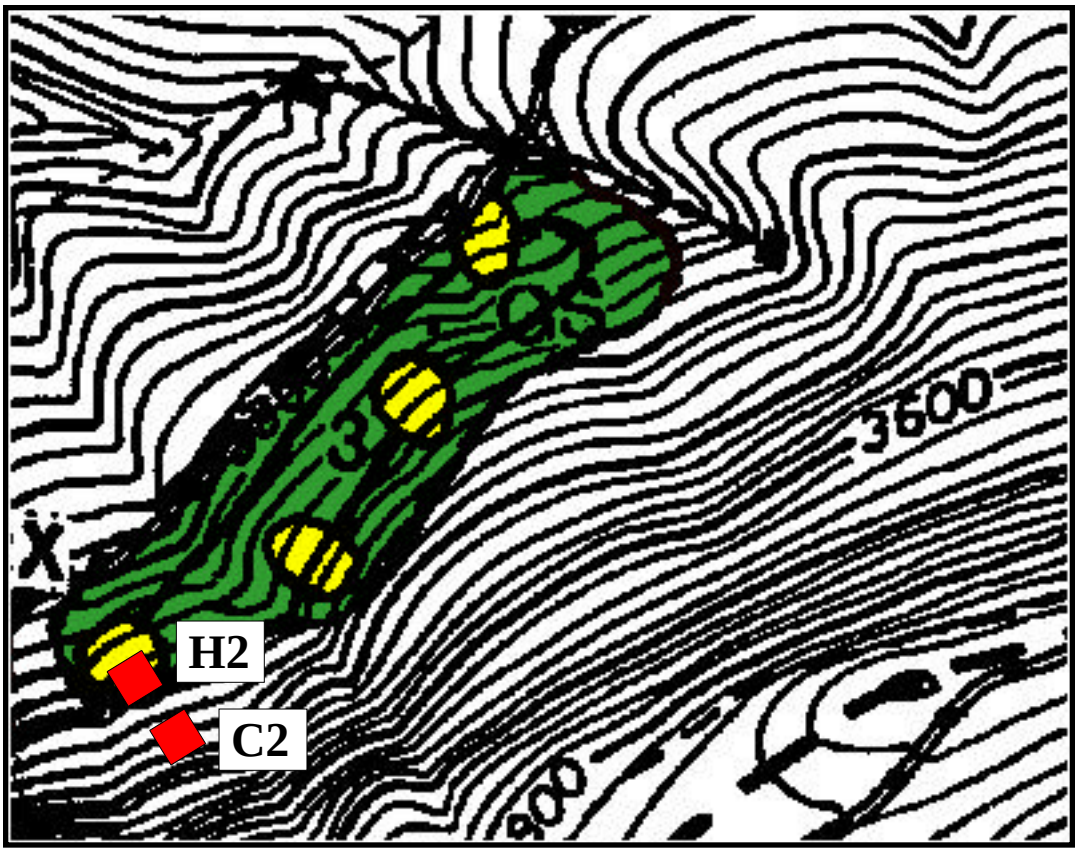

Figure 3. 2. Overview of Site 2. Yellow areas are group selection cuts. Green areas are where thinning occurred. Red squares are sampling plots. H indicates a harvested plot; C indicates a control plot. Plots H2 and C2 are approximately 50 m apart. The two most distant group selection cuts are approximately 0.3 km apart.

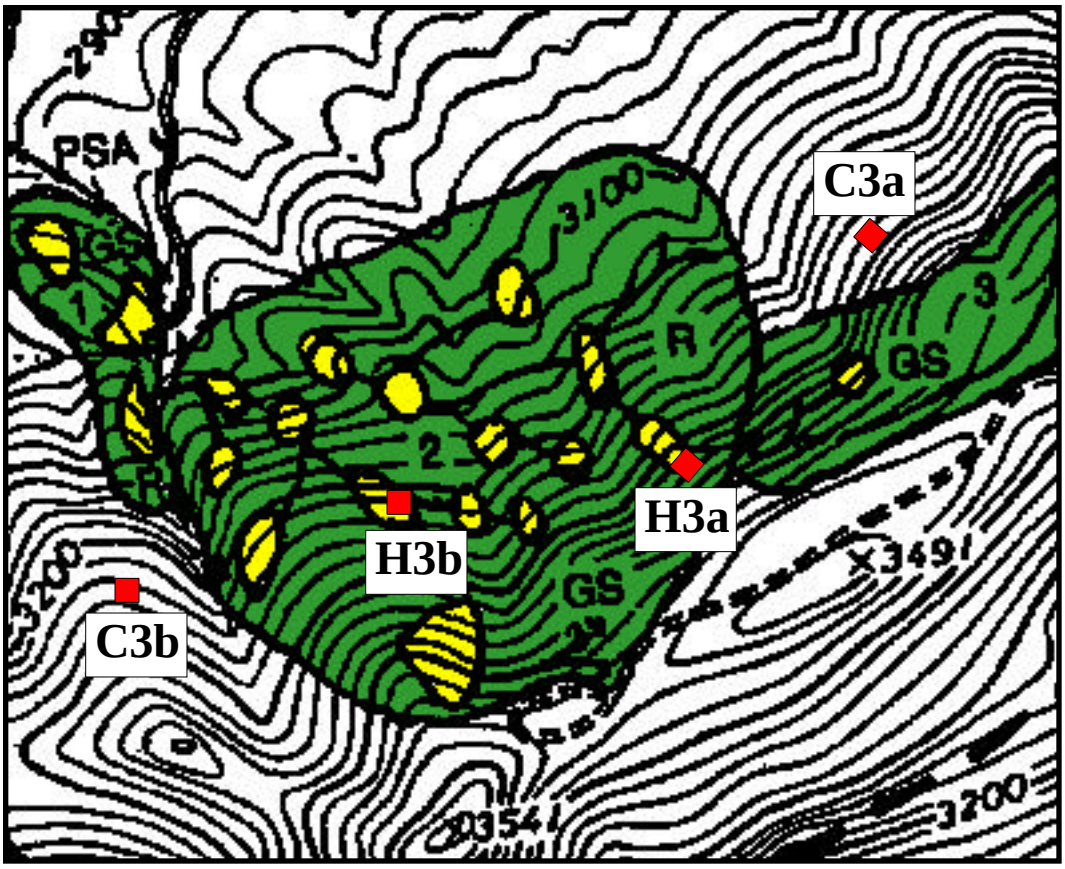

Figure 3. 3. Overview of Site 3. Yellow areas are group selection cuts. Green areas are where thinning occurred. Red squares are sampling plots. H indicates a harvested plot, C indicates a control plot. Plots C3b and C3a are approximately 1 km apart.

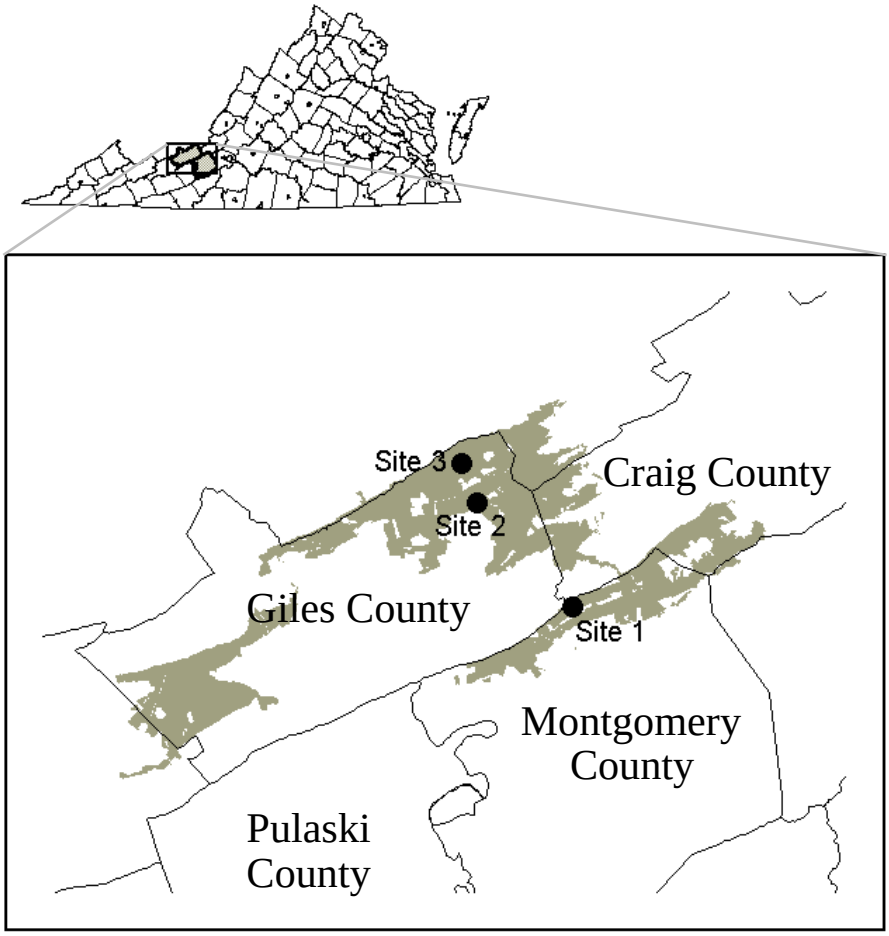

Figure 3. 4. Site locations. Shaded area on enlarged map indicates the Blacksburg Ranger district of the George Washington and Jefferson National Forest.

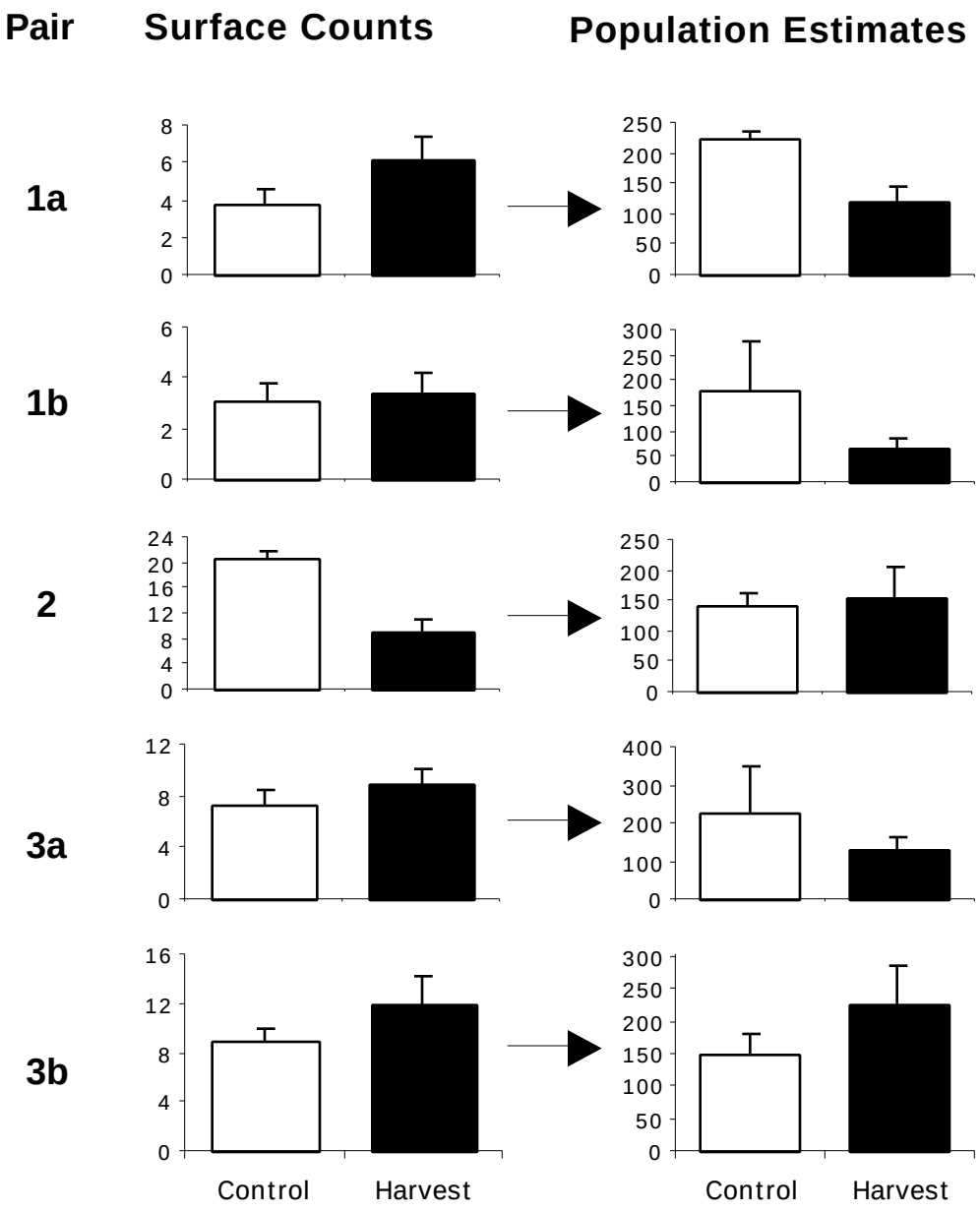

Figure 3. 5. Relative abundances (mean + SE) of redback salamanders (*Plethodon cinereus*), from surface counts and population estimates. Values are in salamanders per 100 m^2. See Table 3.1 and Figure 3.4 for description of site locations.

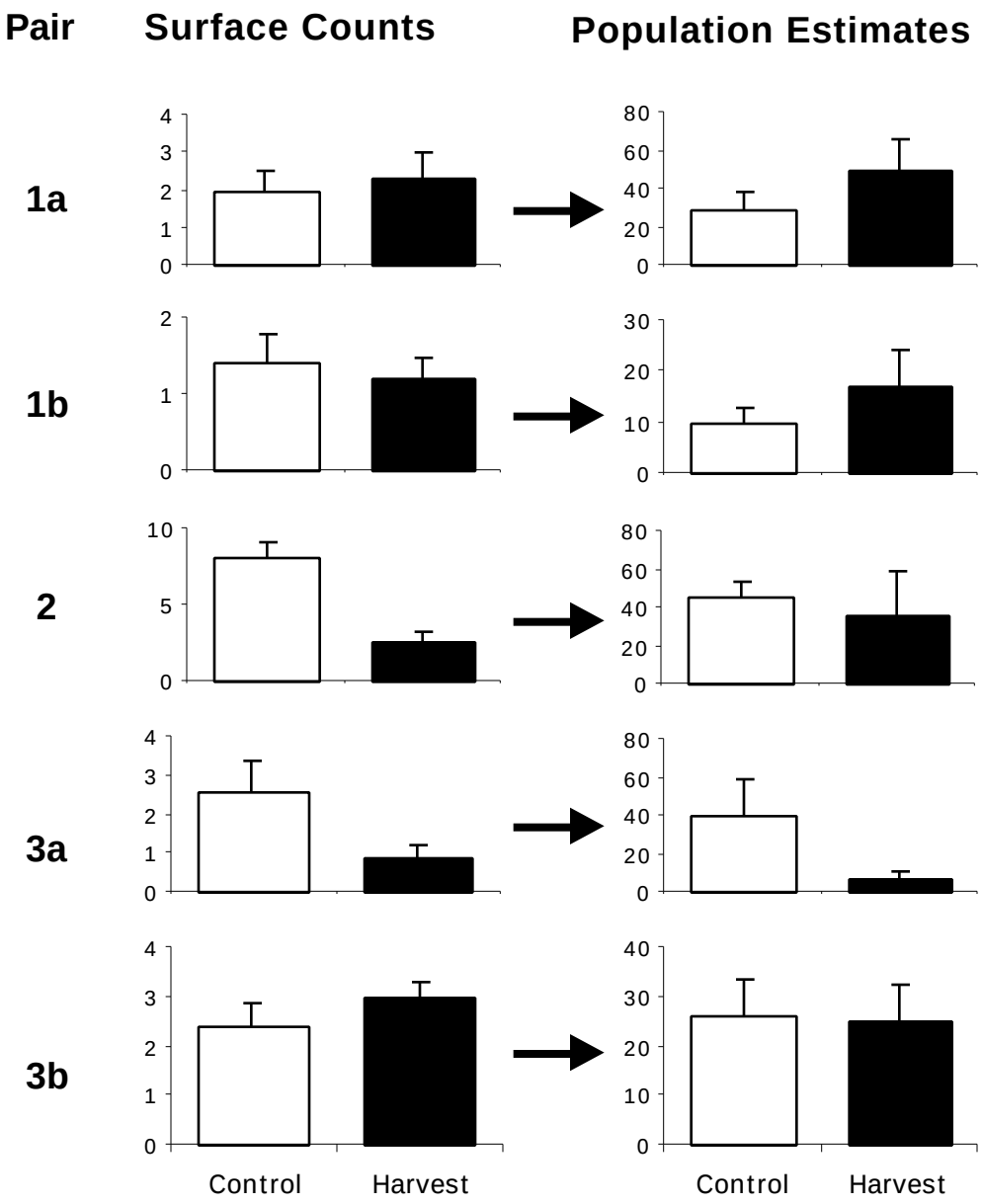

Figure 3. 6. Relative abundances (mean + SE) of slimy salamanders (*Plethodon glutinosus*), from surface counts and population estimates. Values are in salamanders per 100 m^2. See Table 3.1 and Figure 3.4 for description of site locations.

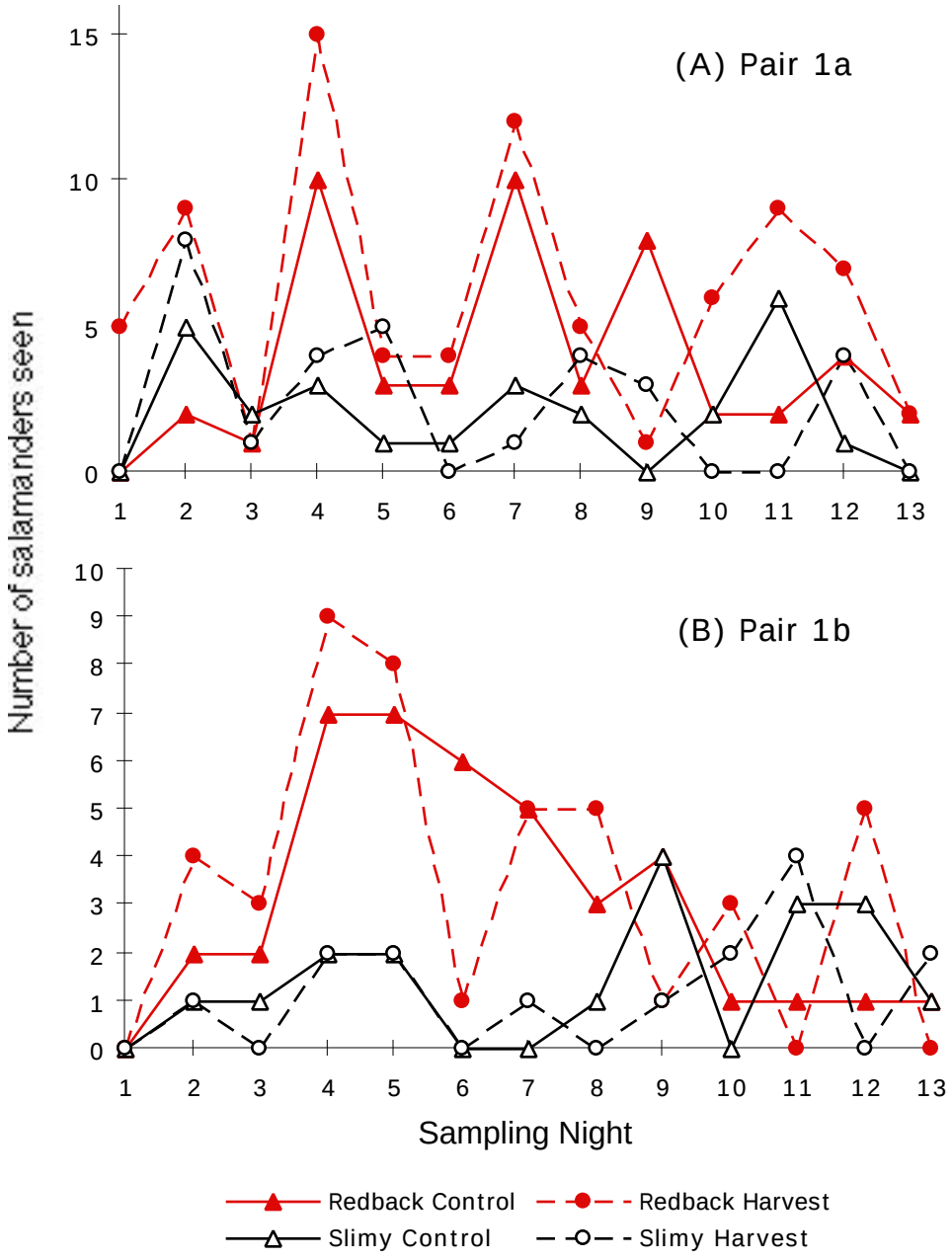

Figure 3. 7. Number of salamanders seen per night for (A) Pair 1a and (B) Pair 1b. Only sampling nights when both plots of a pair were sampled wet are shown.

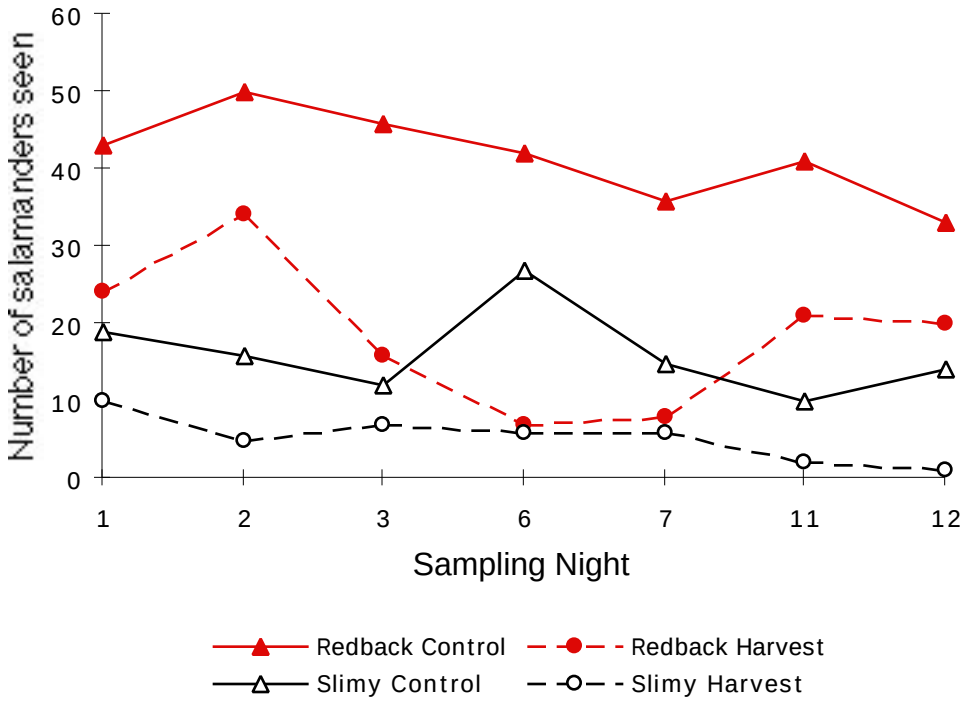

Figure 3. 8. Number of salamanders seen per night for Pair 2. Only sampling nights when both plots were sampled wet are shown.

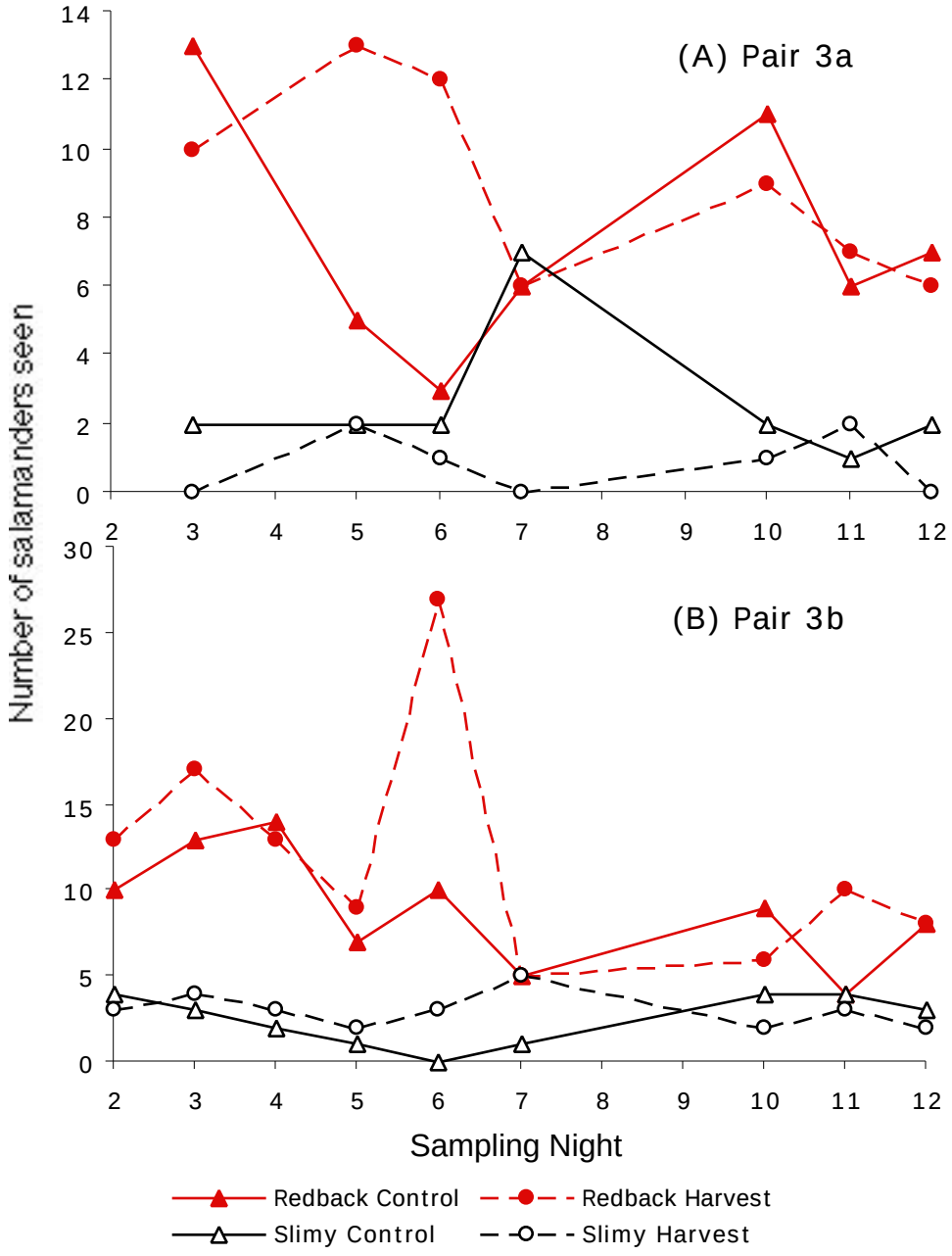

Figure 3. 9. Number of salamanders seen per night for (A) Pair 3a and (B) Pair 3b. Only sampling nights when both plots of a pair were sampled wet are shown.

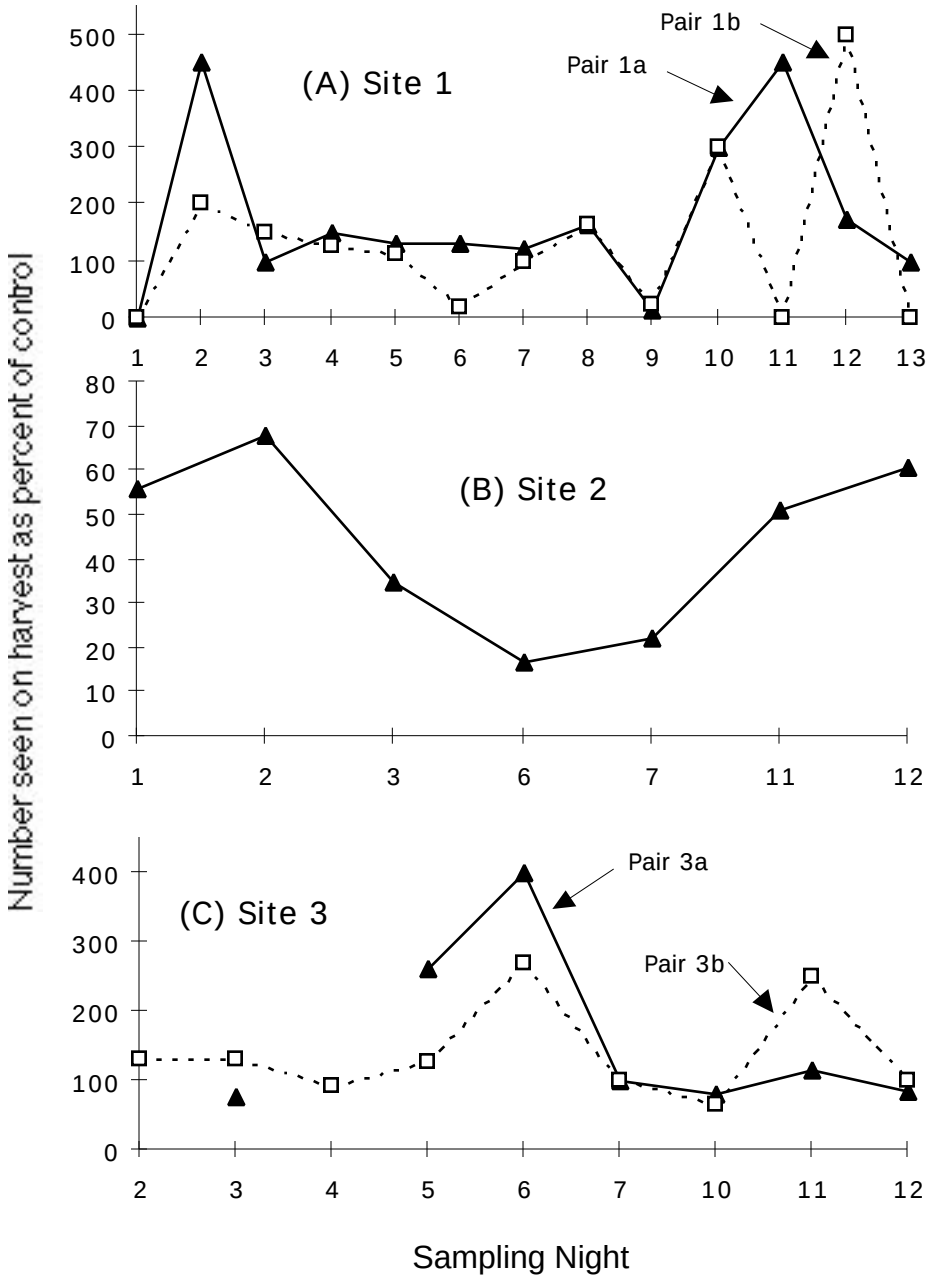

Figure 3. 10. Number of redback salamanders (*Plethodon cinereus*) on the harvested plot as a percent of the control for (A) Site 1, (B) Site 2, and (C) Site 3. Only nights when both plots of a pair were wet are included.

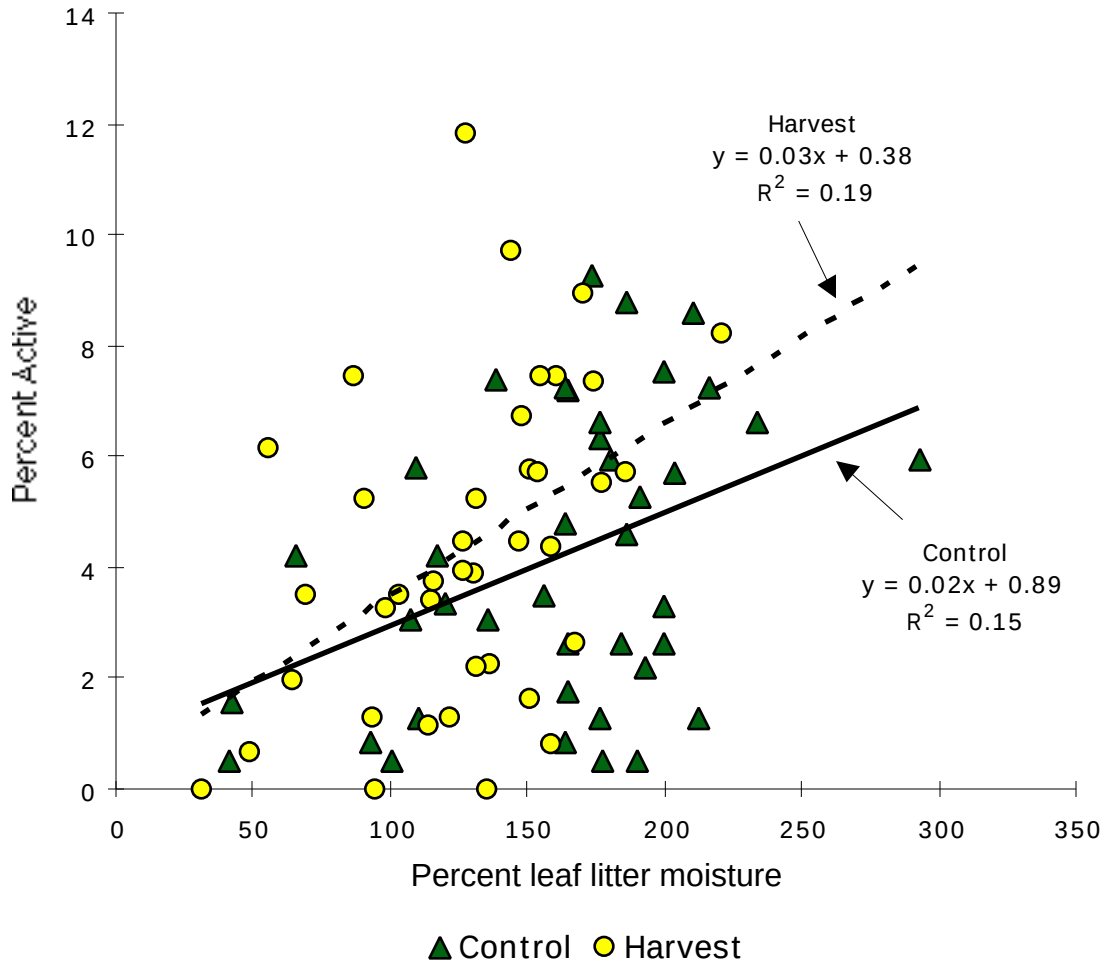

Figure 3. 11. Percent of redback salamanders (*Plethodon cinereus*) active per night versus percent leaf litter moisture. Percent active calculated as the number active on the surface divided by the population estimate.

CHAPTER 4 - RISK-SENSITIVE FORAGING IN THE REDBACK SALAMANDER (*PLETHODON CINEREUS*)

INTRODUCTION

In the previous chapter, I examined whether salamander activity levels differed during favorable "wet" nights in response to timber harvesting. Differences in activity may have been due to differences in the average suitable foraging time after rain, differences in prey quantity or quality, or differences in the nutritional condition or level of hunger of the salamander population due to the harvest. In this chapter, I address whether terrestrial salamanders, particularly the redback salamander (*Plethodon cinereus*), with different hunger levels differ in activity level in unfavorable, "dry" conditions. I used a controlled, laboratory experiment to assess whether the redback salamander exhibits risk-sensitive foraging.

Salamanders subjected to severe conditions, as may occur after timber harvesting, may be willing to engage in more risky foraging behavior, allowing them to compensate for the shorter wet period. Risk-sensitive foraging theory states that animals on negative-energy budgets should engage in risk-prone foraging behavior while those on a positive energy budget should be risk-averse. In much of the work done on this theory, the risk involves a variable food source (Kacelnik and Bateson 1996). However, some work has been done where the risk involves predation or simulated predation threats. Fifteen-spined sticklebacks (*Spinachia spinachia*) were found to reduce foraging at a food source after exposure to a simulated predator; however, increased hunger level and profitability of the food source reversed this effect (Croy and Hughes 1991). In the threespine stickleback (*Gasterosteus aculeatus*) increased hunger levels led to higher feeding rates and increased frequency of initiating solitary predator inspection (Godin and Crossman 1994). In juvenile Atlantic salmon (*Salmo salar*) it was found that the hungrier fish would be the first to resume foraging after a simulated predator attack (Gotceitas and Godin 1991). Studying carcasses in the field, Sweitzer (1996), found porcupines (*Erethizon dorsatum*) of low nutritional condition were more willing to forage in high risk habitat, risking predation over starvation. This relationship between hunger-level

and predation-risk may not be a universal law of nature. Horat and Semlitsch (1994) found no risk trade-offs in two species of tadpoles, *Rana lessonae* and *R. esculenta*

METHODS

I collected 120 redback salamanders (*Plethodon cinereus*) with snout-vent length (SVL) > 35 mm in Giles County, Virginia, in May 1998. They were measured, weighed, and randomly assigned to a low caloric (LOW) or high caloric (HIGH) treatment. Individuals were placed in 15 x 100 mm petri dishes on wet paper towels and kept in an environmental chamber at 10˚C and a 15:9 light:dark cycle, with onset of dark at 1900 EST. I chose 10˚C because Merchant (1970) found this to be the temperature at which the highest net energy gain occurred in the redback salamander. I allowed salamanders to acclimate for 5 to 10 d before feeding. Salamanders were fed *Drosophila melanogaster* fruit flies twice per week. HIGH salamanders were fed at least 66 flies per week; LOW salamanders were fed 1 fly every other week. Numbers of flies were based on maintenance level requirements computed using equations derived by Jaeger (1980a). I intended to feed HIGH salamanders at twice maintenance level and LOW salamanders at less than maintenance level.

At each feeding, the petri dishes were cleaned out and any uneaten flies were counted. All flies were removed 5 days before behavioral tests were run to allow time for digestion. After at least 11 weeks of maintaining this feeding schedule, I began the behavioral tests. Due to a number of escapes and mortalities, the tests ultimately were run with 52 salamanders in the HIGH treatment and 53 in the LOW treatment.

Tests were conducted in experimental chambers, which consisted of plastic, 5.6 L, lidded boxes with base dimensions 15 x 29 cm. A 20 x 150 mm test tube was inserted through one end, and suspended at roughly a 45 degree angle. This was lined with strips of water-saturated paper towel and served as an artificial burrow. I placed salamanders in the experimental chambers before lights-out 1 d prior to testing, allowing 1 night for acclimation to the chambers. During the acclimation period, the test tube was covered with a black paper sheath. The remainder of the chamber was covered with several layers

of paper towel and taped at the edges to prevent the salamander from "burrowing" under or between the paper towels. Leaf litter also was added. In preliminary tests, we found that recently captured (less than 1 week) salamanders would spend virtually no time foraging in either wet or dry test chambers that lacked leaf litter. Leaf litter used was cleared of insects using a Berlese funnel extraction for at least 24 h and was dried for at least one week at 65˚C. Less than 1 h before the onset of dark on the night of observation, each experimental chamber was misted with approximately 2-4 ml of water. This was added because preliminary tests showed that recently captured salamanders spent virtually no time in a totally dry chamber with leaf litter, but some time was spent foraging if small amounts of water were added. We believed that a totally dry chamber would result in too great of a risk even for hungry salamanders, so no effect of risk-sensitive foraging could be observed. Earlier tests indicated the test chamber with only a small amount of water added was indeed a "risk" to the salamanders in that they emerged from the burrows at significantly lower rates than in thoroughly wet chambers (see Appendix 6).

I made observations every 15 min for 7.5 h (30 observations total), beginning 30 min after lights out (1930 to 0245 EST). I removed the paper sheaths at the first observation. For each observation, I checked the test tube burrow with a headlamp and recorded the presence or absence of the salamander from its burrow. Presence was defined by the salamander having both forelegs within the test tube. Salamanders were re-weighed immediately after the observation period. Due to space constraints, I tested salamanders in 3 batches from 22 August to 28 August 1998. I assigned test night randomly within treatment so that each night equal numbers of salamanders from each treatment were tested. There were no apparent differences in scores among batch nights.

At the end of the observation period, each salamander had a score from 0 to 30, representing the number of observations during which the salamander was not in its burrow. I used a two-tailed Wilcoxon rank sum test and the Z-distribution to test the hypothesis that the feeding treatment did not affect the level of activity in the dry test chamber.

RESULTS

The median scores for the Risk-sensitive Foraging experiment were 3.5 and 2 out of the possible 30 for the HIGH and LOW treatments respectively. This was not a significant difference ($p = 0.60$). However, in both groups, there were a number of salamanders with scores of zero, which means they never left their burrows. When I removed these nonresponsive salamanders from the test, the median scores were 13 for the HIGH treatment and 7.5 for the LOW treatment ($p = 0.02$). There was, however, no difference in the proportion of salamanders that were nonresponsive between treatments ($p = 0.63$) with 44% of the HIGH salamanders and 40% of the LOW salamanders nonresponsive.

When scores were plotted against Snout-Vent Length (SVL), there was no apparent trend in the data, except that there was little activity in the salamanders with SVL < 40 mm (Figure 4.1). I divided the salamanders into 3 size classes, 35-39.9, 40-44.9, and >45 mm SVL, and looked at the average score of responsive salamanders and percent nonresponsive in each size class. The median score of responsive salamanders increased with increasing size class in the HIGH group, but peaked in the middle size class in the LOW group (Table 4.1). Within each size class, the HIGH group had a higher median score. Looking at the percent nonresponsive by size class, there was a decrease in nonresponsiveness with increasing size class in both groups, and roughly the same percent nonresponsive between treatments within each size class (Table 4.2).

Although the treatments differed greatly in diet, both had salamanders that gained and lost weight. As a group, the HIGH salamanders gained significantly more weight than LOW salamanders ($p < 0.01$ two-tailed). There was no obvious relationship between an individual salamander's score and percent change in mass (Figure 4.2).

I also divided the data by sex. Looking only at responsive salamanders, males and females within a treatment had similar median scores, with the HIGH group having a higher median score in both sexes, and differences in median scores between treatments was greater in females than in males (Table 4.3). The percent nonresponsive also did not

differ greatly by treatment or sex, although there was a slightly higher percent of females non-responsive than males for both treatments (Table 4.4).

DISCUSSION

Results suggest redback salamanders on low caloric diets are risk-averse. This is contrary to similar studies that show amphibians are risk-neutral (Horat and Semlitsch 1994) and fish, a more thoroughly studied ectothermic group, are either risk-prone (Croy and Hughes 1991, Godin and Crossman 1994, and Gotceitas and Godin 1991) or risk neutral (to a variable food source, not to predation risk) (Wildhaber and Crowder 1995) to differences in energy budget. Because salamanders, like fish, can survive for weeks and more without food, risk-neutral behavior may be expected. However, the risk studied here is not the risk of predation, but a risk of desiccation.. The probability of predation is never 100% for any risk-prone behavior. Conversely, desiccation is physiologically guaranteed for salamanders that forage too long in conditions that are too warm, dry, or windy. Additionally, because salamanders have very low metabolic rates (Pough 1980), the evolutionarily safe strategy may have always been to wait for more favorable physical conditions. Therefore, there are several reasons to expect an absence of this sort of risk-sensitive foraging behavior in salamanders.

The lack of any apparent relationship between percent change in mass and time spent foraging (Figure 4.2) draws into question whether the response variable, the number of times a salamander was observed out of the burrow, was truly dependent on hunger level. Although the treatment groups differed significantly in average percent mass change, the difference was only 8% (HIGH increased 5%, LOW decreased 3%). Because salamanders are able to survive long periods without eating, the 11-week feeding period may have been insufficient to create biologically significant differences in nutritional condition and hunger levels. Differences observed in median response between responsive salamanders may have been a statistical anomaly. Another explanation is that, although salamanders were maintained under the same basic conditions, the regular presence of 30 or more flies in the petri dish during the 11 week feeding period may have had unmeasured effects on the HIGH salamanders such as disease or stress, simulating a

physiologically poor condition similar to what I was attempting to create in the LOW salamanders.

Alternatively, it is possible that after periods of little or no food, salamanders revert to an inactive or nonfeeding state for energy conservation. Although LOW salamanders were fed, the low calorie intake could have simulated conditions that normally trigger the summer or winter estivation and the related metabolic slow down. It is known that salamanders physiologically acclimate to a given temperature and thus maintain low metabolism at relatively high temperatures (Fitzpatrick 1973b, Feder 1978)

Results from this experiment may help explain the striking difference in results in Chapter 3 between Sites 1 and 3 and Site 2. At Site 2, the salamanders had only been exposed to the presumably hostile environment for a few months, comparable to the feeding period in this experiment. Their change in mass would have been minimal (again, much like the LOW salamanders in this experiment) and not yet worth risking desiccation. The risk-averse behavior observed here may be the immediate response strategy of this species.

Table 4.1. Median scores of responsive salamanders by size class and treatment. Number of salamanders in each group in parentheses. Scores represent the number of observations out of 30 that a salamander was observed out of its test-tube burrow. Responsive salamanders are those that were observed at least once out of their burrows. HIGH salamanders were fed 2x maintenance level, LOW salamanders were fed 1 fruit fly per week (much less than maintenance level). Feeding treatments lasted 11 weeks.

Size class (mm SVL)	HIGH	LOW
35 – 39.9	9.5 (2)	2.0 (3)
40 – 44.9	12.0 (11)	10.0 (17)
45 +	16.5 (16)	6.0 (12)

Table 4.2. Percent of nonresponsive salamanders by size class and treatment. Number of salamanders in each group in parentheses. Nonresponsive salamanders are those that were observed in their test tube burrows in all 30 observations. HIGH salamanders were fed 2x maintenance level, LOW salamanders were fed 1 fruit fly per week (much less than maintenance level). Feeding treatments lasted 11 weeks.

Size class (mm SVL)	HIGH	LOW
35 – 39.9	78% (9)	50% (6)
40 – 44.9	48% (21)	45% (31)
45 +	27% (22)	25% (16)

Table 4.3. Median scores of responsive salamanders by sex and treatment. Number of salamanders in each group in parentheses. Scores represent the number of observations out of 30 that a salamander was observed out of its test-tube burrow. Responsive salamanders are those that were observed at least once out of their burrows. HIGH salamanders were fed 2x maintenance level, LOW salamanders were fed 1 fruit fly per week (much less than maintenance level). Feeding treatments lasted 11 weeks.

Sex	HIGH	LOW
Female	13 (16)	6 (19)
Male	12 (13)	9 (13)

Table 4.4. Percent of nonresponsive salamanders by sex and treatment. Number of salamanders in each group in parentheses. Nonresponsive salamanders are those that were observed in their test tube burrows in all 30 observations. HIGH salamanders were fed 2x maintenance level, LOW salamanders were fed 1 fruit fly per week (much less than maintenance level). Feeding treatments lasted 11 weeks.

Sex	HIGH	LOW
Female	48% (31)	42% (33)
Male	38% (21)	35% (20)

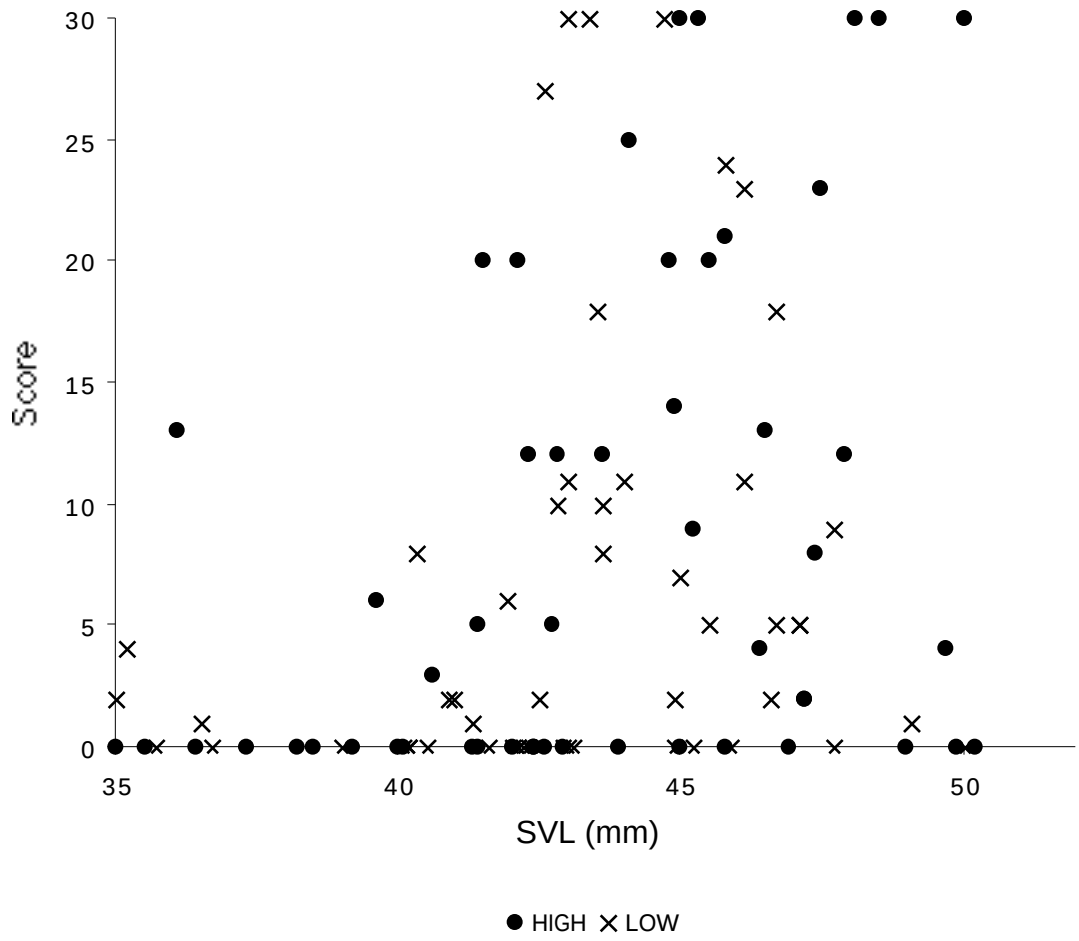

Figure 4.1. Results of tests in experimental chambers for amount of time spent foraging by redback salamanders fed a HIGH caloric or LOW caloric diet. Individual scores versus snout-vent length (SVL), where scores represent the number of observations out of 30 that a salamander was observed out of its test-tube burrow.

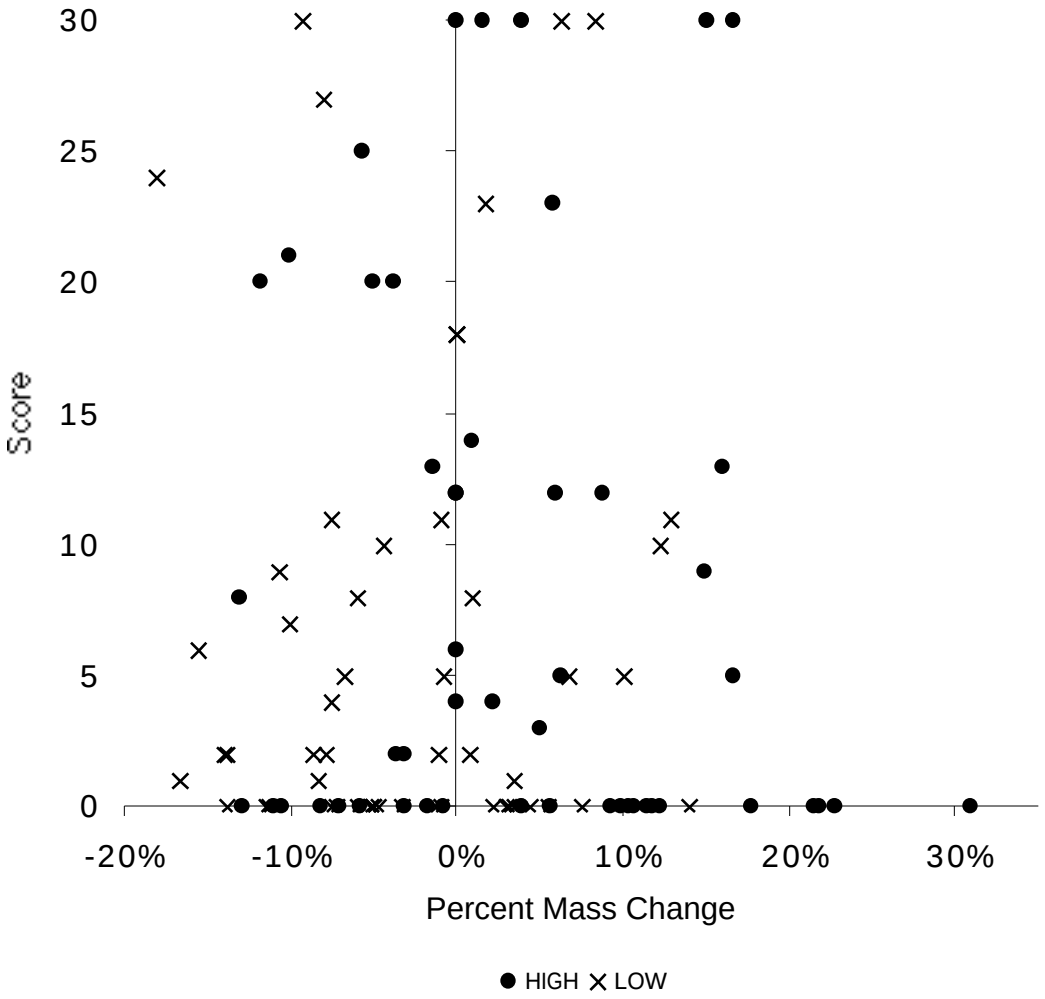

Figure 4.2. Results of tests in experimental chambers for amount of timber spent foraging by redback salamanders fed a HIGH caloric or LOW caloric diet. Individual scores versus percent mass change, where scores represent the number of observations out of 30 that a salamander was observed out of its test-tube burrow.

CHAPTER 5 - CONCLUSIONS

SUMMARY

In this thesis I examined the effects of timber harvesting on terrestrial salamander abundance, fecundity, activity rates, and foraging behavior, and tested for behavioral and visibility induced biases in a commonly used census technique.

In Chapter 2, I examined the short term effects (1 to 4 years postharvest) of 6 silvicultural treatments compared to a Control from 4 sites in southwest Virginia and West Virginia. First year postharvest results showed no significant treatment effect on salamander abundance, but all treatments with canopy removal had fewer salamanders than the Control. When I included data from later years, the treatment effect on salamander abundance was significant. All treatments with canopy removal had fewer salamanders than the Control, and the 3 treatments with the most drastic canopy removal (4-7 Shelterwood, Leavetree, and Clearcut) had significantly fewer salamanders than the Control. Although there was nearly a 2-fold difference in average abundance among treatments with canopy removal, they did not differ significantly. Differences in short-term response among treatments with canopy removal may be detectable with further replication. Further sampling over time may also reveal differences in rates of salamander recovery among these treatments. Evidence from size distributions, age class composition, and reproductive rates suggest that timber harvesting impacts the entire terrestrial salamander community equally without targeting a particular species, a specific age class, or reproduction.

In Chapter 3, I examined the short term effects (less than 18 months postharvest) of timber harvesting on activity rates in redback and slimy salamanders. Instantaneous activity rates for redback salamanders ranged from 1.3% to 9.2% and for slimy salamanders ranged from 3.6% to 11.7%. There was roughly a 2-fold difference in average instantaneous activity rates between treatments, but activity on one treatment was not consistently higher or lower than on the other. A possible explanation for the inconsistency in results is that (1) on low quality sites (Site 1) after a full year, timber

harvesting leads to an increase in activity; (2) on high quality sites (Site 3) after a full year, timber harvesting does not have a strong effect on activity rates; and (3) on recently harvested, high quality sites (Site 2), timber harvesting leads to a decrease in activity (alternatively, the results from Site 2 may represent the response at an extremely high quality site).

In Chapter 4, I investigated risk-sensitive foraging in terrestrial salamanders in a laboratory environment. I maintained 105 redback salamanders at either HIGH or LOW caloric levels for 11 weeks, then observed the amount of time they spent in a dry test chamber. Results indicate redback salamanders are risk-averse, with salamanders maintained at LOW caloric levels spending significantly less time in the dry test chamber than salamanders maintained at HIGH caloric levels. This response may be attributable to the fact that this taxonomic group has adapted to regularly spending seasons in a mostly nonfeeding state. Females and small adults tended to be slightly more risk-averse than males and larger adults.

RECOMMENDATIONS AND FUTURE DIRECTION

The current data on the relative impacts of various timber harvest methods will be improved with further replication and sampling over time. Increased replication may reveal significant differences among treatments with canopy removal. Sampling these sites over several years will reveal differences in rates of salamander population recovery over time, which may be of greater importance than the short term response to these treatments. Despite the evidence of biases in the night sampling method, I believe the results obtained in Chapter 2 are generally reliable. True relative impacts of the 7 treatments may differ somewhat from those presented here, with differences in salamander relative abundances between harvested treatments and the control being slightly larger or smaller than presented, because of treatment induced biases in observability or activity. However, I do believe the conclusion that salamander populations are reduced with timber harvesting is valid, because half of the study sites used were low quality, so surface counts likely overestimated the relative abundance of salamanders on the harvested treatments and on the one high quality site (Clinch 2) most

of the treatments had been harvested for a full year before sampling so there was probably no strong effect of timber harvesting.

The response of non-game wildlife, including salamanders, should be incorporated along with economic, aesthetic, legal, and other ecological considerations in forest management. Alternatives to clearcuts, although they carry less negative connotations and may be more acceptable to the public, may be more detrimental to salamander populations because a larger area must be affected to obtain the same total lumber. For example, to compare the cost of the 12-14 Shelterwood to the Clearcut on salamanders, first consider that the Shelterwood requires 2.5 times the land to produce the same amount of lumber as a Clearcut, based on target basal area removals of 40% and near 100% respectively (Chapter 2: Methods: Treatments). Next consider that the 12-14 Shelterwood costs 46% of the salamander population and the Clearcut costs 65% of the salamander population, based on the adjusted mean number of salamanders postharvest on these treatments relative to numbers on the Control. Given this, the 12-14 Shelterwood costs 115 (46 times 2.5 units of land) salamander units compared to only 65 (65 times 1 unit of land) on the Clearcut. Alternatively, because shelterwood and group selection regeneration methods typically involve removing the remaining basal are after 10-20 years, recovery of salamanders may be stunted, with numbers cut in half again, while salamanders numbers on a clearcut increase steadily.

Because the ecology of terrestrial plethodontid salamanders is based on very low metabolism, similar prey, and predictable dehydration rates, the response of endangered plethodontid species (e.g. *Plethodon hubrichti* and *P. nettingi*) to these timber harvest methods should be similar to that of the common species in this study. However, when known, the different ecological tolerances of these species should be accounted for. For example, the Shenandoah salamander (*Plethodon shenandoah*) is more tolerant of dryness than the redback salamander; the Shenandoah salamander is able to persist in dry talus slopes where the redback salamander cannot and is excluded from the surrounding area because of competition with the redback salamander (Jaeger 1972). This suggests that this species would be less susceptible to the drying effects of timber harvesting.

However, drought lead to the extinction of several populations of the Shenandoah salamander because they were unable to burrow down to moist soil in the shallow soil of the talus (Jaeger 1980c), which suggests they would be even more susceptible to timber harvesting than the redback salamander.

Managers and researchers should be aware of and make an effort to account for possible biases in any wildlife survey. In this study, I tested for biases in nighttime, surface counts for terrestrial salamanders due to differences in observability and in salamander activity in different environments created by timber harvesting. Daytime, cover object, salamander surveys should also be tested for biases in detection levels between habitats. Between-habitat biases in the day search method may arise from differences in cover object, leaf litter, and soil drying rates, or per capita or absolute differences in cover object density. Day search surveys should also be examined for differences in abundance associated with the number of days since the last rain, differences in age ratios between habitats, and differences among observers. It is particularly important to consider the effect of time since the last rain in both high and low quality sites (see below).

Differences in response to timber harvesting and nutritional condition in survival and activity between age classes should be investigated further. There appeared to be differences in foraging strategies and activity levels between juvenile and adult slimy salamanders (Chapter 3: Discussion: Trends and Predictability). There were also size and sex specific differences among adult salamanders in risk taking by foraging under dry conditions (Chapter 4), but these differences were slight and not statistically significant. Although small adults would be expected to have lower energy reserves than larger adults and, therefore, a higher need to forage even under poor conditions, salamanders of the smallest adult size class (35 - 39.9 mm SVL) were slightly more risk-averse than larger adults. Similarly, females which have the added energetic demands of yolking and brooding eggs, and therefore have a high need to forage, were actually more risk-averse than were males. Conversely, salamanders on low quality sites (Chapter 3: Site 1) with potentially low nutritional condition had statistically significant increases in activity following timber harvesting; however, this increase was during suitable, wet nights, not

under unsuitable, dry conditions. Closer investigation of the response of juveniles, small adults, and females to timber harvesting may be fruitful. However, in Chapter 2, I found no effects of timber harvest on age class ratios (except in slimy salamanders), the percent of adult females that were gravid, or the mean clutch sizes of gravid females.

The effects of site quality on salamander behavior and response to timber harvesting should also be examined. Salamander populations on high quality sites appear to show substantial declines in response to timber harvesting and are not biased by differences in activity levels, although salamander declines at high quality sites may be overestimated if sampled immediately after the harvest (see Chapter 2: Discussion: Trends and Predictability). Declines at low quality sites are less substantial but appear to be underestimated due to differences in activity levels.

High quality sites for salamanders are most likely high-elevation, north-facing slopes and wet, supplied by groundwater seeps, high annual rainfall, or low drying rates. These factors should be related to the regeneration rate of forest canopy and, therefore, the recovery rate of a salamander population following timber harvest. Elevation is known to affect salamander survival and reproduction rates (Tilley and Bernardo 1993). Site quality (canopy coverage) may also affect selection of cover objects (Gabor 1995) which could influence results of studies relying on day searches. In Chapter 3, timber harvest on a low quality site (Site 1) lead to large increases in surface activity, while there was little difference in activity on a high quality site (Site 3). Differences in site quality may also explain the larger declines in the first year postharvest on a high quality site Clinch 2 compared to low quality sites Blacksburg 2 and West Virginia 1 (Chapter 2).

We must also question what is truly “high quality” or a “low quality” salamander habitat. The “high quality” label has been given to sites with high surface count densities; however, in Chapter 3, the plot with the highest redback salamander surface density (Plot C2) had a population size estimate no larger than any other control plot. If actual salamander population sizes vary little across these sites, is a “high quality” site one with

a large portion of its population active or one in which salamanders do not need to be active very often or very long?

The study sites in Chapter 2 were chosen to be representative of hardwood forests of the Southern Appalachians. Sites in Chapter 3 were chosen based largely on the availability of recently harvested areas. Study sites are often chosen for areas of high subject density, to obtain sufficient sample sizes, increasing the likelihood of finding "meaningful" (statistically significant and publishable) results. However, choosing study sites that are more representative of the range of species' habitats may yield more interesting and truly meaningful results.

In conclusion, any canopy removal reduced average salamander abundance by 40 to 60%, but only the 3 treatments with the most canopy removal (4-7 Shelterwood, Leavetree, and Clearcut) showed statistically significant reductions. Although I found activity induced biases in the night sampling technique, these were not sufficient to explain the reductions in salamander numbers; therefore, reductions in salamander numbers due to timber harvesting in this and similar studies reflect actual reductions in the salamander population.

LITERATURE CITED

Angleberger, M. P. and J. P. Chinnici. 1975. Dimorphism in the red-backed salamander *Plethodon cinereus* (Green) at Mountain Lake, Virginia. The Virginia Journal of Science 26: 153-158.

Ash, N. A. 1988. Disappearance of salamanders from clearcut plots. The Journal of the Elisha Mitchell Scientific Society 104: 116-122.

_____. 1997. Disappearance and return of plethodontid salamanders to clearcut plots in the southern Blue Ridge Mountains. Conservation Biology 11: 983-989.

_____ and R. C. Bruce. 1994. Impacts of timber harvesting on salamanders. Conservation Biology 8: 300-301.

Bayliss, P., G. J. W. Webb, P. J., P. J. Whitehead, K. Dempsey, and A. Smith. 1986. Estimating the abundance of saltwater crocodiles, *Crocodylus porosus* Schneider, in tidal wetlands of the Northern Territory: a mark-recapture experiment to correct spotlight counts to absolute numbers, and the calibration of helicopter and spotlight counts. Australian Wildlife Research 13: 309-320.

_____ and K. M. Yeomans. 1989. Correcting bias in aerial survey population estimates of feral livestock in northern Australia using the double-coutn technique. Journal of Applied Ecology 26: 925-933.

Blaustein, A. R. 1994. Chicken little or Nero fiddle - a perspective on declining amphibian populations. Herpetologica 50: 85-97.

_____ and D. B. Wake. 1990. Declining amphibian populations: a global phenomenon? Trends in Ecology and Evolution 5: 203-204.

Bobka, M. S., R. G. Jaeger, and D. C. McNaught. 1981. Temperature dependent assimilation of two species of terrestrial salamanders. Copeia 1981: 417-421.

Bogert, C. M. 1952. Relative abundance, habitats, and normal thermal levels of some Virginian salamanders. Ecology 33: 16-30.

Bruce, R. C. 1967. A study of the salamander genus *Plethodon* on the southeastern escarpment of the Blue Ridge Mountains. The Journal of the Elisha Mitchell Scientific Society 83: 74-82.

Bury, R. B. 1983. Differences in amphibian populations in logged and old growth redwood forest. Northwest Science 57: 167-178.

Cohn, J. P. 1994. Salamanders slip-sliding away or too surreptitious to count? BioScience 44: 219-223.

Conant R. and J. T. Collins. 1991. A Field Guide to Reptiles and Amphibians: Eastern and Central North America. Houghton Mifflin Company. 450 pp.

Croy, M. I., and R. N. Hughes. 1991. Effects of food supply, hunger, danger and competition on choice of foraging location by the fifteen-spined stickleback, *Spinachia spinachia* L. Animal Behaviour 42: 131-139.

deMaynadier, P.G. and M.L. Hunter. 1995. The relationship between forest management and amphibian ecology: a review of the literature. Environmental Reviews 3: 230-261.

Dunn, E. R. 1972. Salamanders of the Family Plethodontidae. Society for the Study of Amphibians and Reptiles. 446 pp.

Feder, M. E. 1978. Environmental Variability and thermal acclimation in neotropical and temperate zone salamanders. Physiological Zoology 51(1): 7-16.

_____. 1983. Integrating the ecology and physiology of plethodontid salamanders. Herpetologica 39: 291-310.

Fitzpatrick, L. C. 1973a. Energy allocation in the alleghany moutain salamander, *Desmognathus ochrophaeus*. Ecological Monographs 43: 43-58.

_____. 1973b. Influence of seasonal temperatures on the energy budget and metabolic rates of the northern two-lined salamander Eurycea bislineata bislineata. Comparative Biochemistry and Physiology 45A: 807-818.

Fraser, D. F. 1976. Empirical evaluation of the hypothesis of food competition in salamanders of the genus Plethodon. Ecology 57: 459-471.

Gabor, C. R. 1995. Correlational test of Mathis' hypothesis that bigger salamanders have better territories. Copeia 1995: 729-735.

Godin, J.-G. J., and S. L. Crossman. 1994. Hunger-dependent predator inspection and foraging behaviours in the threespine stickleback (*Gasterosteus aculeatus*) under predation risk. Behavioral Ecology and Sociobiology 34: 359-366.

Gotceitas, V. and J.-G. J. Godin. 1991. Foraging under the risk of predation in juvenile Atlantic salmon (*Salmo salar* L.): effects of social status and hunger. Behavioural Ecology and Sociobiology 29: 255-261.

Grover, M. C. 1998. Influence of cover and moisture on abundances of the terrestrial salamanders Plethodon cinereus and Plethodon glutinosus. Journal of Herpetology 32(4): 489-497.

Hairston, N. G., Sr. 1980. The experimental test of an analysis of field distributions: competition in terrestrial salamanders. Ecology 61: 817-826.

_____. 1981. An experimental test of a guild: salamander competition. Ecology 62: 65-72.

_____. 1983. Growth, survival and reproduction of *Plethodon jordani* : trade-offs between selective pressures. Copeia 1983: 1024-1035.

_____. 1986. Species packing in desmognathus salamanders: experimental demonstration of predation and competition. The American Naturalist 127: 266-291.

_____. 1987. Community Ecology and Salamander Guilds. Cambridge University Press. 230 pp.

Harper, C. A. and D. C. Guynn, Jr. 1999. Factors affecting salamander density and distribution within four forest types in the Southern Appalachian Mountains. Forest Ecology and Management 114: 245-252.

Harpole, D. N. 1996. Effects of silviculture on terrestrial salamanders in southern Appalachian forests. M.S. Thesis Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

_____ and C.A. Haas. 1999. Effects of seven silvicultural treatments on terrestrial salamanders. Forest Ecology and Management 114: 349-356.

Heatwole, H. 1960. Burrowing ability and the behavioral response to desiccation of the salamander, *Plethodon cinereus*. Ecology 41: 661-668.

_____. 1962. Environmental factors influencing local distribution and activity of the salamander, *Plethodon cinereus*. Ecology 43: 460-472.

Horat, P., and R. D. Semlitsch. 1994. Effects of predation risk and hunger on the behaviour of two species of tadpoles. Behavioural Ecology and Sociobiology 34: 393-401.

Huhta, V. 1976. Effects of clear-cutting on numbers, biomass and community respiration of soil invertebrates. Annales Zoologici Fennici 13: 63-80.

Jaeger, R. G. 1972. Food as a limited resource in competition between two species of terrestrial salamanders. Ecology 53: 535-546.

_____. 1978. Plant climbing by salamanders: periodic availability of plant-dwelling prey. Copeia 1978: 686-691.

_____. 1980*a*. Fluctuations in prey availability and food limitation for a terrestrial salamander. Oecologia 44: 335-341.

_____. 1980*b*. Microhabitats of a terrestrial forest salamander. Copeia 1980: 265-268.

_____. 1980*c*. Density-dependent and density-independent causes of extinction of a salamander population. Evolution 34: 617-621.

_____ and D. C. Forester. 1993. Social behavior of plethodontid salamanders. Herpetologica 49: 163-175.

Johnson, J. E., D. W. Smith, and J. A. Burger. 1985. Effects on the forest floor of whole-tree harvesting in an Appalachian oak forest. American Midland Naturalist 114: 51-61.

Kacelnik, A., and M. Bateson. 1996. Risky theories - the effects of variance of foraging decisions. American Zoologist 36: 402-434.

Kaplan, R. H. 1980. The implications of ovum size variability for offspring fitness and clutch size within several populations of salamanders (*Ambystoma*). Evolution 34: 51-64.

_____. 1985. Maternal influences on offspring development in the California Newt, *Taricha torosa*. Copeia 1985: 1028-1035.

Kittredge, J. 1948. Forest Influences. McGraw-Hill Book Company. 394 pp.

Kokko, H. and W. J. Sutherland. 1998. Optimal floating and queing strategies: consequences for density dependence and habitat loss. The American Naturalist 152: 354-366.

Kramer, P., N. Reichenbach, M. Hayslett, and P. Sattler. 1993. Population dynamics and conservation of the Peaks of Otter Salamander, *Plethodon hubrichti*. Journal of Herpetology 27: 431-435.

Krohn, W. B. and E. G. Bizeau. 1989. An estimate of bias in tail-fan surveys of Rocky Mountain Canada Geese. Northwest Science 63: 1-4.

Liechty, H. O., M. J. Holmes, D. D. Reed, and G. D. Mroz. 1992. Changes in microclimate after stand conversion in two northern hardwood stands. Forest Ecology and Management 50: 253-264.

Martin, D. and H. Hong. 1991. The use of Bactine® in the treatment of open wounds and other lesions in captive anurans. Herpetological Review 22: 21.

Mathis, A. 1990. Territoriality in a terrestrial salamander: the influence of resource quality and body size. Behaviour 112: 162-175.

_____. 1991. Territories of male and female terrestrial salamanders: costs, benefits, and intersexual spatial associations. Oecologia 86: 433-440.

Means, D. B., J. G. Palis, and M. Baggett. 1996. Effects of slash pine silviculture on a Florida population of flatwoods salamander. Conservation Biology 10: 426-437.

Merchant, H. C. 1970. Estimated energy budget of the red-backed salamander, *Plethodon cinereus* . Ph.D. Dissertation. Rutgers University, New Brunswick, New Jersey.

_____. 1972. Estimated population size and home range of the salamanders *Plethodon jordani* and *Plethodon glutinosus*. Journal of the Washington Academy of Science 62: 248-257.

Messere, M. and P.K. Ducey. 1998. Forest floor distribution of northern redback salamanders, *Plethodon cinereus,* in relation to canopy gaps: first year following selective logging. Forest Ecology and Management 107: 319-324.

Mitchell, J. C., J. A. Wicknick, and C. D. Anthony. 1996. Effects of timber harvesting practices on Peaks of Otter salamander (*Plethodon hubrichti*) populations. Amphibian and Reptile Conservation 1: 15-19.

Nagel, J. W. 1979. Life History of the ravine salamander (*Plethodon richmondi*) in northeastern Tennessee. Herpetologica 35: 38-43.

Nishikawa, K. C. 1985. The ecology and evolution of aggressive behavior in two species of terrestrial salamander. Ph.D. Dissertation. University of North Carolina, Chapel Hill, North Carolina.

_____. 1990. Intraspecific spatial relationships of two species of terretrial salamanders. Copeia 1990: 418-426.

Ott, R. L. 1993. An Introduction to Statistical Methods and Data Analysis. 4th ed. Duxbury Press. 1051 pp.

Petranka, J. W. 1994. Response to impact of timber harvesting on salamanders. Conservation Biology 8: 302-304.

_____. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press. 587 pp.

_____. 1999. Recovery of salamanders after clearcutting in the southern Appalachians: a critique of Ash's estimates. Conservation Biology 13: 203-205.

_____, M. E. Eldridge, and K. E. Haley. 1993. Effects of timber harvesting on southern Appalachian salamanders. Conservation Biology 7: 363-370.

_____, M. P. Brannon, M. E. Hopey, and C. K. Smith. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. Forest Ecology and Management 67: 135-147.

Pough, F. H. 1980. The advantages of ectothermy for tetrapods. The American Naturalist 115: 92-112.

_____, E. M. Smith, D. H. Rhodes, and A. Collazo. 1987. The abundance of salamanders in forest stands with different histories of disturbance. Forest Ecology and Management 20: 1-9.

Samuel, M. D., R. K. Steinhorst, E. O. Garton, and J. W. Unsworth. 1992. Estimation of wildlife population ratios incorporating survey design and visibility bias. Journal of Wildlife Management 56: 718-725.

Sattler, P. and N. Reichenbach. 1998. The effects of timbering on *Plethodon hubrichti*: short-term effects. Journal of Herpetology 32: 399-404.

Sayler, A. 1966. The reproductive ecology of the red-backed salamander, *Plethodon cinereus*, in Maryland. Copeia 1966: 183-193.

Seastedt, T. R., and D. A. Crossley, Jr. 1981. Microarthropod response following cable logging and clear-cutting in the southern Appalachians. Ecology 62: 126-135.

Semlitsch, R. D. 1980. Geographic and local variation in population parameters of the slimy salamander, *Plethodon glutinosus*. Herpetologica 36: 6-16.

Short, J. and P. Bayliss. 1985. Bias in aerial survey estimates of kangaroo density. Journal of Applied Ecology 22: 415-422.

Smith, J. N. M. and P. Arcese. 1989. How fit are floaters? Consequences of alternative territorial behaviors in a nonmigratory sparrow. The American Naturalist 133: 830-845.

Smith, S. 1978. The underworld of the sparrow: adaptive strategy for floaters. The American Naturalist 112: 571-582.

Spotila, J. R. 1972. Role of temperature and water in the ecology of lungless salamanders. Ecological Monographs 42: 95-124.

Stebbins, R. C. 1954. Natural history of the salamanders of the plethodontid genus *Ensatina*. University of California Publications in Zoology 54: 47-124.

Sweitzer, R. A. 1996. Predation or starvation: consequences of foraging decisions by porcupines (*Erethizon dorsatum*). Journal of Mammology 77: 1068-1077.

Taub, F. B. 1961. The distribution of the red-backed salamander, *Plethodon c. cinereus*, within the soil. Ecology 42: 681-698.

Thurow, G. 1976. Aggression and competition in Eastern Plethodon (Amphibia, Urodela, Plethodontidae). Journal of Herpetology 10(4): 277-291.

Tilley, S. G. and J. Bernardo. 1993. Life history evolution in plethodontid salamanders. Herpetologica 49: 154-163.

Travis, J. 1983. Variation of *Hyla gratiosa* larvae in experimental enclosures. Copeia 1983: 232-237.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47(4): 893-901.

Vernberg, F. J. 1953. Hibernation studies of two species of salamanders, *Plethodon cinereus cinereus* and *Eurycea bislineata bislineata*. Ecology 34: 55-62.

Wake, D. B. 1991. Declining amphibian populations. Science 253: 860.

White, G. 1998. Program MARK. www.cnr.colostate.edu/~gwhite/mark/mark.htm.

Wildhaber, M. L. and L. B. Crowder. 1995. Bluegill sunfish (*Lepomis macrochirus*) foraging behavior under temporally varying food conditions. Copeia 1995(4): 891-899

Zack, S. and B. J. Stutchbury. 1992. Delayed breeding in avian social systems: the role of territory quality and “floater” tactics. Behavior 123: 194-219.

APPENDIX 1 - ACCURACY OF SILVICULTURE TREATMENTS

Table A1. 1. Post-treatment basal area (m^2/ha) by treatment for Blacksburg 1, Blacksburg 2, and Newcastle sites. Basal area includes merchantable and submerchantable timber. Table adapted from Bryan Wender, Virginia Tech Department of Forestry, unpublished data.

Treatment	Blacksburg 1	Blacksburg 2	Newcastle
Control	21.2	21.5	28.8
Herbicide	33.0	28.3	27.1
Group Selection	9.6	26.2	2.4
12-14 Shelterwood	17.7	11.2	7.8
4-7 Shelterwood	3.4	3.9	2.5
Leavetree	3.0	3.9	3.4
Clearcut	4.4	< 0.1	2.2

APPENDIX 2 - EFFECTS OF 7 SILVICULTURAL TREATMENTS IN TERRESTRIAL SALAMANDER BIOMASS

Because changes in population size could be manifested in biomass as well as in changes in abundance, particularly in ectothermic organisms such as fish or salamanders, I also analyzed the effect of the 7 silvicultural treatments from Chapter 2 on salamander biomass.

METHODS

I describe the 7 sivilculture treatments and sampling methods of salamanders in Chapter 2. Salamander biomass on a treatment was calculated for each site as the average abundance per transect within a year multiplied by the average mass in grams within a year. As in the abundance analysis, only data from postharvest years were used. For sites with multiple years, the within year averages were averaged to yield the overall average for that site. For this analysis, I did not subdivide the data by species. Statistical analysis was parallel to the abundance analysis in Chapter 2; I used an ANCOVA with treatment as the main effect, site as a blocking factor, and the preharvest biomass as a covariate.

RESULTS

There was preharvest variation in biomass at all sites (Figure A2. 1a) and biomass was positively correlated with abundance (Figure A2. 2b). Yearly biomass within a site closely paralleled the yearly abundance seen at a site (Figure A2. 3 compared to Figure 2. 2). Combining all sites, the average biomass in the Control was 5.77 g per 30-m^2 transect. Biomass varied from a high of 7.13 g on the Herbicide to a low of 2.96 g on both the Clearcut and the 4-7 Shelterwood (Figure A2. 3). However, there was no significant treatment effect ($p = 0.22$).

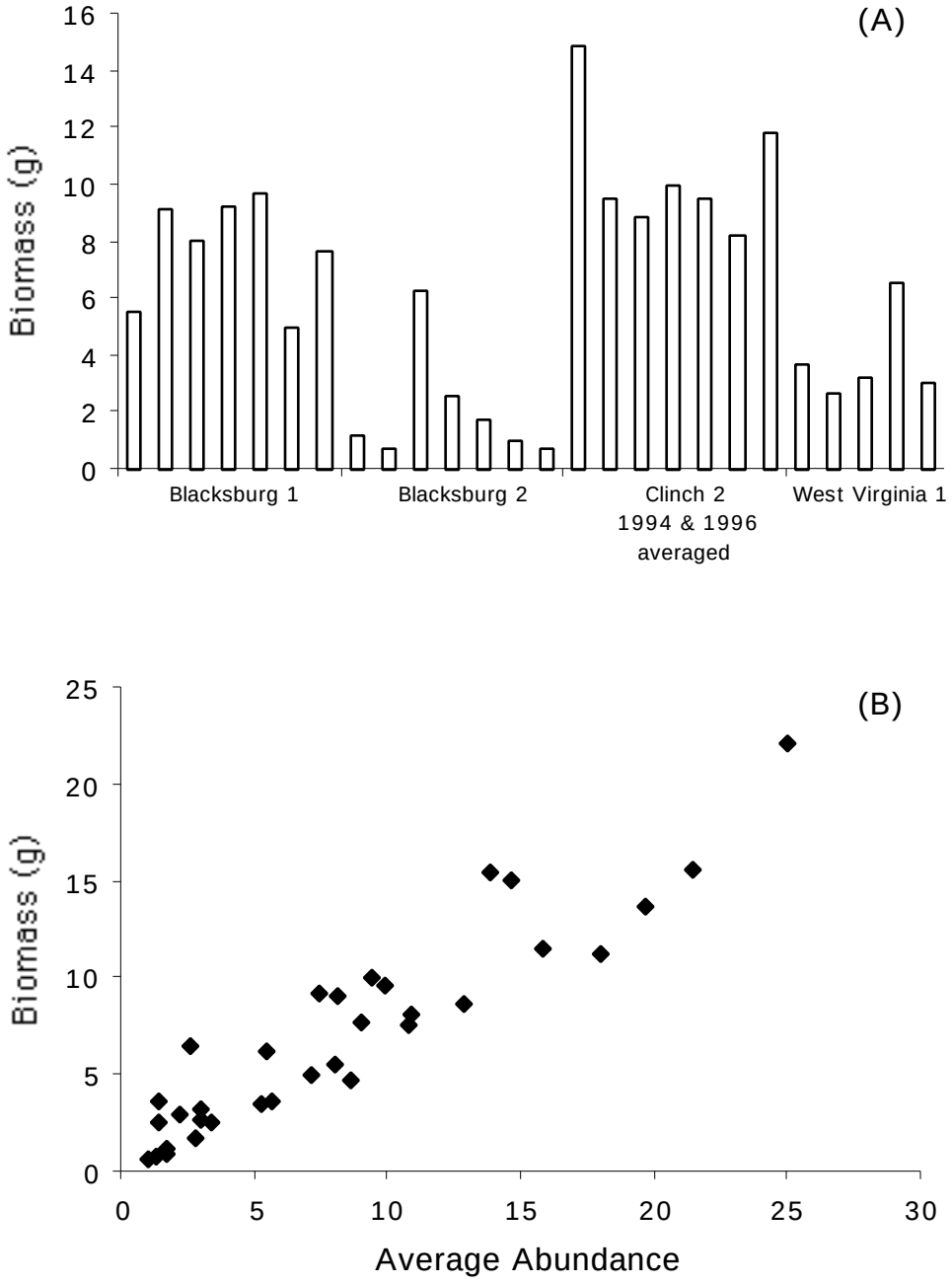

Figure A2. 1. Preharvest salamander biomass per 30-m^2 transect (A) by site and treatment plot and (B) versus preharvest abundance.

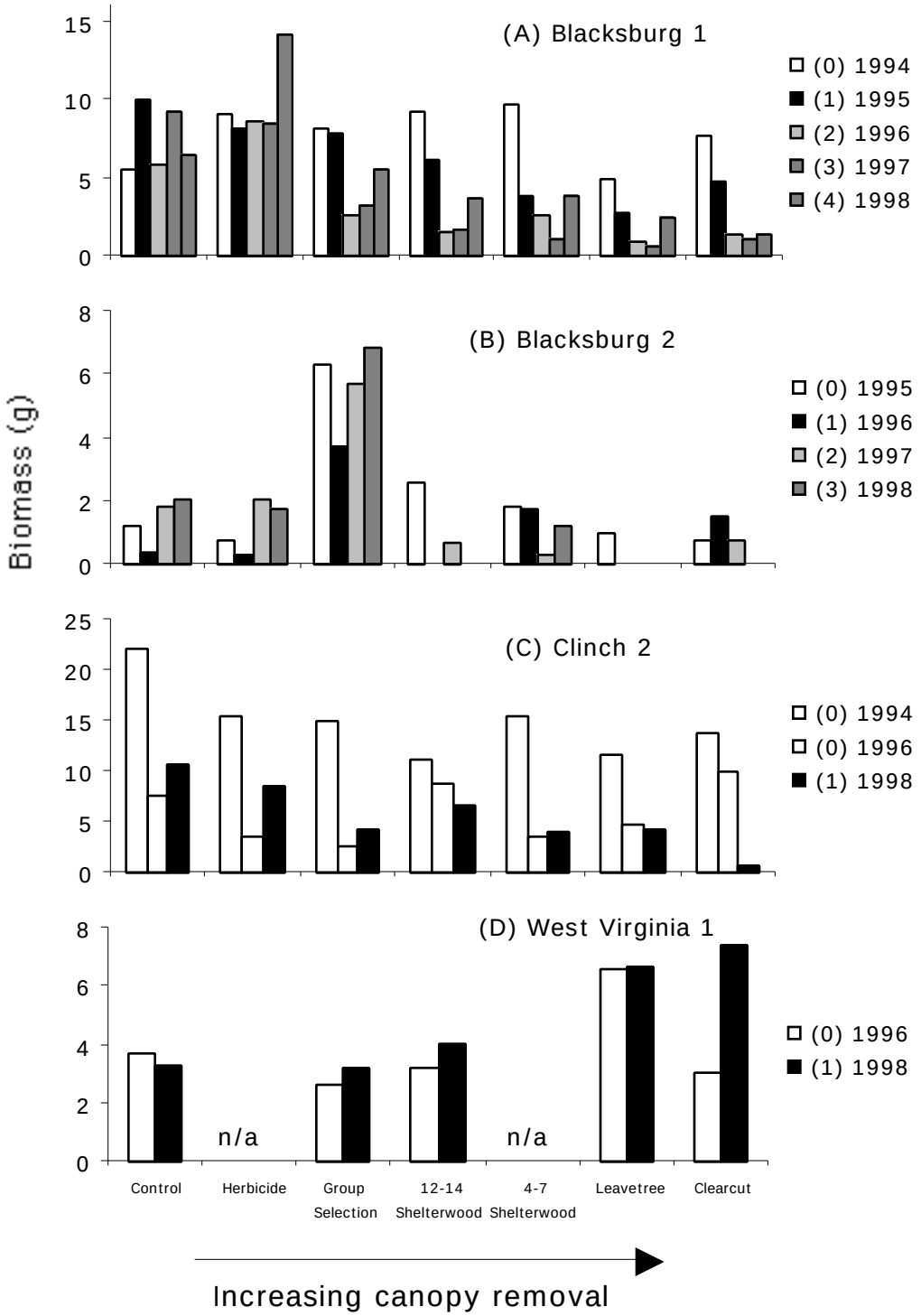

Figure A2. 2. Annual salamander biomass per 30-m^2 transect at (A) Blacksburg 1, (B) Blacksburg 2, (C) Clinch 2, and (D) West Virginia 1.

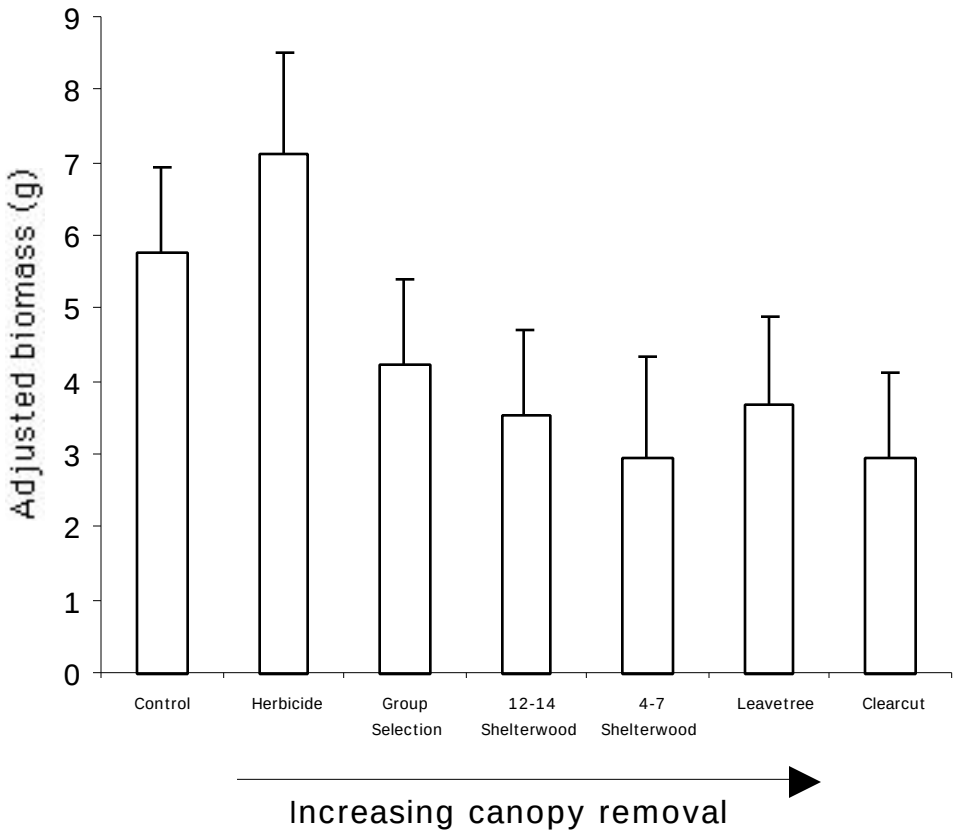

Figure A2. 3. Salamander biomass per 30-m^2 transect (mean + SE) by treatment. Values given include all species, all sites, and all years and are adjusted for preharvest biomass. Treatments did not differ at p = 0.10.

APPENDIX 3 - TOE CLIPPING PATTERN

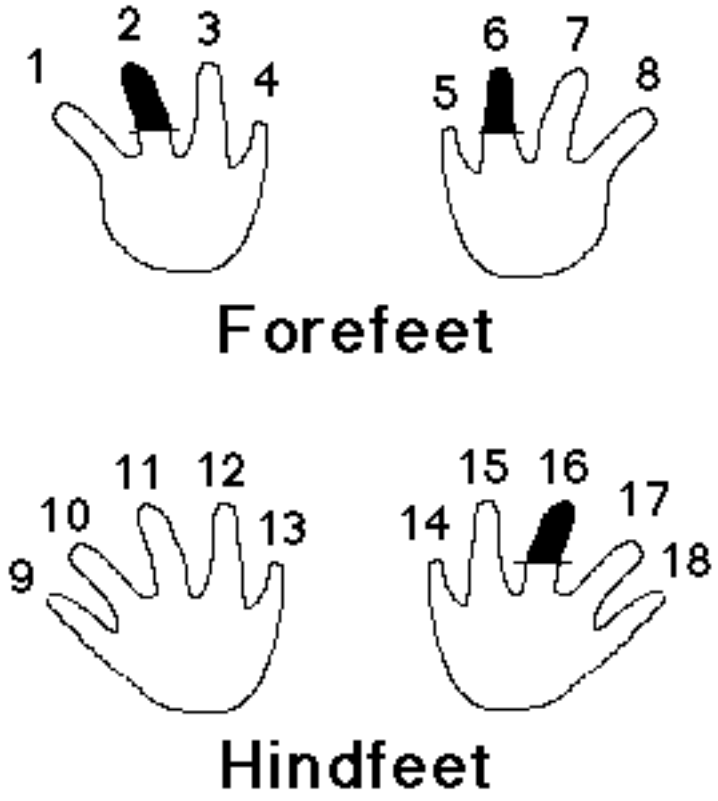

Figure A3. 1. Toe-marking pattern for mark-recapture, shown from dorsal view. Smaller inner toes (Numbers 4, 5, 13, 14) were not used. Numbers were read in sequential order, from lowest to highest. The blackened toes would represent salamander 2-6-16 or 020616.

APPENDIX 4 - MARK CAPTURE PROBABILITIES

Table A4. 1. Probability of capture for redback salamanders in Chapter 3 from Program MARK. See Table 3.1 for descriptions of study plots.

Pair	Control	Harvest	Higher Activity on
1a	1.6	4.6	Harvest
1b	1.5	4.5	Harvest
2	5.4	2.6	Control
3a	2.2	5.8	Harvest
3b	5.2	3.9	Control

Table A4. 2. Probability of capture for slimy salamanders in Chapter 3 from Program MARK. See Table 3.1 for descriptions of study plots.

Pair	Control	Harvest	Higher Activity on
1a	5.3	4.3	Control
1b	9.6	5.5	Control
2	7.0	2.7	Control
3a	5.7	12.0	Harvest
3b	8.2	9.2	Harvest

APPENDIX 5 - STUDY SITE DESCRIPTIONS OF VARIOS STUDIES ON EASTERN PLETHODONTID SALAMANDERS

Table A5. 1. Location, elevation, aspect, slope, and salamander density of various studies on eastern plethodontid salamanders where at least elevation was given.

Citation	Study Location	Elevation (m)	Other Site Quality Parameters	Focus of study
Angleberger and Chinnici 1975	Mtn. Lake Biological Station, Giles Co., VA	945 - 1255		color morphs, *Plethodon cinereus*
Ash 1988	Macon Co., NC	975	230-260˚ aspect, 15-25˚ slope	timber harvest, *P. jordani*, *P. glutinosus*
Bogert 1952	SW Virginia	1580 - 1740		habitats, various plethodontids
Bruce 1967	Oconee Co., SC and Jackson and Transylvania Cos., NC	490 - 1280		*P. glutinosus*, *P. jordani*, *P. cinereus* (only above 900 m)
Fraser 1976	Augusta Co., VA	820	E aspect	competition, *P. cinereus* and *P. hoffmani*
Grover 1998	Mtn. Lake Biological Station, Giles Co., VA	1180 - 1200 m	Salamander density up to 0.6/m^2	habitat-relationships, *P. cinereus* and *P. glutinosus*
Hairston 1980	Highlands Biological Station, NC	1036 - 1128	Salamander density 0.1/m^2	competition, *P. jordani* and *P. glutinosus*
Hairston 1981	Transylvania and Swain Cos., NC	1036 - 1066	Salamander density 0.08/m^2	Competition, various species
Jaeger 1978	Shenandoah National Park, VA	1077	Salamander density 0.1/m^2	plant climbing in *P. cinereus*
Jaeger 1980*c*	Hawksbill Mtn., VA	900+	N aspect, Salamander density 0.5/m^2	competition, *P. cinereus* and *P. shenandoah*
Kramer *et al* 1993	Blue Ridge Parkway, VA	1067	45˚ slope, SE aspect, Salamander density 4.5/m^2	population dynamics, P. *hubrichti*

Table A5. 1. Continued.

Citation	Study Location	Elevation (m)	Other Site Quality Parameters	Focus of study
Mathis 1990	Mtn. Lake Biological Station, Giles Co., VA	1200		territoriality, *P. cinereus*
Merchant 1972	Swain Co., NC	1220	Salamander density 0.2-0.9/m^2	home range, *P. jordani* and *P. glutinosus*
Messere and Ducey 1998	Onandaga Co., NY	150 - 200	Salamander density 0.4-0.7/m^2 in forest control	selective logging, *P. cinereus*
Nagel 1979	Washington Co., TN	760		life history, *P. richmondi*
Nishikawa 1990	Transylvania and Swain Cos., NC	1065 - 1370		spatial relations, *P. teyahalee* and *P. jordani*
Petranka *et al* 1993	Buncombe Co., NC	817 - 1667	Salamander density 0.01/m^2	timber harvesting
Petranka *et al* 1994	Blue Ridge Escarpment, NC	384 - 1159	Salamander density up to 0.01/m^2	timber harvesting

APPENDIX 6 - RISK-SENSITIVE FORAGING EXPERIMENT 1997

Preliminary experiments on Risk-sensitive Foraging in the plethodontid salamanders were conducted in the Fall of 1997. Results were inconclusive. This was possibly a result of having used the same salamanders repeatedly as there was a statistically significant trial effect. This experiment was repeated in the Fall of 1998 with larger sample sizes and not using the same individuals in more than one test. The 1998 replication of this experiment is presented in Chapter 4. Below, I discuss the methods and results from the 1997 replication.

METHODS

I collected 40 redback salamanders (*Plethodon cinereus*), with snout-vent length 35 to 45 mm in Giles County, Virginia, on 21 September 1997. They were immediately measured, weighed and randomly assigned to a low caloric (LOW) or high caloric (HIGH) treatment. Individuals were placed in 15 x 100 mm petri dishes on wet paper towels and kept in an environmental chamber at 10˚C and a 15:9 LD cycle, with onset of dark at 1900 EST. I chose 10˚C because Merchant (1970) found this to be the temperature at which the highest net energy gain occurred in the redback salamander. I allowed salamanders to acclimated for 5 to 10 d before feeding. Salamanders were fed *Drosophila virilis* fruit flies once per week. HIGH salamanders were fed at least 19 flies per week; LOW salamanders were fed 1 fly per week. Numbers of flies were based on maintenance level requirements computed using equations derived by Jaeger (1980a). It was intended that HIGH salamanders be at greater than maintenance level and LOW salamanders be at less than maintenance level.

Each week, the petri dishes were cleaned out and any uneaten flies were counted. After at least 7 weeks of maintaining this feeding schedule, I began the behavioral tests. Tests were conducted in experimental chambers as in Chapter 4. I placed salamanders in the experimental chambers before lights-out 2 days prior to testing, allowing 2 full nights for acclimation to the chambers.

I applied a second layer of experimental conditions, WET and DRY, at the time of observations. Half the salamanders of each feeding treatment were given approximately 150 mL of water in their experimental chambers (WET), enough to saturate the paper towels. Water was added using a plastic watering can equipped with a sprinkler nozzle. The other half of the salamanders (DRY) had 2 squirts, approximately 2-4 mL, of water sprayed-on with a misting bottle. This misting brought the humidity level in the dry chamber nearly to the level in a wet chamber, and resulted in a small but reasonable amount of foraging in the DRY treatment. Water was added within 1 h before lights-out on the night of observation. Observations were made as in Chapter 4.

After the 7.5 hour observation period, I returned all salamanders to their petri dishes. I gave HIGH salamanders 25 flies, and did not feed LOW salamanders. After 5 d salamanders were returned to experimental chambers. Moisture level treatments were switched, so salamanders that had previously been observed under wet conditions were observed dry and those previously observed dry were observed wet. Procedures were repeated four times, so that all salamanders were tested wet twice and dry twice.

I tested the hypothesis that LOW salamanders engage in riskier foraging than HIGH salamanders. The expectation was that LOW-DRY salamanders will spend more time out of their burrows than HIGH-DRY salamanders. Further, I expected the DRY treatment to represent a risk to the salamanders. Therefore, HIGH -WET salamanders are expected to spend more time out of their burrows than HIGH-DRY salamanders

As in Chapter 4, each salamander, per night had a score from 0 to 30, representing the number of observations during which the salamander was not in its burrow. I used SAS PROC MIXED analysis of variance (ANOVA) in a split-plot design with diet (HIGH or LOW), environment (WET or DRY), trial number (1 through 4), and subject as components. I used the slice option to test for statistical difference between HIGH-WET and HIGH-DRY and between HIGH-DRY and LOW-DRY.

RESULTS

Average scores for each treatment combination are given in Table A6. 1 for each replicate night and all nights combined. Within feeding levels, WET salamanders had consistently higher scores than DRY salamanders, indicating they spent more time out of their burrows "foraging" ($p < 0.01$). Combining all nights, LOW-DRY salamanders had slightly higher scores than HIGH-DRY salamanders. However, variance was large and this difference was not significant ($p = 0.63$). In the overall ANOVA, only environment ($p < 0.01$) and trial ($p = 0.04$) effects were significant (Table A6. 2).

Table A6. 1. Average number of observations out of 30 that salamanders spent out of their burrows for the Risk-sensitive Foraging 1997 replicate.

		Feeding level	
Night	Moisture level	HIGH	LOW
1	WET	17.6	11.1
	DRY	1.8	3.2
2	WET	4.6	7.0
	DRY	2.8	3.2
3	WET	17.3	12.0
	DRY	1.2	7.0
4	WET	7.5	11.2
	DRY	6.3	2.5
ALL	**WET**	**11.8 (SE = 1.56)**	**10.1 (SE = 1.58)**
	DRY	**2.8 (SE = 1.57)**	**3.9 (SE = 1.58)**

Table A6. 2. ANOVA table for Main Effects of the 1997 replicate of the Risk-sensitive Foraging experiment.

Source	Numerator DF	Denominator DF	F	p-value
Diet	1	37.8	0.03	0.88
Environment	1	109	36.14	< 0.01
Trial	3	110	2.92	0.04
Diet * Order	3	110	0.54	0.67
Diet * Environment	1	109	1.16	0.28

VITA

Shannon M. Knapp was born in San Diego, California in 1974, and lived in the San Diego area until graduating from Grossmont High School in 1992. Her parents, Keith Knapp and Paula Ames, and brother, Michael Knapp, still live in San Diego. Shannon attended college at American University in Washington, D.C., spent summers working in Gulf Breeze, Florida and Bethel, Minnesota, and received a B.S. in Biology in 1996. In 1999, Shannon completed her M.S. in Wildlife Science in the Department of Fisheries and Wildlife Science at Virginia Polytechnic Institute and State University.

Shannon M. Knapp