MODEL VALIDATION AND IMPROVEMENT USING NEW DATA ON HABITAT CHARACTERISTICS IMPORTANT TO FOREST SALAMANDERS, AND SHORT-TERM EFFECTS OF FORESTRY PRACTICES ON SALAMANDER MOVEMENT AND POPULATION ESTIMATES

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ABSTRACT

Amphibians, because of their semi-permeable skin, sensitivity to changing microclimates, and important role in ecosystems, are often viewed as indicators of ecosystem health. They make excellent organisms for studies on the effects of silvicultural practices. My goal was to provide recommendations for forest management in the southern Appalachians so that harvesting operations are compatible with maintaining healthy populations of forest amphibians.

I tested previously created habitat models that determined the most important habitat characteristics for salamanders. I counted salamanders in 240 10 x 10 m plots located in the MeadWestvaco Wildlife and Ecosystem Research Forest in north-central West Virginia. We also collected a variety of habitat data in these plots to predict salamander abundance with previously created models. These simple linear regression analyses of predicted versus observed values suggest for most models (7 out of 9) a weak relationship between predicted and observed values (R^2 from 0.0033 to 0.2869, p from < 0.0001 to 0.7490). However, one of the models showed characteristics suggesting that it predicted new data as well or better than the original data, and therefore was the most accurate at predicting salamander abundance, and could be used for management purposes, although there was still much unexplained variation. This model included the variables woody stems (< 7.5 cm DBH), available rock, riparian status (i.e., within 15 m of a stream), percent overstory canopy cover, and available highly decomposed woody debris (decomposition classes 3 to 5). All of these relationships were positive except for woody stems, suggesting that in order to maintain healthy populations of salamanders, we should protect areas next to streams, with high amounts of rock, decomposed woody debris, overstory canopy cover, and few woody stems.

I also examined the immediate effects of clearcuts on salamander movement and population estimates. I batch marked salamanders in plots at the edges of a clearcut, and in a control plot. Using the Schnabel estimator, I estimated population sizes in each plot. I then compared population estimates pre- and post-harvest on the interior (harvested) and exterior (unharvested) sides of the plots, taking into account the control plot. I also examined adult-juvenile ratios and movements from one side of the plot to the other. I found no significant changes ($p > 0.05$) following harvest in any of these measures, suggesting that salamanders do not move out of the harvested area post-harvest, at least over the short term (10 months of this study). This suggests that a longer period of time (> 1 year) is required to observe the population declines detected in most studies.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: INTRODUCTION

PROJECT BACKGROUND

Project Goals and Justification

Amphibians, as described in further detail in Chapter 2, are often viewed as indicators of habitat health: their semi-permeable skin, limited dispersal ability, and sensitivity to microclimate changes make them ideal organisms for studies on the effects of silvicultural practices on native wildlife. In particular, the lungless salamanders of the family Plethodontidae, which depend on cutaneous surfaces for gaseous exchange, are sensitive to the higher temperatures and lower moisture on the forest floor (Heatwole and Lim, 1961; Feder and Pough, 1975), such as those caused by silvicultural practices. However, they are rarely included in forest management plans (Pough *et al.*, 1987; Blaustein and Wake, 1990; Wake, 1991; Blaustein, 1994; deMaynadier and Hunter, 1995; Pauley *et al.*, 2000).

My research, funded by the MeadWestvaco Corporation and the National Council for Air and Stream Improvement (NCASI), was a continuation of the amphibian component of the Appalachian Landscape Ecology Project (ALEP), begun by Lori Williams (Williams, 2003). Overall, I hope my research will provide forest managers with recommendations for forest management, particularly harvesting operations, in the southern Appalachians that are compatible with maintaining healthy populations of forest amphibians.

Specifically, my research had two primary objectives: (1) to test habitat-amphibian abundance models developed by Williams (2003), in order to provide better recommendations to forest managers, and (2) to examine the immediate effects of clearcuts on terrestrial salamander movement and population size.

Study Site

The MeadWestvaco Corporation, a leading global company in the paper products industry, devoted 3,413 hectares of working forest to research projects focusing on the effects of silviculture on biodiversity and forest ecosystem health in 1994. This forest (the MeadWestvaco Wildlife and Ecosystem Research Forest, MWERF) is located in east-central (Randolph County) West Virginia (Appendix A). For purposes of the Appalachian Landscape and Ecology Project, the MWERF was divided into six 1300-acre compartments (numbers 4-9, Appendix A). Three additional (annex) compartments (numbers 1-3, Appendix A) were located north of the MWERF. These compartments were blocked based on elevation (1-3, 4-6, and 7-9); within each block three treatments were applied (intensive, moderate, and light disturbance, or 20-, 40-, and 80-year harvest rotations, respectively). Within each compartment, an approximately 28-acre clearcut ("reference cut") was established. These reference cuts had a south-east aspect, and were harvested on a rotating schedule (see Williams, 2003 for harvest dates). The goal of the ALEP reference cuts was to follow plant and animal recolonization of timber harvested areas over time.

The MWERF is located between 734 m (2275 ft) and 1180 m (3540 ft) elevation, and is dominated by mid- to high-elevation forest communities. The majority of the forest overstory consists of northern/Allegheny hardwoods: beech, yellow birch, black cherry, Fraser magnolia, red maple and sugar maple occurring at elevations above 850 meters. Other types of forest overstory are described in Williams (2003). Typical topography on the MWERF includes narrow valleys with high-gradient streams, steep slopes, and plateau-like ridge tops. Soils are acidic and well-drained. There is often > 160 cm of precipitation a year, which is paired with a cool and humid climate (Keyser *et al.*, 2003).

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CHAPTER 2: MODEL VALIDATION AND IMPROVEMENT USING NEW DATA ON HABITAT CHARACTERISTICS IMPORTANT TO FOREST SALAMANDERS

INTRODUCTION

Recent worldwide amphibian population declines (Blaustein and Wake, 1990; Blaustein, 1994) have caused increased concern about the effects of human activities on amphibian populations. Amphibians, because of their semi-permeable skin and their reliance on multiple habitat types, are often viewed as indicators of habitat condition. Because of their sensitivity to changing microclimates (in particular, temperature and moisture conditions that are directly affected by timber harvest), terrestrial amphibians make excellent study organisms for examining the effects of silvicultural practices. Additionally, amphibians play an important role in ecosystems because of their abundance in the food web. Not only do they comprise the majority of vertebrate biomass (more than that of birds and equal to that of small mammals; Burton and Likens, 1975), but they also play an important role in the food web by consuming small arthropods and potentially structuring the detritivore community (Wyman, 1998), by having a high biomass conversion rate, and by acting as "good" prey for other vertebrates (Pough, 1983).

I hope to provide recommendations for forest management, particularly harvesting operations, in the southern Appalachians that are compatible with maintaining healthy

populations of forest amphibians. To this end, Williams (2003) developed nine habitat models based on two years of habitat and amphibian abundance data on the MeadWestvaco Wildlife and Ecosystem Research Forest (MWERF) located in the Allegheny Mountains and Plateau Physiographic province of east-central West Virginia (Randolph County).

I will first describe the models I will test. I included variables known to directly or indirectly influence habitat quality for salamanders. I did not make a priori assumptions about their relative importance, but used an iterative process to develop models for testing. Models were created using multiple linear regressions with stepwise selection (criteria of $p < 0.10$ for entry and $p > 0.10$ for removal).

The original models (Williams 2003, Tables 2.1, 2.15, and 2.16) included some variables that could not be used in this validation (such as "year", soil pH, and percent herbaceous cover, which were not measured every year). Therefore, Williams's (2003) data were used to re-create nine models using the variables: percent overstory canopy cover, riparian status (≤ 15 m from perennial or intermittent stream), percent cover of woody stems (< 7.5 cm DBH), percent cover of woody debris, count of available rocks along diagonal transects, count of decomposition class 1-2 woody debris along diagonal transects, count of decomposition class 3-5 woody debris along diagonal transects, leaf litter depth, stand age, and site index. These nine models included three types for each of three time periods (2001, 2002, and both years combined). The three types of model for each time period were as follows: (1) all plots within 15 m of a perennial or intermittent

stream (that would be designated as a streamside management zone, SMZ, for forest management purposes), (2) terrestrial plots (> 15 m from a stream), and (3) combined streamside and terrestrial plots. Plots that were greater than 15 m from a perennial or intermittent stream, even if on a seep or wet area, were placed in the terrestrial category because they would not have been designated as a SMZ during normal forestry operations. Sample sizes and models are listed in Table 2.1. Generally, these models show significant positive correlations between amphibian abundance and riparian status (≤ 15 m from perennial or intermittent stream), available rock cover, percent overstory canopy cover, and woody debris (decomposition class 3). They show negative relationships with woody stems (< 7.5 cm DBH). Using the same data collection methods as Williams (see below), I collected a third year of data on the same study site, but at different locations, and tested how well the previous models could predict salamander abundance from new data.

METHODS

Terrestrial Sampling

Data was collected from mid-May to mid-August, 2003. As per Williams's (2003) methods, we used area-constrained searches in 10 x 10 m quadrats (Jaeger, 1994; Jaeger and Inger, 1994; Dupuis *et al.*, 1995; Smith and Petranka, 2000) located on constrained randomly located transects. These transects began at constrained random starting points along the study sites' roads, and were oriented in an east-west direction, such that they

ran perpendicular to the prevailing topography. Transect start points were constrained so that they did not overlap with those covered by Williams (2003). Each transect was separated from adjacent transects by a distance greater than 400 meters.

We established 10 x 10 m quadrats along each transect in a random-systematic manner. The first quadrat was randomly placed between 50 and 300 m from the start point (Figure 2.1). We placed quadrats > 50 meters from the forest boundaries to minimize edge effects (deMaynadier and Hunter, 1998; DeGraaf and Yamasaki, 2002; Figure 2.1). Subsequent quadrats were located approximately 300 m away from the first quadrat along each transect. We regularly sampled riparian habitats by establishing an additional quadrat at every second riparian habitat ($\leq$ 15 m from perennial or intermittent stream) along the transect, regardless of the proximity of other quadrats (Figure 2.1).

At each quadrat, we recorded our location (Universal Transverse Mercator units) using a Global Positioning System (GPS) unit set in North American Datum 27 (NAD27) satellite projection. We also recorded our bearing along the transect using a hand-held compass.

An area-constrained search was used to locate amphibians within each 10 x 10 m quadrat (Petranka *et al.*, 1993; Jaeger and Inger, 1994; Herbeck and Larsen, 1999; Jung *et al.*, 2000; Smith and Petranka, 2000). We turned natural cover objects within each quadrat, including logs and branches (at least 5 cm wide), other woody debris (e.g., movable stumps), and rocks (at least 10 cm wide). Objects that were too large or awkward to

move (e.g., wider than 0.75 m or longer than 5 m) were not sampled. If cover objects fell on the boundaries of the quadrat, those on the north and west boundaries were included in sampling, while those on the south and east edges were not.

Salamander relative abundance was simply the count of salamanders within each quadrat. Because terrestrial salamanders have similar ecological requirements at the coarse scale at which this study was conducted, I summed values for all species captured. As described below (in "Statistical Analyses"), counts were transformed to meet normality assumptions.

Habitat Characteristics

Habitat data were also gathered at each quadrat. We visually estimated percent cover of woody stems (< 7.5 cm DBH) for the quadrat, which was roughly the percent of the plot that the woody stems' canopy covered. We used a spherical densiometer to measure overstory canopy closure from the center of the quadrat.

Leaf litter depths at three random points in the quadrat were measured. Using a marker thrown overhead into the plot to randomly select three locations, we dug small holes and measured litter depth with a ruler. Site index (*Quercus rubra* base age 50) and stand age were obtained from MeadWestvaco's Geographic Information System layers. If stand age and site index data were missing, those plots were excluded from the analysis.

To obtain a description of available cover objects, we stretched a meter tape diagonally across the quadrat, and counted any cover object (rock or woody debris) that fell on this diagonal. In addition to the counts, woody debris was ranked based on extent of decomposition, after Maser *et al.* (1979) and Shifley *et al.* (1991). The variables I used in my models were a count of all rocks, a count of woody debris in decomposition classes 1-2, and a count of woody debris in decomposition classes 3-5.

Statistical Analyses

Using SAS® software to analyze the new 2003 habitat data, I predicted amphibian abundance using each of Williams's (2003) nine regression models. Due to the large spread of the relative abundance counts (0 to >20 in Williams, 2003; 0 to 13 in my 2003 data), I square-root transformed amphibian abundance (plus 0.5), as per Williams (2003), to meet normality assumptions and reduce the effect of a few extreme values. Williams examined the habitat variables for multicollinearity, ensuring that the variables were not correlated with each other (Williams, 2003; p. 23). I then regressed predicted on observed salamander abundance, and used a variety of techniques to evaluate model performance.

Slope, Intercept, and R^2 Values

First, I examined the slope, intercept, and R^2 produced from a simple linear regression of predicted on observed values. Ideally, the slope of the line would be 1 (if predicted and

observed values matched exactly), intercept would be 0, and R^2 value would be 1. I also

report p-values, although they were not used to examine the fit of the models (as they

relate to the accuracy of the model in relation to the population of models, more than to

the fit of the model).

Residual Mean Square Compared to Average Squared Prediction Error

Second, I compared the residual mean square from the fitted model with the mean

squared prediction error from the new prediction data. If the mean squared prediction

error from the new prediction model is larger than the residual mean square (which can

be considered the average variance of the residuals from the fit of the original model), the

model did not predict new data as well as it fit the original data.

Reduction of R^2

Third, I examined the R^2 value from the original model, and compared this to the

percentage of variability in the new data explained by the model ($R^2_{Prediction}$). This value

is calculated by the formula:

$$1 - \frac{\sum(y_i - \hat{y}_i)^2}{\sum(y_i - \bar{y})^2}$$

and is the equivalent of the formula, $1 - \dfrac{PRESS}{SST}$ [1-(predicted residual sum of

squares/total sum of squares)]. If the reduction of R^2 from the original model to the

$R^2_{Prediction}$ is large, then the model does not predict new observations as well as it fits the original data.

RESULTS

A summary of the habitat data we collected in 2003 is given in Table 2.2. Also shown is the average salamander abundance for these quadrats. Some of these variables (in particular, site index, percent overstory canopy cover, and stand age) varied little between quadrats.

Slopes of Lines

The slopes of lines from the simple linear regressions of predicted on observed values did not approach 1 in any of the models (Table 2.3, Figure 2.2). The model with the highest slope (closest to 1) was the "all plots 2001" model (0.3600, Table 2.3, Figure 2.2g), followed closely by the "all plots 2002" model (0.3565, Table 2.3, Figure 2.2h).

Intercepts of Lines

None of the intercepts were close to the ideal value of zero. The "all plots 2002" model had the lowest intercept (0.8798, Table 2.3, Figure 2.2h). All of the other models had intercepts greater than 1 (Table 2.3).

R² Values

The "all plots 2002" model had the highest R^2 value (0.2802), compared to the next

highest values of 0.2529 and 0.1479 (Table 2.3), implying that approximately 28% of the

variation in observed values was explained by the model.

Residual Mean Square Compared to Average Squared Prediction Error

In 5 of the 9 models, the residual mean square was smaller than the mean squared

prediction error (Table 2.3), suggesting that these models did not predict new data as well

as they fit the original data. The difference between the two values ranged from 0.0705

in the "streamside plots 2001" model to 0.4897 in the "streamside plots 2002" model. In

four models ("streamside plots both years," "all plots 2001," "all plots 2002," and "all

plots both years," Table 2.3), the residual mean square was larger than the mean squared

prediction error, suggesting that those models predicted the new data as well or better

than they fit the original data. Of these models, the "all plots 2002" model had the lowest

mean squared prediction error, implying that it had the best fit of the models.

Reduction of R^2

Because the discrepancy between observed and predicted values (y_i and $\hat{y}_i$) was often

very great in relation to the difference between the observed and average observed values

(y_i and $\bar{y}$), the R^2 predicted values were often (in 6 out of 9 models) negative (Table

2.3). This is somewhat counterintuitive, as one cannot in theory have an R^2 value that is

less than 0 or greater than 1. I interpret this to mean that very little or none of the variability in the new data is explained by these models. This leads me to conclude that 6 of the 9 models did not perform well. Of the three models that had positive R^2 prediction values ("terrestrial plots 2002," "all plots 2002," and "all plots both years"), one ("all plots both years") showed a large reduction of R^2 (0.3400, Table 2.3), implying that it did not predict new observations as well as it fits the original data. The remaining two models ("terrestrial plots 2002" and "all plots 2002") showed approximately equivalent reductions of R^2 (0.0567 and 0.0607, respectively, Table 2.3). However, the "all plots 2002" model had a much higher original R^2 (0.2992 as opposed to 0.1279 in the "terrestrial plots 2002" model).

DISCUSSION

Overall, these data suggest that the most appropriate model is that from all plots in 2002. This model showed a relatively high original R^2 and low reduction of R^2, in addition to a larger residual mean square than mean squared prediction error (MSPE), and a low MSPE, suggesting that it predicted new data as well or better than the original data. It had the highest R^2 value of all the models in the simple linear regression of predicted on observed values. Finally, it had a steep slope in the simple linear regression (0.3565), and the lowest intercept (0.8798).

Management Implications

This model ("all plots 2002") included the variables woody stems (< 7.5 cm DBH), available rock, riparian status (if within 15 m of a stream), percent overstory canopy cover, and available highly decomposed woody debris (decomposition classes 3 to 5). All of the relationships with abundance were positive, except for woody stems (Table 2.1). These data suggest that in order to make harvesting operations compatible with maintaining healthy populations of salamanders, we should protect areas next to streams, with high amounts of rock, decomposed woody debris, overstory canopy cover, and few woody stems. We could also actively manage areas by increasing amounts of decomposed woody debris (see chapter 4 for a more in-depth discussion of these management actions).

Many other studies in eastern forests have examined the relationship between habitat variables and amphibian abundance, diversity, or activity frequency. Their results often show variables similar to those in my study to be important to amphibians, suggesting that my model could be useful in other areas (Tables 2.4 and 2.5). I will discuss each of the significant variables in my model in turn, followed by a brief discussion of variables that have been found to be significant in other studies. For each variable, I will summarize the results of studies performed in the eastern United States that examined the relationship between that variable and amphibian abundance, diversity, or activity frequency. When studies examined multiple amphibian species, I attempted to summarize only the results for terrestrial salamanders, as this was the focus of my study. In Table 2.5, I give the location of these other studies, as well as the major species from which the data and summaries were drawn.

Riparian status, a significant variable in my model, has been shown to be important in many previous studies (Table 2.4). Despite being positively related to amphibian abundance in five studies (Petranka *et al.*, 1994, Hyde and Simons, 2001; Ford *et al.*, 2002; Grover and Wilbur, 2002; Petranka and Smith, 2005), four studies showed no significant relationship between riparian status and salamander abundance (DeGraaf and Rudis, 1990; Grover and Wilbur, 2002; Brenner *et al.*, 2005; Petranka and Smith, 2005). All four of these studies were examining terrestrial-breeders (*Plethodon* spp.), which logically showed little or no significant increase in abundance near streams or seeps, as they are not dependent on water for breeding. However, some of the studies that found a positive relationship with riparian status were also examining primarily terrestrial-breeders, so this distinction is not entirely clear-cut. Overall, it seems that the relationship we saw with this variable is applicable to most other areas, especially when considering multiple species (not just terrestrial-breeders).

Percent overstory canopy cover, another variable with a significant positive relationship with salamander abundance in my study, has been well-documented as an important habitat variable to salamander abundance. Studies such as those by Pough *et al.* (1987), Wyman (1988), DeMaynadier and Hunter (1998), Harpole and Haas (1999), and Knapp *et al.* (2003) have shown the importance of intact overstory canopy cover to salamander abundance. However, three studies (Harper and Guynn, 1999; Greenberg, 2001; Hyde and Simons, 2001) found no significant relationship between percent overstory canopy cover and salamander abundance, and one (Ford *et al.*, 2002) actually found a negative

relationship for *Plethodon glutinosus* and *P. serratus*. Ford *et al.* (2002) offer little explanation for this conflicting result, although it appears that their measure of canopy cover may have included understory canopy cover, which could obscure the general pattern we saw in most other studies. The positive relationship seen in most studies seems to hold across multiple areas, implying that this variable is likely important to salamanders throughout the eastern United States.

A count of highly decomposed coarse woody debris was also significant in my model. In previous studies, it sometimes had a significant positive relationship with salamander abundance (Petranka *et al.*, 1994; Herbeck and Larsen, 1999), but in some cases no relationship was found (Petranka *et al.*, 1994; Greenberg, 2001; Ford *et al.*, 2002). In the Petranka *et al.* study (1994), a positive relationship was found only on dry plots, with no relationship on wet plots. This could be because moisture was limiting only on the dry plots, meaning that salamanders were more dependent on coarse woody debris on dry plots. A related variable, percent cover of woody debris (which had no significant relationship in my model), showed a positive correlation with salamander abundance in three studies, while four showed no relationship (Table 2.4). One study (DeMaynadier and Hunter, 1998) showed a negative relationship between percent cover of woody debris and salamander abundance. Because their study focused on recent (2 to 11-year-old) clearcuts and disturbed areas, it is likely that the majority of the woody debris in their study was not highly decomposed, and did not make good habitat for salamanders. The lack of suitable decomposed woody debris explains the negative relationship they saw with salamander abundance.

Available rock, which had a significant positive relationship with relative abundance in this study, has been shown to be important to salamander abundance in other studies as well (Herbeck and Larsen, 1999; Ford *et al.*, 2002), though one (DeMaynadier and Hunter, 1998) found no significant relationship. Three other studies that examined a variety of cover objects (artificial cover objects or rock and coarse woody debris combined) found a positive relationship with salamander abundance, while one found no significant relationship (Table 2.4). Of all these studies (examining the importance of cover objects), most (10) showed a positive relationship between cover objects and salamander abundance, closely followed by those (nine) that showed no relationship with salamander abundance. The importance of cover objects to salamander abundance is less clear-cut than the importance of riparian status and overstory canopy cover, and is affected by other variables (such as moisture of plots, and possibly the species examined). However, when examining the number of studies showing positive and negative relationships between cover objects and salamander abundance, there is a clear skew towards positive relationships; cover objects are not negatively correlated with salamander abundance (Table 2.4). This implies that my model may be applicable to other areas, although the cover object variables will likely not be as consistently related to salamander abundance across locations in the eastern United States.

An increase in the percent cover of small woody stems, which had a significant negative relationship with relative abundance in my model, was frequent on recently harvested stands in this study. Our results agree with those of DeGraaf and Yamasaki (2002), but

most studies found no significant relationship between these variables (DeGraaf and Rudis, 1990; Harper and Guynn, 1999). Other studies looking at vegetation cover (often hardwood stems) show mixed results, with approximately equal numbers of studies showing positive relationships (two studies), no relationship (three studies), and negative relationships (two studies) (Table 2.4). Therefore, the relationship we saw in our study is likely not applicable across many other areas of the eastern United States.

Other variables that I examined in this study that showed no significant relationship with salamander abundance were site index, stand age, and leaf litter depth. Most studies (five of six) found a positive correlation between salamander abundance and site/soil moisture, a characteristic described by site index, so my result here was somewhat surprising (Table 2.4). Stand age was another variable with a similar pattern (the two studies that examined it both found positive relationships with salamander abundance, Table 2.4, while I found no significant relationship). Both of these seemingly erratic results could be related to the limited variability in site index and stand age (see "Variation in Data" below).

Leaf litter depth, the other variable I examined that showed no significant relationship with salamander abundance, has generally shown no significant relationship with salamander abundance in other studies (six of nine studies, Table 2.4). However, three studies revealed a positive relationship between leaf litter depth and salamander abundance or, in one study, activity frequency (Table 2.4). My results with this variable

are consistent with most other studies' results, and therefore may be valid in other areas of the eastern United States.

Other variables that have been frequently studied (and were not examined in my study) include percent ground cover of leaf litter, exposed soil, moss, and herbs. Percent cover of leaf litter and herbs have generally shown a bias towards a positive relationship (two studies each positive relationship and no relationship, zero studies with a negative relationship, Table 2.4). However, percent cover of exposed soil and moss have shown no pattern across studies, with nearly equal numbers of studies revealing positive, no, and negative relationships (two, three, and two studies, respectively). This suggests that the relationships between percent cover of litter or herbs and salamander abundance are not as clear-cut as are some variables' relationships, although most studies do find a positive relationship between these variables. Percent cover of exposed soil or moss would be unlikely to show the same relationship with salamander abundance across locations in the eastern United States.

In addition, soil depth, tree DBH (or stand basal area, BA), and elevation have been examined in some studies. None of these variables show clearcut patterns across studies, with most studies finding no significant correlation, and approximately equal numbers of studies showing positive and negative relationships (Table 2.4). I suggest, therefore, that these variables are likely not consistent across locations in the eastern U.S., and models including them are not likely applicable to other areas.

Overall, my examination of other studies in the eastern U.S. suggests that our results may be applicable to other areas. Although the parameter estimates associated with each variable would certainly change from location to location, the general trend of these variables (especially riparian status and overstory canopy cover) being important to salamander abundance will likely hold across many areas in the eastern United States.

Variation in Data

Although it is likely that the results of this study will apply to other areas, it is worth noting that in some cases, I sampled a relatively limited range of habitats. For example, site index ranged only from 62 to 80 (Table 2.2). In comparison to the mean, the three variables that showed the least variation were site index, percent overstory canopy cover, and stand age. The MWERF in general is a mesic, relatively mature forest with a common disturbance history. This could have affected our results by decreasing the likelihood that some variables were significant in the models. A wider range of habitats could have increased the chance that some variables were significant in the models.

Despite this lack of variability in some habitat characteristics, there is still a large amount of unexplained variability in these data (Figure 2.2, low R^2 values). The general lack of consensus between predicted and observed values suggests that there are some un-measured variables that greatly affect salamander abundance. I suggest that this variation falls into two classes: salamander detectability (such as weather or observer variation) and true variation (caused by factors such as landscape variables).

Detectability

Detectability is a problem in many studies, especially when animal behavior and detectability vary with season, weather, observers, or other factors. In this study, 2001 had lower-than-average precipitation levels (103.28 cm precipitation, compared to an average of 112.22 cm). 2002 had above-average precipitation levels (125.37 cm precipitation), as did 2003 (153.29 cm) (National Climatic Data Center, 2004). Weather factors have been shown to affect salamander abundance and detectability (Grover, 1998; Williams and Berkson, 2004). Williams and Berkson (2004) showed that average daily humidity can affect the probability of detection of *Plethodon cinereus* during nighttime surveys. Higher mean daily temperatures were correlated with lower detection probabilities during daytime cover object searches. By collecting data in both streamside and terrestrial plots during the same day, we minimized some detectability issues due to weather and season differences.

However, it was difficult to control for other causes of variation in detectability. For example, while turning natural cover objects in recently cut stands, it was very difficult at times to see the ground (and therefore any salamanders), due to downed logs and vegetation growth. Therefore, it was likely that we missed more animals in these plots than in plots in mature forest. To address this problem, other techniques such as drift-fences and pitfall trapping, or the use of artificial cover objects should be considered, although both are more long-term techniques. These techniques would provide more

equal detectability across plots, but would require much more labor to install, and would greatly decrease the number of plots sampled in a given time period. In addition, artificial cover objects have the disadvantage of adding cover into the natural environment, and thereby potentially influencing actual population sizes (Grover, 1998). Both natural and artificial cover object searches are probably biased towards sampling territorial males than are nighttime visual surveys (Marsh and Goicochea, 2003). Despite increasing detectability, both of these techniques are inefficient and expensive. In a comparison of detection probabilities associated with daytime, natural cover object searches, and nighttime visual surveys of *Plethodon cinereus*, Williams and Berkson (2004) determined that cover object searches have a lower bias (fewer nondetections) but higher variability in the probability of detection. Nighttime visual surveys had a higher bias (more nondetections) but lower variability in the probability of detection. They suggested that cover-object searches are most effective for determining presence if few observations can be made at a sampling area (such as in this study).

Bailey *et al.* (2004a) showed that random temporary vertical emigration occurs with plethodontid salamanders, and that capture probabilities vary due to a trap-shy response and possibly environmental conditions or size of surface populations. In this study, we avoided the trap-response bias by sampling each plot only once. Bailey *et al.* (2004b) showed that vegetation type and elevation were correlated with detection probabilities. To the extent possible, studies should be designed to minimize variation in detectability, by only sampling during specific weather conditions or seasons, and by collecting data in all habitat types during similar weather conditions (as in this study). Bailey *et al.* (2004a

and 2004b) also suggest using a double-sampling design, and always calculating detection probability as part of studies. If sampling rare species (in which low sample sizes make it difficult to accurately estimate detection probability), MacKenzie *et al.* (2005) recommend borrowing information about detectability from other times, places, or species, and using state variables other than abundance. Overall, detectability is an important issue in studies such as this, and needs to be addressed so that the data collected are not biased samples.

Un-measured Variables

Un-measured variables that may affect abundance also should be considered. In this study, these variables could include such things as landscape-level variables [such as slope and aspect of hills, type of ridge (concave or convex), and distance to streams], soil pH and moisture, leaf biomass, presence/number of underground tunnels/holes, and type and amount of understory vegetation. These variables may lend more predictive power to the models. However, there is a trade-off between the amount of data collected and the time, energy, and money spent collecting those data.

CONCLUSIONS

Ultimately, to improve model performance, detectability must be addressed in study design and while collecting data, and the feasibility of collecting a large number of variables for model development must be examined. To maximize the predictive abilities

of a model, detectability must be held as constant as possible, and major variables that could influence the response variable should be measured. Despite the limitations of this model, it is the most accurate model we have. Although it may not predict accurately the exact number of salamanders in an area, it should be useful for predicting areas of high salamander abundance.

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Table 2.1. Regression models describing the relationship between salamander relative abundance and habitat parameters (Williams, 2003). Williams began with ten variables; variables below were selected using stepwise selection. Shown is sample size (number of quadrats sampled), variables included in the model, parameter estimates, and p-values.

Model	Sample Size	Variable	Parameter Estimate	p[1]
Terrestrial plots 2001	44	Intercept	-2.24325	0.2214
		Available Rock	0.06164	**
		Site Index	0.05517	*
Terrestrial plots 2002	142	Intercept	0.68086	**
		Woody Stems	-0.17017	*
		Available Woody Debris, Decomposition Class 3-5	0.03835	0.0663
		Overstory Canopy Cover	0.00619	**
Terrestrial plots both years	195	Intercept	-0.04276	0.9563
		Site Index	0.0187	0.0921
		Available Woody Debris, Decomposition Class 1-2	-0.12963	**
		Available Woody Debris, Decomposition Class 3-5	0.07777	**
Streamside plots 2001	43	Intercept	-7.25911	0.0542
		Site Index	0.13989	*
Streamside plots 2002	65	Intercept	-6.12835	*
		Available Rock	0.10831	**
		Overstory Canopy Cover	0.08459	*
Streamside plots both years	108	Intercept	1.85263	**
		Available Woody Debris, Decomposition Class 1-2	-0.11587	0.0926
		Available Woody Debris, Decomposition Class 3-5	0.10552	**
		Available Rock	0.05009	*
All plots 2001	92	Intercept	-3.13817	0.0984
		Riparian Status	0.96773	**
		Available Rock	0.02763	0.0945
		Site Index	0.06899	*
All plots 2002	214	Intercept	0.46222	*
		Woody Stems	-0.18684	*
		Available Rock	0.04162	**
		Available Woody Debris, Decomposition Class 3-5	0.03771	0.0981
		Overstory Canopy Cover	0.00785	**
		Riparian Status	0.75661	**
All plots both years	319	Intercept	-0.28745	0.7094
		Riparian Status	0.0989	**
		Site Index	0.02074	0.0572
		Available Rock	0.03286	**
		Available Woody Debris, Decomposition Class 1-2	-0.11655	**
		Available Woody Debris, Decomposition Class 3-5	0.07926	**

[1] * indicates $p < 0.05$, ** indicates $p < 0.005$

Table 2.2. Summary of habitat data collected on 211 quadrats in 2003. Also shown is a summary for the count (untransformed) of salamanders captured per quadrat. Shown for each variable is the mean, standard deviation, minimum and maximum values, and means for the 10% of (21) quadrats with the highest and lowest numbers of salamanders captured.

Variable	Mean	SD	Median	Min. Value	Max. Value	Mean Lowest 10%	Mean Highest 10%
Percent Overstory	87.58	23.53	95.75	0	100	71.60	95.62
Percent Cover of Woody Stems	0.60	0.97	0	0	5	1.38	0.14
Percent Cover of Woody Debris	1.00	0.87	1	0	5	1.29	0.86
Count of Available Rocks	3.00	4.14	2	0	26	1.24	5.24
Count of Decomposition Class 1-2 Woody Debris	1.83	2.39	1	0	17	2.48	1.81
Count of Decomposition Class 3-5 Woody Debris	4.80	3.97	4	0	32	4.33	5.00
Leaf Litter Depth (cm)	2.47	1.39	2.33	0	9.66	2.47	2.76
Stand Age	68.59	24.11	77	0	92	57.96	75.05
Site Index	70.50	4.27	70	62	80	69.20	72.22
Salamander (Count)	2.49	2.89	2	0	13	0.00	9.14

Table 2.3. Data from analyses of each of nine models developed by Williams (2003). Slopes, intercepts, R^2, and p-values from simple linear regression of predicted on observed amphibian abundance values. Mean squared residuals (MS_{Res}) from original model, mean squared prediction error (MSPE), and the difference between the two. R^2 values from original model and model with new data ($R^2_{Prediction}$). Also shown is the "loss" of R^2. The "all plots 2002" model shows a high slope, low intercept, and high R^2 value, a MSPE higher than MS_{Res}, a small loss of R^2, and a high original R^2, implying that it is best at predicting new data.

Model	Slope	Intercept	R^2	p	MS_{Res}	MSPE	Difference	Original R^2	$R^2_{Prediction}$	"Loss" of R^2
Terrestrial plots 2001	0.0722	1.4800	0.0033	0.0001	0.3995	0.6276	-0.2281	0.2640	-0.2803	0.5443
Terrestrial plots 2002	0.1589	1.0394	0.1162	< 0.0001	0.3599	0.4553	-0.0954	0.1279	0.0712	0.0567
Terrestrial plots both years	0.0735	1.3049	0.0134	0.1381	0.5026	0.6207	-0.1181	0.1308	-0.2662	0.397
Streamside plots 2001	0.2254	2.2745	0.0850	0.0492	0.8575	0.9280	-0.0705	0.1578	-0.8733	1.0311
Streamside plots 2002	0.1525	1.0751	0.0371	0.1200	0.7934	1.2831	-0.4897	0.3097	-1.5901	1.8998
Streamside plots both years	0.0320	2.3777	0.0023	0.7490	1.0679	0.7672	0.3007	0.1366	-0.5487	0.6853
All plots 2001	0.3600	1.4661	0.2529	< 0.0001	0.9040	0.7109	0.1931	0.3226	-0.1694	0.492
All plots 2002	**0.3565**	**0.8798**	**0.2802**	**< 0.0001**	**0.5898**	**0.4629**	**0.1269**	**0.2992**	**0.2385**	**0.0607**
All plots both years	0.2935	1.1270	0.1479	< 0.0001	0.7006	0.6064	0.0942	0.3425	0.0025	0.34

Table 2.4. Summary of studies in eastern forests examining the importance of habitat variables to salamander abundance and/or diversity. Variables that were examined by fewer than three studies are not included (unless they were significant in this study). In cases where a study's variable was slightly different than the variable listed, or when the same study found different results for different species/habitat variables, clarification is given in parentheses. The signs +, 0, and – indicate the type of relationship between the variable and salamander abundance or diversity.

Group of Variables	Habitat Variable	This Study	+	0[a]	-
Moisture	Riparian Status	+	5 studies[6, 15, 17, 18, 21] (aquatic-breeders)	4 studies[5, 18 (*P. glutinosus*), 20, 21] (terrestrial-breeders)	
	Site Index (Site Moisture)	0	5 studies[1, 4, 9, 11, 15]	1 study[6]	
Canopy Cover	Overstory Canopy Cover	+	5 studies[3, 5, 8 (hardwood + conifer), 12, 19]	3 studies[11, 14, 15]	1 study[17]
	Stand Age	0	2 studies[6, 7]		
Cover Objects	Coarse Woody Debris 3-5	+	2 studies[6 (dry plots), 13]	3 studies[6 (wet plots), 14, 17]	
	Coarse Woody Debris 1-2	0			
	Woody Debris Cover (%)	0	3 studies[8 ("Bole-root"), 9, 10 (count & avg. area)]	4 studies[13, 14, 16, 17 (or large CWD)]	1 study[8 (woody cover)]
	Available Rock	+	2 studies[13, 17]	1 study[8]	
	Cover Objects		3 studies[9 (artificial cover objects), 15 (rock & CWD), 18 (*P. cinereus*)]	1 study[18 (*P. glutinosus*)]	
Leaf Litter	Leaf Litter Depth	0	3 studies[5, 6 (activity frequency), 8]	6 studies[2, 11, 14, 15, 16, 17]	
	Litter Cover (%)		2 studies[8 (deciduous), 12]	2 studies[8 (conifer), 13]	
Ground/ Understory Canopy Percent Cover (Increasing Height from Ground)	Exposed Soil		1 study[13]	1 study[14]	1 study[8]
	Moss Cover		1 study[8 (Nonvascular plants)]	2 studies[8, 13]	1 study[5]
	Herbaceous Cover		2 studies[5, 16]	2 studies[11, 14]	
	Woody Stems Cover	-		2 studies[5 (<1.5 m), 11]	1 study[16 (all understory stems/ha)]
	Vegetation Cover (0-1 m)		1 study[6 (correlated with activity frequency)]	2 studies[8, 16 (hardwood stems 0.5-1 m)]	1 study[13]
	Vegetation Cover (1-2 m)		1 study[10 (hardwood stems >1 m)]	1 study[16 (hardwood stems 1-2 m)]	1 study[8 (0.5-3 m)]
	Soil Depth		1 study[16 (organic layer)]	3 studies[2, 10, 17]	
	Tree DBH (or BA)		2 studies[5 (deciduous BA), 17 (overall BA)]	3 studies[5, 13, 14 (snags and live trees)]	2 studies[5] (coniferous BA, 17 (*E. bislineata*)
Landscape-Level	Elevation		2 studies[17, 21] (terrestrial-breeders)	2 studies[5, 15] (quadratic relationship)	2 studies[21] (aquatic-breeders)

[a]Unless otherwise noted; see exception under Elevation

[1]Heatwole, 1962; [2]Jaeger, 1980; [3]Pough *et al.*, 1987; [4]Wyman, 1988; [5]DeGraaf and Rudis, 1990; [6]Petranka *et al.*, 1994; [7]Mitchell *et al.*, 1997; [8]DeMaynadier and Hunter, 1998; [9]Grover, 1998; [10]Brooks, 1999; [11]Harper and Guynn, 1999; [12]Harpole and Haas, 1999; [13]Herbeck and Larsen, 1999; [14]Greenberg, 2001; [15]Hyde and Simons, 2001; [16]DeGraaf and Yamasaki, 2002; [17]Ford *et al.*, 2002; [18]Grover and Wilbur, 2002; [19]Knapp *et al.*, 2003; [20]Brenner, 2005; [21]Petranka and Smith, 2005

Table 2.5. List of studies corresponding to Table 2.4, with location of study and major species from which summaries in Table 2.4 were made. For studies that examined both salamanders and frogs, I summarized results only for salamanders.

#	Author, Year	Location of Study	Species Studied
1	Heatwole, 1962	northern part of the Lower Peninsula of Michigan	*P. cinereus*
2	Jaeger, 1980	Shenandoah National Park, Virginia	*P. cinereus*
3	Pough *et al.*, 1987	central New York	*P. cinereus, N. viridescens*
4	Wyman, 1988	south-central New York	*P. cinereus, D. fuscus*
5	DeGraaf and Rudis, 1990	White Mountain National Forest, New England	*P. cinereus*
6	Petranka *et al.*, 1994	Pisgah National Forest, western North Carolina	*P. glutinosus, P. jordani, D. ochrophaeus*
7	Mitchell *et al.*, 1997	George Washington National Forest, Virginia	*P. cinereus*
8	DeMaynadier and Hunter, 1998	Penobscot County, Maine	*P. cinereus, Ambystoma* spp.
9	Grover, 1998	Mountain Lake, Giles County, Virginia	*P. cinereus, P. glutinosus*
10	Brooks, 1999	southern New England	*P. cinereus*
11	Harper and Guynn, 1999	western North Carolina	*P. jordani, D. aeneus, D. ochrophaeus*
12	Harpole and Haas, 1999	southwest Virginia	*P. cinereus, P. cylindraceus, D. fuscus*
13	Herbeck and Larsen, 1999	southeastern Ozarks, Missouri	*P. cinereus, P. glutinosus*
14	Greenberg, 2001	western North Carolina	*P. teyahalee*
15	Hyde and Simons, 2001	Great Smoky Mountains National Park, Tennessee	*P. glutinosus, P. jordani, P. serratus, Desmognathus* spp.
16	DeGraaf and Yamasaki, 2002	northern New Hampshire	*P. cinereus*
17	Ford *et al.*, 2002	northern Georgia	*P. glutinosus and Desmognathus*
18	Grover and Wilbur, 2002	Mountain Lake, Giles County, Virginia	*P. cinereus, P. glutinosus, D.fuscus*
19	Knapp *et al.*, 2003	southwestern Virginia and West Virginia	*P. cinereus, P. glutinosus, P. richmondi, D. ochrophaeus*
20	Brenner *et al.*, 2005	Venango County, western Pennsylvania	*P. cinereus*
21	Petranka and Smith, 2005	western North Carolina & eastern Tennessee	*Plethodon and Desmognathus*

34
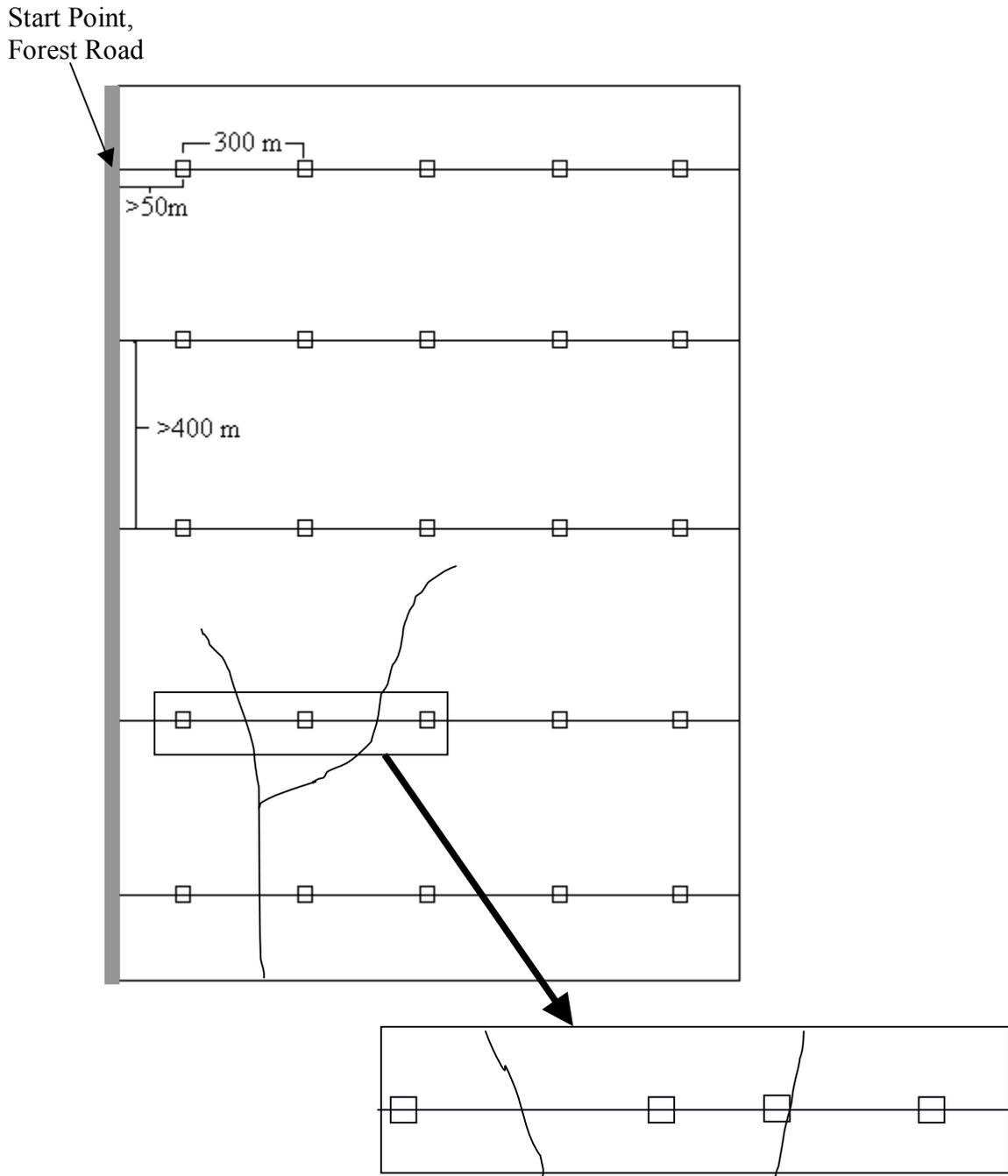
Figure 2.1. Example of transects placed along a road (not to scale). Transects are greater than 400 m apart. Quadrats (10 x 10 m) are greater than 50 m from the edge of the forest, and approximately 300 m from each other. Additional quadrats were sampled at every second stream crossed (inset).
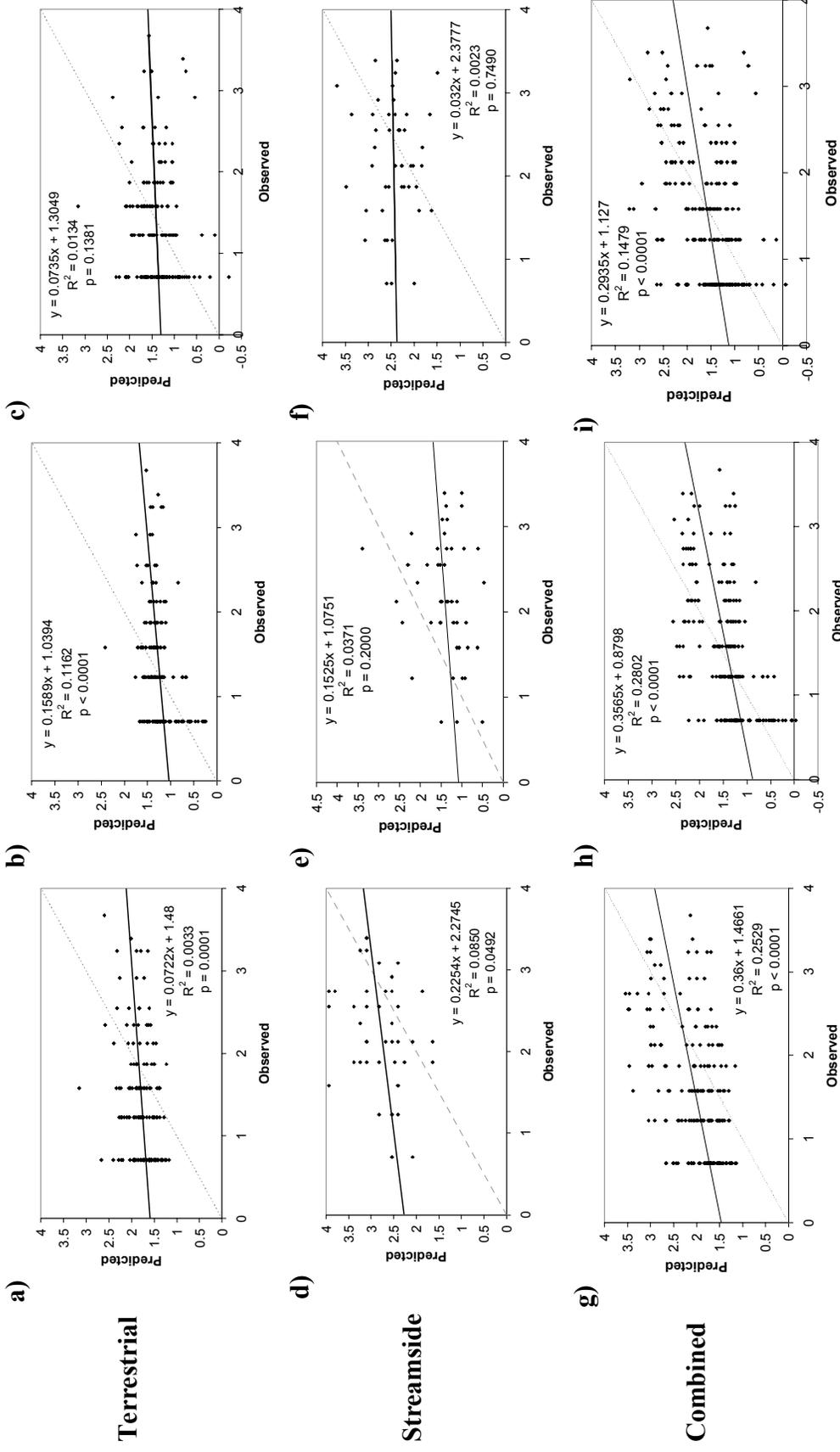
Figure 2.2. Simple linear regressions of predicted on observed amphibian abundance for all 9 models. All values were square-root transformed to reduce variability associated with extreme values, and to meet normality assumptions. The solid line is the regression line; the dotted line is the ideal situation (slope of 1, intercept of 0).

CHAPTER 3: SHORT-TERM EFFECTS OF FORESTRY PRACTICES ON SALAMANDER MOVEMENT AND POPULATION ESTIMATES

INTRODUCTION

Many studies have documented lower amphibian abundance in timber-harvested areas (e.g., Enge and Marion, 1986; Petranka *et al.*, 1993, 1994; Petranka, 1994; Ash and Bruce, 1994; Dupuis *et al.*, 1995; Means *et al.*, 1996; Ash, 1997; Sattler and Reichenbach, 1998; Harpole and Haas, 1999; Herbeck and Larsen, 1999; Petranka, 1999; Knapp *et al.*, 2003). However, none have examined the immediate effects of forestry practices on amphibian movement and survival. Many of these studies (in particular, Petranka *et al.*, 1993) have assumed that the decreased abundance of salamanders observed post-harvest was caused by death. However, there are other possible alternatives, including movement of salamanders out of the harvested area or a decrease in detectability due to movement underground.

Such alternatives are important to consider when determining the severity of effects on terrestrial salamander populations, as well as the recolonization rates following a cut (DeGraaf and Yamasaki, 2002). Some have suggested that movement occurred out of cuts (Sattler and Reichenbach, 1998; DeGraaf and Yamasaki, 2002), while others do not believe that successful movement occurs (Petranka, 1999). If salamanders successfully move out of cuts (e.g., survive, at least in the short term), this is evidence that the

population size is not necessarily decreasing. This could imply that the effects of cutting are not as severe as suggested by some studies (see Petranka *et al.*, 1993).

Possible outcomes for salamanders involving mortality include: (1) dying immediately following the cut, or (2) going underground to await better conditions and dying eventually. Alternatively, (3) salamanders may survive within the cut, which would allow sooner recolonization of the harvested area. They could also move out of the cut when the habitat becomes poor. If the surrounding habitat is not saturated (at carrying capacity), these salamanders may (4) survive outside the cut and be able to eventually recolonize the cut. If the surrounding habitat is saturated, competition would increase, likely leading to (5) the eventual death of salamanders least able to compete. Ideally, it is possible to differentiate among these alternatives (Table 3.1). However, if salamanders are not moving, it would be difficult to differentiate between the alternatives (survival, immediate death, or eventual death/movement out of the plot), because surviving salamanders probably spend much of their time underground (decreasing detectability), which would have the same effect on our measures of relative abundance as would death. To differentiate among the "no movement" alternatives mentioned above, I intended to use caged salamanders to see if they could survive within the cut. However, the timing of the harvest did not make this possible. To differentiate between "movement" and "no movement" alternatives, I conducted a mark-recapture experiment to see if individual salamanders move out of the cut area. To differentiate between the "movement" alternatives, I used population estimates.

If salamanders are able to move, their survival is potentially dependent on whether the surrounding forest is at carrying capacity. Few studies have examined the evidence for populations of terrestrial salamanders being at carrying capacity. However, there is a large body of research showing territoriality in terrestrial salamander species.

Of the terrestrial or semi-terrestrial salamander species that I studied (eastern red-backed salamander, *Plethodon cinereus*, northern slimy salamander, *Plethodon glutinosus*, northern dusky salamander, *Desmognathus fuscus*, Allegheny mountain dusky salamander, *Desmognathus ochrophaeus*, and northern two-lined salamander, *Eurycea bislineata*), some are known to be territorial. The eastern red-backed salamander is known to defend territories with agonistic displays and biting (Jaeger, 1981, 1984), which can expel intruders of either sex (Jaeger *et al.*, 1982). Juvenile *P. cinereus* often enter adult territories during rainless periods, and adults are more tolerant of juveniles with whom they had previous cohabited than juvenile "strangers" (Jaeger *et al.*, 1995). *P. cinereus* aggression can be directed interspecifically as well as intraspecifically (e.g., *P. cinereus* defended territories against same-size juveniles of *P. glutinosus*, Lancaster and Jaeger, 1995). However, adults of these two species apparently do not influence each other's distributions on the forest floor (as they are not aggressive or predatory towards each other, Jaeger *et al.*, 1998).

It appears that most members of the genus *Desmognathus* are territorial. *D. fuscus* is territorial, both intraspecifically and interspecifically (predatory on *P. cinereus*, Jaeger *et*

al., 1998). Male *D. ochrophaeus* also exhibit territorial behavior (Jaeger, 1988). Grant

(1955) reported territorial behavior for *E. bislineata*.

These studies suggest that most of the members of the family Plethodontidae that occur

on the MWERF are territorial. This has two implications for my study: (1) movement

may not occur because of site fidelity, (2) if movement does occur, salamanders that

move may not survive due to aggressive behavior or predation by territorial salamanders

in the surrounding habitat. However, some studies have suggested that cohabitation

occurs (Jaeger *et al.*, 1995; Lang and Jaeger, 2000; Jaeger *et al.*, 2001; Jaeger and

Peterson, 2002) and therefore is a possibility in the surrounding habitat. Additionally,

female salamanders attempting to brood may show decreased growth when forced to

share territories with other females, or reproduction may be decreased (Ng and Wilbur,

1995).

I hoped to expand our knowledge about the behavior of terrestrial salamanders under

stressful conditions. Jaeger *et al.*'s (1995) study showed that when conditions were dry,

more juveniles cohabited with adults than expected. The non-territorial juvenile floaters

seemed to be tolerated by adults (especially when they had previously cohabited, Jaeger

et al., 1995). Similarly, female red-backed salamanders were more tolerant of (spent less

time in threat displays with) familiar females than with strangers (Jaeger and Peterson,

2002). If, as suggested by Jaeger *et al.* (1995), juveniles are allowed to move into adult

territories during dry conditions, but perhaps strange adults are not tolerated (Jaeger,

1981, 1984), this could imply that juveniles moving out of cut areas could survive in the

surrounding habitat, while adults could not. I examined the abundance of juveniles versus adults in this study to test this hypothesis.

METHODS

Four ten by ten meter plots were established in June 2003 at the four edges of one future clearcut (Figure 3.1, Appendices A & B). The use of all four sides of the clearcut minimized the potential for bias if salamanders all move in one direction following the harvest (Phillips, 1986). One additional plot was established approximately 60 meters away from the edge of the harvest in mature forest as a control (Figure 3.1). The literature suggests that edge effects only extend to between 25-35 m (DeMaynadier and Hunter, 1998) and 50 m (Matlack, 1993) outside the harvested area, so our control plot 60 m outside should have been unaffected by the harvest. Home ranges are relatively small for the species in this study: 6.52 m^2 (female) – 14.39 m^2 (male) for *Plethodon glutinosus* (Merchant, 1972), 3.9 m^2 (male) – 4.8 m^2 (female) for *Plethodon cinereus* (Kleeberger and Werner, 1982), and less than 3 m^2 for *Desmognathus fuscus* (Barthalmus and Bellis, 1972), which is presumably similar to that of *Desmognathus ochrophaeus*. Therefore, these plots (100 m^2) were large enough to incorporate the home ranges of multiple individuals of these species.

The sampling order of these plots was randomly selected, and all were sampled in one night in order to avoid temporal bias. In addition to the four edges of these plots being marked, the edge of the future cut was marked. Up to five people crawled along the plot

at the same pace, capturing surface-active amphibians on rainy nights. We crawled from one side of the plot to the other (not back), with individuals occasionally using a zigzag pattern to cover their section of the plot, depending on the number of people sampling. Morphological data (sex, snout-vent length, total length, and mass) were recorded, and each salamander was batch-marked using elastomer dye injected subcutaneously (Donnelly *et al.*, 1994; Davis and Ovaska, 2001; Marold, 2001). If a salamander was captured on the "inside" (harvested) side of the plot, it received a mark behind one of its front legs. If it was captured on the "outside" (unharvested) side of the plot, it received a mark in front of one of its hind legs. For the control plot, one "side" was randomly labeled as the harvested side, and salamanders captured there received the corresponding batch mark, although that half of the plot was not actually harvested.

The plots were sampled six times pre-harvest, between 8 July and 5 August 2003. The planned harvest was completed in early September 2003. The plots were re-sampled once in late September 2003, and twice in early August 2004, yielding three post-harvest sample dates. To ensure that it was appropriate to combine post-harvest samples over a long time period, I used paired t-tests to compare minimum number of animals captured on each post-harvest sample date. Post-harvest estimates, consequently, were from approximately 10 months post-harvest (late September 2003-early August 2004).

Population Estimates

Population estimates were calculated using the adjusted Schnabel estimator, which allows analysis of batch marked animals and accounts for capturing/marking a small proportion of the total population (Krebs, 1999). Because my interest was in primarily in the effect of harvest on terrestrial salamanders, not necessarily on specific species, the five species (*Desmognathus ochrophaeus*, *Plethodon glutinosus*, *Plethodon cinereus*, *Desmognathus fuscus*, and *Eurycea bislineata*) were lumped for data analysis. Additionally, relatively small sample sizes did not allow for population estimates to be calculated for each species individually. Both pre- and post-harvest population estimates were calculated. Significant increases from pre- to post-harvest on the uncut side could indicate that salamanders had moved into the uncut area. If significant decreases on the cut side occurred in conjunction with increases on the uncut side, this would provide evidence of movement. If external abundance increased temporarily then returned to pre-harvest levels (in conjunction with decreased internal abundance), this would suggest that the uncut habitat was saturated, and therefore that moving salamanders either could not survive there or moved through our plots so that we could no longer detect them. Due to only three post-harvest sampling occasions, we were not able to observe such an occurrence (temporary increase then decrease).

I noticed during my analyses that population estimates were often influenced by the number of sampling occasions. If I calculated population estimates after three sampling occasions (the earliest sampling date when I could estimate population size), it was, in 8 of 10 cases, lower than the estimate after six sampling occasions. Because we sampled six times pre-harvest, and only three post-harvest, I chose to re-run the population

estimate analyses using only the first three pre-harvest sampling occasions (8, 9, and 10 July). Because the same marks were used for each sampling occasion, it was not possible to subsample the data using any other sampling occasions besides the first three.

Capture probabilities are generally not calculable using the Schnabel estimator. However, I calculated an estimate of capture probability using the formula:

$$\overline{\sum m_i \Big/ \sum M_i}$$

where m_i = the number of recaptures each night and M_i = the number of animals marked previous to that night. In other words, the "capture probability" is the proportion of recaptured animals to total number of marks available in the population. Capture probabilities were averaged for the four experimental plots, but not for the control plot (as there was only one control).

In order to examine whether abundance closer to the center of a clearcut declines greater than that at the edge (and if this could help explain our results), I examined data from the coverboard study described in Williams (2003) (hereafter referred to as the "reference cut coverboard study"). In that study, coverboards were located on each of nine reference cuts referred to in Chapter 1 (one on each of the nine compartments on the MWERF, Appendix A). Coverboards were located at 4 "stations": 50 meters outside the edge of the clearcut, 5-10 meters inside the edge (the approximate equivalent of the locations of plots in this study), 50 meters inside the edge, and 100 meters inside the edge. The data from Williams's (2003) study were combined with two subsequent years of data collection, leading to at least one year each of pre-harvest and post-harvest data for each

of 7 compartments (compartments 2 and 8 were lacking pre-harvest data so were excluded from the analyses; compartments 1 and 3 had two years of pre-harvest data and one of post-harvest data; compartments 4-6 had one year of pre-harvest data and one year of post-harvest data; compartments 7 and 9 had one year of pre-harvest data and two years of post-harvest data). In order to compare the results of the reference cut coverboard study more directly to my study, I examined only data from one year post-harvest for all 7 compartments (not including the second year of post-harvest data collection on compartments 7 and 9). I calculated relative abundance of salamanders at each station by averaging the total number of animals counted at each sampling period within a year (usually 3-4 sampling events).

Finally, in order to test if the decline in population estimates we observed on both our experimental and control plots could have been an area-wide decline in abundance, I examined 2003 and 2004 relative abundance data which I obtained using nighttime area-constrained searches conducted on two 14-ha study sites also located on the MWERF (West Virginia 1 and West Virginia 2, described in Knapp *et al.*, 2003). These data will hereafter be referred to as the "biodiversity plot data."

Adult-Juvenile Ratio

To identify adults, we used the following minimum snout-vent lengths: *Plethodon* c*inereus* males = 32 mm, females = 34 mm; *Plethodon glutinosus* males = 45 mm, females = 58 mm; *Desmognathus ochrophaeus* adults = 30 mm; *Desmognathus fuscus*

adults = 30 mm; *Eurycea bislineata* adults = 35 mm (Williams, 2003). The proportion of adults captured each night per plot was calculated.

If there was a trend in the proportion of adults from pre- to post-harvest, I proposed that it could have been because post-harvest sampling occasions were, on average, later in the year than the pre-harvest sampling occasions. The mean of the pre-harvest sampling occasions (using calendar days) was on July 19. The mean of the post-harvest sampling occasions was on August 24. In order to examine whether trends could be explained by seasonal changes in the proportion of adults, I examined a different data set, in combination with the data from this study. These data came from an artificial cover objects study I conducted on the MWERF (hereafter referred to as the "patch study"). In that study, artificial cover objects were located in mature forest. Six coverboards less than 2.5 cm apart made up a station, and stations were located 12.5 m from each other. Boards were sampled on 4 occasions between 21 June and 9 August 2004, and the number of each sex (male, female, or juvenile) captured was recorded. In order to minimize small sample sizes, I did not include dates on which fewer than 30 animals were captured. The data from the patch study were compared to those from this study in order to verify the trend. The data from these two studies were then combined (again not including those dates with fewer than 30 overall captures), and the data were graphed in order to examine seasonal trends in the proportion of adults. Because female *Plethodon cinereus* lay their eggs in late spring and brood them until hatching 6-9 weeks later (Ng and Wilbur, 1995), it could have been that the proportion of adults increased due to females emerging from brooding when we were sampling post-harvest. I hoped to

elucidate the causes behind the seasonal change (whether due to an increase in the numbers of females emerging from brooding, or to death of young juveniles during the sampling season).

Movement

As another method to detect whether movement was occurring, I tallied the recaptured animals that had moved in either direction (from one side of the plot to the other). These pre- and post-harvest numbers were used to determine whether movement patterns changed from pre- to post-harvest. I also compared pre-harvest movement rates to those observed on a nearby site (hereafter referred to as "movement site 2", sampled the following year (18 May to 18 June 2004) using the same methods. This site was only sampled pre-harvest, and due to miscommunication, the plots were destroyed by the harvest in late June and July 2004. These plots were located in stand 105, south of the intersection of the Kittle Creek and Camel Back roads, at approximately 581360 mE, 4284920 mN.

Statistical Analyses

Repeated measures ANOVAs were performed to test two sets of null hypotheses. The first set of hypotheses addressed population estimates, and follow: (1) harvest vs. control: population estimates on the harvested sides of the plots, taking into account normal fluctuations reflected by population estimates on the control plot, did not change from

pre- to post-harvest, (2) unharvest vs. control: population estimates on the unharvested sides of the plots, taking into account normal fluctuations reflected by population estimates on the control plot, did not change from pre- to post-harvest, and (3) harvest vs. unharvest: population estimates on the harvested sides of the experimental plots, taking into account normal fluctuations reflected by population estimates on the unharvested sides of the experimental plots, did not change from pre- to post-harvest. The second set of hypotheses addressed relative proportion of adults to juveniles, and follow: (4) harvest vs. control: proportion of adults on the harvested sides of the plots, taking into account normal fluctuations reflected by proportion of adults on the control plot, did not change from pre- to post-harvest, (5) unharvest vs. control: proportion of adults on the unharvested sides of the plots, taking into account normal fluctuations reflected by proportion of adults on the control plot, did not change from pre- to post-harvest, and (6) harvest vs. unharvest: proportion of adults on the harvested sides of the experimental plots, taking into account normal fluctuations reflected by proportion of adults on the unharvested sides of the experimental plots, did not change from pre- to post-harvest.

In order to examine the results of the reference cut coverboard study, I used ANOVAs (with compartments as a blocking factor) to test whether treatment (harvest) affected salamander relative abundance at each coverboard station. Two Tukey honestly significant difference (HSD) tests were used to show which stations differed from each other.

I used a Wilcoxon signed rank test on the biodiversity plot data, in order to test whether a site-wide decline occurred from 2003 to 2004.

I used a power calculation on the harvested sides of the plots (that does not take into account the change observed on the control plots) to determine the power I had to observe a 40% decrease in salamander populations over one year (Gerrodette, 1993). The 40% value was derived from results of Harpole and Haas (1999), which showed that five experimental treatments (group selection, 12-14 m^2 shelterwood, 4-7 m^2 shelterwood, leavetree, and clearcut) during year 1 post-harvest showed an average of 40% decline (Harpole and Haas, 1999). For my analysis I used a one-tailed t-distribution with $\alpha = 0.10$, assumed the coefficient of variation (CV) to be proportional to the inverse of the square root of population abundance, and assumed CV = 0.20 (estimated from my data).

Additionally, three Wilcoxon signed-rank tests were performed to examine the movement of salamanders in the experimental plots. In the first analysis (pre-harvest uni-directional movement), the proportion of salamanders moving from harvested to unharvested sides of the experimental plots, pre-harvest, was A. The proportion of salamanders moving from unharvested to harvested sides, pre-harvest, was B. I tested the null hypothesis that (A - B) = 0, or that salamanders were not moving in one direction pre-harvest. In the second analysis (post-harvest uni-directional movement), the proportion of salamanders moving from harvested to unharvested sides of the experimental plots, post-harvest, was A. The proportion of salamanders moving from unharvested to harvested sides, post-

harvest, was B. I tested the null hypothesis that (A - B) = 0, or that salamanders were not moving in one direction post-harvest. In the third analysis (post-harvest movement out of cut sides of plots), the proportion of salamanders moving from harvested to unharvested sides of the experimental plots, pre-harvest, was A. The proportion of salamanders moving from harvested to unharvested sides, post-harvest, was B. I tested the null hypothesis that (A - B) = 0, or that salamanders were not moving out of the plots post-harvest.

RESULTS

The total number of captures and recaptures by sample occasion and plot is shown in Table 3.2. Two Mann-Whitney U tests showed that the minimum number of animals captured was not significantly different between the September 2003 sample date (mean ranks = 4.7 and 4.9) and each of the August 2004 sample dates (mean ranks = 6.3 and 6.1) (U(4) = 16.5 and U(4) = 15.5, $p > 0.05$). Therefore, I combined these sample dates in order to estimate post-harvest population size.

Population Estimates

The mean population size estimates (from all six pre-harvest sampling occasions) and capture probabilities are shown in Table 3.3. Results from the repeated measures ANOVAs are given in 3.4. For population estimates (hypotheses 1 & 2 above), there was no significant interaction of plot type (harvested or unharvested vs. control) and time

(F(1,3) = 2.78, $p > 0.05$ and F(1,3) = 4.68, $p > 0.05$, respectively). Additionally, there was no significant interaction of side of plot and time, when examining only the experimental plots (hypothesis 3 above) (F(1,6) = 0.39, $p > 0.05$).

Mean population size estimates (using only the first three pre-harvest sampling dates) and capture probabilities and given in Table 3.3. Results from the repeated measures ANOVAs are shown in Table 3.5. There was no significant interaction of plot type (harvested or unharvested vs. control) and time (F(1,3) = 1.54, $p > 0.05$ and F(1,3) = 4.81, $p > 0.05$, respectively). Additionally, there was no significant interaction of side of plot and time, when examining only the experimental plots (F(1,6) = 1.74, $p > 0.05$).

The ANOVAs on the reference cut coverboard study showed that, for each station, treatment (harvesting) significantly affected relative abundance of salamanders ($p < 0.06$, Table 3.6). Pre-harvest relative abundances at each station were similar; the only significant difference was that relative abundance at station 1 (50 m outside harvest) was higher than that at station 4 (100 m inside cut) (HSD, $p < 0.05$, Figure 3.2). Post-harvest relative abundance at station 1 (50 m outside cut) was significantly higher than those at stations 2 (edge), 3 (50 m inside), and 4 (100 m inside), which were not significantly different from each other (Figure 3.2). The relative abundance at station 1 increased by 148% from pre- to post-harvest (Figure 3.2). The relative abundance at stations 2, 3, and 4 decreased by 77.3%, 89.2%, and 53.7%, respectively.

In examining the biodiversity plot data, the number of captures on control plots showed a marginally significant decline based on a Wilcoxon signed rank test (from 2.67 salamanders/plot to 0.83 salamanders/plot, $p = 0.0625$).

Over the course of one year, I had 38% power to observe the 40% decline. In order to obtain the desired 80% power to observe a 40% overall decline, CV would need to be decreased to 0.10 (perhaps by doubling the number of plots, thereby increasing the number of salamanders captured and minimizing variation). I chose 0.10 because it is unlikely that CV could be decreased much below this level, given the 0.20 CV in this study. If CV was decreased to 0.10, and all other variables in the power calculation were held constant, it would require four years of monitoring to have the desired 80% power to observe this decline.

Adult-Juvenile Ratio

For proportion adults (hypotheses 4 & 5 above), there was no significant interaction of plot type (harvested or unharvested vs. control) and time ($F(1,3) = 0.048$, $p > 0.05$ and $F(1,3) = 0.094$, $p > 0.05$, respectively). Additionally, there was no significant interaction of side of plot and time, when examining only the experimental plots (hypothesis 6 above) ($F(1,6) = 1.66$, $p > 0.05$, Table 3.4).

Despite the lack of significant interaction in the repeated measures ANOVA, it appears that there is a trend toward a greater proportion of adults post-harvest (Table 3.4). In the

patch study (used here to examine whether trends could be explained by seasonal changes in the proportion of adults), samples were taken on June 21, June 28, July 17, and August 9, 2004. The proportions of adults on those dates were 0.500, 0.447, 0.636, and 0.667. This supported the increasing trend we observed in this study, and allowed us to combine these data (from the patch study and this study) in Figure 3.3, in order to examine the reason behind the trends. Figure 3.3 shows a decrease in number of females and juveniles captured, and an increase in number of males captured during the sampling season.

Movement

We observed some movement of salamanders within the plots. Pre-harvest on all plots, 12 salamanders moved from the inside of the plot to the outside, and 16 moved from outside to inside (9.76% and 13.00%, respectively, of 123 recaptures). Post-harvest on the control plots, 1 animal moved from inside to outside, and 1 moved from outside to inside (9.09% and 9.09%, respectively, of 11 recaptures). The first Wilcoxon signed-rank test showed that the difference in the proportion of salamanders pre-harvest moving from harvested to unharvested and moving from unharvested to harvested sides of the plots was not different from zero ($Z = -1.095$, $p > 0.05$). The second test showed that the difference in the proportion of salamanders post-harvest moving from harvested to unharvested and moving from unharvested to harvested sides of the experimental plots was not different from zero ($Z = 0.000$, $p > 0.05$). The third test showed that the difference in the proportion of salamanders moving from harvested to unharvested sides

of the experimental plots between pre- and post-harvest was not different from zero ($Z =$ -0.730, $p > 0.05$).

Examining the pre-harvest data from movement site 2 (sampled in 2004), we had 5 animals switch sides of the plots (of 20 recaptures). Given the movement rate observed pre-harvest on the 2003 plots, we would have expected to see 4.6 movements, approximately the number we observed.

DISCUSSION

Movement

The results from these analyses show that, over the short-term (July 2003-August 2004), harvesting has little effect on the movement of salamanders near the edge of those harvested areas. There was no significant movement in either direction pre- or post-harvest, and the proportion of salamanders moving from harvested to unharvested sides of the experimental plots did not change from pre- to post-harvest. The data from movement site 2 (5/20 or 25% of recaptures moving) agrees with the approximate rate of movement we saw pre-harvest in this study (28/123 or 23% of recaptures). Because the movement site 2 sampling occurred earlier in the season (May 18-June 18 2004, versus July 8-August 5 2003 in this study), it suggests that this rate of movement is relatively consistent across time (from mid-May to early August) and location (within the constraints of this study). Rate of movement post-harvest in this study was 18% (2/11

recaptures). Because I used batch marks in this study, it was impossible to tell how far each animal moved when they did switch sides of the plots. However, I know from the patch study that some animals are capable of moving more than 10 meters within 3.5 weeks. Of thirty-one recaptures in that study, three movements were made 12.5 m to the nearest coverboard station (by two juvenile *Plethodon cinereus*). Other individuals (25 of 31 recaptures, 81%) moved from board to board (less than 1 m) within the same coverboard station. Additionally, Marsh *et al.* (2004) found that red-backed salamanders (in particular, young adults) naturally traversed open field areas in order to colonize suitable habitat (within 25 m of the edge). This implies that salamanders (at least juveniles) are capable of making movements beyond the area of an average home range, and could have moved well outside our 10 x 10 m plots.

Population Estimates

The results of the population estimates mirrored the movement results, showing no significant interaction of plot type and time, or of side of plot and time. In other words, population size estimates did not change due to harvesting. However, it appears that there is a trend toward decreased population size post-harvest (on both the control and experimental plots, Table 3.4), despite the lack of significant interaction in the repeated measures ANOVA. This could be a consequence of the seasonal differences in pre- and post-harvest sampling. Pre-harvest sampling occurred primarily in July 2003, which had above-average precipitation (15.49 cm, compared to an average of 12.22 cm) (National Climatic Data Center, 2005). The previous spring and early summer (March-June) of

2003 had well above average precipitation (50.37 cm, average 41.10 cm, NCDC, 2005).

We sampled post-harvest in late September 2003 and in August 2004. September's

precipitation (17.17 cm) was above average (8.23 cm), while August 2004's precipitation

was exactly average (10.29 cm). June and July 2004, like August, had average

precipitation levels (23.70 cm, average 23.14 cm). This suggests that during the two

months prior to pre- and post-harvest sampling, there were differences in the amount of

precipitation (well above average pre-harvest, only slightly above average post-harvest).

Weather factors have been shown to affect salamander abundance and detectability

(Grover, 1998; Williams and Berkson, 2004). Williams and Berkson (2004) showed that

average daily humidity can affect the probability of detection of *Plethodon cinereus*

during nighttime surveys. These seasonal weather differences could have affected the

apparent decreased population size post-harvest observed on both control and

experimental plots, if detection probability were affected.

The biodiversity plot data which I collected during the two sampling years (2003 and

2004) to follow up on the Knapp *et al* (2003) study, suggest a decline in relative

abundance, so it is possible the decline I observed in population estimates was a change

observed over the entire study area. However, these data had similar problems to the

current study's data, in that 2004 data were collected earlier in the season on average than

the 2003 data (July 2 versus July 26). Therefore, I can not be sure that this decline was

not also an artifact of sampling season.

The results of the analyses using the first three pre-harvest sampling occasions (Table 3.5) were similar to those using all six pre-harvest sampling occasions. For two of the three tests (unharvested and only experimental plots), p-values decreased with the tests using only three pre-harvest sampling occasions. However, there were still no significant interactions (the closest to significance was $p = 0.12$ in the unharvested plots analysis, indicating a decline from 64 to 23 individuals on the unharvested sides of the experimental plots).

These results are somewhat surprising, considering that previous work in the area by Williams (2003) showed significant decreases in relative abundance in year 1 post-harvest (using coverboard and night sampling, at two of three sites). This sampling was performed between six and eight months post-harvest. Similarly, Ash (1997) saw a 30-50% decline in plethodontid salamanders on clearcut plots in the first year after harvest. One might expect that my 10-month post-harvest population estimates would show comparable declines. However, other studies (Harpole and Haas, 1999; Knapp *et al.*, 2003) have shown the greatest effect on relative abundance at 2 years or later post-harvest. Sattler and Reichenbach (1998) saw a 70% decline in Peaks of Otter (*Plethodon hubrichti*) salamander abundance two years post-harvest at clearcut sites. A lag in response to timber harvesting could be explained by characteristics of terrestrial salamanders: they are both long-lived and have low metabolisms. They generally do not reach sexual maturity until 3-6 years of age (Hairston, 1987), and *P. cinereus* uses only 8.3 calories/g/day at 15°C (Merchant, 1970). Additionally, *P. cinereus* has been known

to survive for months in captivity without eating, implying that they should be able to survive a full season under altered habitat conditions (Stebbins, 1954; Feder, 1983).

It is unclear why differences exist between studies in the amount of time it takes to see a population decline. Potentially, the weather conditions of the years following harvest could affect abundance, due either to actual population changes, or to changes in detectability because the salamanders emerge more or less often. Similarly, the physical aspects of the clearcut could have a large influence on the length of time it takes to observe a population change. The size of the clear-cut was relatively small in this study (12.7 ha). A larger cut, or one exposed to more sun and wind or higher temperatures, could have a drier forest floor, causing more abrupt population declines. Additionally, location of sampling points could affect estimates of abundance. For example, the reference cut study (part of ALEP) sampling points were, on average, closer to the center of the clearcut than were our plots (coverboard stations in the reference cut study were located 5-100 m inside the edge of the harvest, on average 51 meters from the edge; night transects were located at least 50 m from the edge, while ours were centered on the edge, and extended no more than 5 m in either direction from the edge; Williams, 2003). I suspected that Williams (2003) saw a greater effect in the reference cut study because conditions were harsher closer to the middle of the clearcuts than they were at the edge where this study was concentrated. The reference cut coverboard study data show clearly that harvests affect relative abundance at any distance from the edge (Table 3.6). However, there is little evidence that stations closer to the center of the harvest are more affected than those near the edge (Figure 3.2).

It is also possible that the time frame used in my study was simply too short to observe changes in population size. Similarly, the size of the plots could have been too small to be strongly affected (in microhabitat or microclimate characteristics) by the harvest (Messere and Ducey, 1998). The survey plots were, on average, only 2.5% of the length of each side of the harvest. In order to solve these problems in the future, it might be useful to change the shape and location of the plots, in order to increase the chances of observing changes in abundance. For example, two longer, narrower plots separated by a buffer including the edge of the harvest might be more likely to pick up movement, and could show changes in abundance more easily, due to greater differences in microhabitat characteristics. Although none of my results were significant, they were all in a negative direction (as was the control plot). Future studies should use multiple control plots. There is the possibility of significance with a larger sample size (more plots). In order to obtain the desired 80% power to observe a 40% overall decline, CV would need to be decreased to 0.10 (perhaps by doubling the number of plots, or changing their shape, thereby increasing the number of salamanders captured and minimizing variation), and it would still require four years of monitoring to have the power to observe this decline. It seems, therefore, that such a short-term study may not be able to obtain 80% power. However, the use of individual (as opposed to batch) marks would be useful in order to perform more detailed mark-recapture analyses.

Adult-Juvenile Ratio

Similar to the trends observed with population estimates, the proportion of adults did not change due to harvesting (relative to control or unharvested plots). The trend we observed in the increasing proportion of adults from pre-to post-harvest (Table 3.4) appeared to be due to increased mortality of young (juvenile) animals during their first year, not due to females emerging from brooding, as female proportions showed no noticeable increase in mid- to late-summer (Figure 3.3). However, the data also show an increase in the numbers of males captured in mid- to late-summer. This could be due to recruitment of adult males into the population, as juveniles matured later in the season.

CONCLUSION

Overall, this study found no evidence of an effect over the short-term of harvesting on salamander movement and population estimates within 5 m of the edge. My control plot, 60 m from the edge, showed a population estimate decline (as did the experimental plots). Because I saw no significant effect of the harvest on abundance or movement, my results are consistent with the second and third no movement alternatives in Table 3.1 ("No movement, eventual death" or "No movement, survival"). However, because I was unable to complete experiments with caged salamanders, I was unable to differentiate between these two alternatives. Unless declines happened on a greater scale than expected, this study lacked power to detect declines, and so cannot provide evidence to support or refute any of the alternatives. It is possible that the effects on population estimates would be significant if the study design was changed or if monitoring continued for the longer term. The trends observed suggests that it may take some time (> 1 year)

for harvests to affect salamanders and cause the population declines seen in many other studies.

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Table 3.1. Potential alternatives available to forest salamanders following a timber harvest, and differentiation among these alternatives.

Alternative	Result
No movement, immediate death	Abundance outside cut (external abundance) remains constant, and abundance inside cut (internal abundance) decreases; caged animals show decreased survival and body condition in cut
No movement, eventual death	External abundance remains constant, and internal abundance remains constant over the short term of this study, decreases eventually; caged animals show decreased survival and body condition in cut
No movement, survival	External abundance remains constant, and internal abundance remains constant; caged animals survive in cut
Movement, eventual death or movement out of plot	External abundance increases temporarily then decreases to original level, and internal abundance decreases; observe movement of marked salamanders
Movement, survival	External abundance increases and remains high, and internal abundance decreases; observe movement of marked salamanders

Table 3.2. Total and mean number of captures and recaptures of salamanders per sampling occasion, on all experimental and control plots, 8 July 2003-12 August 2004, Randolph County, WV.

Sample Occasion	Total Number of Captures/Recaptures on Plot #					Mean Number of Captures/ Recaptures	Total Number of Captures/Recaptures
	1	2	3	4	Control		
Pre-harvest 1	4 / 0	8 / 0	15 / 0	18 / 0	22 / 0	13.4 / 0.0	67 / 0
2	11 / 0	7 / 1	21 / 1	35 / 3	16 / 1	18.0 / 1.2	90 / 6
3	6 / 5	5 / 2	5 / 5	27 / 9	19 / 5	12.4 / 5.2	62 / 26
4	5 / 1	4 / 2	10 / 8	21 / 6	21 / 8	12.2 / 5.0	61 / 25
5	8 / 1	4 / 2	12 / 10	13 / 7	15 / 4	10.4 / 4.8	52 / 24
6	3 / 3	1 / 1	7 / 6	27 / 14	23 / 17	12.2 / 8.2	61 / 41
Post-harvest 7	5 / 0	4 / 0	6 / 0	4 / 0	2 / 0	4.2 / 0.0	21 / 0
8	4 / 0	1 / 0	9 / 0	13 / 0	9 / 2	7.2 / 0.4	36 / 2
9	7 / 0	2 / 0	2 / 2	13 / 2	9 / 5	6.6 / 1.8	33 / 9
MEAN	5.9 / 1.1	4.0 / 0.9	9.7 / 3.6	19.0 / 4.6	15.1 / 4.7	10.7 / 3.0	53.7 / 14.8
TOTAL	53 / 10	36 / 8	87 / 32	171 / 41	136 / 42	96.6 / 26.6	483 / 133

Table 3.3. Population estimates and capture probabilities on all experimental (E) and control (C) plots, for both unharvested (U) and harvested (H) sides of plots, 8 July 2003-12 August 2004, Randolph County, WV.

Pre-harvest capture occasions	Plot	Side of Plot	Population Estimates		Capture Probabilities	
			Pre-harvest	Post-harvest	Pre-harvest	Post-harvest
All six	E	U	71.00	22.75	0.101	0.042
		H	63.75	29.50	0.112	0.036
	C	U	124.00	20.00	0.127	0.400
		H	115.00	8.50	0.106	0.375
First three	E	U	64.09	22.75	0.154	0.042
		H	41.58	29.5	0.184	0.036
	C	U	146.00	20.00	0.065	0.400
		H	59.30	8.50	0.172	0.375

Table 3.4. Mean population estimates of salamanders (using all six capture occasions pre-harvest, 8 July-5 August 2003; sampled September 2003-August 2004 post-harvest, Randolph County, WV) and proportion adults per plot or side of plot (with standard errors when available) from pre- or post-harvest, and results from repeated measures ANOVA.

Variable	Repeated Measures Analysis	Plot or Side	Pre-harvest	Post-harvest	Mean Square (T, T*G, E)[1]	df (T, T*G, E)[1]	F (T, T*G)[1]	p (T, T*G)[1]
	Harvested sides of plots: 2 (plot type) x 2 (time)	Control Plot	115.00	8.50	7924.23	1	10.56	0.048
		Experimental Plots	63.75 (26.26)	29.50 (11.18)	2088.03	1	2.78	**0.194**
					750.46	3		
Population estimate	Unharvested sides of plots: 2 (plot type) x 2 (time)	Control Plot	124.00	20.00	9272.03	1	34.93	0.010
		Experimental Plots	71.00 (25.53)	22.75 (14.23)	1243.23	1	4.68	**0.119**
					265.46	3		
	Experimental plots: 2 (side of plot) x 2 (time)	Unharvested Side	71.00 (25.53)	22.75 (14.23)	6806.25	1	13.40	0.011
		Harvested Side	63.75 (26.26)	29.50 (11.18)	196.00	1	0.39	**0.557**
					507.96	6		
	Harvested sides of plots: 2 (plot type) x 2 (time)	Control Plot	0.365	0.636	0.0965	1	4.348	0.128
		Experimental Plots	0.424 (0.119)	0.644 (0.099)	0.0106	1	0.048	**0.841**
					0.0222	3		
Proportion adults	Unharvested sides of plots: 2 (plot type) x 2 (time)	Control Plot	0.476	0.579	0.00800	1	0.458	0.547
		Experimental Plots	0.531 (0.112)	0.570 (0.092)	0.00165	1	0.094	**0.779**
					0.0175	3		
	Experimental plots: 2 (side of plot) x 2 (time)	Unharvested Side	0.531 (0.112)	0.570 (0.092)	0.0668	1	3.37	0.360
		Harvested Side	0.424 (0.119)	0.644 (0.099)	0.0328	1	1.66	**0.246**
					0.0198	6		

[1] T = Time, T*G = Time*Group, E = Error(Time)

Table 3.5. Mean population estimates of salamanders (using only the first three capture occasions pre-harvest, 8 July-10 July 2003; sampled September 2003-August 2004 post-harvest, Randolph County, WV) from pre- or post-harvest, and results from repeated measures ANOVA.

Variable	Repeated Measures Analysis	Plot or Side	Pre-harvest	Post-harvest	Mean Square (T T*G E)[1]	df (T T*G E)[1]	F (T T*G)[1]	p (T T*G)[1]
	Harvested sides of plots: 2 (plot type) x 2 (time)	Control Plot	59.30	8.50	1581.31	1	4.05	0.138
		Experimental Plots	41.58 (17.72)	29.5 (11.18)	599.85	1	1.54	**0.303**
					390.37	3		
Population estimate	Unharvested sides of plots: 2 (plot type) x 2 (time)	Control Plot	146.00	20.00	11201.41	1	18.79	0.023
		Experimental Plots	64.09 (23.75)	22.75 (14.23)	2866.76	1	4.81	**0.116**
					596.23	3		
	Experimental plots: 2 (side of plot) x 2 (time)	Unharvested Side	64.09 (23.75)	22.75 (14.23)	2853.43	1	5.78	0.053
		Harvested Side	41.58 (17.72)	29.5 (11.18)	856.59	1	1.74	**0.236**
					493.30	6		

[1] T = Time, T*G = Time*Group, E = Error(Time)

Table 3.6. Results of four ANOVA (with compartments as a blocking factor) of effect of harvest on relative abundance of salamanders, from the reference cut coverboard study, 2001-2004, Randolph County, WV. For each, harvest had a significant effect on relative abundance ($p < 0.06$).

Source	df	MS	F	*p*
Station 1				
Treatment	1	16.286	3.85	**0.0559**
Compartment	6	37.175	8.79	< 0.0001
Error	45	4.227		
Station 2				
Treatment	1	146.962	16.799	**0.0002**
Compartment	6	19.228	2.198	0.0606
Error	45	8.748		
Station 3				
Treatment	1	180.494	21.077	**< 0.0001**
Compartment	6	34.983	4.085	0.0024
Error	45	8.564		
Station 4				
Treatment	1	14.728	3.924	**0.0537**
Compartment	6	8.322	2.217	0.0586
Error	45	3.753		

Station 1 = 50 meters outside edge of clearcut, Station 2 = 5-10 m inside edge, Station 3 = 50 m inside edge, Station 4 = 100 m inside edge.
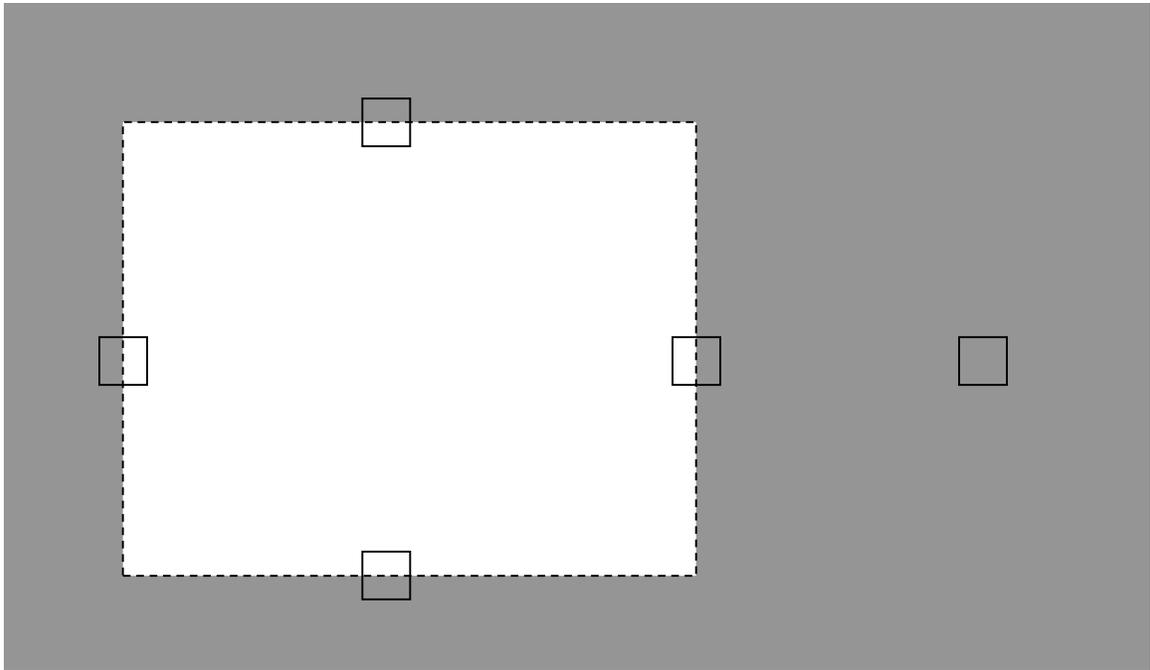
Figure 3.1. Schematic diagram of 10 x 10 m plots on the edge (dotted line) of future clearcut (white). Gray color indicates the uncut area. The control plot is approximately 60 m away from the edge of the cut (not to scale).
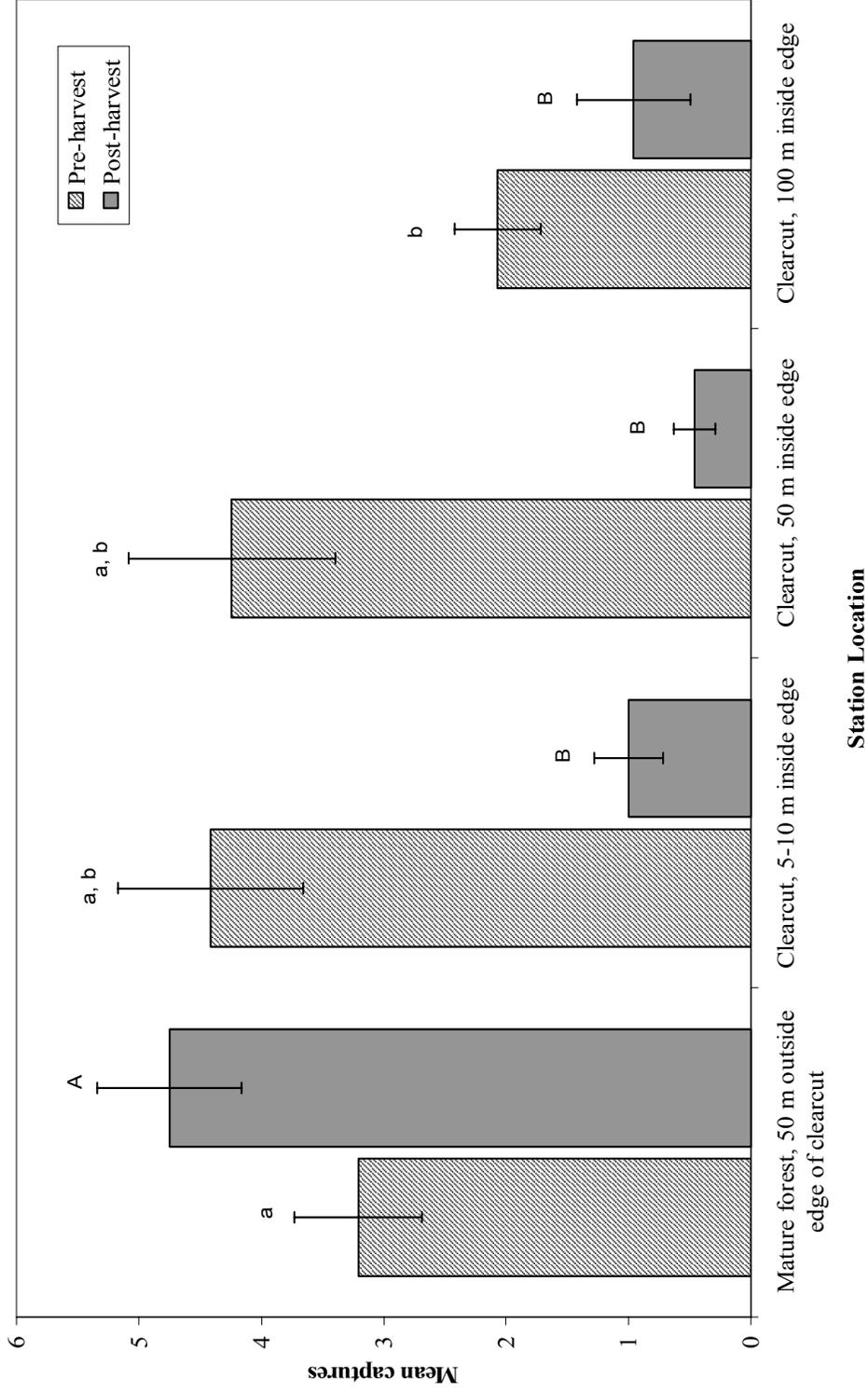
Figure 3.2. Mean number of individuals captured ($\pm$ 1 S.E.) at combined coverboard stations, pre- and post-harvest of seven 28-ha clearcuts. Each cut had at least one pre-harvest and one post-harvest year of data. Two separate Tukey HSD tests (lower case and capital letters above bars) showed that there were few significant differences in relative abundance pre-harvest (lower case letters). Post-harvest, stations inside the clearcut had significantly fewer salamanders than the station outside the clearcut (capital letters).
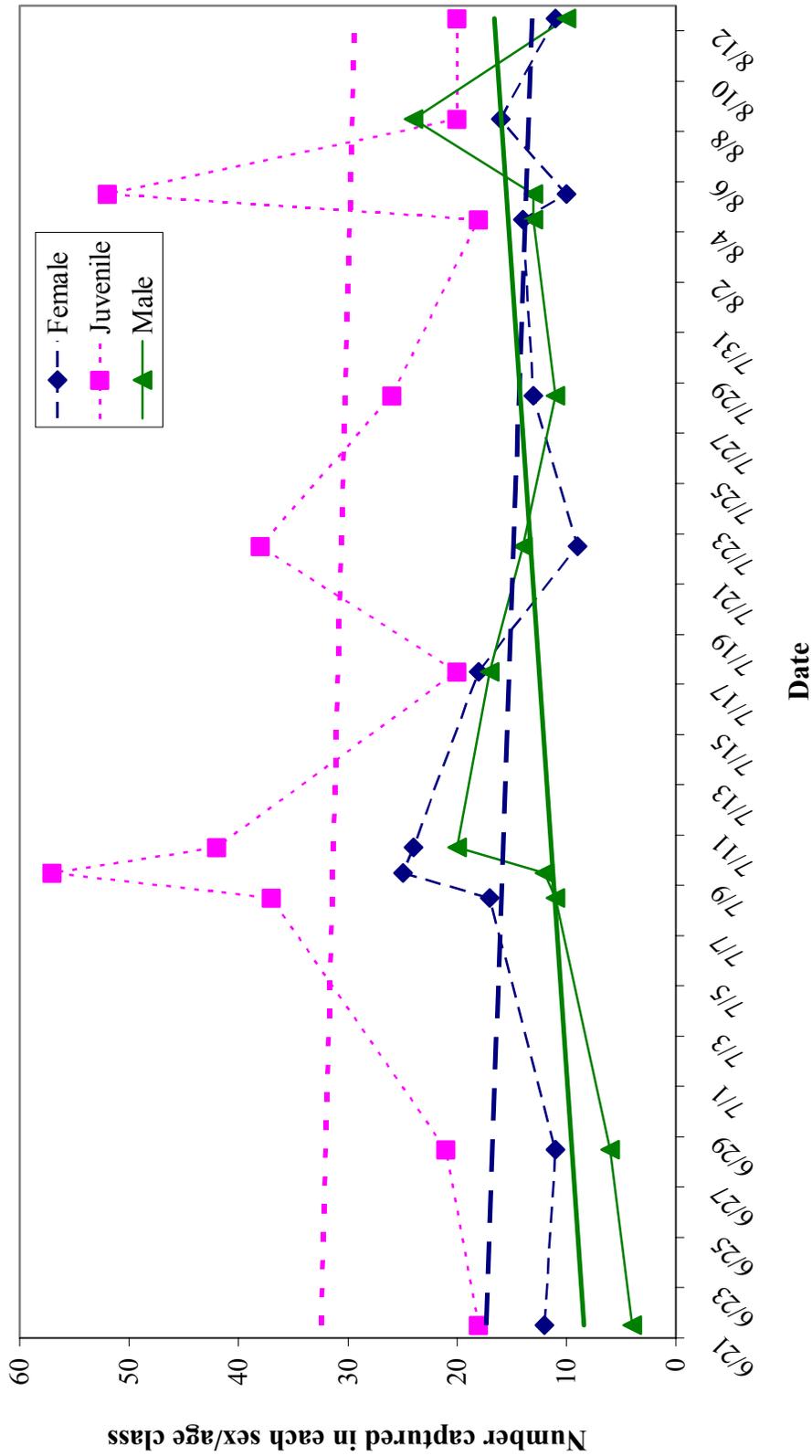
Figure 3.3. Numbers of juvenile, female, and male salamanders, compiled from this study and the patch study (both studies conducted in 2004, Randolph County, WV). The data exclude dates when fewer than 30 individuals were captured. Linear trend lines are included for each sex/age class. The data show a decrease of female and juveniles, suggesting that the trend toward a greater proportion of adults post-harvest was due to increased mortality of young (juvenile) animals during their first year, as well as an increase in males, which could be explained by maturing of juveniles (becoming males) late in the year.

CHAPTER 4: CONCLUSIONS

INTRODUCTION

My foremost goal in this research was to provide forest managers with recommendations for forest management, particularly harvesting operations, in the southern Appalachians that are compatible with maintaining healthy populations of forest amphibians. I proposed to do this through the validation of previous habitat models (Chapter 2), and the use of population estimates to determine the immediate effects of clearcuts on salamander movement (Chapter 3). Below, I will summarize the pertinent results, and give management recommendations based on them.

In my validation of Williams's (2003) habitat models (Chapter 2), I determined that one model was better than all others at predicting salamander abundance with new data. This model included the variables percent cover of woody stems (< 7.5 cm DBH), available rock, riparian status (if within 15 m of a stream), percent overstory canopy cover, and available highly decomposed woody debris (decomposition classes 3 to 5). All of the relationships with abundance were positive, except for woody stems.

My research into the short-term effects of clearcuts on salamander movement and population estimates (Chapter 3) revealed no significant changes in population estimates, adult-juvenile ratio, or movement following harvest. This supported the hypothesis that

salamanders were not moving post-harvest, although the eventual fate (survival or death) of these salamanders was unclear.

MANAGEMENT RECOMMENDATIONS

Retain Overstory Canopy Cover

As suggested by the habitat model that most accurately predicted salamander abundance using new data (Chapter 2), percent overstory canopy cover is very important to salamanders. Although decreasing the amount of overstory canopy cover is inherent to timber harvesting, one potential compromise is to minimize canopy removal in areas with other characteristics of high-quality habitat. This would involve protecting areas with a large amount of rock, highly decomposed woody debris, and near streams or seeps.

However, it is worth noting that there is no guarantee that partial removal of canopy is any better than complete removal. Knapp *et al.* (2003), in a comparison of seven silvicultural alternatives, showed that all treatments with canopy removal had significantly fewer salamanders than the control and herbicide treatments. The relative landscape-level effect of a group-selection cut was 1.8 times that of a clearcut; shelterwood 1 was 1.2 times more, leavetree was 1.3 times more, and shelterwood 2 was 1.4 times more. Given that these alternative silvicultural practices (to clearcutting) require multiple entries into a stand and/or more extensive disturbance to access a more dispersed resource, Knapp *et al.*'s study showed that clearcutting (complete canopy

removal) in small areas minimized the effects on salamander abundance. In the context

of this study, Knapp *et al.*'s (2003) research implies that clearcutting may affect

populations the least, and may be the best choice for managers. However, if group

selection or other alternative silvicultural methods are to be used, areas of canopy

retention should be chosen carefully and placed in areas with other characteristics of

high-quality habitat (high amounts of rock, highly decomposed coarse woody debris, and

in riparian areas).

Riparian Areas

Riparian areas (≤ 15 m from perennial or intermittent stream) are very important for

maintaining healthy populations of salamanders. These areas are used by many species

for egg-laying, foraging, and over-wintering (e.g., *Desmognathus* spp., Green and Pauley,

1987; Harding, 1997). Other riparian areas (those surrounding ponds and temporary

pools) are important for species that breed in the temporary pools, and use the

surrounding areas as foraging and over-wintering sites (e.g., *Ambystoma* spp.).

A suitable width for a buffer area around streams and ponds seems to vary based on the

species. Semlitsch and Bodie (2003), in their literature review, found that amphibians

(anurans and salamanders) required core habitat of 159-290 m from the water's edge,

plus a 50 m buffer (to protect the core area). Within amphibians, salamanders required

117-218 m, plus a 50 m terrestrial buffer. However, the plethodontid stream salamanders

(*Desmognathus* spp. and *Eurycea* spp.) showed a much smaller dispersal distance than

other amphibian species (seldom more than 20-30 m from the stream). This suggests that pond-breeders require a larger buffer and greater connectivity between breeding and upland habitat than do stream- and seep-dependent species. Most of the species examined in this thesis were stream- and seep-dependent, and Semlitsch and Bodie's review (2003) suggests that at a minimum, the 20-30 m surrounding these areas is essential, and an additional buffer of 50 m would be ideal to protect the species' core area. Petranka and Smith's (2005) research agrees, as they suggest that a 30 m area, with a 10 m buffer, would provide a core area for some stream-dependent species, and a source of terrestrial-breeding species for recolonization into adjacent harvested areas. It is worth noting that we found many animals in small seep areas; if at all possible, managers should attempt to protect these areas in addition to larger streams. However, there is a trade-off in the size of the buffer and the land available for timber harvest. A wider core area and buffer would allow less land to be harvested, although it would protect more amphibians. Another tradeoff is in the distribution of "protected areas." If a landowner is willing to set aside 10-25% of land to protect wildlife habitat or provide other ecosystem services, we need to consider whether those protected areas are best distributed as narrow strips (riparian buffers) or large patches on the landscape. The latter may be preferable for wildlife species that require large areas or are sensitive to edge effects. Managers will have to balance these opposing issues, in order to minimize effects on amphibians, while maximizing profits from timber harvest. I suggest that a minimal buffer around streams of 30 m on each side of the stream would protect the core area for many species; a 50-75 m buffer would be more ideal, to minimize the effects of timber harvesting on amphibians and promote recolonization.

Corridors

My results in Chapter 3 suggest that salamanders do not move any more post-harvest than pre-harvest in the short-term in response to a clearcut. This implies that the use of corridors to facilitate movement away from disturbance may not be useful. Marsh *et al.* (2004) found that red-backed salamanders, when displaced, returned as often through open habitat as through forested habitat, also suggesting that corridors are not necessary to survival or movement of individuals. Marsh *et al.* (2004) also found that red-backed salamanders (in particular, young adults) naturally traversed open field areas in order to colonize suitable habitat (within 25 m of the edge). However, some research has shown that juvenile pond-breeding amphibians partially avoid open habitats (and prefer forested habitats) for dispersal (deMaynadier and Hunter, 1999; Rothermel and Semlitsch, 2002). Rosenberg *et al.* (1998) showed that a terrestrial salamander (*Ensatina eschscholtzii*) chose corridors more often, spent more time in them, and moved slower through them than through bare (harsh) environments. However, the number of salamanders reaching target patches (an estimate of survival) through corridors was only significantly higher than those through bare pathways in situations where the matrix was most severe. This research suggests that corridors could be useful for colonization purposes, especially in very severe environments. It is unclear if rates of colonization or movement are affected by the use of corridors; i.e., although animals may be able to move across unsuitable habitat in order to colonize (Marsh *et al.*, 2004), they may colonize much faster (or slower, Rosenberg *et al.*, 1998) with a corridor. Overall, the use of corridors for

recolonization or movement away from disturbance appears to be an unresolved debate. Further study may settle this question, and provide managers with a definitive answer as to whether corridors are useful, and if so, in which habitats/for which species they should be used.

Increase Available Highly Decomposed Woody Debris

My data (Chapter 2) show that highly decomposed woody debris (class 3-5) is important for salamanders. They use this debris for refuge from dry conditions, egg-laying, and foraging. In order to protect salamander populations, managers should attempt to leave more snags standing, or fell them and leave them on-site. These dead (and beginning to decompose) trees would provide important habitat for recolonizing salamanders, long before live felled trees would. Additionally, it could be possible to import dead limbs and trees from other areas to decompose on-site, and increase the amount of woody debris. Leaving a duff and slash layer on the site (by not practicing whole-tree harvesting, and leaving the tops of trees on site) may help moderate some of the severe effects of the harvest on temperature and soil surface moisture. Additionally, grapple skidders could be used to distribute tops and branches to areas with other high-quality characteristics (near streams, with large amounts of rock), in order to maximize the populations of salamanders in those areas likely to have a high abundance.

SUMMARY

I have provided recommendations for managing industrial forest land in Appalachian hardwood forests in order to maintain healthy populations of amphibians. Based on my research and other published studies, I suggest management techniques including: 1) minimizing canopy removal in high-quality sites, such as those near riparian areas, and potentially developing corridors, especially for pond-breeding amphibians, and 2) increasing highly decomposed woody debris through leaving or felling snags, minimizing whole-tree harvesting, and strategically placing slash using grapple skidders. Although these recommendations are based on considerable research, they have not been demonstrated to increase or maintain amphibian populations. Further research may be needed, and managers should record the success or failure of attempted management techniques, in order to provide a better understanding of the most effective management methods.

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APPENDIX A: LOCATION OF MWERF

Appendix A. Location of the MWERF in north-central West Virginia. The MWERF has been divided into 6 compartments (4-9); the annex compartments are located north of the MWERF (compartments 1-3). The movement study was located in compartment 9, and is highlighted in blue. Further data, collected to compare movement rates to those in the original study, were collected on stand 105 in compartment 6 (also highlighted in blue).

APPENDIX B: MOVEMENT PLOT LOCATIONS & DETAILS

Appendix B. UTM locations of plots used in the movement study, including time harvested, and colors used for marking. Experimental plots were located one on each side of the stand, with the control plot approximately 60 m from the plot on the south-west facing side of the stand. The plot on the north-west facing side of the stand bordered a stream; the other plots were not near water.

Plot Number	UTM Zone	UTM mE	UTM mN	Harvested	Mark Color Used		
					Pre-harvest	Post-harvest 2003	Post-harvest 2004
Experimental 1	17S	582780	4283052	Early September 2003	Yellow	Red	Orange
Experimental 2	17S	582797	4282902	Early September 2003	Yellow	Red	Orange
Experimental 3	17S	582420	4282420	Early September 2003	Yellow	Red	Orange
Experimental 4	17S	582389	4282593	Early September 2003	Yellow	Red	Orange
Control	17S	582406	4282385	Early September 2003	Yellow	Red	Orange

VITA

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