ECOLOGICAL INTERACTIONS OF PLETHODONTID SALAMANDERS AND VEGETATION IN MISSOURI OZARK FORESTS

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by

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The undersigned, appointed by the Dean of the Graduate School, have examined the thesis entitled:

ECOLOGICAL INTERACTIONS OF PLETHODONTID SALAMANDERS AND VEGETATION IN MISSOURI OZARK FORESTS

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a candidate for the degree of Master of Science, and hereby certify that in their opinion it is worthy of acceptance.

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ABSTRACT

Salamanders are a seldom seen but important component of forested ecosystems. They are the primary predators of forest floor invertebrates and their abundance is a measure of ecosystem health. I examined management impacts on plethodontid salamander abundance in oak-pine and oak-hickory forest ecosystems in the southeastern Ozarks of Missouri. Relationships between coarse woody debris, canopy cover, ground area cover, herbaceous vegetation, woody vegetation, and plethodontid salamanders occurring among 42 sample plots distributed within three distinct forest structural stages were determined. I measured salamander abundance in regenerating forests < five years old, second growth forests 70-80 years old, and old-growth forests >120 years old. Salamander density was lowest in newly regenerated stands and highest in stands more than 120 years old. Comparisons of regenerating forests < five years old with mature stands more than 70 years old suggest that terrestrial salamanders are reduced to very low numbers when mature forests are intensively harvested. Stand age comparisons further suggest that salamander abundance slowly increases over time after stands are regenerated. Using Poisson regression, models were constructed based on data collected to describe the relationship between plethodontid salamanders and vegetation structure within each forest structural stage.

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CHAPTER 1

INTRODUCTION

The vegetation in the Central Hardwood region (Bailey 1995, Johnson 1997) is a reflection of past disturbance patterns. Fire, wind, insect, and disease outbreaks are natural disturbances that occurred prior to European settlement that greatly influenced the composition of vegetation (Guyette and Larsen In preparation). European settlement resulted in widespread clearcutting of the forest resource in the nineteenth and early twentieth centuries (Cunningham and Hauser 1989, Guyette and Larsen In preparation). Trees were cut and processed for fuel, railroad ties, building materials, and various other uses (Guyette and Larsen In preparation). Presently, forests are managed to achieve a particular objective by implementing various silvicultural practices (Forest Land Management Guidelines, Missouri Department of Conservation (MDC) 1986). Silvicultural prescriptions result in a pattern of disturbance across the landscape resulting in patches of evenaged, unevenaged, and non-manipulated forests of various sizes and ages.

Traditionally, management of trees and game species have been the focal point of natural resource agencies and the public. Natural resource agencies in the mid twentieth century concentrated their efforts on habitat restoration, by eliminating arson wildfires and destructive harvest practices as well as restoring various game species populations. Presently, public attitudes have changed considerably in support of a stronger conservation and stewardship ethic in forest management decisions (Missouri Department of Conservation 1996, Palmer 1996) and in particular, harvest impacts on non-timber forest resources. Research programs have been developed that investigate many biotic and abiotic ecosystem attributes. Moreover, research is being implemented to begin understanding ecosystem function rather than focusing on individual attributes. Natural resource agencies have begun to embrace ideas such as ecosystem management, which requires an understanding of the entire system rather than just its individual parts. One area of interest, in particular, is the response of all components of a system to forest management practices conducted today, and the importance of these components to the function of the system.

Amphibians are integral components in many ecosystems. They occupy trophic positions of both aquatic and terrestrial systems, and function as a primary predator upon invertebrates and serve as prey for larger vertebrates (Pough et al. 1987, Corn and Bury 1989). Salamanders alone are the most abundant vertebrate animals, and they comprise the major component of vertebrate biomass in many forest ecosystems (Burton and Likens 1975).

More than half of all species of salamanders are purely terrestrial lacking an aquatic larval stage in their life cycle (Hairston 1987). These species comprise the family Plethodonidae. Plethodontids lack lungs and exchange gases almost entirely through cutaneous respiration. This type of respiration limits terrestrial salamander distribution to environments that provide microhabitats with high levels of moisture. Microhabitat availability is largely a response to vegetation structure. Timber harvesting drastically alters vegetation structure and results in changes to the salamander community structure.

Sensitivity of salamanders to timber harvesting is well known in the Pacific Northwest and eastern U.S.; older, more mature forests support higher densities (Bury 1983, Enge and Marion 1986, Corn and Bury 1989, Welsh 1990, Welsh and Lind 1991, Blymer and McGinnes 1977, Bennett et al. 1980, Pough et al. 1987, Raphael 1988, Ash 1988, Corn and Bury 1991, Petranka et al. 1994, Dupuis et al. 1995). Older forests that have relatively large amounts of down and dead wood and leaf litter providing optimal microhabitats for terrestrial salamanders (Pough et al. 1987, Bury and Corn 1988, Aubry et al. 1988).

Timber harvesting removes a portion of large, dominant canopy trees within a stand. Removal of canopy trees results in increased light penetration to the forest floor, reduction in soil moisture, and increased soil temperature (Gieger 1965). Decreases in soil surface moisture and increases in temperature following timber harvesting forces salamanders to limit time spent foraging on the surface (Heatwole and Lim 1961, Spotila 1972). Because their skin is highly permeable, salamanders must utilize microhabitats that minimize water loss when conditions are unfavorable and the risk of desiccation is high (Spotila 1972). Jaeger (1972) suggested that salamanders moved horizontally from within the litter layer to under cover objects. However, Fraser (1976) indicates that salamanders primarily move vertically from within the litter layer to underground retreats.

Because plethodonids are the dominant salamanders in forests (Burton and Likens 1975) and habitat alterations restrict surface activity, reducing the abundance of salamanders could affect the resource base for birds and small mammals. Feder (1983) describes plethodontid salamanders as opportunistic exploiters of moisture. Plethodontids will forage widely and climb understory vegetation and tree trunks to capture prey when the forest is wet. As the forest becomes drier, foraging activity is restricted and salamanders are forced under cover objects and ultimately underground where they do not feed (Jaeger 1972, 1980a, 1980b). The inability to forage reduces biomass production of salamanders and limits the ecological role of salamanders in the system. The reduction in surface activity resulting from forest management practices reduces salamander numbers and availability as prey.

Because the physiological aspects and life history of plethodontid salamanders makes them sensitive to alterations in forest vegetation structure, natural resource managers can benefit from using plethodontids in management decisions. Plethodontids can provide information on the condition of the ecosystem after forest management practices have been implemented by indicating the impact significance, forest recovery process, and forest recovery time. This information can be utilized to effectively manage forests for timber production while maintaining biodiversity, forest productivity, and other features that reflect ecosystem health.

My thesis reports research results of two papers describing plethodontid salamander density and habitat characteristics within three distinct forest structural stages in the Missouri Ozarks. The first paper is a study of the habitat characteristics associated with plethodontid salamander densities. I use the physical structure of three distinct forest structural stages to discuss the impacts of forest management practices on salamander densities. In the second paper, I modeled relationships between salamander density and vegetation structure within each forest structural stage. I use Poisson regression to describe the habitat characteristics explaining salamander densities in each forest type.

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CHAPTER 2

PLETHODONTID SALAMANDER RESPONSE TO FOREST MANAGEMENT PRACTICES IN MISSOURI OZARK FORESTS

INTRODUCTION

Even-aged silviculture has been the primary management technique in Missouri since the mid 1970's (Gingrich 1967, Forest Land Management Guidelines, Missouri Department of Conservation (MDC) 1986). Even-aged silviculture has traditionally been used to regenerate shade intolerant tree species, such as oaks and hickories, that presently occupy the Ozark Highlands. This practice encompasses one or all of the following cutting methods: (1) clearcuts, (2) shelterwood cuts, (3) intermediate cuts, and (4) seed tree cuts (Smith 1986). All of these methods remove a significant portion of large, dominate canopy trees within a stand. Removal of canopy cover results in increased light penetration to the forest floor, reduction of leaf litter, reduction in soil moisture, and increased soil temperature (Gieger 1965). This type of abrupt alteration to vegetation structure greatly modifies the microclimate of the stand (Chen et al. 1997, Xu et al. 1997) and surrounding forest. Consequently, species composition (plants and animals) will change with changes in the microhabitat of the forest. The recovery time for many plants and animals will require decades until suitable microhabitats exist on the site.

Forest management practices modify forest structure and in turn affect salamander communities. This study focuses on the family of plethodontid salamanders and their response to alterations in forest structure through harvesting practices for three reasons: (1) plethodontid salamanders are abundant and widely distributed within the Ozark Highlands (Johnson 1992); (2) plethodontid salamanders lack lungs and exchange gases almost entirely through cutaneous respiration. For gas exchange to occur, respiration requires exposed, permeable skin (Spotila 1972, Feder 1983). This attribute causes salamanders to seek moist microhabitats making them sensitive to environmental disturbances that modify the prevailing temperature, humidity, and soil moisture regime; (3) plethodontid salamanders are important components in the energy flow of forest systems (Burton and Likens 1975). Because of their small size, salamanders exploit prey that is too small for birds and mammals, and efficiently convert biomass of prey into that which can be captured by larger animals (Pough 1983). Reducing the abundance of salamanders could affect the trophic structure of the system.

Plethodontid salamander biology makes them sensitive to alterations in structural and vegetation characteristics of a forest. Because plethodontid salamanders are completely terrestrial and lack an aquatic larval stage the forest must provide microhabitats for all stages of the life history of these species. Forest management practices that alter the canopy and modify temperature and moisture regimes of the forest floor will determine the microclimate and, therefore, microhabitats available for salamanders (Heatwole 1962, Spotila 1972).

I examine the impacts of past forest management practices on plethodontid salamander abundance in southeastern Missouri. Specifically, I examined plethodontid salamander abundance in old-growth forests with no past timber harvest, second growth forests that had not been manipulated in the past 40 years, and regenerating forests less than five years old. I test the null hypothesis that no differences in salamander abundance and habitat characteristics exist among the three forest structural stages. I measured microhabitat conditions within these distinctly different structural stages while also measuring the density of salamanders.

STUDY AREA

This study was conducted in oak-hickory forests of the Ozark Highland region (Nelson 1987) of Missouri, USA. Second growth and regeneration cut sites were located on Missouri Department of Conservation lands in Reynolds and Shannon counties. Old-growth sites were located on lands owned by the National Park Service in Carter County and Pioneer Forest in Shannon County (Figure 2.1). Pioneer Forest is the largest privately owned land base in Missouri, consisting of 160,000 contiguous acres.

Geologically, these counties are underlain mainly by Ordovician age dolomite (Missouri Geological Survey 1979). Areas of Cambrian age dolomite and Precambrian igneous rock are also present. Soils are dry to xeric chert or limestone, and well to excessively drained (Meinert et al. 1997, Sauer 1920). This region receives an average of 112 cm of precipitation annually and has a mean annual temperature of 13.5° C. The daily temperature during summer months (June, July, August) can reach a mean maximum of 32.5° C and a mean minimum of 4.8° C in winter (December, January, February).

FIELD METHODS

Data were collected from twenty-one 144-m^2 plots in 1995 and 21 additional plots in 1996 (Figure 2.2). Three distinct forest structural stages were used to determine response of plethodontid salamanders to alterations in vegetation structure. Structural stages consisted of newly regenerated stands less than five years old, second growth stands 70-80 years old, and mature old-growth stands greater than 120 years old. I located seven plots in each structural stage in 1995 and 1996. All plots were established mid-slope on north aspects ranging from 120° to 330°. Each plot was surrounded by a 50 m buffer of similar habitat to avoid forest edge effects. After a plot was established, down wood measurements were taken across the plot. Length and midpoint diameters were recorded for each piece of down wood at least 10 cm (4 inches) in diameter.

Measurements were used to estimate volume and percent cover of down wood on the forest floor. The extent of decomposition was ranked for each piece of down wood by using decay classes one through five as described by Maser et al. (1979). Decay class one consisted of newly fallen limbs and snags with little decay. Decay class five included nearly completely decomposed logs that were faded, oval shaped, soft, and powdery.

In April of each year, area / time-constrained searches for salamanders (Campbell and Christman 1982, Corn and Bury 1990, Heyer et al. 1994) were conducted on each established plot for up to six person hours. Salamanders were located by tearing open down wood, rolling logs, turning over rocks, and raking through the leaf litter. When a salamander was encountered it was identified to species and measured for snout-to-vent length. Type of cover object was also recorded. In 1996, rocks 7.6 cm (3 inches) in length or greater, that were turned over while searching for salamanders, were counted for each plot. The distances to neighboring salamanders and down wood were recorded. Captured individuals were placed in a bucket for the duration of the search and then released.

Soil and humus samples were collected from six points in each plot for pH and moisture analysis. Soil samples were collected down to 3 cm below the surface. Samples were placed in zip lock bags and kept in cold storage until analyzed. Levels of pH were determined by a one to one paste of air dried soil and deionized water (USDA, NRCS 1996) using a digital ionanalizer pH meter and combination electrode. To determine the percent moisture of soil and humus, all samples were weighed to determine soil/water weight, then air dried for five days and weighed again to determine soil weight. Soil and humus moisture was measured as grams of water/grams of dry soil or humus.

I returned to each plot in July to sample woody and herbaceous vegetation and ground cover. Trees ≥ 11.4-cm diameter at breast height (dbh) were sampled across each plot. Tree dbh and species were recorded. A 36-m^2 plot was established in the center of the 144-m^2 plot to measure dbh and identify species of trees between 3.8-cm and 11.4-cm dbh (Figure 2.2). Trees at least one-meter tall to < 3.8-cm dbh were measured and identified across a 9-m^2 plot established in the center of the 36-m^2 plot. Eight 1-m^2 quadrats systematically placed outside and three meters from the border of the 144-m^2 plot (Figure 2.2) were utilized to sample ground cover and herbaceous and woody vegetation less than one meter tall. Vegetation was grouped into categories including sedges, grasses, legumes, forbs, ferns, woody vegetation, and total vegetation. Woody vegetation was identified to species and the area of each 1-m^2 quadrat covered by each group was estimated to the nearest percent. I visually estimated percent ground cover of rock, down wood, leaf litter, bare ground, basal area, and moss/lichen in each 1-m^2 quadrat. Canopy cover was estimated to the nearest percent using canopy tubes (Robinson 1947, Lemmon 1956) at five points in each plot.

Data Analysis

I used analysis of variance (ANOVA) and Tukey's Honestly Significant Difference procedures to test for differences in salamander abundance and vegetation. The Tukey test is a multiple comparison procedure used to identify significant differences between structural stages (Zar 1984). I used a two-way ANOVA to test for treatment effects, year effects, and treatment by year interactions. Differences in mean salamander densities among forest structural stages were determined by using a single factor ANOVA. Vegetation and ground cover differences among forest structural stages were determined by single factor ANOVA and Tukey tests. Tests with a P-value < 0.05 were defined as significant. Percent data were transformed using the arcsine transformation before analysis. The SAS statistical package was used for analyses (SAS 1985).

The volume of each down log was computed as a cylinder with known length and midpoint diameter. Volumes were summarized for each plot and expanded to a per-hectare basis ($m^3 \cdot ha^{-1}$). Within each forest structural stage, volume was estimated by decay class and diameter class for comparison. Four diameter classes were compared: 10-20 cm, 21-30 cm, 31-40 cm, and > 40 cm.

Percent ground area covered by each log was computed as a product of length and midpoint diameter.

RESULTS

I captured three species and 348 individual plethodontid salamanders in 1995 and 1996. Southern redback salamanders (*Plethodon serratus*) comprised 84 % of individuals and slimy salamanders (*P. glutinosus*) comprised 16 %. One individual of longtail salamander (*Eurycea longicauda)* was captured on an old-growth site located at Big Spring Pines Natural Area. Redback salamander densities were 1205 salamanders / ha (±203.4 s.e.) on old-growth sites and 238 salamanders / ha (±81.6 s.e.) on second growth sites. No redback salamanders were located on regeneration cut sites. Densities of slimy salamanders were 213 salamanders / ha (±48.5 s.e.) in old-growth sites, 55 salamanders / ha on second growth sites (±36.5 s.e.), and 15 salamanders / ha on regeneration cut sites (±10.7 s.e.).

Tests of treatment effects (forest structural stage) indicated statistical differences in salamander density ($F=14.27$, $P<0.001$). There were no year effects or treatment by year interactions ($F=0.81$, $P=0.374$; $F=0.75$, $P=0.477$, respectively). The mean number of salamanders found per plot for old-growth, second growth, and regeneration cut sites was 20.5, 4.14, and 0.214, respectively.

Furthermore, the mean density of plethodontid salamanders in old-growth areas was significantly greater than in second growth or regeneration cut areas ($F=35.12$, $P<0.001$). I estimated the mean densities of old-growth, second growth, and clearcuts as 1422.7 salamanders / hectare (±202.4 s.e.), 287.5 salamanders / hectare (±79.8 s.e.), and 14.87 salamanders / hectare (±10.74 s.e.), respectively (Figure 2.3).

Vegetation and Cover Characteristics

Plethodontid salamanders utilized a variety of cover objects including down wood, rocks, and litter. Seventy-five percent of individuals captured were located under rocks and 5.7 % were located under or in down logs. The remaining 19.3 % were found while raking through the leaf litter, 28 % of which were located 20.3 cm or less from a down log.

Regeneration cut and old-growth sites had the highest volume of down wood per hectare (76 m^3 ha^{-1} and 70 m^3 ha^{-1}, respectively). However, most down wood volume on regeneration cut sites consisted of decay class two and three logs ($F=22.43$, $P<0.001$). Old-growth sites had more down wood volume in decay classes four than other decay classes combined ($F=9.01$, $P=0.004$). The majority of down wood volume on second growth sites was in decay classes three and four ($F=13.97$, $P<0.001$) (Figure 2.4). Regeneration cut sites had significantly more down wood volume in decay classes one and two than either second growth sites or old-growth sites (Tukey test: decay class one, P=0.004; decay class two, P<0.001) (Table 2.1). Old-growth sites had more down wood volume in decay classes four and five than either second growth or regeneration cut sites. Although these differences were biologically apparent they were not statistically significant (P=0.29) (Table 2.1) (Figure 2.4).

Most of the down wood on the forest floor for all sites was between 0.02-m and 3-m long and between 11-cm and 15-cm in diameter. Logs on second growth sites were longest (mean=3.7 m). Largest diameter logs were found on old-growth sites (mean=19 cm). Across all sites, logs 8 to 9-m long with diameters between 15 to 20 cm and 40 to 45 cm comprised the majority of down wood volume. Volume of down wood across forest structural stages varied by diameter class. Most down wood volume on regeneration cut sites had a diameter ranging from 10 cm to 20 cm than all other diameters combined (F=12.77, P=<0.001). Most down wood volume on second growth sites had a diameter ranging from 31 cm to 40 cm (F=57.51, P<0.001). Logs with a diameter of 31 cm and greater comprised the greatest volume on old-growth sites (F=54.26, P<0.001) (Figure 2.5). The percentage of ground area covered by down wood was not significantly different (F=3.07, P=0.058) between old-growth (4.3 %), second growth (3.1 %), and regeneration cut sites (2.7 %).

The mean density of trees 11.4-cm dbh or greater was significantly different among forest structural stages (P<0.001) (Table 2.1). Old-growth sites averaged 267.9 trees/hectare, second growth averaged 396.8 trees/hectare, and 19.84 trees/hectare were estimated for regeneration cut sites. Oak trees greater than 11.4-cm dbh dominated the canopy for old-growth sites and second growth sites. Few white oak and short-leaf pine were located in regeneration cut sites, however, most trees found on these sites were snags. The percent of the ground surface covered by the canopy differed significantly between regeneration cut sites (20.6%) and both old-growth (79.2%) and second growth (77.4%) sites (Tukey test: P<0.001) (Table 2.1).

The density of trees in size classes 3.8-cm to 11.4-cm dbh and 1-m tall to 3.8-cm dbh observed for old-growth and second growth sites differed significantly from that observed for regeneration cut sites (Tukey test: size class 3.8 to 11.4 cm P<0.001; size class 1m tall to 3.8 cm P<0.001) (Table 2.1). In size class 3.8-cm to 11.4-cm dbh, old-growth sites had a mean density of 272.8 trees/hectare, second growth sites had 233.1 trees/hectare, and regeneration cut sites had 29.8 trees/hectare. Flowering dogwood (*Cornus florida*) was the most abundant tree species within this size class for all treatments. In size class 1 m tall to 3.8 cm, I estimated a mean density of 163.7 trees/hectare in old-growth sites, 238.1 trees/hectare in second growth sites, and regeneration cut sites estimated a mean density of 1026.8 trees/hectare. Flowering dogwood was the most abundant tree species within this size class for old-growth and second growth sites and sassafras was the most abundant tree species for regeneration cut sites.

Herbaceous plant cover less than one meter tall was significantly different among treatments (P=0.004) (Table 2.1). Generally, regeneration cut sites had significantly greater percent cover of grass (Tukey test: P=0.008) and forbs (Tukey test: P=0.031) than old-growth and significantly greater percent cover of sedges (Tukey test: P=0.004) and ferns (Tukey test: P=0.014) than either second growth or old-growth sites (Table 2.1). Second growth sites had significantly greater percent cover of legumes than regeneration cut and old-growth sites (Tukey test: P<0.001) (Table 2.1). There were no differences in the percent cover of moss between forest structural stages (Tukey test: P=0.24) (Table 2.1).

There was no difference in the percentage of exposed soil between old-growth (0.39%) and regeneration cut sites (0.40%), but second growth sites differed from old-growth sites and regeneration cut sites by having a low percentage of exposed soil (0.12%) (Tukey test: P=0.039) (Table 2.1). More of the soil surface was covered by litter in second growth sites (88.1%) than either old-growth sites (71.8%) or regeneration cut sites (74.9%) (Tukey test: P<0.001) (Table 2.1). Rocks covered 11.8 percent of the ground surface on old-growth sites. This was significantly greater than the 3.8 percent and 4.3 percent of rock cover on second growth and regeneration cut sites, respectively (Tukey test: P<0.001) (Table 2.1).

The number of rocks 3 inches or greater in length turned over on each plot in 1996 averaged 900 rocks / plot on old-growth sites, 355 rocks / plot on second growth sites, and 244 rocks / plot on regeneration cut sites. In 1996, 109 salamanders were located under rocks in old-growth sites and 17 were located under rocks in second growth sites. No salamanders were located under rocks in regeneration cut sites. I estimate 57 rocks turned / salamander on old-growth sites and 146 rocks turned / salamander on second growth sites.

Soil Characteristics

There were no significant differences in soil (P=0.81) or humus (P=0.99) pH among sites (Table 2.1). Analysis of the soil for moisture content indicated no significant differences among sites (P=0.41) (Table 2.1) in 1996. Significant differences were realized for the moisture content of humus between second growth and regeneration cut sites (Tukey test: F=8.31, P=0.003) (Table 2.1). The moisture content of humus on old-growth sites was not significantly different from that on second growth or regeneration cut sites (Table 2.1).

DISCUSSION

Previous studies have shown that factors such as temperature, moisture, and available cover affect the distribution of plethodontid salamanders (Heatwole 1962, Spotila 1972, Feder and Pough 1975, Jaeger 1980, Feder 1983). I found a significant difference in the species composition of both vegetation and salamanders and in the structural complexity of the forest immediately following harvest and post-harvest years.

Regeneration cutting reduces microhabitats for salamanders (Bury 1983, Ash 1988, Raphael 1988, Welsch 1990, Ash 1996) through increased temperatures and decreased moisture availability by eliminating the forest canopy. Consequently, mature forests support more salamanders than young newly regenerated forests. I found that newly regenerated areas support few if any salamanders. However, I do not believe all regeneration cut areas are devoid of salamanders. Daytime surface counts exclude individuals in underground retreats making it possible that the numbers observed do not reflect actual population sizes in regeneration cut areas. Decreases in soil moisture and increases in temperature following timber harvest forces salamanders underground during the day. Therefore, few salamanders would be expected to be caught during daytime searches. However, Ash (1988) conducted night searches for *Plethodon jordani* in the Blue Ridge Mountains, North Carolina and by the second summer after timber harvest was not able to find any salamanders. Even if surface activity did not accurately measure abundance, it remains evident that recently regenerated areas do not provide suitable habitat for plethodontid salamanders due to their life history. Spotila (1972) found that salamander distributions may be limited by shortened activity periods at higher temperatures. He reports that salamanders could not survive in areas where energy requirements exceed energy intake. Spotila (1972) and Jaeger (1980) point out that salamanders will seek moist microhabitats to avoid desiccation.

Salamanders were more abundant in old-growth forests than forests with a more recent history of logging. I found five times more salamanders in old-growth than in second growth and 20 times more salamanders in second growth than in regeneration cuts during the spring of 1995 and 1996. My findings are consistent with those from the eastern U.S. (Blymer and McGinnes 1977, Bennett et al. 1980, Enge and Marion 1986, Pough et al. 1987, Ash 1988, Petranka et al. 1994) and Pacific Northwest (Bury 1983, Raphael 1988, Welsh and Lind 1991, Corn and Bury 1991, Dupuis et al. 1995) indicating significant reductions in salamander populations after timber harvesting. Even though few salamanders were found in regeneration cut sites that where five years old or less, repopulation of salamanders can occur on these sites when conditions are suitable. Evidence of this is shown by the significantly higher densities of salamanders on second growth sites that had undergone regeneration cutting 70 to 80 years ago. However, the rate of salamanders returning to harvested areas is slow, perhaps because of long generation time, slow dispersal rates, and high site fidelity (Hairston 1983, Hairston et al. 1992). The recovery rate of the vegetation on a site after harvesting also explains the slow repopulation of salamanders. After a site has been clearcut, it is subject to greater daily fluctuations in temperature and humidity levels, and higher wind speeds than a closed canopy forest. As the overstory canopy forms, climatic conditions become more stable, surface soil moisture increases, and soil temperature decreases (Gieger 1965).

The recovery rate of second growth forests that had undergone regeneration cutting 70 to 100 years ago could be very different from the recovery rate of forests that have been regeneration cut in more recent years. Logging practices of the past consisted entirely of unmanaged even-aged harvesting that was very wide spread across the landscape (Record 1910). These activities along with burning and open range grazing had detrimental impacts to the soil. Approximately 30 years ago, regulated timber management began to play a part in logging activities of the Missouri Ozarks. During the past 10 years strict guidelines have been manifested and followed that control logging activities conducted on public lands (Forest Land Management Guidelines, MDC 1986). Currently, few newly regeneration cut stands are larger than 11 acres in size.

Vegetation and cover characteristics

Salamanders will respond behaviorally to changes in their environment resulting in the occupancy of a certain microhabitat (Heatwole 1960, 1962). Cover objects are an important microhabitat to the survival of individual plethodontid salamanders. When the leaf litter layer becomes dry (degree of dryness is relative to the tolerance limits of the organism) plethodontids tend to remain beneath cover objects and will retreat underground when the leaf litter and soil surface become very dry (Taub 1961, Heatwole 1962, Fraser 1976, Jaeger 1980). An increase in rainfall will shift microhabitat utilization from beneath cover objects and/or sub-surface retreats to the leaf litter layer increasing the surface population and creating conditions suitable for reproductive activity and foraging.

Rocks and down wood were most often used as cover objects for the salamanders observed in this study. The percent of ground surface covered by rock was greatest on old-growth sites when compared to second growth and regeneration cut sites. Perhaps due to the high percent cover of leaf litter on second growth sites, an inaccurate measure of rock was recorded on these sites. However, results of the number of rocks flipped for each site in 1996 concurs that old-growth sites had a higher rock content.

Down wood provides critical microhabitat for terrestrial salamanders. Because down wood has a high water-holding capacity, it offers salamanders an escape from desiccation and a moist location for egg deposition. Log size and state of decay likely influences its use by salamanders. Larger logs provide more cover and a longer duration of use (Cline et al. 1980, Maser and Trappe 1984), and logs toward middle to late stages of decay provide hiding spaces and an abundance of many prey species (Harmon et al. 1986). Available cover in old-growth sites, second growth sites, and regeneration cut sites was ample. Volume of down wood was similar for old-growth and regeneration cut sites. However, most down wood in regeneration cut sites was ranked in decay class two or three, which is unusable to salamanders. Old-growth sites had most logs ranked into decay classes four and five, which are stages of decay salamanders can utilize. Volume of down wood was lowest in second growth sites. Jenkins and Parker (1997) suggest that 80 to 100 year old stands experience little overstory mortality resulting in little input of down trees on the forest floor. Low mortality of overstory trees explains the low volume of down wood in second growth sites.

Second growth sites (70 to 80 years old) are classified within the understory reinitiation stage as described by Oliver (1981). Characteristics of these sites include a dense overstory (trees >11.25 cm dbh) with a high percentage of canopy closure, and a dense understory (trees 3.5 cm to 11.25 cm dbh) that remains small for many years. These sites experience little mortality to dominate overstory trees, and therefore high mortality occurs to suppressed overstory trees and smaller diameter trees in the understory. Small diameter dead trees comprise the majority of down wood on second growth sites explaining lower observed volume. Forest floor herbaceous plants and woody shrubs appear and survive during this stage of forest succession, but growth is slow because of the small amount of direct sunlight able to penetrate the dense overstory canopy.

Old-growth sites (greater than 120 years old) had a significantly lower number of overstory trees per hectare than second growth sites. This follows Oliver's (1981) definition of the old-growth stage, which he describes as having large, old trees; relatively open canopies; trees of varying heights and diameters; diverse understories; and large down logs. Overstory tree mortality is high, which creates openings in the canopy and stimulates rapid growth of understory trees. Overstory mortality produces large, dead trees on the forest floor explaining the high volume of down wood observed on these sites.

Regeneration cut sites (less than five years old) had a significantly higher number of trees 1m tall to 3.5 cm dbh and had a significantly lower number of trees 3.5 cm to 11.25 cm dbh than old-growth and second growth sites. These sites develop quickly with a wide range of herbaceous and woody plant species competing for available growth space. The volume of down wood on these sites was high, however, it was mostly comprised of small diameter, non-merchantable timber and tree tops left on the site.

Each structural stage examined in this study has characteristics and structural features unique to its stage of development. Plethodontid salamanders require those features best suited to support cutaneous and buccal respiration and gelatinous eggs laid on land. Combinations of characteristics and structural features defining older mature forests seem to support the greatest amount of plethodontid surface activity. Plethodontids are non-migratory, highly territorial, and lack an aquatic larval stage in their life cycle. Therefore, not only are these areas inhabited by adult plethodontids, but also harbor egg clutches and juveniles. Disturbance that results in deterioration or loss of habitat may have profound consequences on plethodontid communities in Ozark forests.

CONSERVATION IMPLICATIONS

Plethodontid salamanders are important ecological components of forest floor communities. They function as a primary predator upon invertebrates and serve as prey for larger vertebrates (Pough et al. 1987, Corn & Bury 1989). They are the most abundant vertebrate animals in many forest ecosystems, and their annual production of biomass exceeds that of birds or small mammals (Burton & Likens 1975). Because of their sensitivity to alterations in the environment and high abundance in forested systems, plethodontid salamanders can be utilized to provide information on the condition of the ecosystem. Plethodontids can serve as indicators of the impacts from tree harvest on the ecosystem, as well as the recovery process and recovery time associated with these practices. Moreover, habitat and landscape level management that considers plethodontid salamander abundance is an important component in monitoring ecosystem health.

Even-aged management creates a shifting mosaic of forest age-classes across the landscape. Maximum forest age is determined by the rotation age. Rotation ages have been defined by the optimum size or age that trees should be grown to maximize economic returns (Smith 1986). Length of rotation for tree species in the Central Hardwood region typically ranges from 75 to 120 years, which is often shorter than the average frequency of natural disturbances. As a result, even-aged management may truncate succession and prevent development of structural characteristics associated with older, mature forests (Bunnell & Kremsater 1990) including development of large trees, accumulation of down wood, and development of high density foliage layering. Management activities based on commercial rotations could result in lower plethodontid densities due to lack of suitable habitat. Increasing the rotation length in managed forests would provide older, mature forests that play a critical role in maintaining the relative high densities of plethodontid salamanders.

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Figure 2.1. Location of study areas where salamander abundance was measured in Reynolds, Shannon, and Carter counties in southeast Missouri Ozarks, 1995-1996. Symbols represent forest structural stages.

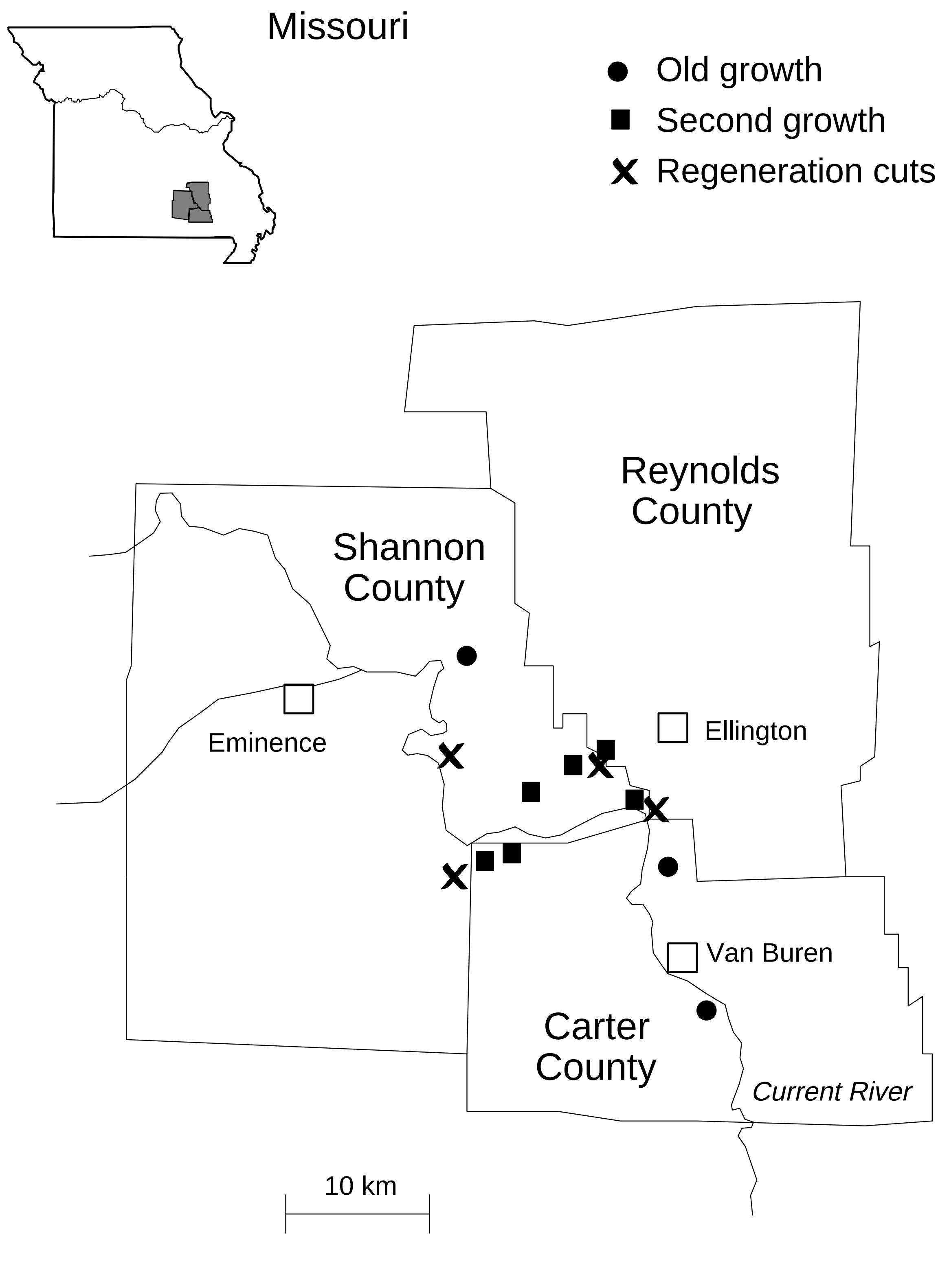

Missouri
Old growth
Second growth
Regeneration cuts
Reynolds County
Shannon County
Eminence
Ellington
Van Buren
Carter County
Current River
10 km

Figure 2.2. Diagram of the vegetation plot layout used to sample woody and herbaceous vegetation and ground cover at salamander sample plots on old-growth, second growth, and regeneration cut sites.

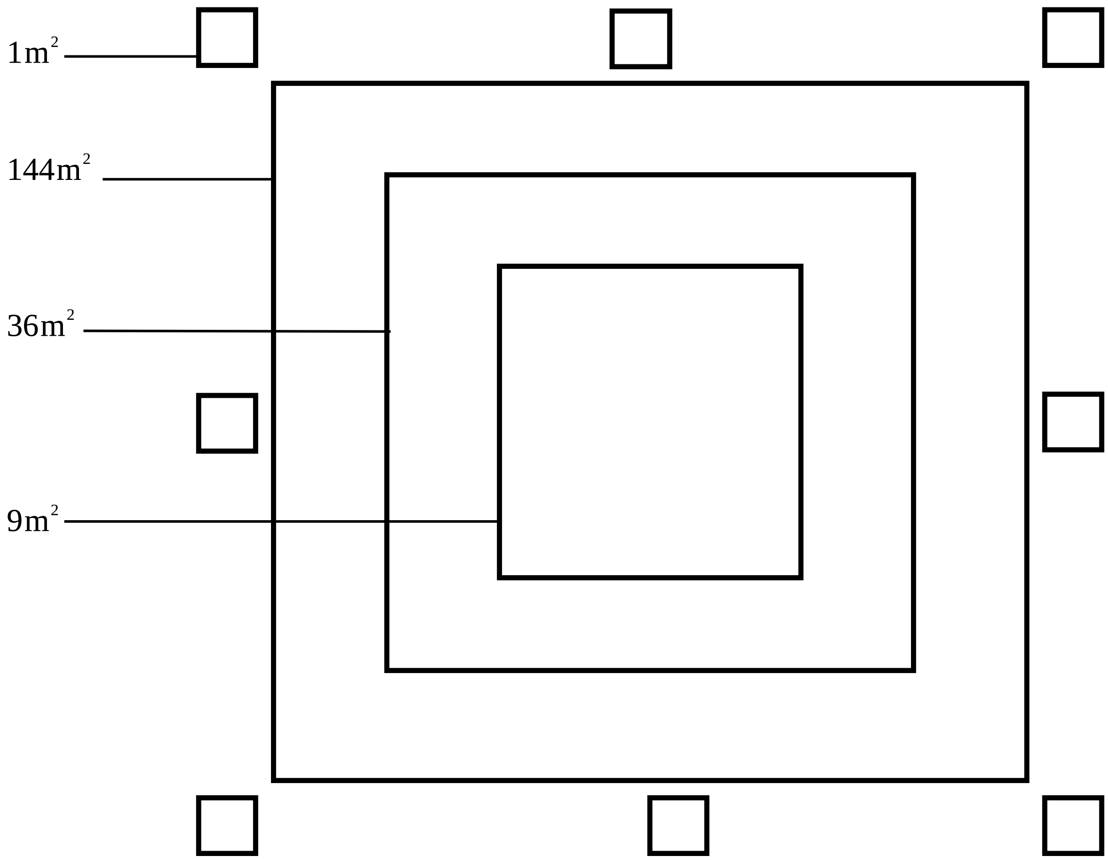
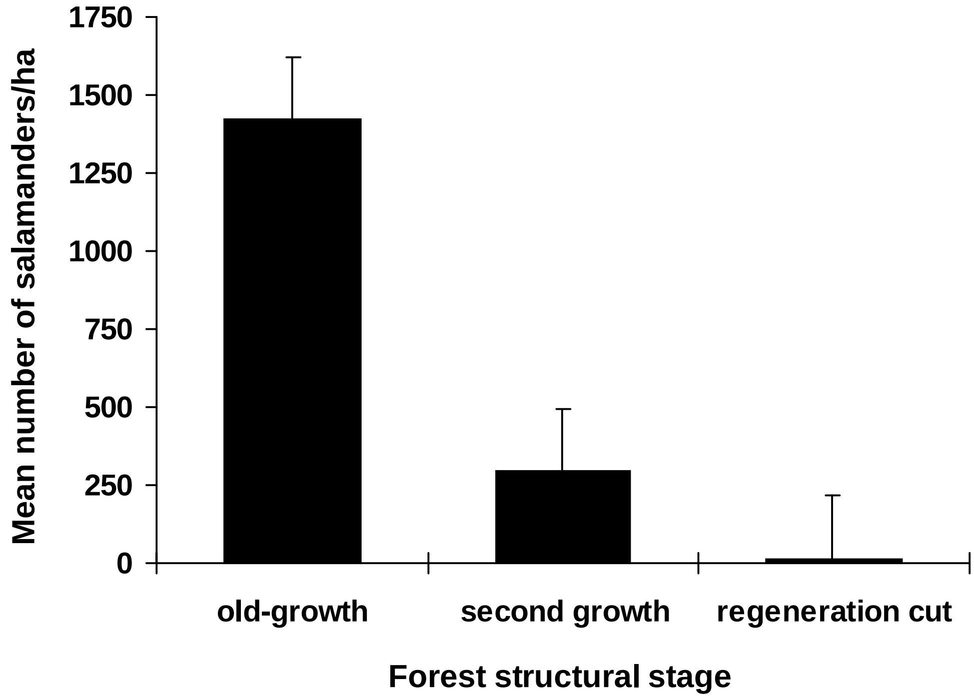

1m2
144m2
36m2
9m2

Figure 2.3. Average salamander density (salamanders/ha with standard error bar) by forest structural stage in the Missouri Ozarks, 1995-1996. Old-growth = >120 years, second growth = 70-80 years post harvest, regeneration cut = ≤ 5 years post harvest.



Mean number of salamanders/ha
1750
1500
1250
1000
750
500
250
0
old-growth
second growth
regeneration cut
Forest structural stage

Figure 2.4. Mean down wood volume of old-growth, second growth, and regeneration cut sites by decay class in the Missouri Ozarks, 1995-1996. Decay class 1 is the least decayed and decay class 5 is the most decayed. OG = old-growth, SG = second growth, RC = regeneration cut.

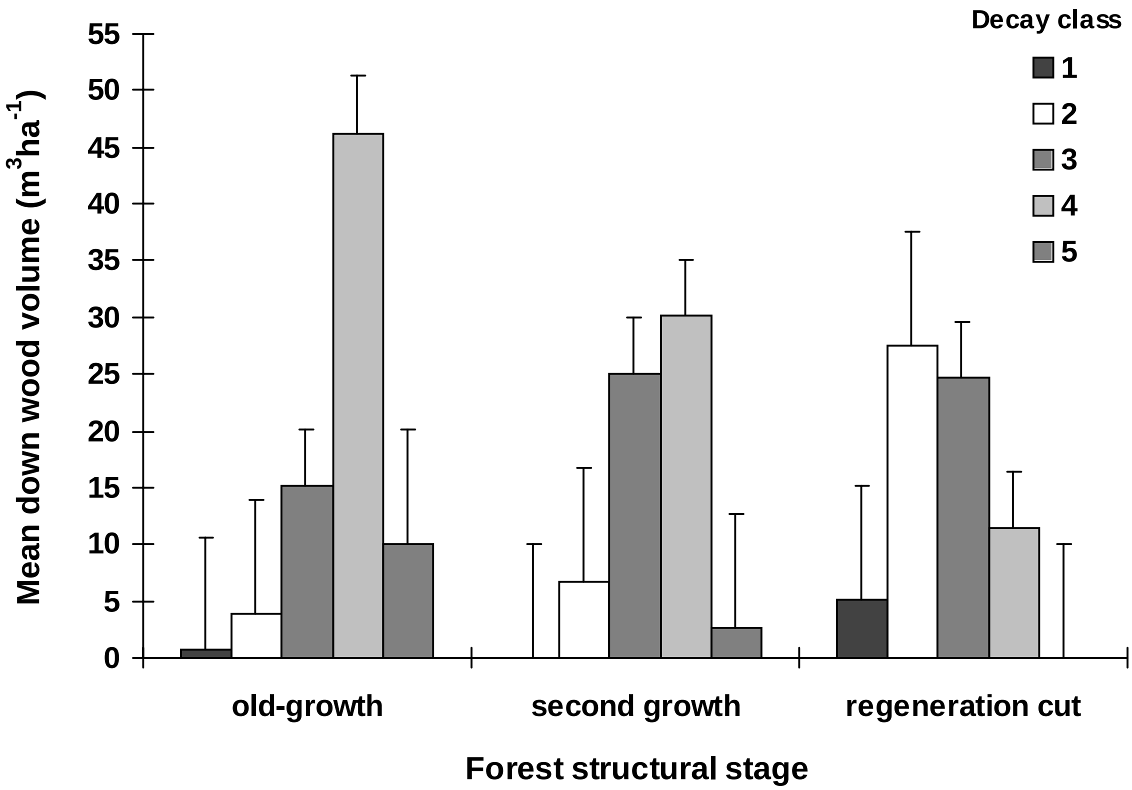

Decay class
1
2
3
4
5
Mean down wood volume (m^3ha^{-1})
0
5
10
15
20
25
30
35
40
45
50
55
old-growth
second growth
regeneration cut
Forest structural stage

Figure 2.5. Mean down wood volume of old-growth, second growth, and regeneration cut sites by diameter class in the Missouri Ozarks, 1995-1996.

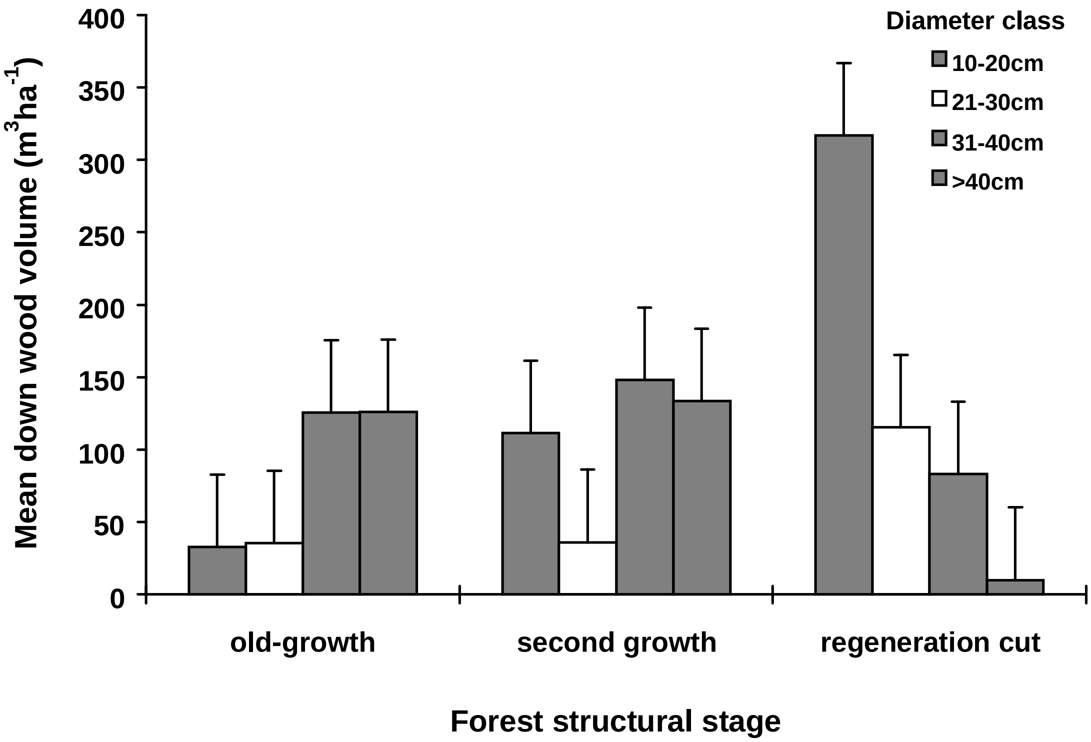

Mean down wood volume (m3ha-1)
400
350
300
250
200
150
100
50
0
Diameter class
10-20cm
21-30cm
31-40cm
>40cm
old-growth
second growth
regeneration cut
Forest structural stage

Table 2.1. Mean vegetation measurements on old-growth, second growth, and regeneration cut sites in the Missouri Ozarks, 1995-1996.

Variable	Old-growth X	Old-growth SE	Second growth X	Second growth SE	Regeneration cut X	Regeneration cut SE	F-value[1]	P-value
Down wood volume (m^3/ha)	76.15	23.33	64.59	16.92	68.79	9.34	0.11	0.895
DDW[2] vol. decay class 1	0.66a	0.51	0a	0	5.19b	1.88	6.32	0.004
DDW vol. decay class 2	3.95a	3.51	6.73a	4.47	27.49b	5.09	8.52	<0.001
DDW vol. decay class 3	15.11	8.22	25.04	10.52	24.63	7.22	0.41	0.666
DDW vol. decay class 4	46.21	23.39	30.09	11.51	11.43	5.56	1.28	0.290
DDW vol. decay class 5	10.05	7.82	2.70	1.44	0	0	1.28	0.290
Down wood cover (%)	3.91	0.87	4.51	0.91	6.65	0.69	3.03	0.059
No. trees >11.4cm dbh/ha	267.86a	32.44	391.86b	49.16	19.84c	13.48	29.48	<0.001
No. trees 3.8-11.4cm dbh/ha	272.65a	27.67	232.99a	28.74	29.73b	14.02	28.49	<0.001
No. trees 1m to 3.8cm dbh/ha	163.68a	40.93	238.12b	58.56	972.22b	117.16	31.82	<0.001
Woody cover <1m tall (%)	6.20a	1.04	10.85a	0.94	34.32b	2.81	68.91	<0.001
Herb cover (%)	8.93a	1.95	15.99ab	1.94	20.56b	2.92	6.41	0.004
Sedge cover (%)	0.30a	0.09	0.10a	0.03	2.39b	0.86	6.43	0.004
Grass cover (%)	0.83ab	0.29	0.10a	0.04	2.39b	0.82	5.45	0.008
Forb cover (%)	1.81ab	0.63	1.62a	0.28	3.95b	0.93	3.78	0.032
Fern cover (%)	0.73a	0.26	0.56a	0.31	5.12b	1.99	4.85	0.013
Legume cover (%)	5.21a	1.32	13.57b	1.89	6.67a	1.13	9.06	<0.001
Moss cover (%)	3.99	0.54	2.67	0.67	2.88	0.81	1.07	0.353
Rock cover (%)	11.84a	1.61	3.81b	1.40	4.31b	0.86	11.48	<0.001
Bare ground cover (%)	0.39	0.12	0.12	0.06	0.40	0.07	3.25	0.049
Litter cover (%)	78.06a	2.24	88.14b	1.66	74.20a	2.34	11.75	<0.001
Canopy cover (%)	79.24a	2.32	77.41a	2.13	20.59b	6.83	58.97	<0.001
Soil pH	5.47	0.16	5.26	0.16	5.31	0.14	0.47	0.629
Humus pH	5.97	0.13	5.92	0.17	5.95	0.14	0.03	0.975
Soil moisture	31.16	1.80	33.74	5.11	27.46	1.61	0.93	0.411
Humus moisture	97.69ab	10.47	124.25a	12.54	63.52b	8.23	8.31	0.003

Means with the same letter within rows were not significantly different (Tukey multiple comparison, P>0.05).

[1]N=42.

[2]DDW=down and dead wood.

CHAPTER 3

PLETHODONTID SALAMANDER AND VEGETATION STRUCTURE RELATIONSHIPS IN MISSOURI OZARK FORESTS

INTRODUCTION

Plethodontids are a non-migratory group of salamanders that are completely terrestrial and lack an aquatic larval stage in their life cycle. These species lack lungs and exchange gases primarily through cutaneous respiration. For gas exchange to occur, respiration requires exposed, permeable skin (Spotila 1972, Feder 1983). This attribute causes salamanders to seek moist microhabitats making them sensitive to environmental disturbances that modify the prevailing temperature, humidity, and soil moisture regime. Microhabitat availability for terrestrial salamanders is linked primarily to vegetation structure. The occurrence, abundance, or absolute density of many plethodontids are correlated with measures of vegetation structure.

Forest regeneration practices manipulate vegetation structure. Even-aged silviculture is used to regenerate central hardwood forests. Tree regeneration results from pre-existing advanced reproduction (seedlings and seedling sprouts) and stump sprouts. Alteration of habitats occurs mostly during the harvest operation because advanced reproduction is present before cutting begins. Harvesting changes the amount of standing timber, changes the timber size class distribution, opens the canopy, and increases the amount of light penetration to the forest floor. Tree reproduction and other understory species quickly respond to these alterations. Knowledge of how plethodontid salamanders respond to changing habitat characteristics in managed forests will help land managers make decisions for integration of wildlife with forest management.

Many studies have examined terrestrial salamander habitat relations using area/time constrained searches (Burton and Likens 1975, Ash 1988, Bury 1983, Petranka 1994, Dupuis et al. 1995, Ash 1996, Meier and Bratton In press, Chapter 2 this thesis). Constrained searches can be used to determine species present in an area, relative abundance, and density (Heyer et al. 1994) by determining the number of individuals on a plot of a specific size. Various analysis techniques have been used to explain salamander densities by describing habitat characteristics of the site. However, analysis of salamander counts is effective when based on the log-linear model. In this model, two components of the classical least-squares model are replaced by having multiplicative systematic effects and a Poisson error distribution (McCullagh and Nelder 1983). This modeling technique follows the basic Poisson distribution for data that are in the form of discrete values. The application of the log-linear Poisson model is the most effective way to use habitat characteristics for describing salamander distribution and abundance when data are derived from counts (McCullagh and Nelder 1983).

In chapter 2, I examined the effects of forest management practices on terrestrial salamanders in Missouri and showed that salamander density is reduced post-harvest. I found that the mean density of plethodontid salamanders in old-growth areas was significantly higher than in second growth or regeneration cut forests. In chapter 3, I focus on modeling relationships between salamander density and vegetation structure in managed Missouri Ozark forests. Study sites were selected in three distinct forest structural stages including old-growth forests >120 years old, second growth forests 70-80 years old, and regenerating forests <5 years old. Our objective was to describe the relationships between the density of salamanders and vegetation structure within each forest type using Poisson regression.

STUDY AREA

This study was conducted in oak-hickory forests of the Ozark Highland region (Nelson 1987) of Missouri, USA. Second growth and regeneration cut sites were located on Missouri Department of Conservation lands in Reynolds and Shannon counties. Old-growth sites were located on lands owned by the National Park Service in Carter County and Pioneer Forest in Shannon County

(Figure 3.1). Pioneer Forest is the largest privately owned land base in Missouri, consisting of 160,000 contiguous acres.

Geologically, these counties are underlain mainly by Ordovician age dolomite (Missouri Geological Survey 1979). Areas of Cambrian age dolomite and Precambrian igneous rock are also present. Soils are dry to xeric chert or limestone, and well to excessively drained (Meinert et al. 1997, Sauer 1920). This region receives an average of 112 cm of precipitation annually and has a mean annual temperature of 13.5° C. The daily temperature during summer months (June, July, August) can reach a mean maximum of 32.5° C and a mean minimum of 4.8° C in winter (December, January, February).

FIELD METHODS

Data were collected from twenty-one square 144m^2 plots in 1995 and 21 additional plots in 1996 (Figure 3.2). Three distinct forest structural stages were sampled to determine response of plethodontid salamanders to alterations in vegetation structure. Structural stages consisted of newly regenerated stands less than five years old, second growth stands 70-80 years old, and mature old-growth stands greater than 120 years old. I located seven plots in each structural stage in 1995 and 1996. All plots were established mid-slope on north aspects ranging from 120° to 330°. To avoid forest edge effects, each plot was surrounded by at least 50 m of forest buffer on all sides. After a plot was established, down wood measurements were taken across the plot. Length and midpoint diameters were recorded for each piece of down wood at least 10-cm (4 inches) in diameter. Volume and percent cover were computed by assuming pieces of down wood were cylindrical. The extent of decomposition was ranked for each piece of down wood using five decay classes as described by Maser et al. (1979). Decay class one consisted of newly fallen limbs and trees with little decay. Decay class five included nearly completely decomposed logs that were faded, oval shaped, soft , and powdery.

In April of each year, area/time-constrained searches for salamanders (Campbell and Christman 1982, Corn and Bury 1990, Heyer et al. 1994) were conducted on each established plot for up to six person hours. Salamanders were located by tearing open down wood, rolling logs, turning over rocks, and raking through the leaf litter. When a salamander was encountered it was identified to species and measured for snout-to-vent length. Type of cover object was also recorded. In 1996, rocks 7.6 cm (3 inches) in length or greater, that were turned over while searching for salamanders, were counted for each plot. The distances to neighboring salamanders and down wood were recorded. Captured individuals were placed in a bucket for the duration of the search and then released.

Soil and humus samples were collected from six points in each plot for pH and moisture analysis. Soil samples were collected down to 3 cm below the surface. Samples were placed in zip lock bags and kept in cold storage until analyzed. Levels of pH were determined by a one to one paste of air dried soil and deionized water (USDA, NRCS 1996) using a digital ionanalizer pH meter and combination electrode. To determine the percent moisture of soil and humus, all samples were weighed to determine soil/water weight, then air dried for five days and weighed again to determine soil and humus weight. Soil and humus moisture was measured as grams of water/grams of dry soil or humus.

I returned to each plot in July to sample woody and herbaceous vegetation and ground cover. Trees ≥ 11.4-cm diameter at breast height (dbh) were sampled across each plot. Tree dbh and species were recorded. A square 36-m^2 plot was established in the center of the 144-m^2 plot to measure dbh and identify species of trees between 3.8-cm and 11.4-cm dbh (Figure 3.2). Trees at least one-meter tall and < 3.8-cm dbh were measured and identified within a square 9-m^2 plot nested in the center of the 36-m^2 plot. Eight 1-m^2 quadrats systematically placed outside and three meters from the border of the 144-m^2 plot (Figure 3.2) were used to sample ground cover and herbaceous and woody vegetation less than one meter tall. Vegetation was grouped into categories including sedges, grasses, legumes, forbs, ferns, woody vegetation, and total vegetation. Woody vegetation was identified to species and the area of each 1-m^2 quadrat covered by each group was estimated to the nearest percent. Percent ground cover of rock, down wood, leaf litter, bare ground, basal area, and moss/lichen was visually estimated in each 1-m^2 quadrat. Total canopy cover was estimated to the nearest percent using canopy tubes (Robinson 1947, Lemmon 1956) at five points in each plot.

DATA ANALYSIS

I used 18 habitat variables derived from field measurements to construct models of expected salamander density. Those variables described the vegetation and physical structure of the forest and represent habitat characteristics believed to be important for terrestrial salamanders. I examined correlations among salamander densities and habitat characteristics. Poisson regression was used to analyze the relationships among salamanders and habitat variables, and to build predictive models of salamander abundance using the sampled vegetation characteristics. Poisson regression is a log-linear modeling process applied to count data that is assumed to follow a Poisson distribution (McCullagh and Nelder 1983). Poisson distribution is a natural model for count data, which are in the form of discrete values (e.g. numbers of salamanders). Poisson regression often works better than linear regression with data transformations when the number of counts is small (McCullagh and Nelder 1983).

Initially, all vegetation and ground cover variables were regressed against salamander abundance to determine the fit of the full model. Then Akaike's information criterion (AIC) selection procedure was used to develop models with smaller sets of independent variables. AIC is the likelihood version of the Cp statistic, and like Cp, changes in AIC due to subsetting a model by a given term reflects both the change in deviance caused by the step as well as the dimension of the term being changed (Chambers and Hastie 1992). The best model is given by the lowest AIC value (Chambers and Hastie 1992). All variables were considered potentially important in explaining salamander abundance and no limits were set for the number of variables to be retained in the final model. Variables retained in the final model produced by the AIC procedure were significant at $P<0.05$ and were biologically interpretable. Habitat variables retained in the model were examined for correlations, and were determined as significant at $P<0.05$. Deviance residuals were examined for use in detecting observations with large influences in the fitting process. No large influences were located. Residual deviance was used as a measure of goodness-of-fit. Residual deviance is similar to the residual sum of squares, and is useful when comparing alternative models (McCullagh and Nelder 1983).

The validity of this model will be tested over time as conditions are realized on the Missouri Ozark Forest Ecosystem Project (MOFEP). MOFEP is a long-term, landscape-scale study of the impacts of forest management practices conducted in Missouri on multiple ecosystem attributes (Brookshire and Hauser 1993, Brookshire et al. 1997).

RESULTS AND DISCUSSION

Species-Habitat Associations

Redback Salamander.-Redback salamanders (*Plethodon serratus*) comprised 83 % of the total number of salamanders captured. Redback salamander densities were 1205 salamanders / ha on old-growth sites and 238 salamanders / ha on second growth sites. No redback salamanders were located on regeneration cut sites. Redback salamander density was positively correlated with percent cover rock (R=0.36; P=0.017), percent canopy cover (R=0.45; P=0.002), and percent slope (R=0.39; P=0.012) and negatively correlated with trees > 1-m tall to 1.5-cm dbh (R=-0.38; P=0.012), percent cover down wood estimated within 1-m^2 quadrats (R=-034; P=0.027), and percent cover woody vegetation < 1 m tall (R=-0.53; P=0.0003).

Slimy Salamander.-Slimy salamanders (*P. glutinosus*) constituted 16 % of the total number of salamanders captured in 1995 and 1996. Densities of slimy salamanders were 213 salamanders / ha in old-growth sites, 55 salamanders / ha on second growth sites, and 15 salamanders / ha on regeneration cut sites. The density of slimy salamanders per ha was positively correlated with density of trees 3.8 cm to 11.4 cm dbh (R=0.43; P=0.004), percent cover of rock (R=0.52; P=0.0004), percent canopy cover (R=0.31; P=0.048), and percent slope (R=0.45; P=0.003), and negatively correlated with percent cover woody vegetation < 1 m tall (R=-0.40; P=0.009).

Predictive Model

Several habitat variables were significantly correlated (Pearson's R absolute values > 0.50) but no habitat variables were highly correlated with salamander density (Table 3.1). Salamander density was moderately correlated with percent cover of woody vegetation <1m tall (R=-0.56; P<0.001), percent canopy cover (R=0.48; P=0.001), and percent cover of rock (R=0.46; P=0.003).

In the Poisson model, salamander abundance was best explained by forest structural stage, percent cover of down wood, basal area of overstory trees ≥ 11.4 cm dbh, density of trees 3.8 cm to 11.4 cm dbh, percent cover of leaf litter, percent cover of herbaceous vegetation, and percent canopy cover. This model had an AIC of 106.4 and residual deviance=88.4 (df=33) (full model null deviance=593.3; df=41). Percent canopy cover was highly correlated with several habitat variables in the final model, including regeneration cuts (R=-0.87; P<0.001), basal area of overstory trees ≥ 11.4 cm dbh (R=0.58; P<0.001), density of trees 3.8 cm to 11.4 cm dbh (R=0.72; P<0.001), and percent cover of leaf litter

(R=-0.58; P<0.001). Consequently, canopy cover was dropped from the model as its effects were largely explained by the other variables. There was no significant difference between models including or excluding canopy cover from the model (F=2.65; P=0.11). The final model including forest structural stage, percent cover of down wood, basal area of overstory trees, density of trees 3.8 cm to 11.4 cm dbh, percent cover of litter, and percent cover of herbaceous vegetation had an AIC of 113.3 and residual deviance=97.3 (df=34) (Tables 3.2 and 3.3).

Plethodontid salamander density was positively related with forest structural stage, negatively related with density of trees 3.8 cm to 11.4 cm dbh, negatively related with basal area of overstory trees, positively related with percent cover of herbaceous vegetation, positively related with percent cover of down wood, and negatively related with percent cover of litter (Table 3.3). Forest structural stage was the most significant parameter (Student's t-test: old-growth, t=4.52; second growth, t=10.67; regeneration cuts t=4.59), and made the greatest contribution to the overall model having a residual deviance of 372.5.

Even though salamander density was not strongly influenced by percent cover of down wood, down wood is an important microhabitat for terrestrial salamanders (Table 3.3). The percent of area covered by down wood was not significantly different (F=3.07, P=0.058) between old-growth (4.3 %), second growth (3.1 %), and regeneration cut sites (2.7 %). However, percent cover of down wood on regeneration cut sites consisted primarily of decay class two logs, and old-growth sites consisted primarily of decay class four logs (Figure 3.3). When salamander density was regressed against down wood decay classes, salamander density was negatively correlated with decay classes one, two, and three and positively correlated with decay classes four and five. This model had a residual deviance of 498.9 (df=36). Regeneration cut sites had a high percent cover of down wood, but because the down wood was in early stages of decomposition it does not provide suitable microhabitat for terrestrial salamanders.

Plethodontid salamanders are non-migratory and highly terrestrial carrying out their entire life history within a relatively small range (Madison 1969, Merchant 1972). Highest densities were found on old-growth sites. Structural characteristics surrounding preferred habitats include large, down logs in later stages of decay, stratified canopy, and diverse understory (Aubry et al. 1988, Raphael 1988, Bury et al. 1991, Corn and Bury 1991, Welsh and Lind 1991, Petranka et al. 1994, Dupuis et al. 1995). Salamander density in this study was highest in habitats possessing high basal area with a well developed midstory and high percent cover of down wood in decay classes 4 and 5. Characteristics of old-growth sites include a stratified canopy and decayed down wood as compared to second growth and regeneration cut sites (Oliver 1981, Shifley et al.

1995, Richards et al. 1995, Shifley et al. 1997). The number of trees/ha is relatively high in the second growth sites with a high percentage of canopy closure. The percent of understory cover decreases considerably in the old-growth and second growth sites as compared to the regeneration cut sites. This model shows a good relationship between plethodontid salamanders and what appears to be suitable habitat, which are forests with low levels of disturbance.

Based on desired information, forest managers can select the most appropriate model to meet particular objectives within time and budget constraints. Table 3.3 indicates the best subset model for each possible number of independent variables in the final model. For example, stage of forest development (old-growth, second growth, or regeneration cut) can be used to get an initial estimate of salamander density. Including more independent variables improves the precision of the estimates (Table 3.3). Forest inventory protocols and procedures vary by agency and even individual. The inventory is typically used to plan tree harvests, determine intermediate cultural activities, implement prescribed fire, designate old growth, etc. For example, the Missouri Department of Conservation (MDC) routinely collects information on tree diameter, tree height, tree species, predominant ground cover species and various environmental parameters (Forest Land Management Guidelines, MDC 1986). In order for salamander densities to be predicted from operational inventory data it is important to correlate their abundance to inventory information collected.

Therefore, as an example, a model was built including forest structural stage, basal area of overstory trees, density of trees 3.8 cm to 11.4 cm dbh, percent cover of herbaceous vegetation, and density of trees one meter tall to 3.8 cm dbh. This model had an AIC of 129.6 and residual deviance=115.6 (df=35). From this model, managers can predict approximate salamander densities in various aged forests by utilizing data collected by field foresters. Moreover, developing these models may lead to utilizing predicted salamander abundance in decisions about ecosystem health and long-term sustainability of management practices.

CONCLUSIONS

Models are important tools that can be utilized by researchers and managers to predict the response of particular ecosystem components to disturbance. I used Poisson regression to build a log-linear based model to describe salamander density and habitat relationships.

Plethodontid salamander density is likely determined by a combination of habitat characteristics. The AIC method of model selection indicated that salamander density could best be explained by describing forest structural stage, percent cover of down wood, basal area of overstory trees, density of trees 3.8 to 11.4 cm dbh, percent cover leaf litter, percent cover of herbaceous vegetation, and percent canopy cover. Canopy cover was dropped from the model because its effects could be explained by other variables in the model. Variables retained in the final model were significant ($P<0.05$).

The stage of forest development strongly influenced salamander density and explained the greatest amount of variation in the model. Old-growth forests supported the highest densities of plethodontid salamanders. Structural characteristics describing old-growth forests include large, old trees; relatively open canopies; trees of varying heights; diverse understories, and large down logs (Oliver 1981). This model shows a strong relationship between plethodontid salamanders and habitat characteristics describing older, more mature forests with no recent history of disturbance.

Ecosystem management is the present and future emphasis of natural resource agencies. Models that describe the relationship between ecosystem components and disturbance are critical in order to evaluate the implications of certain management activities conducted in the Missouri Ozarks. Because the physiological aspects and life history of plethodontid salamanders makes them sensitive to alterations in forest vegetation structure, I feel using plethodontids in these models will help describe the impact of management decisions on the ecosystem. Moreover, plethodontids can provide information on the condition of the ecosystem after forest management practices have been implemented by indicating the impact significance, forest recovery process, and forest recovery time. This information can be utilized to effectively manage forests for timber production while maintaining biodiversity, forest productivity, and other features that reflect ecosystem health.

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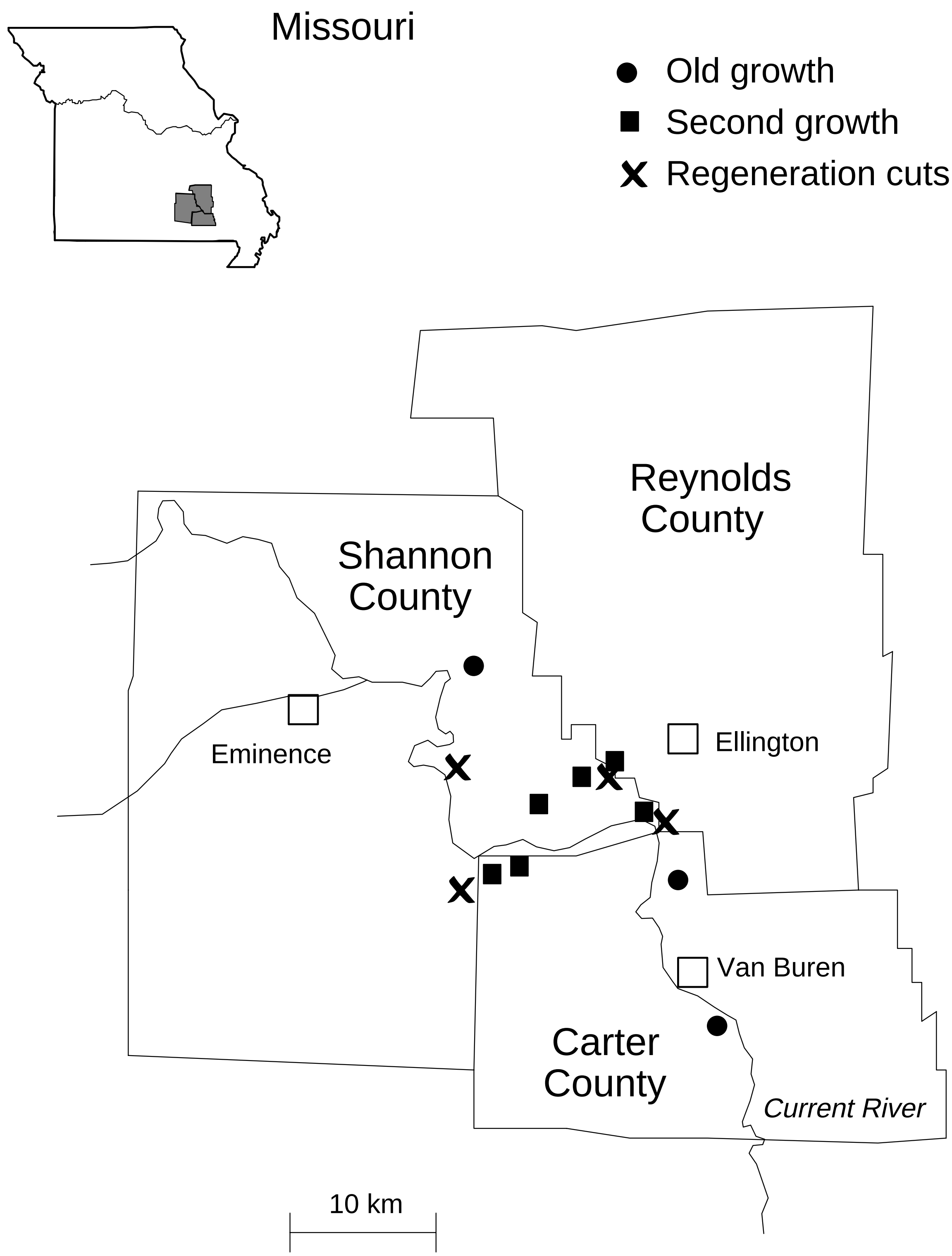
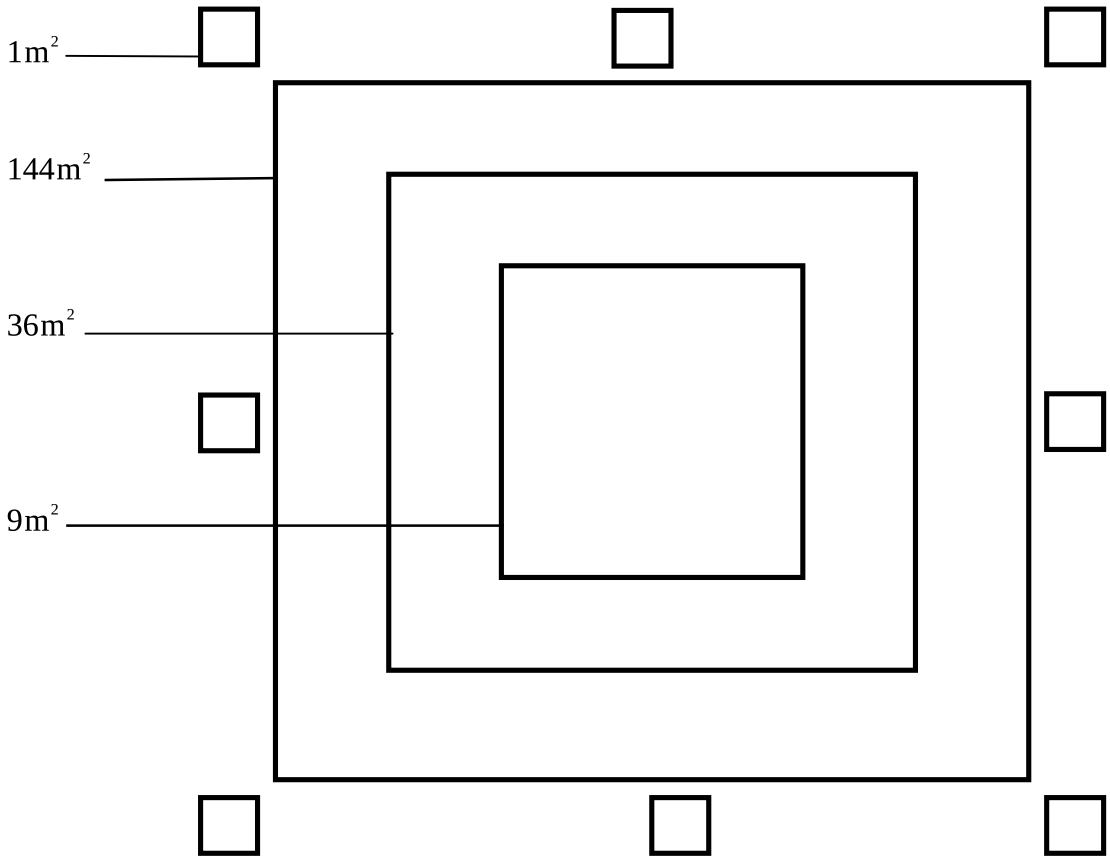
Figure 3.1. Location of study areas where salamander abundance was measured in Reynolds, Shannon, and Carter counties in southeast Missouri Ozarks, 1995-1996. Symbols represent forest structural stages.



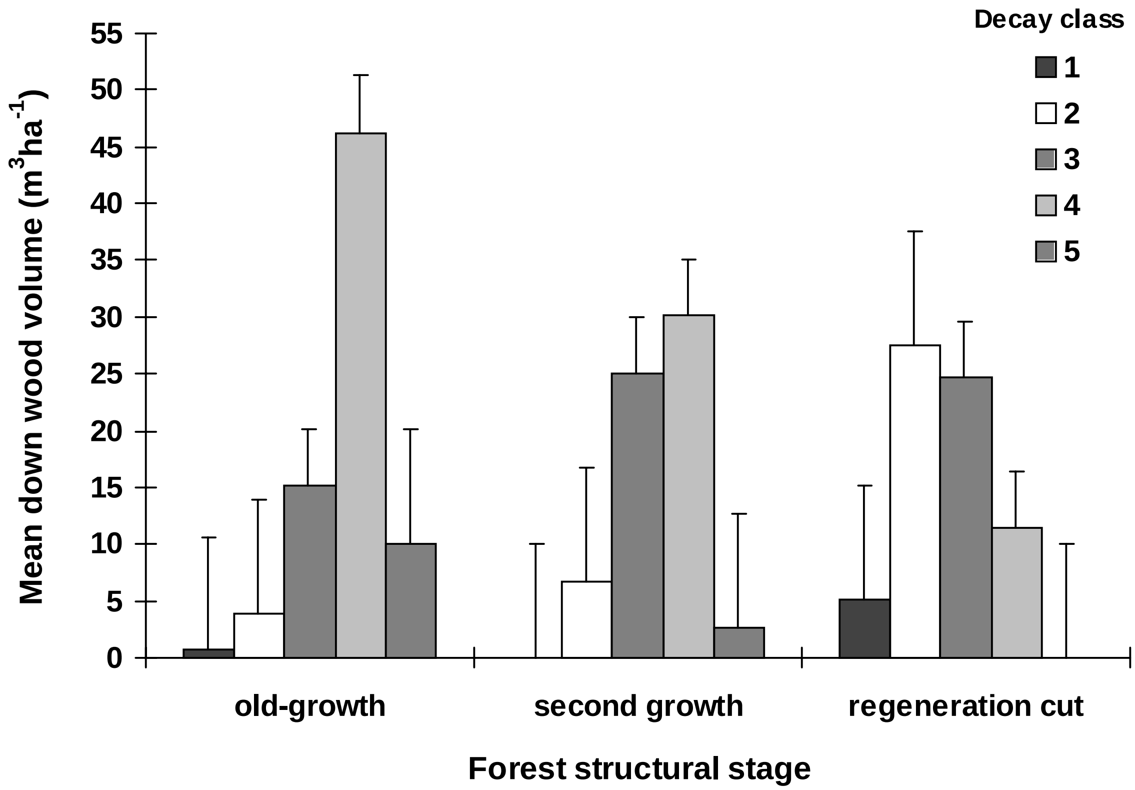
Missouri
Old growth
Second growth
Regeneration cuts
Reynolds County
Shannon County
Eminence
Ellington
Van Buren
Carter County
Current River
10 km

Figure 3.2. Diagram of the vegetation plot layout used to sample woody and herbaceous vegetation and ground cover at salamander sample plots on old-growth, second growth, and regeneration cut sites in the Missouri Ozarks, 1995-1996.



1m²
144m²
36m²
9m²

Figure 3.3. Mean down wood volume of old-growth, second growth, and regeneration cut sites by decay class in the Missouri Ozarks, 1995-1996. Decay class 1 is the least decayed and decay class 5 is the most decayed. OG = old-growth, SG = second growth, RC = regeneration cut.



Decay class
1
2
3
4
5
Mean down wood volume (m³ha⁻¹)
0
5
10
15
20
25
30
35
40
45
50
55
old-growth
second growth
regeneration cut
Forest structural stage

Table 3.1. Correlation coefficients (Pearson's r) among salamander numbers and habitat variables for Missouri Ozark forests, 1995-1996.

Variables	Second growth	Regen. cut	DDW volume	DDW % cover	Basal area trees >11.4	Trees 3.8 to 11.4 cm	Trees 1m tall to 3.8 cm	Rock cover	Bare ground cover	Moss cover	Litter cover
Salamander numbers	-0.27	-0.52	0.20	-0.09	0.26	0.30	-0.39	0.46	0.07	0.17	-0.07
Second growth	1	-0.50	-0.06	-0.11	0.41	0.28	-0.34	-0.33	-0.38	-0.14	0.59
Regeneration cut		1	-0.01	0.36	-0.72	-0.76	0.78	-0.27	0.19	-0.08	-0.44
DDW volume			1	0.80	-0.21	-0.04	-0.05	-0.15	-0.11	-0.21	0.03
DDW % cover				1	-0.36	-0.35	0.27	-0.37	-0.07	-0.30	-0.80
Basal area trees >11.4 dbh					1	0.43	-0.62	0.12	-0.05	0.08	0.31
Trees 3.8-11.4 cm dbh						1	-0.64	0.30	-0.37	0.10	0.30
Trees 1m tall - 3.8cm dbh							1	-0.21	0.12	-0.15	-0.18
Rock cover (%)								1	0.13	0.48	-0.52
Bare ground cover (%)									1	-0.06	-0.18
Moss cover (%)										1	-0.58
Litter cover (%)											1
Herb cover (%)											
Woody veg cover (%)											
Canopy cover (%)											
pH soil											

Table 3.1. Continued.

Variables	Herb cover	Woody veg. cover	Canopy cover	pH soil	pH humus
Salamander numbers	-0.33	-0.56	0.48	0.15	0.13
Second growth	0.06	-0.32	0.41	-0.10	-0.03
Regeneration cut	-0.39	0.87	-0.87	-0.05	0.01
DDW volume	-0.17	0.03	-0.05	-0.07	-0.09
DDW % cover	0.04	0.39	-0.33	-0.09	-0.04
Basal area trees >11.4 dbh	-0.15	-0.63	0.58	-0.02	-0.14
Trees 3.8-11.4 cm dbh	-0.39	-0.73	0.72	0.17	0.08
Trees 1m tall - 3.8cm dbh	0.21	0.70	-0.63	0.01	0.11
Rock cover (%)	-0.44	-0.35	0.20	-0.10	-0.27
Bare ground cover (%)	-0.07	0.05	-0.12	0.45	-0.01
Moss cover (%)	-0.21	-0.12	0.09	-0.12	-0.24
Litter cover (%)	0.09	-0.29	0.36	0.03	0.18
Herb cover (%)	1	0.47	-0.58	0.02	-0.01
Woody veg cover (%)		1	-0.88	-0.09	-0.09
Canopy cover (%)			1	0.11	0.22
pH soil				1	0.59

Table 3.2. Habitat variables used to develop the final model for plethodontid salamanders taken from habitat assessment in the Missouri Ozarks, 1995-1996.

Variable	Units	Mean	SD	Range Min.	Range Max.
Volume down wood	m^3/ha	69.84	64.01	0.52	341.19
Percent cover down wood (across plot)		5.02	3.26	0.08	12.07
Basal area trees >11.4cm dbh	m^2/ha	17.44	14.25	0.00	48.27
Density trees 3.8-11.4cm dbh	#/ha	178.46	139.76	0.00	485.80
Density trees 1m to 3.8cm dbh	#/ha	457.99	469.01	0.00	1944.43
Percent cover rock		6.65	6.11	0.19	20.38
Percent cover bare ground		0.30	0.34	0.00	1.38
Percent cover down wood (1m^2 quads)		10.10	7.74	2.25	31.25
Percent cover basal area		0.93	0.54	0.00	3.06
Percent cover moss		3.18	2.55	0.25	12.44
Percent cover litter		80.14	9.70	56.86	96.13
Percent cover herbaceous veg.		15.16	9.73	1.38	40.0
Percent cover woody veg.		17.12	14.11	0.81	49.75
Percent canopy cover		59.08	31.79	0.00	94.20
Slope		29.56	7.99	14.0	52.0
Humus pH		5.95	0.55	4.19	6.97
Soil pH		5.35	0.57	4.08	6.72

Table 3.3. Poisson regression coefficients for best subset models relating plethodontid salamander density to habitat variables in Missouri Ozark forests, 1995-1996. Predictability is the percent of variance explained by the model.

	Intercept	OG[1]	SG	TREE	BA	HERB	DDW	LITTER	CANOPY	Residual deviance	AIC	Predictability (%)
Model 1	0.967	2.280	0.227	-	-	-	-	-	-	175.7	181.7	70.0
Model 2	1.497	2.647	0.308	-0.221	-	-	-	-	-	142.2	150.2	76.0
Model 3	1.908	2.900	0.398	-0.264	-1.256	-	-	-	-	127.6	137.6	78.5
Model 4	1.582	3.137	0.397	-0.287	-1.443	0.026	-	-	-	116.2	128.2	80.4
Model 5	1.082	3.204	0.389	-0.274	-1.192	0.034	0.053	-	-	108.3	122.3	81.7
Model 6	3.122	3.473	0.539	-0.246	-1.363	0.054	0.085	-0.032	-	97.3	113.3	83.6
Model 7	2.098	2.845	0.329	-0.197	-1.259	0.066	0.120	-0.043	0.022	88.4	106.4	85.1

[1]OG=value is 1 if site is old-growth, 0 otherwise; SG=value is 1 if site is second growth, 0 otherwise; site assumed to be a regeneration cut if SG and RC both = 0; TREE=density of trees 3.8 to 11.4cm dbh; BA=basal area of trees >11.4cm dbh; HERB=percent cover herbaceous vegetation; DDW=percent cover down wood; LITTER=percent cover leaf litter; CANOPY=percent cover canopy.

Null deviance=593.3; df=41. Predictability=1-(residual deviance / null deviance)

APPENDIX

Plot identification by number, site name location, county, USGS topographic quadrangle, harvesting treatment, and year of harvest for study in the Missouri Ozarks, 1995-1996. Plot numbers 1-21 were sampled in 1995, and plot numbers 22-42 were sampled in 1996. OG=old-growth, SG=second growth, and RC=regeneration cut.

Plot No.	Site Name	County	Quad. (MO)	Treatment	Year Cut
1	Big Spring Nat. Area	Carter	Big Spring	OG	
2	Big Spring Nat. Area	Carter	Big Spring	OG	
3	Big Spring Nat. Area	Carter	Big Spring	OG	
4	Big Spring Nat. Area	Carter	Van Buren South	OG	
5	Big Spring Nat. Area	Carter	Big Spring	OG	
6	Big Spring Nat. Area	Carter	Van Buren South	OG	
7	Big Spring Nat. Area	Carter	Van Buren South	OG	
8	Deer Run Conserv. Area	Reynolds	Exchange	SG	
9	Cardareva Conserv. Area	Reynolds	Exchange	SG	
10	Cardareva Conserv. Area	Reynolds	Exchange	SG	
11	Peck Ranch Conserv. Area	Carter	Stegal Mtn.	SG	
12	Peck Ranch Conserv. Area	Carter	Stegal Mtn.	SG	
13	Carrs Creek Conserv. Area	Shannon	Powder Mill Ferry	SG	
14	Deer Run Conserv. Area	Reynolds	Exchange	SG	
15	Deer Run Conserv. Area	Reynolds	Exchange	RC	1992
16	Deer Run Conserv. Area	Reynolds	Exchange	RC	1992
17	Deer Run Conserv. Area	Reynolds	Exchange	RC	1992

APPENDIX (cont.)

Plot identification by number, site name location, county, USGS topographic quadrangle, harvesting treatment, and year of harvest for study in the Missouri Ozarks, 1995-1996. Plot numbers 1-21 were sampled in 1995, and plot numbers 22-42 were sampled in 1996. OG=old-growth, SG=second growth, and RC=regeneration cut.

Plot No.	Site Name	County	Quad. (MO)	Treatment	Year Cut
18	Mule Mtn. Conserv. Area	Shannon	Stegal Mtn.	RC	1993
19	Mule Mtn. Conserv. Area	Shannon	Stegal Mtn.	RC	1993
20	Paint Rock Conserv. Area	Shannon	Van Buren North	RC	1993
21	Deer Run Conserv. Area	Reynolds	Exchange	RC	1992
22	Big Spring Nat. Area	Carter	Big Spring	OG	
23	National Park Service	Carter	Van Buren North	OG	
24	Current River Nat. Area	Shannon	The Sinks	OG	
25	Current River Nat. Area	Shannon	The Sinks	OG	
26	National Park Service	Carter	Van Buren North	OG	
27	Big Spring Nat. Area	Carter	Van Buren South	OG	
28	Big Spring Nat. Area	Carter	Van Buren South	OG	
29	Peck Ranch Conserv. Area	Carter	Stegal Mtn.	SG	
30	Carrs Creek Conserv. Area	Shannon	Powder Mill Ferry	SG	
31	Cardareva Conserv. Area	Reynolds	Exchange	SG	
32	Deer Run Conserv. Area	Reynolds	Exchange	SG	
33	Paint Rock Conserv. Area	Shannon	Exchange	SG	
34	Cardareva Conserv. Area	Reynolds	Exchange	SG	
35	Mule Mtn. Conserv. Area	Shannon	Stegal Mtn.	SG	

APPENDIX (cont.)

Plot identification by number, site name location, UTM coordinates, USGS topographic quadrangle, harvesting treatment, and year of harvest for study in the Missouri Ozarks, 1995-1996. Plot numbers 1-21 were sampled in 1995, and plot numbers 22-42 were sampled in 1996. OG=old-growth, SG=second growth, and RC=regeneration cut.

Plot No.	Site Name	County	Quad (MO)	Treatment	Year Cut
36	Deer Run Conserv. Area	Reynolds	Exchange	RC	1992
37	Deer Run Conserv. Area	Reynolds	Exchange	RC	1992
38	Powder Mill Conserv. Area	Reynolds	Exchange	RC	1994
39	Mule Mtn. Conserv. Area	Shannon	Stegal Mtn.	RC	1993
40	Mule Mtn. Conserv. Area	Shannon	Stegal Mtn.	RC	1993
41	Paint Rock Conserv. Area	Shannon	Van Buren North	RC	1994
42	Paint Rock Conserv. Area	Shannon	Van Buren North	RC	1993