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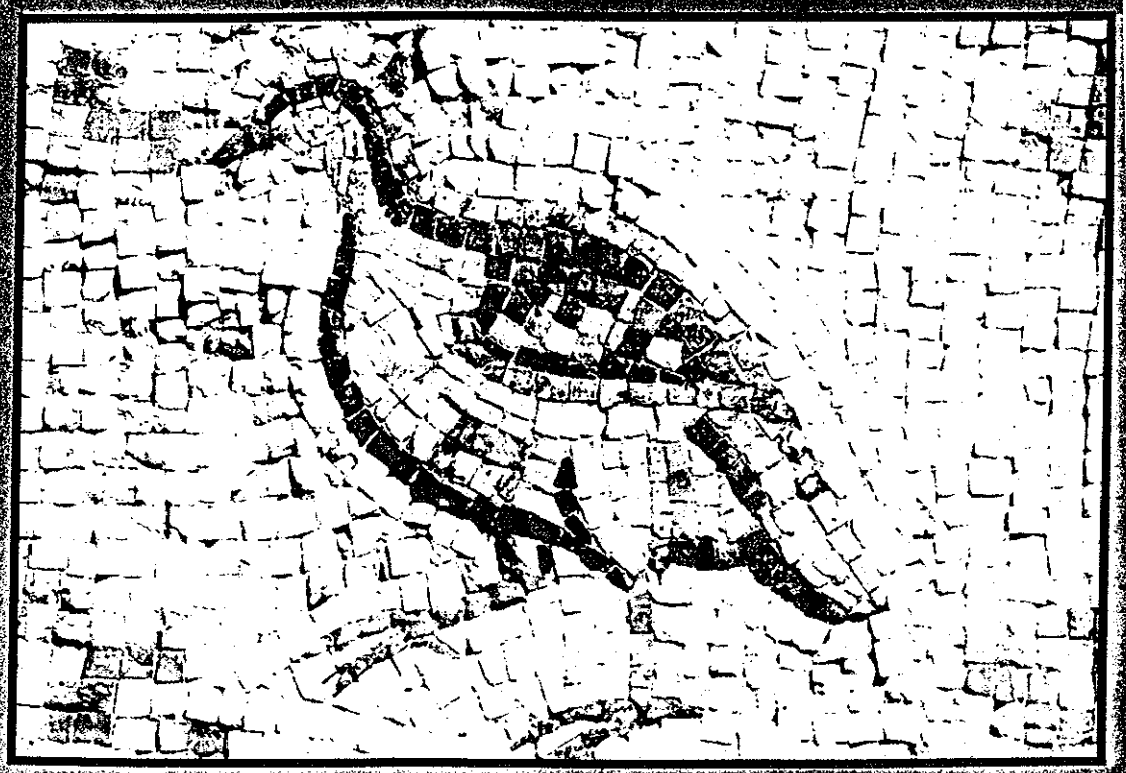

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Cover: Chukar Partridge (*Alectoris chukar*) mosaic from the Byzantine period at Madaba, Jordan, symbolic of the multiple, inter-related components of biodiversity. Rapid urbanization of landscapes in Israel and the region threatens to disrupt unique and perhaps essential connections among chukar populations. Photo by Salit Kark. See pages 542–552.

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Plethodontid Salamander Response to Silvicultural Practices in Missouri Ozark Forests

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Abstract: *There is little information on the effects of tree harvest on salamander populations in the midwestern United States. We present data on plethodontid salamander densities in replicated stands of three forest age classes in the southeastern Ozarks of Missouri. Forest age classes consisted of regeneration-cut sites <5 years old, second-growth sites 70-80 years old, and old-growth sites >120 years old. Salamander abundance on 21, 144-m^2 plots was determined by area- and time-constrained searches. We also compared age-class habitat characteristics, including downed woody debris, canopy cover, ground area cover, herbaceous vegetation, and woody vegetation. Salamander density was lowest in newly regenerated forests and highest in forests >120 years old. Comparisons of recently regenerated forests with mature forests >70 years old indicated that terrestrial salamanders were reduced to very low numbers when mature forests had been intensively harvested. This reduction may result from a decrease in microhabitat availability. Forest age-class comparisons further indicated that salamander abundance slowly increased over time after forests had regenerated. Management decisions that take into account plethodontid salamander abundance and their response to forest structural diversity are important components in sustaining ecosystem integrity while maximizing economic yield.*

Respuesta de una Salamandra Pledodóntida a las Prácticas Silviculturales en los Bosques de Missouri Ozark

Resumen: *Existe poca información sobre los efectos de la cosecha de árboles sobre poblaciones de salamandras del medio Oeste de los Estados Unidos. Presentamos datos de densidades de una salamandra pletodóntida en sitios replicados de tres bosques con diferentes clases de edades en la zona Sureste de Ozark en Missouri. Las clases de edades consistieron en sitios cortados en regeneración <5 años de edad, sitios de segundo crecimiento de 70-80 años de edad y sitios maduros >120 años de edad. La abundancia de salamandras en cuadrantes de 21, 144 m^2 fue determinada mediante búsquedas restringidas en área y tiempo. También comparamos las características del hábitat incluyendo materia muerta en el suelo, cobertura del dosel, área de suelo cubierto, vegetación herbácea y vegetación leñosa. La densidad de salamandras fue más baja en los bosques recientemente regenerados y la más alta se observó en bosques >120 años de edad. Las comparaciones de bosques recientemente regenerados contra bosques >70 años de edad indican que las poblaciones de salamandras terrestres son reducidas a números muy bajos cuando los bosques maduros son cosechados intensamente. Esta reducción puede ser debida a una disminución en la disponibilidad del hábitat. Las comparaciones entre bosques de diferentes clases de edades indicaron además que la abundancia de las salamandras incrementa lentamente con el tiempo una vez que el bosque se ha regenerado. Las decisiones de manejo que consideren la abundancia de salamandras pletodóntidas y su respuesta a la diversidad estructural del bosque son un componente importante en el mantenimiento de la integridad del ecosistema al mismo tiempo que se maximiza una cosecha económica.*

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Introduction

The possible decline of plethodontid salamanders and the effects of land-use practices, such as forest management, on plethodontid salamander populations are growing concerns (Bury 1980; Vitt et al. 1990; Wake 1991; Walls et al. 1992; Blaustein et al. 1994; de-Maynadier & Hunter 1995). Our knowledge of the effects of timber harvesting on salamander populations in Missouri Ozark forests is incomplete. Salamander response to forest management has been comparatively well researched in the Pacific Northwest and eastern United States (Blymer & McGinnes 1977; Bennett et al. 1980; Bury 1983; Enge & Marion 1986; Pough et al. 1987; Ash 1988; Pais 1988; Raphael 1988; Corn & Bury 1991; Welsch & Lind 1991; Diller & Wallace 1994; Petranka et al. 1994; Dupuis et al. 1995; Ash 1997; Mitchell et al. 1997). These studies indicate that plethodontid salamanders appear to be best adapted to conditions characteristic of older, mature forests and that forest management can affect salamander abundance.

Plethodontid salamanders are the dominant group of salamanders inhabiting deciduous Ozark forests (U.S.A.) (Johnson 1992). They lack lungs and exchange gases almost entirely through cutaneous respiration. For gas exchange to occur, respiration requires exposed, moist, permeable skin (Spotila 1972; Feder 1983); therefore, salamanders seek moist microhabitats, making them sensitive to environmental disturbances that modify the prevailing temperature, humidity, and soil moisture regime. Plethodontid salamanders are important components in the energy flow of forest ecosystems (Burton & Likens 1975). Because of their small size, salamanders exploit prey that is too small for birds and mammals and efficiently convert the 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.

Even-aged silviculture has been the primary management technique in Missouri since the mid-1970s (Gingrich 1967; Missouri Department of Conservation 1986). Even-aged silviculture has traditionally been used to regenerate shade-intolerant tree species, such as oaks and hickories, which presently occupy Ozark forests. This harvesting method removes a significant portion of large, dominant canopy trees within a management unit. Removing canopy cover increases light penetration to the forest floor, reduces leaf litter, reduces surface-soil moisture, and increases soil temperature (Gieger 1965). This abrupt alteration of vegetation structure greatly modifies the microclimate of the management unit and surrounding forest (Chen et al. 1997; Xu et al. 1997). Consequently, it is likely that community composition will be altered with changes in the microhabitat of the forest. It may be decades before microhabitats suitable for many plants and animals are reestablished.

Certain plethodontid salamanders, such as *Plethodon* spp., are completely terrestrial and lack an aquatic larval stage; therefore, the forest must provide microhabitats for all stages of the life history of these species. Silvicultural practices that create canopy gaps and subsequently modify temperature and moisture regimes of the forest floor will determine the microclimate and, therefore, the microhabitats available for salamanders (Heatwole 1962; Spotila 1972; Jaeger 1980; Feder 1983). We examined the effects of tree harvest on plethodontid salamander abundance and species richness in southeastern Missouri. Specifically, we examined abundance and richness in old-growth areas with no past timber harvest, second-growth areas that had not been manipulated in the past 70 years, and regenerating forests <5 years old. We tested the null hypothesis that no differences in salamander abundance and habitat characteristics exist among the three forest age classes. We also compared microhabitat conditions within these distinctly different forests.

Methods

Study Area

We conducted our study in oak-hickory forests of the Ozark Mountain region (Nelson 1987) of Missouri. 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 U.S. National Park Service in Carter County and Pioneer Forest in Shannon County (Fig. 1). Pioneer Forest is the largest (6475 ha) privately owned land base in Missouri.

Soils are dry to xeric chert or limestone and well to excessively drained (Sauer 1920; Meinert et al. 1997). The 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 during winter (December, January, February) the mean minimum temperature is 4.8° C.

Data Collection

We collected data from 21, 144-m^2 plots in 1995 and 21 additional plots in 1996. Three distinct forest age-classes were used to determine the response of plethodontid salamanders to alterations in vegetation structure. Forest age classes consisted of newly regenerated stands <5 years old, second-growth stands 70–80 years old, and mature, old-growth stands >120 years old. Seven plots were located within each age class in 1995 and 1996. All plots were established mid-slope on north aspects ranging from 120° to 330°. A 50-m buffer of similar habitat

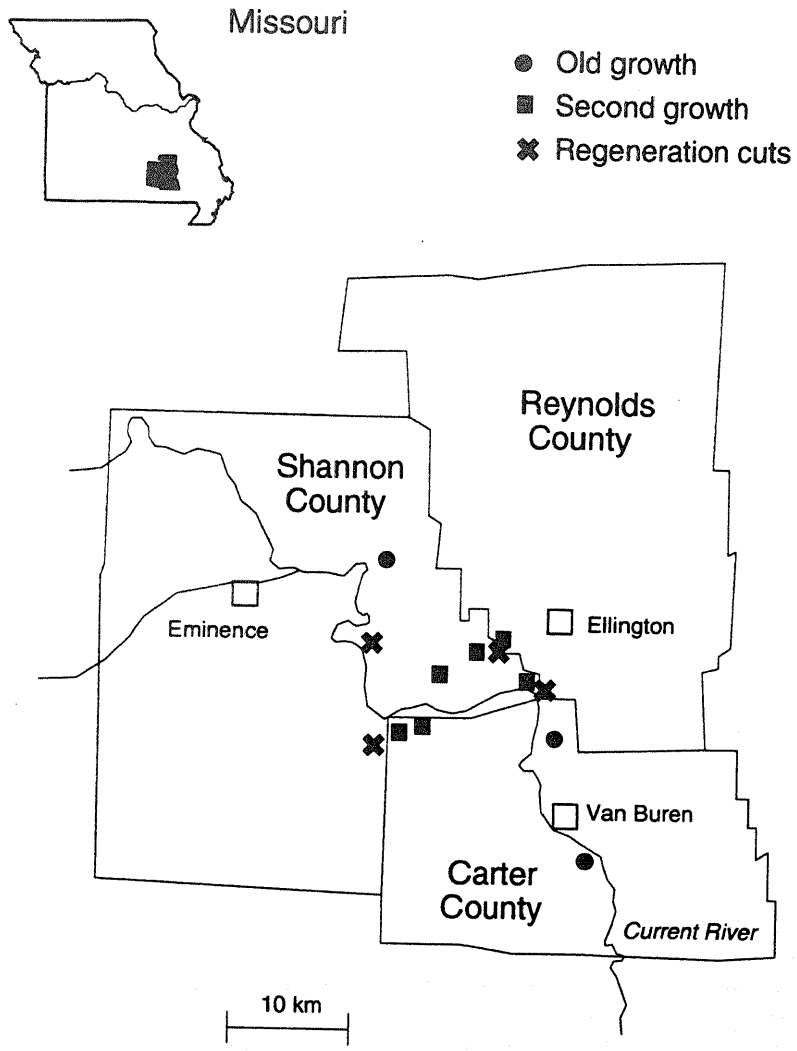

Figure 1. Location of study areas where salamander abundance was measured in Reynolds, Shannon, and Carter counties in the southeast Missouri Ozarks, 1995-1996.

surrounded each plot to avoid forest edge effects. After a plot was established, downed woody debris measurements were recorded across the plot. Length and midpoint diameters were recorded for each piece of downed woody debris at least 10 cm in diameter. We used these measurements to estimate volume and percent cover of downed woody debris on the forest floor. The extent of decomposition was ranked for each piece of debris by decay classes 1-5 as described by Maser et al. (1979). Decay class 1 consisted of newly fallen limbs and snags with little decay. Decay class 5 included almost completely decomposed logs that were faded, oval shaped, soft, and powdery.

In April of each year, we conducted a single area- and time-constrained search for salamanders on each established plot for up to 6 person-hours. Salamanders were located by rolling and tearing open downed woody debris, 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. The type of cover object was also recorded. In 1996 we counted the number of rocks 7.5 cm in length or greater that were turned while searching for salamanders on each plot. The distances to neighboring salamanders, and downed woody debris 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 Ziplock bags and kept in cold storage until analyzed. We air dried soil and mixed one part soil with one part deionized water (National Soil Survey Center 1996). We measured the pH of the paste with a digital ionanalizer pH meter and combination electrode. Soil and humus samples were weighed, air dried for 5 days, and weighed again to determine the samples' moisture per gram.

We 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 tree species between 3.8 cm and 11.4 cm dbh. Trees at least 1 m tall and <3.8 cm dbh were measured and identified across a 9-m^2 plot established in the center of the 36-m^2 plot. We used 8, 1-m^2 quadrats systematically placed outside and 3 m from the border of the 144-m^2 plot to sample ground cover and herbaceous and woody vegetation <1 m 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 percent area of each 1-m^2 quadrat covered by each group was estimated. We visually estimated the percent ground cover of rock, downed woody debris, leaf litter, bare ground, basal area, moss, and lichen in each quadrat. We used canopy tubes to measure percent canopy cover (Robinson 1947; Lemmon 1956) at five points in each plot.

Data Analysis

Analysis of variance (ANOVA) and Tukey's honestly significant difference procedures were used to test for differences in salamander abundance and vegetation. The Tukey test is a multiple comparison procedure used to identify significant differences among age classes (Zar 1984). We used a two-way ANOVA to test for treatment effects, year effects, and treatment-by-year interactions. Differences in mean relative densities among forest age classes of salamanders were determined with a single-factor ANOVA. Single-factor ANOVA and Tukey tests determined vegetation and ground cover differences among forest age classes. Tests with $p < 0.05$ were considered significant. Data recorded in percentages were transformed with the arcsine transformation before analysis. We used the SAS statistical package for analyses (SAS Institute 1985).

The volume of each piece of downed wood 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/ha). Within each forest age-class, volume was estimated by decay class and diameter class for comparison. Four diameter classes were compared: 10–20, 21–30, 31–40, and >40 cm. Percent ground area covered by each log was computed as a product of length and midpoint diameter.

Results

In 1995 and 1996, 348 plethodontid salamanders of three species were captured. Eighty-four percent were southern redback salamanders (*Plethodon serratus*) and 16% were slimy salamanders (*P. glutinosus* complex). One longtail salamander (*Eurycea longicauda*) was captured on an old-growth plot located at Big Spring Pines Natural Area. Redback salamander densities were 1205 salamanders/ha (±203.4 SE) on old-growth sites and 238 salamanders/ha (±81.6 SE) on second-growth sites. No redback salamanders were found on regeneration-cut sites. Densities of slimy salamanders were 213 salamanders/ha (±48.5 SE) in old-growth sites, 55 salamanders/ha on second-growth sites (±36.5 SE), and 15 salamanders/ha on regeneration-cut sites (±10.7 SE).

Tests of treatment effects (forest age-class) indicated statistical differences in salamander density ($F = 34.51$, df = 2, $p < 0.001$). No differences, however, were found in treatment effects for year and treatment-by-year interactions ($F = 0.81$, df = 1, $p = 0.374$; $F = 0.75$, df = 2, $p = 0.477$, 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. The mean surface density of plethodontid salamanders in old-growth areas was significantly greater than in second-growth or regeneration-cut areas (Tukey test; $F = 35.12$, df = 41, $p < 0.001$). We estimated the mean surface densities of old-growth, second-growth, and regeneration cuts as 1422.7 salamanders/ha (±202.4 SE), 287.5 salamanders/ha (±79.8 SE), and 14.87 salamanders/ha (±10.74 SE), respectively.

Vegetation and Cover Characteristics

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

Regeneration-cut and old-growth sites had the highest volume of downed woody debris per hectare (76 m^3/ha and 70 m^3/ha, respectively). Most downed woody debris on regeneration-cut sites consisted of decay classes 2 and 3 ($F = 22.43$, df = 69, $p < 0.001$). Old-growth sites had more downed woody debris in decay class 4 than in other decay classes combined ($F = 9.01$, df = 69, $p = 0.004$). The majority of downed woody debris volume on second-growth sites was in decay classes 3 and 4 ($F = 13.97$, df = 69, $p < 0.001$; Fig. 2). Regeneration-cut sites had significantly more downed woody debris volume in decay classes 1 and 2 than either second-growth or old-growth sites (Tukey test: decay class 1, $p = 0.004$; decay class 2, $p < 0.001$; Table 1). Old-growth sites had more downed woody debris volume in decay classes 4 and 5 than either second-growth or regeneration-cut sites. Although these differences were biologically apparent, they were not statistically significant ($p = 0.29$; Table 1; Fig. 2).

Most downed woody debris on the forest floor for all sites was 0.02–3 m long and 11–15 cm in diameter. Logs on second-growth sites were longest (mean = 3.7 m).

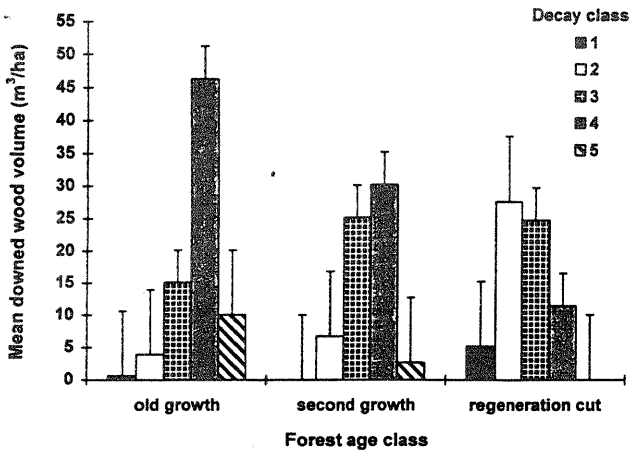

Figure 2. Mean downed wood volume of old-growth, second-growth, and regeneration-cut sites by decay class in the Missouri Ozarks, 1995–1996. Decay class 1 is the least decayed, and decay class 5 is the most decayed.

The largest-diameter logs were found on old-growth sites (mean = 19 cm). Across all sites, logs 8–9 m long with diameters 15–20 cm and 40–45 cm made up the majority of downed woody debris. The volume of downed woody debris across forest age classes varied by diameter class. Most downed woody debris volume on regeneration-cut sites had a diameter ranging from 10 cm to 20 cm ($F = 12.77$, df = 80; $p < 0.001$; Fig. 3). Most downed woody debris volume on second-growth sites had a diameter ranging from 31 cm to 40 cm ($F = 57.51$, df = 33; $p < 0.001$; Fig. 3). Logs with a diameter of >30 cm made up the greatest volume on old-growth sites ($F = 54.26$, df = 13; $p > 0.001$; Fig. 3). The percentage of ground area covered by downed woody debris was not significantly different among old-growth (2.7%), second-growth (3.1%), and regeneration-cut sites (4.6%) ($F = 3.07$, $p = 0.058$; Table 1).

The mean density of trees 11.4 cm dbh or greater was significantly different among forest age classes ($p < 0.001$; Table 1). Old-growth sites averaged 267.9 trees/ha, second-growth 396.8 trees/ha, and regeneration-cut 19.84 trees/ha. Oak trees >11.4 cm dbh dominated the canopy for old-growth and second-growth sites. Few white oak (*Quercus alba*) and short-leaf pine (*Pinus echinata*) were located in regeneration-cut sites; most trees found on these sites were snags. The percentage 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 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 3.8-11.4 cm dbh, $p < 0.001$; size class 1 m tall to 3.8 cm dbh, $p < 0.001$; Table 1). In size class 3.8–11.4 cm dbh, old-growth sites had a mean density of 272.8 trees/ha, second-growth 233.1 trees/ha, and regeneration cuts 29.8 trees/ha. 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 dbh, we estimated a mean density of 163.7 trees/ha in old-growth sites, 238.1 trees/ha in second-growth, and 1026.8 trees/ha in regeneration cuts. Flowering dogwood was the most abundant tree species within this size class for old-growth and second-growth sites, and sassafras (*Sassafras albidum*) was the most abundant tree species for regeneration-cut sites.

Herbaceous plant cover <1 m tall was significantly different among treatments ($p = 0.004$; Table 1). Generally, regeneration-cut sites had a significantly greater percent cover of grass (Tukey test: $p = 0.008$) and forbs (Tukey test: $p = 0.031$) than old growth and a 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 1). Second-growth sites had a significantly greater percent cover of legumes than regeneration-cut and old-growth sites (Tukey test: $p < 0.001$; Table 1). There were no differences in the percent cover of moss between forest age classes (Tukey test: $p = 0.24$; Table 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 in that they had a low percentage of exposed soil (0.12%) (Tukey test: $p = 0.039$; Table 1). More of the soil surface was covered by litter in second growth (88.1%) than either old growth (71.8%) or regeneration cuts (74.9%) (Tukey test: $p < 0.001$; Table 1). Rocks covered 11.8% of the ground surface on old-growth sites. This was significantly greater than the 3.8% and 4.3% of rock cover on second-growth and regeneration-cut sites, respectively (Tukey test: $p < 0.001$; Table 1). The number of rocks 7.5 cm 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, and 244 rocks/plot on regeneration cuts. 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. We estimate 57 rocks turned per salamander on old-growth sites and 146 rocks turned per salamander on second-growth sites.

Soil Characteristics

There were no significant differences in soil ($p = 0.81$) or humus ($p = 0.99$) pH among forest age classes (Table 1). Analysis of the soil for moisture content indicated no significant differences among forest age classes ($p =$

Table 1. Measurements of mean vegetation and ground cover on old-growth, second-growth, and regeneration-cut sites in the Missouri Ozarks, 1995–1996.[a]

	Old growth		*Second growth*		*Regeneration cut*			
Variable[b]	$\bar{x}$	*SE*	$\bar{x}$	*SE*	$\bar{x}$	*SE*	F[c]	p
DWD volume (m^3/ha)	76.15	23.33	64.59	16.92	68.79	9.34	0.11	0.895
DWD volume decay class 1	0.66a	0.51	0a	0	5.19b	1.88	6.32	0.004
DWD volume decay class 2	3.95a	3.51	6.73a	4.47	27.49b	5.09	8.52	<0.001
DWD volume decay class 3	15.11	8.22	25.04	10.52	24.63	7.22	0.41	0.666
DWD volume decay class 4	46.21	23.39	30.09	11.51	11.43	5.56	1.28	0.290
DWD volume decay class 5	10.05	7.82	2.70	1.44	0	0	1.28	0.290
DWD cover (%)	3.91	0.87	4.51	0.91	6.65	0.69	3.07	0.058
No. trees >11.4 cm dbh/ha	267.86a	32.44	391.86b	49.16	19.84c	13.48	29.48	<0.001
No. trees 3.8–11.4 cm dbh/ha	272.65a	27.67	232.99a	28.74	29.73b	14.02	28.49	<0.001
No. trees 1 m to 3.8 cm dbh/ha	163.68a	40.93	238.12b	58.56	972.22b	117.16	31.82	<0.001
Woody cover <1 m 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[d]	31.16	1.80	33.74	5.11	27.46	1.61	0.93	0.411
Humus moisture[d]	97.69ab	10.47	124.25a	12.54	63.52b	8.23	8.31	0.003

[a] *Means with the same letter within rows were not significantly different (Tukey multiple comparison,* $p < 0.05$*).*
[b] *DWD, downed woody debris.*
[c] $n = 42$.
[d] $n = 21$.

0.41; Table 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 1). The moisture content of humus on old-growth sites was not significantly different from that on second-growth or regeneration-cut sites (Table 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 & Pough 1975; Jaeger 1980; Feder 1983; Feder & Londos 1984). We found a significant difference in the species composition of both vegetation and salamanders among forest age classes.

Regeneration cutting reduces microhabitats for salamanders (Bury 1983; Ash 1988; Raphael 1988; Welsch 1990; Petranka et al. 1994; Ash 1997) because temperatures increase and surface moisture decreases with elimination of the forest canopy. Consequently, mature forests support more salamanders than young, regenerating forests. We found that newly regenerated forests <5 years old support few if any salamanders. We do not believe, however, that all regeneration-cut areas are devoid of salamanders. Daytime surface counts excluded individuals in underground retreats, so the numbers observed may not necessarily reflect actual population sizes. Decreased soil moisture and increased surface temperature following timber harvest force salamanders underground during the day. Therefore, fewer salamanders would be detected during daytime searches. Ash (1988), however, 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 because of physiological constraints. 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.

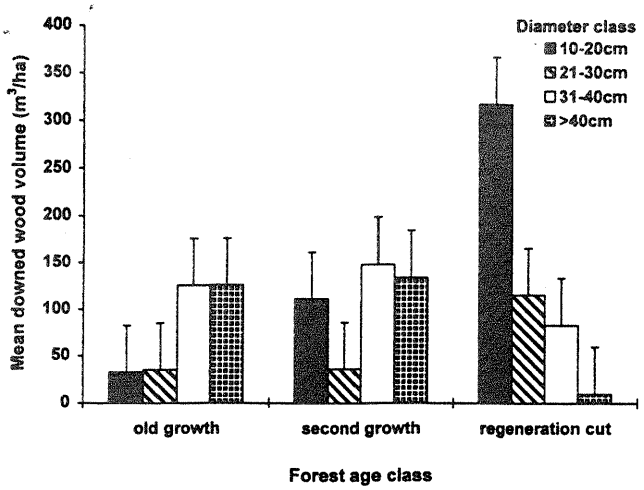

Figure 3. Mean downed wood volume of old-growth, second-growth, and regeneration-cut sites by diameter class in the Missouri Ozarks, 1995-1996.

Salamanders were more abundant in old-growth forests than in forests with a more recent history of logging. During the springs of 1995 and 1996, we found five times more salamanders in old growth than in second growth and 20 times more salamanders in second growth than in regenerating forests. These findings are consistent with those from the eastern United States (Blymer & McGinnes 1977; Bennett et al. 1980; Enge & Marion 1986; Pough et al. 1987; Ash 1988; Petranka et al. 1994) and Pacific Northwest (Bury 1983; Raphael 1988; Corn & Bury 1991; Welsch & Lind 1991; Dupuis et al. 1995), which indicate significant reductions in salamander populations after timber harvesting. Even though we found few salamanders in regeneration-cut sites that were ≤5 years old, repopulation of salamanders can occur on these sites when conditions are suitable. We see evidence of this in the significantly higher densities of salamanders on second-growth sites that had undergone regeneration cutting 70 to 80 years earlier. The rate of salamanders returning to harvested areas is slow, however, perhaps because of long generation times, slow dispersal rates, and high site fidelity (Hairston 1983; Hairston et al. 1992), coupled with the slow recovery rate of the vegetation on a site after harvesting. 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 have undergone regeneration cutting 70-100 years ago could be very different from the recovery rate of forests that have been regenerated in more recent years. Logging practices of the past consisted entirely of unmanaged, even-aged harvesting that was widespread across the landscape (Record 1910). These activities, along with burning and open-range grazing, had detrimental effects on 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 (Missouri Department of Conservation 1986). Currently, few newly cut regeneration stands are larger than 4.5 ha.

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 provide a microhabitat important to the survival of individual plethodontid salamanders. When the leaf litter 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). These conditions may result in short-term negative energy budgets. An increase in rainfall will shift microhabitat utilization from beneath cover objects or subsurface retreats to the leaf litter layer, which increases the surface population and creates conditions suitable for reproductive activity and foraging.

Rocks and downed woody debris were the cover objects used most often by salamanders observed in our study. The percentage of ground surface covered by rock was greater on old-growth sites than on 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. Results of the number of rocks flipped for each site in 1996, however, showed that old-growth sites had a higher rock content. Even though old-growth sites had more rocks to serve as cover objects, we do not believe that rock content alone is responsible for determining salamander abundance. The combination of characteristics that constitutes mature, old-growth forests provides optimal conditions for plethodontid salamanders. In addition, wholesale removal of essentially all merchantable trees at the turn of the century most likely drastically altered the surface structure and composition of the ground. Remnant old-growth forests exist predominately where harvest crews had limited access to trees because of steep terrain or other landscape features. Therefore, old growth was surrounded by landscape-level harvesting and may have provided points of accumulation for surface rock displaced due to poor management practices employed at the turn of the century.

Downed woody debris provides critical microhabitat for terrestrial salamanders. Because downed wood has a

high water-holding capacity, it offers salamanders an escape from desiccation and a moist location for egg deposition. The size and state of decay of a log likely influences its use by salamanders. Larger logs provide more cover and a longer opportunity for use (Cline et al. 1980; Maser & Trappe 1984), and logs at middle to late stages of decay provide hiding spaces and an abundance of prey species (Harmon et al. 1986). Available cover in old-growth, second-growth, and regeneration-cut sites was ample. The volume of downed woody debris was similar for old-growth and regeneration-cut sites. But, most downed woody debris in regeneration-cut sites was ranked in decay class 2 or 3, which is unusable to salamanders. Old-growth logs primarily ranked into decay class 4 and 5, which are stages of decay useful to salamanders. The volume of downed woody debris 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 downed trees on the forest floor. Low mortality of overstory trees explains the low volume of downed woody debris in second-growth sites.

Characteristics of second-growth sites (70–80 years old) include a dense overstory (trees >11.25 cm dbh) with a high percentage of canopy closure and a dense understory (trees 3.5-11.25 cm dbh) that remains small for many years (Oliver 1981). These sites experience little mortality among dominant overstory trees and therefore high mortality among suppressed overstory trees and smaller-diameter trees in the understory. Small-diameter dead trees comprise the majority of downed woody debris on second-growth sites, explaining the lower observed volume. Herbaceous plants and woody shrubs of the forest floor appear and survive during this stage of forest succession, but growth is slow because of the small amount of direct sunlight that penetrates the dense overstory canopy.

Old-growth sites (>120 years) had a significantly lower number of overstory trees per hectare than second-growth sites. Oliver (1981) describes the old-growth stage as being characterized by large, old trees; a relatively open canopy; trees of various heights and diameters; a diverse understory; and large downed logs. Overstory tree mortality is high, which creates openings in the canopy and stimulates rapid growth among understory trees. Overstory mortality produces large, dead trees on the forest floor, explaining the high volume of downed woody debris observed on these sites.

Regeneration-cut sites (<5 years old) contained a significantly higher number of trees 1 m tall to 3.5 cm dbh and had a significantly lower number of trees 3.5–11.25 cm dbh than did 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 downed woody debris on these sites was high, however, and mostly composed of small-diameter, nonmerchantable timber and tree tops left on site.

Each forest age class we examined had 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. *Plethodon* species are nonmigratory and highly territorial and lack an aquatic larval stage in their life cycle. Therefore, forest microhabitats must be available to support all stages of the life cycle. Disturbance that results in deterioration or loss of habitat may have profound consequences for 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 1991). They are the most abundant vertebrate animals in many forest ecosystems, and their annual production of biomass may exceed that of birds or small mammals (Burton & Likens 1975). Because of their sensitivity to alterations in the environment and their high abundance in forested systems, plethodontid salamanders can provide information on the condition of the ecosystem. Plethodontids can serve as indicators of the effects of tree harvest on the ecosystem and of 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). The length of rotation for tree species in Missouri Ozark forests 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 the development of structural characteristics associated with older, mature forests (Bunnell & Kremsater 1990), such as the development of large trees, the accumulation of downed woody debris, and the 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 relatively high densities of plethodontid salamanders.

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