# Effects of Forest Management on Amphibians and Reptiles in Missouri Ozark Forests

ROCHELLE B. RENKEN,*§ WENDY K. GRAM,† DEBRA K. FANTZ,*
STEPHEN C. RICHTER,† TIMOTHY J. MILLER,* KEVIN B. RICKE,*
BRADLEY RUSSELL,* AND XIAOYIN WANG‡

*Wildlife Research Section, Missouri Department of Conservation, 1110 S. College Avenue,
Columbia, MO 65201, U.S.A.
†Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, 2401 Chautauqua Avenue,
Norman, OK 73072, U.S.A.
‡Department of Statistics, University of Missouri, 222 Mathematical Sciences Building, Columbia, MO 65211, U.S.A.

---

**Abstract:** *As part of the Missouri Ozark Forest Ecosystem Project (MOFEP), we experimentally evaluated the impacts of forest management on the relative abundance of amphibians and reptiles in Missouri's Ozark forests (U.S.A.). Using large study sites (average size of 400 ha) as the experimental unit, we tested the effects of uneven-aged and even-aged forest management treatments compared with no-harvest management (i.e., control) on the relative abundance of 13 focal amphibian and reptile species. Within even-aged management sites, we also focused on the local-scale effects of clearcutting on these species by comparing relative abundance among plots located within clearcut stands, 50 m away from clearcut stands, and 200 m away from clearcut stands. Pretreatment sampling of species abundance occurred from 1992 through 1995, and post-treatment sampling occurred from 1997 through 2000. At the landscape scale, treatment significantly affected the abundance of* Bufo americanus. *This species declined less on even-aged management sites than on control sites, but the general decline on all sites suggests that other factors may have contributed to this result. Within even-aged management sites, most amphibian species declined and some reptile species increased relative to pretreatment abundances within clearcut stands. We found significant effects of distance from clearcut for two amphibian species,* Ambystoma maculatum *and* Rana clamitans, *and two reptile species,* Scincella lateralis *and* Sceloporus undulatus. *In general, we conclude that clearcuts within even-aged management sites locally affected amphibian and reptile species but, at a larger spatial scale, we did not detect significant effects of even-aged and uneven-aged forest management. These findings represent relatively short-term data but suggest that forest management and maintenance of biodiversity may be compatible when relatively small amounts of the landscape are disturbed.*

Efectos de la Gestión de Bosques Sobre Anfibios y Reptiles en los Bosques Ozark, Missouri

**Resumen:** *Como parte del Proyecto Ecosistema del Bosque Ozark de Missouri (PEBOM), evaluamos experimentalmente los impactos de la gestión de bosques sobre la abundancia relativa de anfibios y reptiles en los bosques Ozark, Missouri (E.U.A.). Utilizando sitios de estudio extensos (es decir, de tamaño promedio de 400ha) como la unidad experimental, estudiamos los efectos de tratamientos de manejo de bosques de edad uniforme y dispar comparados con el manejo sin cosecha (es decir, control) sobre la abundancia relativa de 13 especies focales de anfibios y reptiles. En los sitios de manejo de edad uniforme, también analizamos los efectos a escala local de la tala completa sobre estas especies comparando la abundancia relativa entre parcelas localizadas dentro de los claros talados, a 50 m y 200 m de los claros. Para determinar la abundancia de especies, se tomaron muestras previas al tratamiento de 1992 a 1995, y muestras posteriores al tratamiento de 1997 a 2000. A la escala de paisaje, el tratamiento afectó significativamente la abundancia de* Bufo americanus.

---

§*email rochelle.renken@mdc.mo.gov*
*Paper submitted July 20, 2002; revised manuscript accepted April 24, 2003.*

Conservation Biology, Pages 174–188
Volume 18, No. 1, February 2004

*La abundancia de esta especie disminuyó menos en sitios de manejo de edad uniforme que en los sitios control, pero la disminución general en todos los sitios sugiere que otros factores pudieron haber contribuido a este resultado. En los sitios de manejo de edad uniforme, la abundancia de la mayoría de las especies de anfibios disminuyó y algunas especies de reptiles incrementaron en relación con las abundancias previas al tratamiento dentro de los claros talados. Encontramos efectos significativos de la distancia del claro para dos especies de anfibios,* Ambystoma maculatum *y* Rana clamitans*, y dos especies de reptiles,* Scincella lateralis *y* Sceloporus undulatus*. En general, concluimos que la tala en sitios de edad uniforme afectó localmente a las especies de anfibios y reptiles, pero a una mayor escala espacial, no detectamos impactos significativos entre el manejo de sitios de edad uniforme y dispar. Estos hallazgos representan datos de relativamente corto plazo pero sugieren que la gestión de bosques y el mantenimiento de la biodiversidad pueden ser compatibles cuando se perturban superficies relativamente pequeñas del paisaje.*

## Introduction

Forest management may involve the temporary loss of mature forest habitat through timber removal. Ecologically, forest management changes the vegetation structure and environmental conditions of the forest (Chen et al. 1999; Zheng et al. 2000), which, in turn, may affect the composition and structure of forest animal communities (Huhta 1976; Monthey & Soutiere 1985; Healy & Brooks 1988; Yahner 1992; Theenhaus & Schaefer 1995; Thompson et al. 1995; Annand & Thompson 1997). The impacts of forest management on associated amphibian and reptile communities are usually evaluated at a local scale; many comparative studies assess amphibian and reptile populations in harvested areas after timber removal (see review by deMaynadier & Hunter 1995). Few studies, however, address the larger-scale impacts of forest management on amphibian and reptile communities. Many species move beyond the boundaries of a forest stand or cut, and the persistence of a population is dependent on population dynamics across a landscape (Raymond & Hardy 1991). Furthermore, forest-management strategies, such as even-aged and uneven-aged forest management, are often applied to large areas that contain a hundred or more forest stands harvested over time (Missouri Department of Conservation 1986). This type of disturbance results in a landscape in which temporary patches of regenerating forest are surrounded by older forest. Some forest-management strategies may meet the goals of both resource managers and conservation biologists by combining economically feasible forest-management strategies with maintenance of viable amphibian and reptile communities.

Local, stand-level studies of amphibian and reptile responses to forest management have generally demonstrated that the loss of forest cover adversely affects amphibian species (e.g., Blymer & McGinnes 1977; Enge & Marion 1986; Ash 1988; Petranka et al. 1994; Harpole & Haas 1999; Herbeck & Larsen 1999) and differentially affects reptiles, depending on species. For example, some lizard species increase in abundance on recently cut stands (e.g., Enge & Marion 1986; Bury & Corn 1988; Raphael 1988; Greenberg et al. 1994; Goldingay et al. 1996), whereas other lizard species decline on recently cut stands (Greenberg et al. 1994).

At a landscape scale, forest fragmentation, as indicated by percent forest cover, distance to forest edge, patch size, and tree basal area, is associated with reduced species distribution and diversity for some amphibians and reptiles in temperate (Gibbs 1998; Hager 1998; Guerry & Hunter 2002) and tropical (Marsh & Pearman 1997; Pearman 1997) regions. Little is known, however, about how amphibians and reptiles respond to habitat and environmental edges created by timber harvests. Schlaepfer and Gavin (2001) note that lizards were more abundant at a forest edge than in the forest interior. Although Messere and Ducey (1998) found no difference in salamander density within and at the edges of small gaps created by tree harvests, it appears that the environmental and structural changes observed in a stand after timber removal may deflect salamanders away from cuts (Raymond & Hardy 1991), and these effects may reach into adjacent uncut forest to reduce salamander abundance for a small distance (<65 m) into the forest (DeGraaf & Yamasaki 1992, 2002; deMaynadier & Hunter 1998, 1999). These local-scale changes may accumulate into larger-scale impacts as the number of harvested patches increases within the landscape.

Most researchers who evaluate the effects of forest management on associated animal communities rely on correlation or comparative analyses of data collected after timber harvest, with no reference to preharvest conditions (e.g., Petranka et al. 1993; Greenberg et al. 1994). The inherent variation in population abundance through time (Pechmann et al. 1991; Marsh 2001) and the patchy distribution of many amphibian and reptile species further limit interpretation of results from postdisturbance studies. A more robust experimental design includes pre- and postharvest data collected over multiple years and spatial scales.

We sought to experimentally evaluate the impact of uneven-aged and even-aged forest management on the relative abundance of amphibians and reptiles in Missouri's Ozark forests (U.S.A.). Temporally, we focused on 6 years of data, comparing 3 years of pretreatment data with 3 years of post-treatment data following timber removal. We approached this question from two different spatial scales. From a landscape-scale perspective, we tested the effects of uneven-aged and even-aged forest-management treatments on the abundance of amphibian and reptile species by using abundance per study site as the experimental unit. Within even-aged management sites, we focused on local-scale, distance-from-clearcut effects by evaluating the impact of clearcutting on the relative abundance of amphibian and reptile species within 200 m of clearcut stands.

## Methods

### Study Area

We conducted this research on the nine study sites that comprise the Missouri Ozark Forest Ecosystem Project (MOFEP), a multi-investigator, landscape-scale experiment administered by the Missouri Department of Conservation (Brookshire et al. 1997). The sites ranged in size from 312 to 514 ha and were located in Carter, Reynolds, and Shannon counties in the Ozark hills of south-central Missouri (91°01′–91°13′W, 37°00′–37°12′N), a region that was 84% forested (Brookshire & Hauser 1993: Xu et al. 1997). Before 1880 these forests were dominated by continuous short-leaf pine *(Pinus echinata* Milli.) communities, but intensive harvesting during 1880–1920, followed by repeated burning and grazing, altered the landscape and produced the mature upland oak-hickory and oak-pine communities of today (Cunningham & Hauser 1989; Guyette & Larsen 2000). In the Ozarks, white oak *(Quercus alba* L.) shares the canopy with other species of oak, including post oak *(Q. stellata* Wang.), black oak *(Q. velutina* Lam.), scarlet oak *(Q. coccinea* Muenchh.), and with short-leaf pine and mockernut hickory (*Carya tomentosa* [Poir.] Nutt.; Kurzejeski et al. 1993). At the start of this project in 1990, most overstory trees were 50–70 years old (Brookshire & Dey 2000).

### Forest-Management Applications

The Missouri Department of Conservation designed MOFEP as a 100-year experiment to evaluate the effects of three forest-management treatments: even-aged, uneven-aged, and no-harvest (i.e., control) management. Each site was randomly assigned to a management treatment or control, resulting in a randomized complete block design (Fig. 1). Each study site was composed of approximately 70 forest stands that ranged in size from 0.16 to 62 ha (mean of 5 ha). Treatments were designed to mimic forest-management practices commonly administered by the Missouri Department of Conservation. In the even-aged treatment, approximately 10–15% of the total forest area was clearcut. Forest thinning was conducted at the same time as clearcutting to increase growing space for residual trees. In the uneven-aged treatment, foresters used small-group and single-tree selection cuts. In both even-aged and uneven-aged sites, a patch of approximately 10% of each site was permanently designated as a reserve and left uncut.

The Missouri Department of Conservation harvested trees from even-aged and uneven-aged sites from May 1996 to May 1997 (i.e., first round of harvesting, with future harvests scheduled for every 15 years). In even-aged sites, clearcuts were 3–13 ha in size, resulting in seven to nine clearcut stands per even-aged site (Brookshire et al. 1997). In addition, foresters thinned 5–24% of each site to promote tree growth of selected size classes and to maintain species diversity. A total of 68–121 ha were harvested on even-aged sites, resulting in a harvested tree volume of 1.8–2.2 $10^3 m^3$ per site (Brookshire et al. 1997). The goal of even-aged management was to create a specific distribution of tree size classes in study sites: 10% in regeneration, 20% in small trees (6–14 cm diameter at breast height [dbh]), 30% in poletimber (14–29 cm dbh), and 40% in sawtimber ($>29$ cm dbh; Kabrick et al. 2002).

In uneven-aged sites, foresters harvested trees from a combination of small-group and single-tree selection cuts across an average of 57% of each site. Small-group cuts ranged from 21 to 43 m in diameter, depending on aspect. Five percent of the harvested area per uneven-aged site was treated with small-group cuts (153–267 small-group cuts per site). Foresters used single-tree selection cuts to obtain a balance of size classes, with 1.5 times more small trees than large trees in the next size class. During the harvest, foresters cut an estimated 9,300–25,800 trees per uneven-aged site. The combination of small-group and single-tree selection cuts yielded a tree volume of 2.2–3.2 $10^3 m^3$ per site (Brookshire et al. 1997). Thus, in even-aged sites, foresters harvested 15–34% of the forest area, and large blocks of cut or thinned forest were interspersed in a matrix of uncut forest. For uneven-aged sites, harvesting occurred in 41–69% of each site, and small areas of cut or thinned forest were scattered throughout uncut forest (Fig. 1; Kabrick et al. 2002).

Following tree harvest, habitat structure on even-aged and uneven-aged sites differed from that of control sites by changes in canopy cover, basal area of larger trees, and number of large trees. Canopy cover on even-aged and uneven-aged sites decreased after tree harvest by 26% and 24%, respectively, whereas canopy cover on control sites in the post-treatment period decreased by 13% from that observed during pretreatment (Kabrick et al. 2002). The basal area of trees of $\geq 4$ cm dbh and the number of trees of $\geq 11$ cm dbh remained the same from pretreatment to post-treatment on control sites, but they decreased by 3.2 $m^2$/ha and 42 trees/ha and by 3.7 $m^2$/ha and 54 trees/ha, respectively, for even-aged and uneven-aged sites (Kabrick et al. 2002).

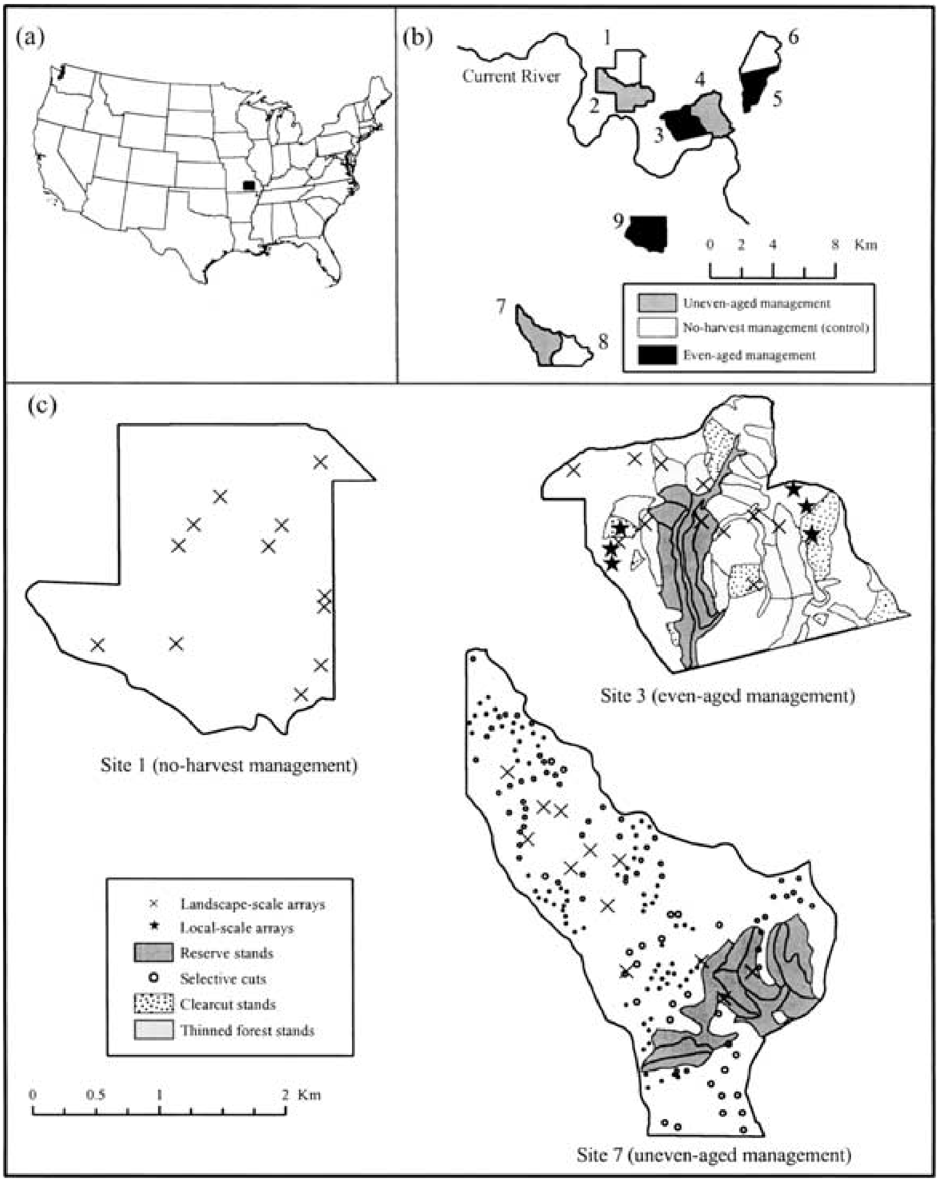

*Figure 1. (a) Map of the United States with Missouri Ozark Forest Ecosystem Project (MOFEP) study area depicted in black. (b) Map of MOFEP study area with study sites 1–9 and management treatments. (c) Configuration of drift-fence arrays, reserve stands (which will never be cut), selective cuts, clearcut stands, and thinned forest stands on a no-harvest (i.e., control), even-aged, and uneven-aged management site.*

### Amphibian and Reptile Data Collection

We captured amphibians and reptiles on MOFEP sites from March through June (spring) and September through early November (fall) in 1992–1995 (pretreatment) and 1997–2000 (post-treatment) for both the landscape and local-scale experiments. We trapped animals with drift-fence arrays (modified from Jones 1981). Each array consisted of nine funnel traps and one pitfall trap. Funnel traps were placed along the sides and ends of three 7.5 × 0.75 m aluminum-flashing drift fences buried 10 cm in the ground. We arranged the three fences 120° apart with the pitfall trap in the middle. Field assistants checked traps every 3–5 days, identified captured animals to species, uniquely marked each animal by toe clipping or ventral-scale clipping (except for *Bufo americanus* and *Notopthalmus viridescens*, which were given a batch mark) and released all animals (see Renken 1997). We chose this sampling technique because it (1) provided information about most of the species of forest amphibians and reptiles, (2) did not interfere with sample plots for other MOFEP investigations, (3) enabled long-term, repeated sampling of a plot, and (4) had the least investigator bias possible for a long-term project.

To examine the landscape-level impacts of forest management, we erected 12 arrays in each of the nine study sites. During project design, we determined that we could logistically and financially sample a maximum of 12 arrays per site per year. We placed 6 of the 12 arrays at random locations throughout each site on an ecological land type (ELT; Meinert et al. 1997) 17 slopes, defined as side slopes with south to west aspect and dry chert forest (SWELT) and six others at random locations throughout each site on ELT 18 slopes, defined as side slopes with north to east aspect and dry-mesic chert forest or dry-mesic sand forest (NEELT), resulting in a split-plot design. We determined random locations for arrays by using a dot grid and numbers from a random-numbers table to select random sample points on study site maps. We sampled SWELT and NEELT because 73% of the MOFEP study area consisted of these ELTs (Meinert et al. 1997). Thus, arrays were randomly located throughout each study site without consideration of whether a particular stand would be harvested during this first round of treatment (Fig. 1). For each study species, we used relative abundance per site and ELT as the replicate unit, resulting in a total sample size of 18 response variables per year (i.e., 9 sites × 2 ELTs).

We examined the local-scale impacts of clearcuts on amphibian and reptile abundances within the three even-aged management sites. In 1991 we randomly selected two forest stands designated to be clearcut in 1996 in each of the three sites: one stand in each site was on SWELT slope and one stand was on NEELT slope. Stands ranged in size from 3 to 13 ha. For each designated clearcut stand, we established three drift-fence arrays: (1) one array randomly located within the designated clearcut stand, (2) one array within adjacent forest 50 m from the clearcut boundary, and (3) one array within adjacent forest 200 m from the clearcut boundary (Fig. 1). We placed these three arrays within the same ELT and at approximately the same elevation. For each study species, we used relative abundance per ELT and distance class as the replicate unit, resulting in a total sample size of 18 response variables per year (i.e., 3 sites × 3 distance classes × 2 ELTs).

### Data Analysis

Of the 43 species we captured (see Renken & Fantz 2002), we report results for seven focal amphibian species (*Ambystoma maculatum* [spotted salamander], *Bufo americanus* [American toad], *Notopthalmus viridescens* [central newt], *Plethodon albagula* [western slimy salamander], *Plethodon serratus* [southern red-backed salamander], *Pseudacris crucifer* [northern spring peeper], *Rana clamitans* [green frog]) and six focal reptile species (*Eumeces fasciatus* [common five-lined skink], *Eumeces laticeps* [broad-headed skink], *Sceloporus undulatus* [northern fence lizard], *Scincella lateralis* [little brown skink], *Storeria occipitomaculata* [northern red-bellied snake], *Virginia valeriae* [smooth earthsnake]) that have a variety of life histories and habitat preferences. To standardize trapping effort, we expressed the relative abundance of each species per study site and ELT as mean abundance (based on first-time captures only) per 100 trap days per year (1 trap day = 1 array open for 1 day). We grouped together fall and spring trapping seasons of consecutive years to represent a sampling year. For the pretreatment sampling years of 1992, 1993, and 1994, we trapped for 178, 182, and 183 days, respectively, and for the post-treatment years of 1997, 1998, and 1999, we trapped for 187, 189, and 184 days, respectively.

For the landscape-scale data, we used a split-plot repeated-measures analysis of variance to analyze the effects of forest-management treatments on the relative abundance of each species. We used a multivariate repeated-measures approach because this approach is more powerful than the univariate approach when the sphericity assumption is violated (von Ende 1993). In this model, block and treatment (i.e., even-aged management, uneven-aged management, or control) were the main effects (tested over an error term of block × treatment), each treatment was split into ELT effects (tested over an error term of block × ELT), and year effects were a repeated measure of ELT within each treatment (Tables 1 & 2; Sheriff & He 1997). The dependent variables for each species were difference scores per site, ELT, and year based on mean pretreatment abundance minus post-treatment abundance per site, ELT, and year. That is, we calculated a mean abundance per site and ELT for pretreatment years (1992–1994) and subtracted each post-treatment year (1997–1999) abundance from the pretreatment mean. In earlier repeated-measures analyses of pretreatment data, we did not find a significant year effect (Renken 1997). Thus, we used mean pretreatment abundance in these analyses. We used difference scores in this model because we did not meet the assumptions necessary to include pretreatment abundance as a covariate in this model.

For the stand-level experiment, we used a similar split-plot repeated-measures analysis of variance to test the local distance effects of clearcutting on species abundances. In this model, site (a blocking term in this model) and ELT were the main effects (tested over an error term of site × ELT), each ELT was split into distance-from-clearcut classes (tested over an error term of site × distance), and year effects were a repeated measure of distance class within each ELT (Tables 3 & 4). The dependent variables for each species were difference scores per stand, distance class, and year based on mean pretreatment abundance minus post-treatment abundance.

We followed tests of main effects in both models with contrasts to test for differences among treatments and distance classes across years. For all tests including contrasts, we used an overall significance level of $\alpha = 0.10$ (for contrasts, $p < 0.033$ was necessary for significance after a Bonferroni adjustment of alpha) because sample size was small in these experiments (and thus power was low), and we were interested in detecting an effect if one existed (i.e., minimizing Type II error; Sheriff & He 1997). All analyses were performed with SAS (version 8.01).

## Results

We captured 25,677 individual amphibians and reptiles during pre- and post-treatment sampling. The 13 focal species accounted for 22,605 (88%) of these captures. In general, we did not detect significant effects of even-aged or uneven-aged management treatments on amphibian and reptile species' abundances at the landscape scale (Tables 1 & 2). Amphibian species' abundances declined

**Table 1. Split-plot repeated measures analysis of variance testing the effects of even-aged and uneven-aged forest management on amphibian species abundance at the landscape scale.**[a]

| | | Ambystoma maculatum | | Bufo americanus | | Notopthalmus viridescens | | Plethodon albagula | | Plethodon serratus | | Pseudacris crucifer | | Rana clamitans | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Source of variation* | *Ndf,Ddf*[b] | F | p | F | p | F | p | F | p | F | p | F | p | F | p |
| Between subjects | | | | | | | | | | | | | | | |
| treatment[c,d] | 2,4 | 2.96 | 0.163 | 8.38 | 0.037 | 1.09 | 0.419 | 0.31 | 0.748 | 0.08 | 0.924 | 0.13 | 0.874 | 0.43 | 0.677 |
| block[d] | 2,4 | 0.09 | 0.920 | 10.10 | 0.027 | 7.02 | 0.049 | 0.96 | 0.456 | 0.87 | 0.485 | 0.96 | 0.456 | 0.95 | 0.461 |
| ELT[e] | 1,2 | 2.39 | 0.263 | 0.56 | 0.531 | 1.33 | 0.367 | 0.33 | 0.622 | 0.01 | 0.916 | 0.42 | 0.584 | 0.01 | 0.947 |
| treatment × ELT[f] | 2,4 | 2.62 | 0.187 | 28.31 | 0.004 | 0.94 | 0.463 | 0.13 | 0.880 | 0.44 | 0.674 | 0.51 | 0.635 | 0.58 | 0.603 |
| Within subject[g] | | | | | | | | | | | | | | | |
| year | 2,3 | 17.43 | 0.022 | 284.95 | 0.0004 | 8.92 | 0.012 | 46.46 | 0.006 | 25.80 | 0.013 | 127.95 | 0.001 | 6.28 | 0.085 |
| year × treatment | 4,6 | 0.72 | 0.608 | 0.55 | 0.705 | 1.86 | 0.236 | 0.13 | 0.968 | 0.41 | 0.794 | 1.21 | 0.397 | 2.44 | 0.158 |
| year × ELT | 2,1 | 0.52 | 0.699 | 1.05 | 0.569 | 3.13 | 0.371 | 0.11 | 0.905 | 1.80 | 0.466 | 0.47 | 0.719 | 1.51 | 0.499 |
| year × treatment × ELT | 4,6 | 0.41 | 0.798 | 0.38 | 0.815 | 6.51 | 0.023 | 3.79 | 0.072 | 1.21 | 0.398 | 0.11 | 0.975 | 0.43 | 0.784 |

[a] *Difference scores of mean abundance of pretreatment years (1993, 1994, 1995) minus abundance each post-treatment year (1997, 1998, 1999) are the repeated measure (i.e., pretreatment - 1997; pretreatment - 1998; pretreatment - 1999). Main effects in the model are block and treatment, and each treatment is split into effects of ecological land type (ELT).*

[b] *The Ndf and Ddf are the numbers of degrees of freedom in the numerator and denominator, respectively, for calculating* F.

[c] *The treatment main effect compares even-aged management, uneven-aged management, and control (no-harvest management) sites.*

[d] *Error term is treatment × block interaction.*

[e] *Error term is block × ELT interaction.*

[f] *Error term is treatment × block × ELT interaction.*

[g] *The* F *approximations of within-subjects are based on the multivariate Wilks' lambda test statistic.*

**Table 2. Split-plot repeated measures analysis of variance testing the effects of even-aged and uneven-aged forest management on reptile species abundance at the landscape scale.[a]**

| | | Eumeces fasciatus | | Eumeces laticeps | | Sceloporus undulatus | | Scincella lateralis | | Storeria occipitomaculata | | Virginia valeriea | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Source of variation* | *Ndf,Ddf*[b] | F | p | F | p | F | p | F | p | F | p | F | p |
| Between subjects | | | | | | | | | | | | | |
| treatment[c,d] | 2,4 | 0.94 | 0.464 | 0.89 | 0.480 | 3.58 | 0.129 | 2.92 | 0.165 | 1.92 | 0.261 | 0.68 | 0.556 |
| block[d] | 2,4 | 0.26 | 0.785 | 1.35 | 0.356 | 0.76 | 0.524 | 1.44 | 0.339 | 1.69 | 0.294 | 1.19 | 0.393 |
| ELT[e] | 1,2 | 0.07 | 0.814 | 0.27 | 0.654 | 0.97 | 0.429 | 0.07 | 0.815 | 0.56 | 0.533 | 2.42 | 0.260 |
| treatment × ELT[f] | 2,4 | 1.58 | 9.94 | 0.06 | 0.939 | 3.00 | 0.160 | 3.16 | 0.151 | 1.88 | 0.266 | 0.67 | 0.560 |
| Within subject[g] | | | | | | | | | | | | | |
| year | 2,3 | 4.64 | 0.121 | 6.46 | 0.082 | 1.05 | 0.452 | 968.42 | <0.0001 | 42.17 | 0.006 | 15.15 | 0.027 |
| year × treatment | 4,6 | 0.73 | 0.602 | 0.81 | 0.564 | 0.13 | 0.968 | 0.58 | 0.682 | 0.81 | 0.564 | 3.79 | 0.072 |
| year × ELT | 2,1 | 3.03 | 0.376 | 24.50 | 0.141 | 101.68 | 0.070 | 0.94 | 0.420 | 29.88 | 0.128 | 2.44 | 0.413 |
| year × treatment × ELT | 4,6 | 0.24 | 0.906 | 0.74 | 0.596 | 3.54 | 0.082 | 9.38 | 0.009 | 1.53 | 0.306 | 1.68 | 0.271 |

[a] *Difference scores of mean abundance of pretreatment years (1993, 1994, 1995) minus abundance of each post-treatment year (1997, 1998, 1999) are the repeated measure (i.e., pretreatment – 1997; pretreatment – 1998; pretreatment – 1999). Main effects in the model are block and treatment, and each treatment is split into effects of ecological land type (ELT).*

[b] *The Ndf and Ddf are the numbers of degrees of freedom in the numerator and denominator, respectively, for calculating* F.

[c] *The treatment main effect compares even-aged management, uneven-aged management, and control (no-harvest management) sites.*

[d] *Error term is treatment × block interaction.*

[e] *Error term is block × ELT interaction.*

[f] *Error term is treatment × block × ELT interaction.*

[g] *The* F *approximations of within subjects are based on the multivariate Wilks' lambda test statistic.*

after tree harvest, but abundances also declined on control sites (Fig. 2). Reptile abundance increased 1 or 2 years after treatment for many species, but the patterns among species and ELT were not consistent (Fig. 3). In the local distance-from-clearcut experiment, most amphibian species declined and some reptile species increased relative to pretreatment abundances within clearcut stands, but distance from clearcut (i.e., local-scale treatment) significantly affected two species of amphibians and two species of lizards (Tables 3 & 4).

At the landscape scale, treatment significantly affected one amphibian species and no reptile species (Tables 1 & 2). Abundance differed between control sites and even-aged management sites for *Bufo americanus* (treatment contrasts: $F_{1,4} = 16.62, p = 0.015$; Fig. 2). In addition, the treatment-by-ELT interaction was significant for *B. americanus*, with populations on SWELT experiencing steeper declines on treatment sites than populations on NEELT (Fig. 2). The steepest abundance declines occurred on control sites (Table 1; Fig. 2). Relative abundance was significantly different among years for all amphibian species and four species of reptiles (Tables 1 & 2). Lastly, the year-by-treatment interaction was significant for *Virginia valeriae* (Table 2), with higher abundance on even-aged sites in 1997 than on either uneven-aged or control sites (Fig. 3).

Within even-aged management sites, distance from clearcut significantly affected the abundance of two amphibian species and two reptile species (Tables 3 & 4). *Ambystoma maculatum* were more abundant at 50 m and 200 m than at 0 m from clearcuts (treatment contrasts: $F_{1,4} = 5.78, p = 0.074$, and $F_{1,4} = 9.57, p = 0.036$, respectively; Fig. 4), whereas *Rana clamitans* were most abundant at 50 m from clearcuts, particularly in NEELT (treatment contrasts: $F_{1,4} = 7.59, p = 0.051$, and $F_{1,4} = 5.98, p = 0.071$, for 50 m vs. 0 m and 50 m vs. 200 m, respectively; Fig. 4). The relative abundance of *Scincella lateralis* initially increased in uncut forest 50 m and 200 m from clearcuts, whereas its abundance did not change within clearcuts (treatment contrasts; $F_{1,4} = 10.35, p = 0.032$, and $F_{1,4} = 11.20, p = 0.029$, respectively; Fig. 5). The relative abundance of *Sceloporus undulatus* sharply increased within clearcuts but remained unchanged in surrounding uncut forest at 50 m and 200 m from cuts (treatment contrasts: $F_{1,4} = 230.57, p < 0.001$, and $F_{1,4} = 264.30, p < 0.001$, respectively; Fig. 5).

## Discussion

At the relatively large spatial scale of this experiment, we did not detect a significant impact of even-aged or uneven-aged forest management on the abundance of most amphibian and reptile species in Missouri Ozark forests. These data represent short-term findings from MOFEP, and future harvests on these sites may affect these species more dramatically. Some species were affected in directly disturbed areas, as many other studies have demonstrated (e.g., Blymer & McGinnes 1977; Enge & Marion 1986; Pough et al. 1987; Ash 1988; Petranka et al. 1994; Harper & Guynn 1999; Harpole & Haas 1999; Herbeck & Larsen 1999) and our local-scale results showed, but populations

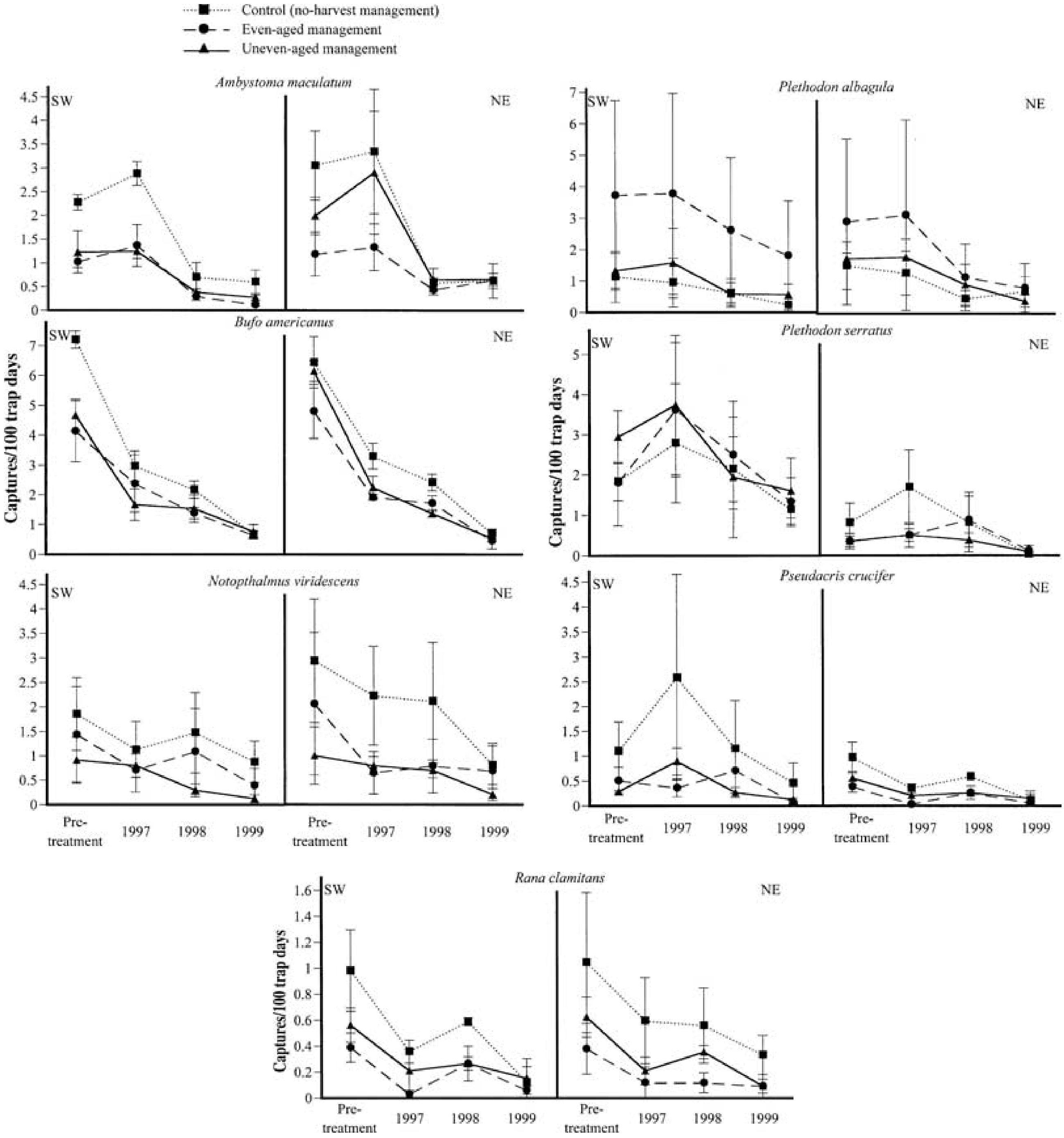

*Figure 2. Mean relative abundance (±1 SE) at the landscape scale of focal amphibian species on control (i.e., no-harvest), even-aged, and uneven-aged forest treatment sites during pretreatment (mean of years 1993–1995) and post-treatment years 1997, 1998, and 1999 on ecological land type (ELT) 17 slopes (SW) and ELT 18 slopes (NE).*

of most species persisted at a relatively stable abundance (within the range of normal population variability) across the study area.

We expected to observe declines in salamander abundances and no response by frogs and toads after timber harvest on even-aged treatment sites. On uneven-aged treatment sites, we did not expect to see impacts after timber harvest for amphibians in general because the disturbance, although widespread throughout the study sites, affected relatively small patches of forest (Fig. 1). Many studies have documented a positive relationship between salamander abundance and age of forest stand (Petranka

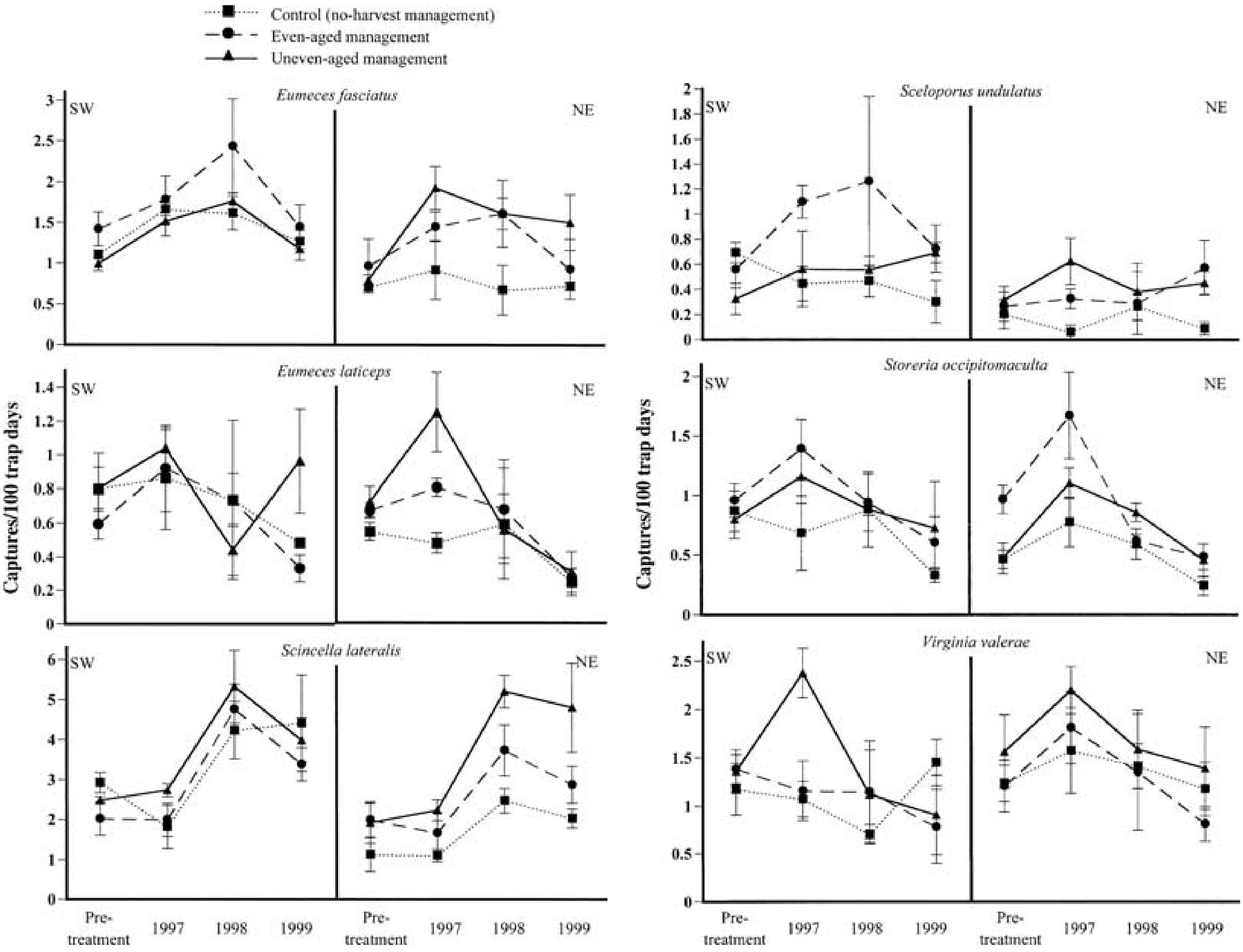

*Figure 3. Mean relative abundance (±1 SE) at the landscape scale of focal reptile species on control (i.e., no-harvest), even-aged, and uneven-aged forest treatment sites during pretreatment (mean of years 1993–1995) and post-treatment years 1997, 1998, and 1999 on ecological land type (ELT) 17 slopes (SW) and ELT 18 slopes (NE).*

et al. 1993; Petranka et al. 1994; Dupuis et al. 1995; Herbeck & Larsen 1999; Grialou et al. 2000) or proximity to forest interior (DeGraaf & Yamasaki 1992; deMaynadier & Hunter 1998, 1999). Other researchers have suggested that salamanders may shift their habitat use after tree harvest from clearcuts to uncut forest (Raymond & Hardy 1991) and may decline in abundance in response to smaller patch size and fragmentation (Gibbs 1998; Hager 1998). Toads and frogs, conversely, tend to be unaffected by and more tolerant than salamanders of forest edges, tree harvests, and declining patch size (deMaynadier & Hunter 1998; Gibbs 1998; Hager 1998).

For the focal species in our study, landscape-scale treatments significantly affected *B. americanus*. This toad species declined in abundance after timber harvest on both even-aged and uneven-aged treatment sites (relative to pretreatment means), yet the significant treatment effect was largely influenced by the concurrent steep decline in abundance on control sites (Fig. 2). Toads on harvested sites may have benefited from an increase in invertebrate density in clearcuts (Harper & Guynn 1999) and declined less sharply on harvested sites than control sites. This finding also suggests that some of the changes observed on treatment sites may not have been the result of the management treatments but rather may have been the result of a regional environmental event. Other MOFEP studies detected similar patterns for birds, mammals, and caterpillars (Gram et al. 2001).

Southern Missouri experienced a mild drought for several years immediately following timber harvest in 1996. For instance, during our pretreatment period, a weather station 8 km from the study area received an average of 135 cm of rainfall per year compared with 132 cm, 118 cm, and 93 cm of rainfall during the 1997, 1998, and 1999 post-treatment years, respectively (National Oceanic and Atmospheric Administration Climatological Data for Ellington, Missouri). The dry conditions created by the mild drought may have had more effect on aphibian

**Table 3. Split-plot repeated measures analysis of variance comparing amphibian abundance among plots located within a clearcut stand, 50 m away from a clearcut stand, and 200 m away from a clearcut stand (distance).**[a]

| | | Ambystoma maculatum | | Bufo americanus | | Notopthalmus viridescens | | Plethodon albagula | | Plethodon serratus | | Pseudacris crucifer | | Rana clamitans | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Source of variation* | *Ndf,Ddf*[b] | F | p | F | p | F | p | F | p | F | p | F | p | F | p |
| Between subjects | | | | | | | | | | | | | | | |
| site[c] | 2,2 | 1.35 | 0.426 | 12.21 | 0.076 | 4.46 | 0.183 | 0.65 | 0.606 | 0.44 | 0.694 | 6.41 | 0.1349 | 7744.14 | 0.001 |
| ELT[c] | 1,2 | 2.22 | 0.275 | 0.24 | 0.675 | 2.66 | 0.244 | 0.46 | 0.569 | 0.07 | 0.815 | 1.77 | 0.315 | 2015.14 | 0.001 |
| distance[d] | 2,4 | 5.49 | 0.071 | 2.01 | 0.249 | 0.37 | 0.710 | 2.35 | 0.211 | 0.40 | 0.697 | 0.57 | 0.605 | 4.58 | 0.092 |
| ELT × distance[e] | 2,4 | 0.53 | 0.625 | 0.96 | 0.458 | 0.17 | 0.847 | 0.55 | 0.615 | 2.80 | 0.174 | 0.55 | 0.617 | 0.02 | 0.983 |
| Within subject[f] | | | | | | | | | | | | | | | |
| year | 2,3 | 15.17 | 0.027 | 88.67 | 0.002 | 0.64 | 0.587 | 19.98 | 0.019 | 9.47 | 0.051 | 132.40 | 0.001 | 3.57 | 0.161 |
| year × ELT | 2,1 | 0.53 | 0.695 | 3.62 | 0.348 | 0.33 | 0.775 | 0.15 | 0.880 | 662.37 | 0.028 | 0.52 | 0.701 | 1.00 | 0.577 |
| year × distance | 4,6 | 1.01 | 0.469 | 1.28 | 0.375 | 1.32 | 0.362 | 1.00 | 0.475 | 0.18 | 0.940 | 1.14 | 0.423 | 0.24 | 0.904 |
| year × distance × ELT | 4,6 | 1.58 | 0.293 | 3.04 | 0.109 | 0.47 | 0.756 | 0.40 | 0.803 | 1.09 | 0.439 | 2.24 | 0.181 | 0.84 | 0.546 |

[a] *Difference scores of mean abundance of pretreatment years (1993, 1994, 1995) minus abundance of each post-treatment year (1997, 1998, 1999) are the repeated measure (i.e., pretreatment – 1997; pretreatment – 1998; pretreatment – 1999). Main effects in the model are site (blocking unit) and ecological land type (ELT), and each ELT is split into distance effects.*

[b] *The Ndf and Ddf are the numbers of degrees of freedom in the numerator and denominator, respectively, for calculating* F.

[c] *Error term is site × ELT.*

[d] *Error term is site × distance.*

[e] *Error term is site × ELT × distance.*

[f] *The* F *approximations of within subjects are based on the multivariate Wilks' lambda test statistic.*

**Table 4. Split-plot repeated measures analysis of variance comparing reptile abundance among plots located within a clearcut stand, 50 m away from a clearcut stand, and 200 m away from a clearcut stand (distance).[a]**

| | | Eumeces fasciatus | | Eumeces laticeps | | Sceloporus undulatus | | Scincella lateralis | | Storeria occipitomaculata | | Virginia valeriea | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Source of variation* | *Ndf,Ddf*[b] | F | p | F | p | F | p | F | p | F | p | F | p |
| Between subjects | | | | | | | | | | | | | |
| site[c] | 2,2 | 6.99 | 0.125 | 0.43 | 0.699 | 0.27 | 0.790 | 2.72 | 0.269 | 1.48 | 0.403 | 1.18 | 0.460 |
| ELT[c] | 1,2 | 0.23 | 0.678 | 0.04 | 0.856 | 0.04 | 0.860 | 1.40 | 0.359 | 0.69 | 0.494 | 1.72 | 0.321 |
| distance[d] | 2,4 | 0 | 1.000 | 1.08 | 0.421 | 163.19 | 0.0001 | 7.22 | 0.047 | 0.83 | 0.500 | 1.15 | 0.404 |
| ELT × distance[e] | 2,4 | 0.84 | 0.496 | 2.66 | 0.185 | 0.18 | 0.845 | 0.57 | 0.604 | 3.22 | 0.147 | 2.18 | 0.229 |
| Within subject[f] | | | | | | | | | | | | | |
| year | 2,3 | 6.11 | 0.876 | 8.83 | 0.055 | 1.88 | 0.296 | 32.50 | 0.009 | 100.20 | 0.002 | 2.91 | 0.198 |
| year × ELT | 2,1 | 1.24 | 0.537 | 373.94 | 0.037 | 0.52 | 0.700 | 3.02 | 0.377 | 0.95 | 0.587 | 115.96 | 0.066 |
| year × distance | 4,6 | 2.58 | 0.144 | 0.42 | 0.788 | 3.24 | 0.097 | 0.80 | 0.565 | 0.93 | 0.507 | 1.33 | 0.359 |
| year × distance × ELT | 4,6 | 0.80 | 0.566 | 1.32 | 0.362 | 1.28 | 0.373 | 2.60 | 0.142 | 0.89 | 0.524 | 0.72 | 0.608 |

[a] *Difference scores of mean abundance of pre-treatment years (1993, 1994, 1995) minus abundance of each post-treatment year (1997, 1998, 1999) are the repeated measure (i.e., pretreatment - 1997; pretreatment - 1998; pretreatment - 1999). Main effects in the model are site (blocking unit) and ecological land type (ELT), and each ELT is split into distance effects.*

[b] *The Ndf and Ddf are the numbers of degrees of freedom in the numerator and denominator, respectively, for calculating* F.

[c] *Error term is site × ELT.*

[d] *Error term is site × distance.*

[e] *Error term is site × ELT × distance.*

[f] *The* F *approximations of within subjects are based on the multivariate Wilks' lambda test statistic.*

populations and activity, and thus on our relative abundance estimates, than did the forest-management treatments.

Our results demonstrate the importance of sampling control sites over the same time period as treatment sites and including pretreatment data. If we had simply compared pretreatment to post-treatment abundances on treatment sites, we would have concluded that both even-aged and uneven-aged management exerted large treatment effects (Fig. 2). Likewise, without pretreatment data, we may have been less aware of the regional fluctuations in abundances over time. With data from control sites and pretreatment years, we eliminated the effects of these potentially confounding factors from the statistical analyses, which partially explains why we found few treatment effects despite visibly large post-treatment changes in the abundance of many amphibian and reptile species (Figs. 2 & 3). Ecologically, however, we acknowledge that this regional decline complicates interpretation of the results.

Amphibian species in general were affected by clearcutting at the local scale (i.e., many species declined from pre- to post-treatment; Fig. 4). If we consider this result in light of the landscape-scale results, however, it is more likely that the declines in all distance classes reflect a combination of timber harvest and environmental factors. The results for *A. maculatum* fit the predicted pattern, with salamander abundances declining within clearcut stands (Fig. 4). These results support findings from other studies that demonstrate that amphibians decline in stands that have been recently harvested (DeGraaf & Yamasaki 1992; deMaynadier & Hunter 1998), yet confounding environmental factors may have also led to abundance declines at distances up to 200 m from clearcuts. We had low capture rates for *R. clamitans*, and the significant treatment effect was due to an increase in capture rates on NEELTs at 50 m from clearcuts. This result may be a sampling or statistical anomaly that does not have biological significance.

We expected lizard abundance to increase and snake abundance to remain unchanged following even-aged and uneven-aged timber harvest. Many studies report an increase in lizard abundance within harvested areas (Enge & Marion 1986; Bury & Corn 1988; Raphael 1988; Goldingay et al. 1996) or at forest edges (Schlaepfer & Gavin 2001). Among our six reptile species, distance from clearcut significantly affected two lizard species, *S. undulatus* and *S. lateralis*, but landscape-scale treatment affects were not significant (Figs. 3 & 5). We detected a significant year-by-treatment interaction for *V. valeriae*, suggesting that smooth earthsnakes were more active and thus were captured more frequently on SWELTs in uneven-aged management sites immediately following harvest (Fig. 3). Several lizard species, including *Eumeces fasciatus*, *S. lateralis*, and *S. undulatus*, showed a trend toward higher relative abundance in even-aged and/or uneven-aged management treatments (Fig. 3), and, with higher statistical power, we may have detected significant changes. As this experiment continues and more mature forest is harvested for timber, we suspect that we will be able to detect a landscape-scale treatment effect for some of these species.

The significant increase in the abundance of *S. undulatus* within clearcut stands relative to distance classes farther away from harvested stands was not surprising

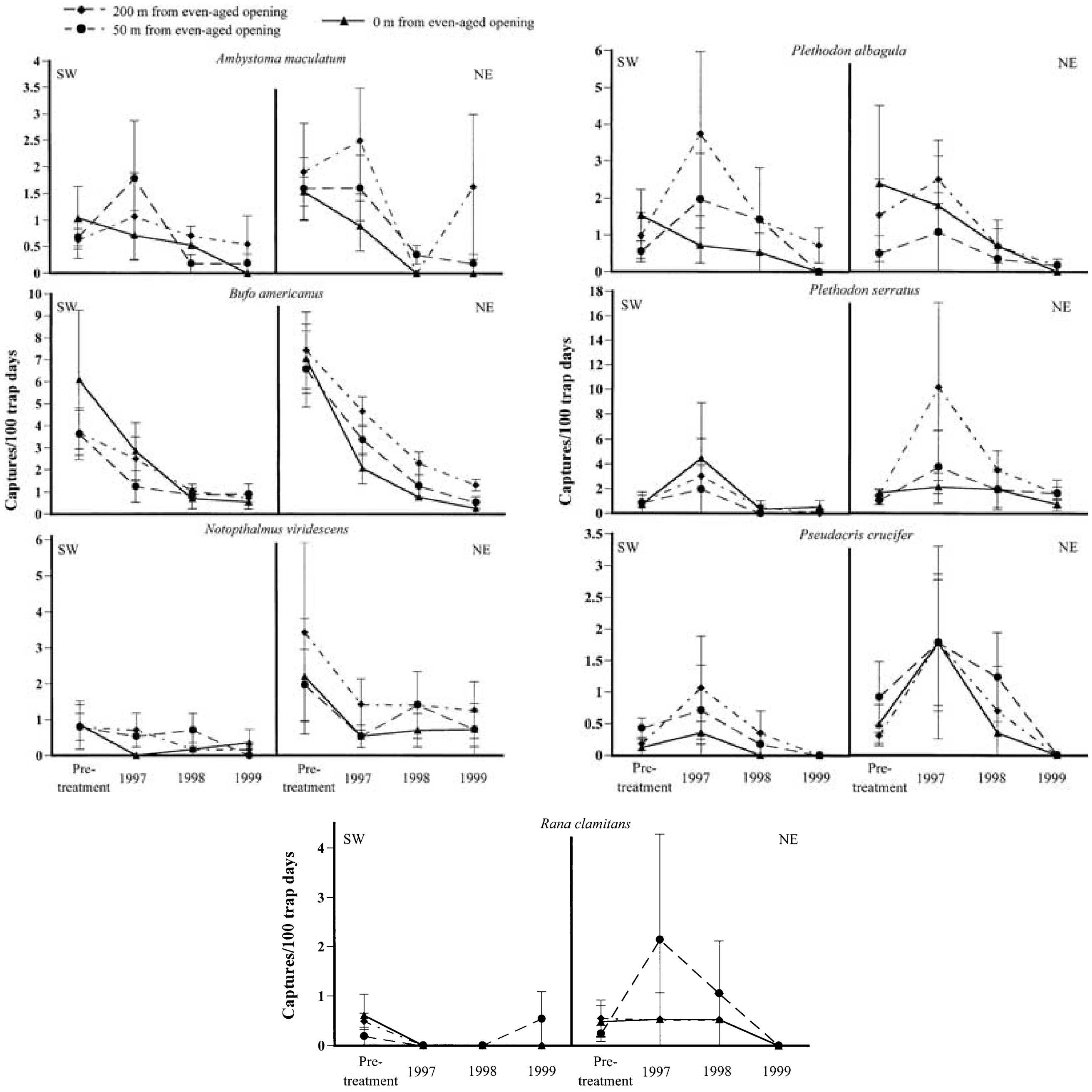

*Figure 4. Mean relative abundance (±1 SE) for focal amphibian species within clearcut stands, 50 m away from a clearcut stand, and 200 m away from a clearcut stand during pretreatment (mean of years 1993–1995) and post-treatment years 1997, 1998, and 1999 on ecological land type (ELT) 17 slopes (SW) and ELT 18 slopes (NE).*

based on results from other studies that focused on the local-scale effects of clearcutting (Bury & Corn 1988). Lizard survival and reproduction are influenced by perch use and food availability (Parker 1994; Ballinger 1977). *S. undulatus* may have experienced increased survival and/or reproductive success within the clearcuts. The altered forest structure and environmental conditions (e.g., slash on the ground, temperature, soil moisture) within cuts may have increased food availability, which may have contributed to increased reproductive success. During the fall months of the post-treatment years, the relative abundance of juvenile *S. undulatus* was nearly twice as high as that of adults (juvenile-to-adult ratio of 1:0.52 during post-treatment years and 1:1.15 during pretreatment years), suggesting that *S. undulatus* experienced increased reproductive success in disturbed areas. Because of the abundance of basking sites within cuts, lizards may have been in better condition, potentially contributing to increased survival and reproductive success in these areas.

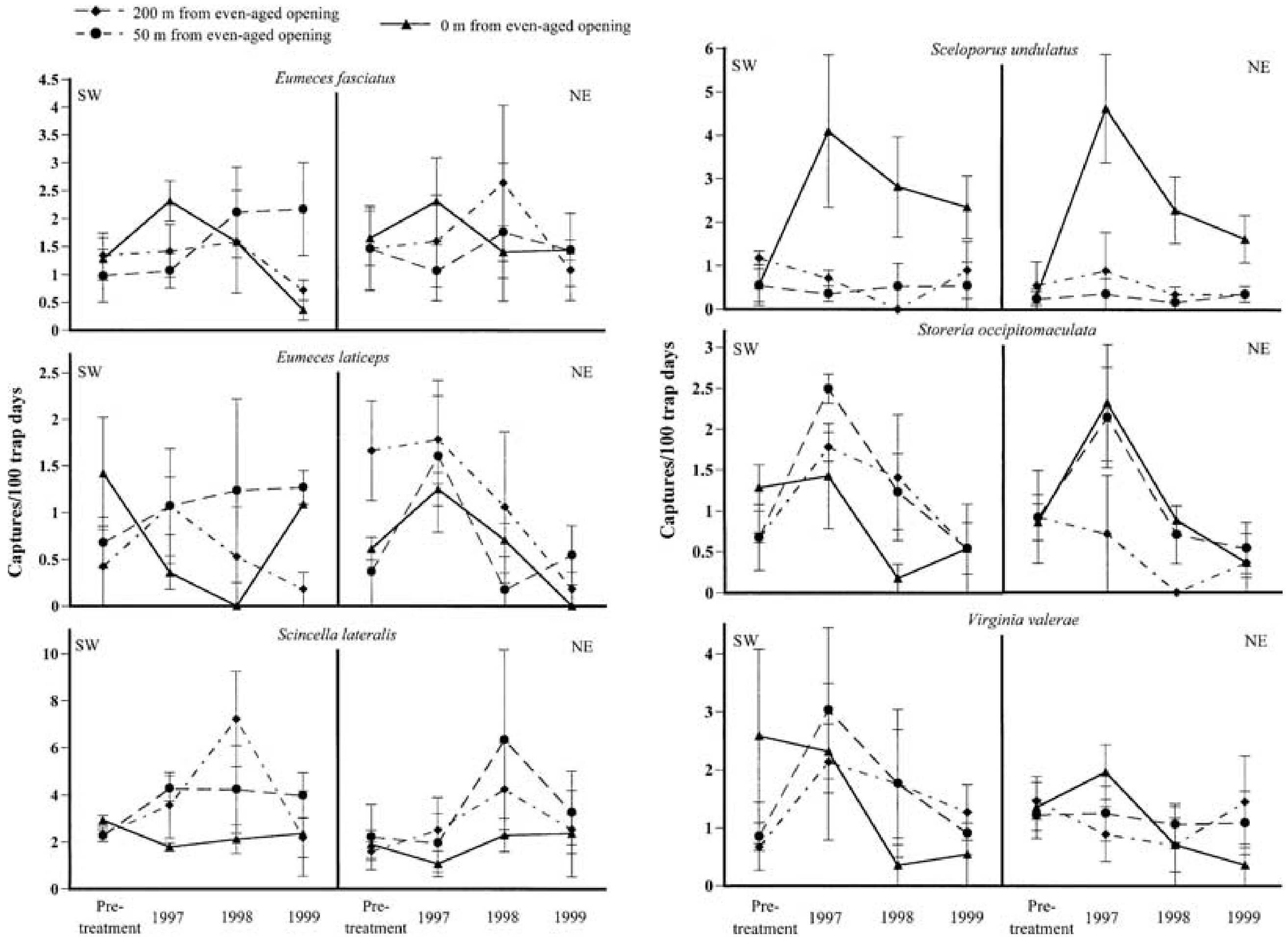

*Figure 5. Mean relative abundance (±1 SE) for focal reptile species within clearcut stands, 50 m away from a clearcut stand, and 200 m away from a clearcut stand during pretreatment (mean of years 1993–1995) and post-treatment years 1997, 1998, and 1999 on ecological land type (ELT) 17 slopes (SW) and ELT 18 slopes (NE).*

The results for *S. lateralis* are more puzzling. *S. lateralis* inhabits the litter layer on the forest floor and eats insects and spiders within the litter (Brooks 1967). Other studies have shown that areas of recent tree harvest have reduced litter cover (Pough et al. 1987; Harpole & Haas 1999), and increases in skink abundance may be the result of changes in local resource availability. The increase in the relative abundance of *S. lateralis* in uncut forest surrounding clearcuts may complement the observed increase in abundance in uneven-aged sites (Figs. 3 & 5). On uneven-aged sites, small openings created by group-selection harvests left a landscape composed of small, disturbed patches dispersed throughout the study site, with abundant uncut forest, or edge, surrounding harvested areas. This patchwork of openings with associated edge may have produced the same response in *S. lateralis* as that observed in uncut forests surrounding clearcuts, only the effect was dispersed throughout the study site.

The maintenance of the biodiversity, or functional diversity (Silver et al. 1996), of ecosystems is a goal of natural resource managers and conservation biologists. Given the preponderance of evidence about the detrimental local-scale impacts of timber harvest on amphibians, there is valid concern that forest management reduces diversity by causing population declines or extirpations across the landscape (Waldick 1997). Our project addressed this issue by testing the effects of several forest-management strategies on amphibians and reptiles at multiple spatial and, eventually, temporal scales. We did not detect a detrimental effect of these initial even-aged and uneven-aged forest-management treatments on the abundance of most amphibians and reptiles in Missouri Ozark forests, but we caution that low statistical power may have limited our ability to detect small yet potentially important effects. We also acknowledge that our conclusions may change as this long-term experiments proceeds. These findings represent relatively short-term data, but they suggest that forest management and maintenance of biodiversity may be compatible when relatively small amounts of the landscape are disturbed.

## Acknowledgments

We thank the more than 50 field assistants who collected data for this project under arduous conditions. Without their dedication, strength, and ingenuity, the amphibian and reptile study of the Missouri Ozark Forest Ecosystem Project would not have occurred. We also thank supervisors and colleagues at the Missouri Department of Conservation who supported and facilitated our work. We appreciate comments on the manuscript by J. Grabner, J. Kabrick, B. McComb, and five anonymous reviewers. This research was funded, in part, by the Federal Aid in Wildlife Restoration Act, under Pittman-Robertson Project W-13-R.

### Literature Cited

Annand, E. M., and F. R. Thompson. 1997. Forest bird response to regeneration practices in central hardwood forests. Journal of Wildlife Management **61:**159–171.

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

Ballinger, R. E. 1977. Reproductive strategies: food availability as a source of proximal variation in a lizard. Ecology **58:**628–635.

Blymer, M. J., and B. S. McGinnes. 1977. Observations on possible detrimental effects of clearcutting on terrestrial amphibians. Bulletin of the Maryland Herpetological Society **13:**79–83.

Brooks, G. R. 1967. Population ecology of the ground skink, *Lygosoma laterale* (Say). Ecological Monographs **37:**71–87.

Brookshire, B. L., and C. Hauser. 1993. The Missouri Forest Ecosystem Project. Pages 289–306 in A. R. Gillespie, G. R. Parker, P. E. Pope, and G. Rink, editors. The 9th central hardwood forest conference. General technical report NC-161. U.S. Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota.

Brookshire, B. L., and D. C. Dey. 2000. Establishment and data collection of vegetation-related studies on the Missouri Ozark Forest Project study sites. Pages 1–18 in S. R. Shifley and B. L. Brookshire, editors. Missouri Ozark Forest Ecosystem Project: site history, soils, landforms, woody and herbaceous vegetation, down wood, and inventory methods for the landscape experiment. General technical report NC-193. U.S. Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota.

Brookshire, B. L., R. Jensen, and D. C. Dey. 1997. The Missouri Ozark Forest Ecosystem Project: past, present and future. Pages 1–25 in B. L. Brookshire and S. R. Shifley, editors. Missouri Ozark Forest Ecosystem Project symposium: an experimental approach to landscape research. General technical report NC-193. U.S. Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota.

Bury, R. B., and P. S. Corn. 1988. Douglas-fir forests in the Oregon and Washington Cascades: relation of the herpetofauna to stand age and moisture. Pages 11–22 in R. C. Szaro, K. E. Severson, and D. R. Patton, editors. Management of amphibians, reptiles, and small mammals in North America. General technical report, RM-166. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Tempe, Arizona.

Chen, J., S. C. Saunders, T. R. Crow, R. J. Naiman, K. D. Brosofske, G. D. Mroz, B. L. Brookshire, and J. F. Franklin. 1999. Microclimate in forest ecosystem and landscape ecology. BioScience **49:**288–297.

Cunningham, R. J., and C. Hauser. 1989. The decline of the Missouri Ozark forest between 1880 and 1920. Pages 34–37 in T. A. Waldrup, editor. Pine hardwood mixtures: a symposium on management and ecology of the type. General technical report 58. U.S. Forest Service, Atlanta.

DeGraaf, R. M., and M. Yamasaki. 1992. A nondestructive technique to monitor the relative abundance of terrestrial salamanders. Wildlife Society Bulletin **20:**260–264.

DeGraaf, R. M., and M. Yamasaki. 2002. Effects of edge contrast on redback salamander distribution in even-aged northern hardwoods. Forest Science **48:**351–363.

deMaynadier, P. G., and M. L. Hunter. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Review **3:**230–261.

deMaynadier, P. G., and M. L. Hunter. 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. Conservation Biology **12:**340–352.

deMaynadier, P. G., and M. L. Hunter. 1999. Forest canopy closure and juvenile emigration by pool-breeding amphibians in Maine. Journal of Wildlife Management **63:**441–450.

Dupuis, L. A., J. M. Smith, and F. Bunnell. 1995. Relation of terrestrial-breeding amphibian abundance to tree-stand age. Conservation Biology **9:**645–653.

Enge, K. M., and W. R. Marion. 1986. Effects of clearcutting and site preparation on herpetofauna of a north Florida flatwoods. Forest Ecology and Management **14:**177–192.

Gibbs, J. P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. Landscape Ecology **13:**263–268.

Goldingay, R., G. Daly, and F. Lemckert. 1996. Assessing the impacts of logging on reptiles and frogs in the montane forests of southern New South Wales. Wildlife Research **23:**495–510.

Gram, W. K., V. L. Sork, R. J. Marquis, R. B. Renken, R. L. Clawson, J. Faaborg, D. K. Fantz, J. Le Corff, J. Lill, and P. Porneluzi. 2001. Evaluating the effects of ecosystem management: a case study in a Missouri Ozark forest. Ecological Applications **11:**1667–1679.

Greenberg, C. H., D. G. Neary, and L. D. Harris. 1994. Effect of high-intensity wildfire and silvicultural treatments on reptile communities in sand-pine scrub. Conservation Biology **8:**1047–1057.

Grialou, J. A., S. D. West, and R. N. Wilkins. 2000. The effects of forest clearcut harvesting and thinning on terrestrial salamanders. Journal of Wildlife Management **64:**105–113.

Guerry, A. D., and M. L. Hunter. 2002. Amphibian distributions in a landscape of forests and agriculture: an examination of landscape composition and configuration. Conservation Biology **16:**745–754.

Guyette, R., and D. Larsen. 2000. A history of anthropogenic and natural disturbances in the area of the Missouri Ozark Forest Ecosystem Project. Pages 19–40 in S. R. Shifley and B. L. Brookshire, editors. Missouri Ozark Forest Ecosystem Project: site history, soils, landforms, woody and herbaceous vegetation, down wood, and inventory methods for the landscape experiment. U.S. Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota.

Hager, H. A. 1998. Area-sensitivity of reptiles and amphibians: are there indicator species for habitat fragmentation? Ecoscience **5:**139–147.

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

Harpole, D. N., and C. A. Haas. 1999. Effects of seven silvicultural treatments on terrestrial salamanders. Forest Ecology and Management **114:**349–356.

Healy, W. M., and R. T. Brooks. 1988. Small mammal abundance in northern hardwood stands of different ages in West Virginia. Journal of Wildlife Management **52:**491–496.

Herbeck, L. A., and D. R. Larsen. 1999. Plethodontid salamander response to silvicultural practices in Missouri Ozark forests. Conservation Biology **13:**623–632.

Huhta, V. 1976. Effects of clearcutting on numbers, biomass and community respiration of soil invertebrates. Annales Zoologici Fennici **13:**63–80.

Jones, K. B. 1981. Effects of grazing on lizard abundance and diversity in western Arizona. Southwestern Naturalist **26:**107–115.

Kabrick, J. M., R. G. Jensen, S. R. Shifley, and D. R. Larsen. 2002. Woody vegetation following even-aged, uneven-aged, and no-harvest treatments on the Missouri Ozark Forest Ecosystem Project (MOFEP). Pages 84–101 in S. R. Shifley and J. M. Kabrick, editors. Proceedings of the second Missouri Ozark forest ecosystem symposium: post-treatment results of the landscape experiment. General technical report NC-227. U.S. Forest Service, St. Paul, Minnesota.

Kurzejeski, E. W., R. L. Clawson, R. B. Renken, S. L. Sheriff, L. D. Vangilder, C. Hauser, and J. Faaborg. 1993. Experimental evaluation of forest management: the Missouri Ozark Forest Ecosystem Project. Transactions of the North American Wildlife and Natural Resource Conference **58:**599–609.

Marsh, D. M. 2001. Fluctuations in amphibian populations: a meta-analysis. Biological Conservation **101:**327–335.

Marsh, D. M., and P. B. Pearman. 1997. Effects of habitat fragmentation on the abundance of two species of Leptodactylid frogs in an Andean montane forest. Conservation Biology **11:**1323–1328.

Meinert, D., T. Nigh, and J. Kabrick. 1997. Landforms, geology and soils of the MOFEP study sites. Pages 56–68 in B. L. Brookshire and S. R. Shifley, editors. Missouri Ozark Forest Ecosystem Project symposium: an experimental approach to landscape research. General technical report NC-193. U.S. Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota.

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

Missouri Department of Conservation (MDC) 1986. Forest management guidelines. MDC, Jefferson City.

Monthey, R. W., and E. C. Soutiere. 1985. Responses of small mammals to forest harvesting in northern Maine. Canadian Field Naturalist **99:**13–18.

Parker, W. S. 1994. Demography of the fence lizard, *Sceloporus undulatus*, in northern Mississippi. Copeia **994:**136–152.

Pearman, P. B. 1997. Correlates of amphibian diversity in an altered landscape of Amazonian Ecuador. Conservation Biology **11:**1211–1225.

Pechmann, J. H. K., D. E. Scott, R. D. Semlitsch, J. P. Caldwell, L. J. Vitt, and J. W. Gibbons. 1991. Declining amphibian populations: the problems of separating human impacts from natural fluctuations. Science **253:**892–895.

Petranka, J. W., M. E. Eldridge, and K. E. Haley. 1993. Effects of timber harvesting on southern Appalachian salamanders. Conservation Biology **7:**363–370.

Petranka, J. W., M. P. Brannon, M. E. Hopey, and C. K. Smith. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. Forest Ecology & Management **67:**135–147.

Pough, F. H., E. M. Smith, D. H. Rhodes, and A. Collazo. 1987. The abundance of salamanders in forest stands with different histories of disturbance. Forest Ecology and Management **20:**1–10.

Raphael, M. G. 1988. Long-term trends in abundance of amphibians, reptiles, and mammals in Douglas-fir forests of northwestern California. Pages 23–31 in R. C. Szaro, K. E. Severson, and D. R. Patton, editors. Management of amphibians, reptiles, and small mammals in North America. General Technical Report RM-166. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Tempe, Arizona.

Raymond, L. R., and L. M. Hardy. 1991. Effects of a clearcut on a population of the mole salamander, *Ambystoma talpoideum*, in an adjacent unaltered forest. Journal of Herpetology **25:**509–512.

Renken, R. B. 1997. Pre-treatment conditions of herpetofaunal communities on Missouri Ozark Forest Ecosystem Project (MOFEP) sites, 1992–1995. Pages 289–308 in B. L. Brookshire and S. R. Shifley, editors. Missouri Ozark Forest Ecosystem Project symposium: an experimental approach to landscape research. General technical report NC-193. U.S. Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota.

Renken, R. B., and D. Fantz. 2002. Immediate, landscape-scale impacts of even-aged and uneven-aged forest management on herpetofaunal communities of the Missouri Ozark forest ecosystem project. Pages 171–183 in S. R. Shifley and J. M. Kabrick, editors. Proceedings of the second Missouri Ozark forest ecosystem symposium: post-treatment results of the landscape experiment. General technical report NC-227. U.S. Forest Service, St. Paul, Minnesota.

Schlaepfer, M. A., and T. A. Gavin. 2001. Edge effects on lizards and frogs in tropical forest fragments. Conservation Biology **15:**1079–1090.

Sheriff, S. L., and Z. He. 1997. The experimental design of the Missouri Ozarks Forest Ecosystem Project. Pages 26–40 in B. L. Brookshire and S. R. Shifley, editors. Missouri Ozark Forest Ecosystem Project symposium: an experimental approach to landscape research. General technical report NC-193. U.S. Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota.

Silver, W. L., S. Brown, and A. E. Lugo. 1996. Effects of changes in biodiversity on ecosystem function in tropical forests. Conservation Biology **10:**17–24.

Theenhaus, A., and M. Schaefer. 1995. The effects of clear-cutting and liming on the soil macrofauna of a beech forest. Forest Ecology and Management **77:**35–51.

Thompson, F. R., J. R. Probst, and M. G. Raphael. 1995. Impacts of silviculture: overview and management recommendations. Pages 201–219 in T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds. Oxford University Press, Oxford, United Kingdom.

von Ende, C. N. 1993. Repeated-measures analysis: growth and other time-dependent measures. Pages 113–137 in S. M. Scheiner, and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman & Hall, New York.

Waldick, R. 1997. Effects of forestry practices on amphibian populations in eastern North America. Herpetological Conservation **1:**191–205.

Xu, M., S. C. Saunders, and J. Chen. 1997. Analysis of landscape structure in the southeastern Missouri Ozarks. Pages 41–55 in B. L. Brookshire and S. R. Shifley, editors. Missouri Ozark Forest Ecosystem Project symposium: an experimental approach to landscape research. General technical report NC-193. U.S. Forest Service, St. Paul, Minnesota.

Yahner, R. H. 1992. Dynamics of a small mammal community in a fragmented forest. American Midland Naturalist **127:**381–391.

Zheng, D., J. Chen, B. Song, M. Xu, P. Sneed, and R. Jansen. 2000. Effects of silvicultural treatments on summer forest microclimate in southeastern Missouri Ozarks. Climate Research **15:**45–59.