Forest Ecology and Management 271 (2012) 124–131

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

# Effects of short-rotation controlled burning on amphibians and reptiles in pine woodlands

Roger W. Perry [a,*], D. Craig Rudolph [b], Ronald E. Thill [b]

[a] Southern Research Station, Forest Service, U.S. Department of Agriculture, P.O. Box 1270, Hot Springs, AR 71902, USA
[b] Southern Research Station, Forest Service, U.S. Department of Agriculture, 506 Hayter Street, Nacogdoches, TX 75965-3556, USA

ARTICLE INFO

*Article history:*
Received 6 December 2011
Received in revised form 2 February 2012
Accepted 3 February 2012

*Keywords:*
Amphibians
Arkansas
Burning
Fire
Lizards
Snakes

ABSTRACT

Fire is being used increasingly as a forest management tool throughout North America, but its effects on reptiles and amphibians in many ecosystems are unclear. Open woodlands with understories dominated by herbaceous vegetation benefit many wildlife species, but maintaining these woodlands requires frequent burning. Although many studies have compared herpetofaunal responses in burned forests to unburned forests, fewer studies have examined changes in the herpetofaunal community during the interval between short-rotation prescribed burns. We examined changes in habitat and relative abundance of reptiles and amphibians each year within a 3-year burn cycle in nine restored pine woodlands of western Arkansas, USA. Overall numbers of reptiles did not change among the three burn years; however, capture rates for one snake species (southern black racer [*Coluber constrictor priapus*]) and three lizards differed among the three post-burn years. Overall capture rate for anurans and all amphibians combined was greatest the first year after burning, mostly because captures of dwarf American toads (*Bufo americanus charlessmithi*) were substantially greater in stands the first year after burning. Salamander captures were infrequent. Capture rates of most reptile and amphibian species declined over the 3-year sampling period. Only minor changes in capture rate occurred among the 36 species we evaluated during the intervening years between frequent burns. Capture rates for only two species were lower the first year after fire. Although not all herpetofaunal species benefited from frequent fire, most species appeared to tolerate the frequent burning necessary for maintaining open pine woodlands in the Ouachita Mountains.

Published by Elsevier B.V.

## 1. Introduction

Fire is an important disturbance that shapes biological communities, resulting in fire-maintained ecosystems in many regions of the world (Friend, 1993; Trainor and Woinarski, 1994; Russell et al., 1999; Means, 2006). Historically, fires were a common occurrence across most of the eastern US, but fire suppression during the past century led to profound changes in these forests (e.g., Sharitz et al., 1992; Lorimer, 2001; Van Lear and Harlow, 2002; Spetich et al., 2011). Fire is currently being used as a tool by forest managers throughout North America for many reasons, including ecological restoration, improving wildlife habitat, reducing hazardous fuel loads and wildfire risk, forest regeneration, and reducing competing vegetation (Hunter, 1990). With this increased use of fire as a management tool, information on its effects on fauna is becoming increasingly important.

Interest in herpetofauna (reptiles and amphibians) has increased in recent years due to worldwide declines in amphibian and reptile populations (e.g., Wake, 1991; Gibbons et al., 2000; Houlahan et al., 2000; McCallum, 2007). There is also increased awareness of the potential effects forest management, including prescribed burning on herpetofauna (e.g., deMaynadier and Hunter, 1995; Ash, 1997; Pilliod et al., 2003). Although fires may affect herpetofauna directly by killing individuals, evidence suggests few herpetofauna are directly killed by fire in fire-maintained ecosystems, and many species have adaptations that allow survival during fires (e.g., Means and Campbell, 1982; Friend, 1993; Russell et al., 1999; Pilliod et al., 2003).

More significantly, habitat alterations resulting from fire (or the lack of fire) may have substantial effects on herpetofauna (Russell et al., 1999). For example, altered fire regimes have been implicated in the extirpation of a number of amphibian species in the US (Bradford, 2005). Although fire-maintained ecosystems are important to many herpetofaunal communities (e.g., Trainor and Woinarski, 1994; Russell et al., 1999; Means, 2006), responses of herpetofauna to the structural changes in forests that occur as a result of fire are unknown for many ecosystems. Forest structure altered by fire may affect predation rates by increasing foraging efficiency of predators (Pilliod et al., 2003), or may reduce the resources needed for survival such as food and shelter, resulting in movements of herpetofauna to areas with more favorable

---

* Corresponding author. Tel.: +1 501 623 1180x108; fax: +1 501 623 0186.
*E-mail address:* rperry03@fs.fed.us (R.W. Perry).

0378-1127/$ - see front matter Published by Elsevier B.V.
doi:10.1016/j.foreco.2012.02.004

conditions (e.g., Semlitsch et al., 2008). Thus, knowing how herpetofauna respond to fire is important for implementing ecologically sensitive burning programs.

Considerable research has examined herpetofauna populations in burned versus unburned areas or in restored fire-dependent communities versus unrestored communities (e.g., McLeod and Gates, 1998; Litt et al., 2001; Moseley et al., 2003; Keyser et al., 2004; Thill et al., 2004; Langford et al., 2007; Perry et al., 2009). Less information is available on effects of fire return intervals on herpetofauna. Some fire frequencies may be better than others for promoting herpetofaunal diversity (Mushinsky, 1985). For example, Mushinsky (1985) found the greatest diversity of herpetofauna in areas burned yearly and those burned every 7 years, but diversity was lowest on areas burned every 2 years in Florida sand-pine (*Pinus clausa*) scrub. Nevertheless, few studies have examined herpetofaunal communities during the interval between short-rotation controlled burns in restored fire-adapted ecosystems such as the Ouachita Mountains of Oklahoma and Arkansas. Our goal was to assess changes in relative abundance of individual reptile and amphibian species in pine woodlands within the 3-year burn interval between recurrent fires to determine short-term changes in the herpetofaunal community within restored, fire-maintained pine woodlands. These woodlands were restored and maintained as part of a program to enhance habitat for the endangered red-cockaded woodpecker (*Picoides borealis*) (Bukenhofer and Hedrick, 1997). Prior studies using these herpetofauna data have compared captures in restored, frequently burned pine woodlands with unrestored, unburned forests (Perry et al., 2009). Preliminary analyses of diversity, richness, and abundance among years after burn (by species groups) were presented by Thill et al. (2004).

## 2. Methods

### 2.1. Study areas

We conducted the study on the Poteau Ranger District (lat 34°45′N, long 94°15′W) of the Ouachita National Forest (ONF), located in the Ouachita Mountains of western Arkansas, USA. The Ouachita Mountain ecological subregion extends from central Arkansas into eastern Oklahoma and consists of east- to west-oriented mountains. Throughout this region, elevation ranges from 100 to 800 m, mean annual precipitation ranges from 112 to 142 cm, mean annual temperature ranges from 16.0 to 17.0 °C, and the growing season is 200–240 days (McNab and Avers, 1994). Soils in the area are derived from shale and sandstone and are typically shallow, rocky, and drought prone (Masters et al., 1993). The predominant forest type in the area is mixed shortleaf pine (*Pinus echinata*)-hardwood forests. The hardwood component in these forests is diverse and includes oaks (*Quercus* spp.), hickories (*Carya* spp.), and red maple (*Acer rubrum*).

All sampling was conducted in restored pine woodlands. We randomly selected nine restored pine-woodland stands from those available. All stands were 10.5–42.1 ha (mean 25.0 ha) in size, generally rectangular in shape, and had slopes less than 20%. Prior to restoration, these stands were mature (>50 years old), second-growth, pine-hardwood forests (Perry et al., 2009). Initial restoration included thinning of the overstory and felling of most midstory trees, which left pine basal areas (BA) of approximately 13–16 $m^2$/ha and residual hardwood BAs of approximately 2 $m^2$/ha. Study stands underwent thinning 9 or more years prior to initiation of our study and had undergone three or more (range 3–7, average = 5.4) prescribed burns. Prescribed burns were previously conducted at 2- to 5-year intervals, usually during winter or early spring. Unthinned 15- to 50-m-wide buffers (greenbelts) were retained around stream drainages for protection of water quality within most stands. Water flow in these drains was usually limited to heavy rain events. Forests in greenbelts were mature (>50 years old), mixed pine-hardwood, and were remnant, second-growth forests. Greenbelts were burned when the surrounding woodlands were burned, but typically burned less intensely and less thoroughly.

### 2.2. Treatments

During the 3 years of our study (1999–2001), stands were burned on a 3-year burning cycle. All prescribed burns were conducted in March and April (during early green up) and all burned stands were part of larger burning units (65–1336 ha). Thus, most study stands were contiguous to large areas of burned forest. Each year, three of the nine stands (those burned 3 years prior) were burned following their third growing season. Thus, each year, we sampled three stands during their first growing season, three stands during their second growing season, and three stands during their third growing season after prescribed burning, and each stand was sampled during every phase of the 3-year burning cycle.

### 2.3. Herpetofauna sampling

We sampled herpetofauna using drift fence arrays connected to central funnel traps. Each array consisted of 4, 15-m-long fences (90° apart) constructed of steel hardware cloth (3.2-mm mesh) with a 1.2- × 1.2- × 0.46-m-high funnel trap in the center (Burgdorf et al., 2005). Bottoms of fences were buried 10–15 cm in the ground. A pitfall (18.9-L plastic bucket) was buried flush with the soil surface at the distal end of each drift fence. We placed elevated plywood covers over pitfalls to provide shade and deflect precipitation and we placed leaf litter in buckets to provide cover and microhabitat for captured animals. We provided a water dispenser in each trap.

In each stand, we installed three arrays. Arrays were >150 m apart, >50 m from roads or stand edges, and >75 m from permanent or intermittent streams, ponds, and greenbelts. We checked traps weekly from early April until late September for 3 years (1999–2001); trapping effort was equal among all stands and years (24 weeks each year). We recorded all captured vertebrates and immediately released them >50 m from the trap array. We followed appropriate animal care guidelines (see Guidelines for Use of Live Amphibians and Reptiles in Field Research; American Society of Ichthyologists and Herpetologists; http://www.asih.org/files/hacc-final.pdf). We did not mark captured individuals because of safety concerns associated with lone field personnel marking venomous snakes in remote areas. Therefore, we used total captures as an index of relative abundance among the three post-burn years.

### 2.4. Habitat sampling

We measured habitat in September and early October at four plots surrounding each array (12 plots in each stand). A plot was located 7 m beyond the distal end of each drift fence. At plot center, we measured canopy closure (%) with a spherical densiometer, and overstory and midstory (conifer and hardwood combined) BA using a prism. In three adjacent 2- × 2-m subplots, we visually estimated (±10%) down wood cover. In three nested 1- × 1-m subplots, we visually estimated percent cover of grass, forbs, leaf litter, rock and bare ground, and woody understory vegetation ($\leqslant$2 m high). In the center of each 1- × 1-m subplot, we measured litter depth and assigned depth to 1 of 6 classes: 1 = 0 cm, 2 = 0.1–2.0 cm, 3 = 2.1– 4.0 cm, 4 = 4.1– 6.0 cm, 5 = 6.1– 8.0 cm, and 6 $\geqslant$ 8.1 cm. Within an 11.3-m-radius semicircle, we measured the volume of each log with an average diameter 10 cm or greater using Smalian's cubic volume estimate (Avery and Burkhart, 1994).

We estimated horizontal vegetation density using a 0.5- × 0.5-m density board (MacArthur and MacArthur, 1961). For horizontal vegetation density, we measured the distance (out to a maximum of 50 m) at which 50% of the density board was obscured by vegetation at three heights: ground level to 0.5 m high (ground level), 0.75–1.25 m above the ground (1 m above the ground), and 1.75–2.25 m above the ground (2 m above the ground). We estimated a modified foliage density index ($k$) for each height, using $k = 10(\ln[2]/D)$, where $D$ = distance from the observer to the density board (MacArthur and MacArthur, 1961). We measured overstory BA in 1999 and 2001 and all understory measures annually.

### 2.5. Analyses

We sampled restored woodland stands 1-, 2-, and 3-growing seasons after burning (Year 1, Year 2, and Year 3) over 3 years (1999–2001). In successive years, Year 1 stands became Year 2 stands, Year 2 stands became Year 3 stands, and Year 3 stands were subjected to prescribed burning to become Year 1 stands again. Thus, each stand was sampled during every phase of the 3-year burning cycle. We determined means for each vegetative parameter by burn year (Year 1-Year 3) to demonstrate changes in habitat throughout the burn cycle. We compared mean values for each vegetative parameter among the three post-burn periods using a repeated measures analysis of variance (ANOVA) in a mixed model (Proc Mixed; Littell et al., 1996); we included time (year) as a random effect and years after burn (Year 1–Year 3) as the fixed treatment effect. Prior to analysis, we tested residuals for each habitat parameter for normality using Shapiro–Wilk tests (SAS Institute Inc., 2000); we transformed data ($\ln[x+]$) to meet the assumptions of normality and used ranks when data could not be normalized. We used Tukey multiple comparisons to separate least squared means when ANOVA indicated a significant difference among treatments (SAS Institute Inc., 2000). For the multiple tests of habitat parameters, we used the Benjamini–Hochberg method to control the positive false discovery rate (FDR) for the overall experiment at 0.05 (Benjamini and Hochberg, 1995; Waite and Campbell, 2006).

To test for year-after-burn effects on each herpetofaunal species, we used ANOVA in a crossover design (Kuehl, 2000). We first tested each species for sequence and carryover effects. We found no significant sequence or carryover effects for any species; thus, we tested for fixed treatment effects (year after burn), year (year of sampling; 1999–2001), and treatment × year effects without carryover or sequence effects. We considered analyses for each species to be independent experiments, and we evaluated all tests at alpha = 0.05. Prior to analysis, we tested residuals for each herpetofaunal species for normality using Shapiro–Wilk tests (SAS Institute Inc., 2000). We transformed data to meet the assumptions of normality using $\ln(x + 1)$ or $1/(x + 0.5)$ transformations, but used ranks when data could not be normalized (Conover and Iman, 1981). We used Tukey multiple comparisons to separate means when ANOVA indicated a significant difference among treatments (SAS Institute Inc., 2000). We conducted analysis only on species with eight or more captures that were captured in six or more stands to reduce the likelihood of making inaccurate inferences from sparse data.

## 3. Results

Among all study sites ($n = 9$), overstory BA averaged 18.83 $m^2$/ha (±0.50 SE), midstory BA averaged 1.63 $m^2$/ha (±0.09), and canopy cover averaged 68.7% (±2.0). Grass cover, down wood, litter depth, volume of down logs, and foliage density index at ground level did not differ among the post-burn years (Table 1). However, Year 1 stands had greater forb cover and less woody plant cover than Year 3 stands. Furthermore, Year 1 stands had less leaf litter cover, more rocks and bare ground, and a lower foliage density index at 1 m and 2 m above the ground than the other two post-burn years.

We captured 2077 reptiles of 33 species and 1962 amphibians of 18 species. Overall numbers of reptiles, snakes, and turtles did not differ among years after burn (Table 2). Southern black racers (*Coluber constrictor priapus*) were the only species of snake that differed in total captures among burn periods, with captures greater in Year 2 and Year 3 stands than Year 1 stands. Among snakes that were too rare for analysis, a total of six brown snakes (*Storeria dekayi*) and five western worm snakes (*Carphophis vermis*) were captured in all 3 years after burn; one western cottonmouth (*Agkistrodon piscivorus leucostoma*) and one western earth snake (*Virginia valeriae elegans*) were captured in Year 3 stands; one flathead snake (*Tantilla gracilis*) was captured in a Year 1 stand; two ringneck snakes (*Diadophis punctatus*) were captured in Year 2 stands; and 5 blotched water snakes (*Nerodia erythrogaster transversa*) were captured in Year 1 and Year 2 stands.

Differences in the overall captures of lizards and skinks among the three post-burn years were just above significant ($P = 0.075$), but three species differed significantly among the burn years (Table 2). Ground skinks (*Scincella lateralis*) were most abundant in Year 1, fence lizards (*Sceloporus undulatus*) were most abundant in Year 2, and southern coal skinks (*Eumeces anthracinus pluvialis*) were most abundant in Year 3 stands.

Overall number of both amphibians and anurans was greatest in Year 1 stands, mostly because of a similar pattern in dwarf American toads, which made up the vast majority of amphibian captures (Table 3). Overall numbers of toads were greatest in Year 1 stands, with both Fowler's toads (*Bufo fowleri*) and dwarf American toads ( *Bufo americanus charlessmithi*) captured most often in Year 1 stands. Among rarely captured anurans, a total of four northern cricket frogs (*Acris crepitans*) were captured in all three periods after burn and two chorus frogs (*Pseudacris fouquettei*) were captured in Year 3 stands.

Most species of salamander were captured too infrequently for analyses. Differences in captures of spotted salamanders (*Ambystoma maculatum*) among the three post-burn periods were just above significant ($P = 0.097$), suggesting captures may have been influenced by time after burn. Among rarely captured salamanders, a total of seven marbled salamanders (*Ambystoma opacum*) were captured in all 3 years after burn; one Ouachita dusky salamander (*Desmognathus brimleyorum*) was captured in a Year 1 stand; and one many-ribbed salamander (*Eurycea multiplicata*) and one western slimy salamander (*Plethodon albagula*) were captured in Year 3 stands.

Nine species and five species groups showed significant effects of sampling year (Table 4). With a few exceptions, species with significant effects of sampling year had greater capture rates during the first year of sampling (1999) and the lowest capture rates during the third year of sampling (2001). Louisiana milk snakes (*Lampropeltis triangulum amaura*) were not captured during the second year of sampling (2000), and Fowler's toads were captured least during 1999. Only one species (ground skink) had a significant year × treatment interaction. Capture rates for ground skinks were greater in Year 1 stands than Year 3 stands during 1999, but were greater in Year 1 stands than in Year 2 stands in 2001 (Fig. 1).

## 4. Discussion

Forests of the southeastern US have been shaped by frequent fires for thousands of years (Sharitz et al., 1992; Lorimer, 2001; Spetich et al., 2011), and many species of reptiles and amphibians

**Table 1**
Structural attributes of nine pine-woodland stands during each year of a 3-year burn cycle (Year 1, Year 2, and Year 3) in the Ouachita Mountains of western Arkansas, 1999–2001. Stands were burned in March or early April of Year 1 and vegetation was measured in late summer (September–early October) each year after burning.

| Variable | Year after burn | | | | | | $F$ | $P$ |
|---|---|---|---|---|---|---|---|---|
| | Year 1 | | Year 2 | | Year 3 | | | |
| | $\bar{x}$ | SE | $\bar{x}$ | SE | $\bar{x}$ | SE | | |
| Forb cover (%) | 22.2A[a] | 2.5 | 15.2AB | 2.4 | 12.5B | 2.4 | 4.64 | **0.020** |
| Grass cover (%) | 19.1 | 2.7 | 23.5 | 4.0 | 21.2 | 2.3 | 0.49 | 0.617[c] |
| Woody plant cover (%) | 24.3A | 2.4 | 27.8AB | 1.2 | 33.1B | 1.7 | 5.91 | **0.009** |
| Leaf litter cover (%) | 91.5A | 1.0 | 96.4B | 0.6 | 97.3B | 0.5 | 11.53 | **<0.001**[d] |
| Rock and bare ground cover (%) | 6.7A | 1.0 | 2.2B | 0.5 | 1.3B | 0.3 | 20.89 | **<0.001**[c] |
| Litter depth[b] | 1.41 | 0.18 | 1.88 | 0.18 | 2.16 | 0.26 | 3.61 | 0.043[c] |
| Down wood (%) | 4.4 | 0.7 | 4.2 | 0.7 | 5.1 | 0.8 | 0.88 | 0.428[c] |
| Log volume ($m^3$/ha) | 37.8 | 12.5 | 31.1 | 6.1 | 32.6 | 5.7 | 0.03 | 0.970[c] |
| Foliage density index at ground level | 2.029 | 0.221 | 2.233 | 0.282 | 1.837 | 0.149 | 0.92 | 0.413 |
| Foliage density index 1 m above ground | 0.171A | 0.008 | 0.452B | 0.045 | 0.626B | 0.079 | 32.78 | **<0.001**[d] |
| Foliage density index 2 m above ground | 0.072A | 0.001 | 0.085B | 0.005 | 0.116C | 0.014 | 15.83 | **<0.001**[d] |

[a] Comparison among the three post-burn periods using mixed-model ANOVA. Within rows, means followed by like capital letters were not significant ($P > 0.05$) using Tukey multiple comparison tests. Bold = significant at alpha < 0.05 controlled for experiment-wise error rate using Benjamini–Hochberg control of the false discovery rate (FDR).

[b] Litter depth in 2-cm class increments. See text for details on measurement.

[c] Data were log-transformed ($\ln[x + 1]$).

[d] Analysis was conducted on ranks.

**Table 2**
Mean total captures per stand of each reptile species in nine restored pine woodlands compared during each year of a 3-year burn cycle (Year 1, Year 2, and Year 3) in the Ouachita Mountains of western Arkansas, 1999–2001. Stands were burned every 3 years in March or April of Year 1. Captures occurred during summer (April–September). Only species with $\geqslant$ 8 captures and captured in at least six stands were compared. Probabilities ($P$) for each species were derived from ANOVA and significantly different means were compared using Tukey tests.

| Species | Year 1 | | Year 2 | | Year 3 | | $F$ | $P$ |
|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | SE | $\bar{x}$ | SE | $\bar{x}$ | SE | | |
| Reptiles (all) | 78.56 | 8.72 | 79.33 | 10.41 | 76.00 | 7.30 | 0.04 | 0.958[a] |
| Snakes (all) | 31.11 | 3.63 | 33.44 | 5.16 | 38.89 | 6.15 | 0.94 | 0.416[a] |
| Eastern coachwhip (*Masticophis flagellum flagellum*) | 2.67 | 1.08 | 1.67 | 0.53 | 1.56 | 0.50 | 0.23 | 0.799[a] |
| Eastern garter snake (*Thamnophis sirtalis sirtalis*) | 1.67 | 0.85 | 1.67 | 0.37 | 1.67 | 0.47 | 0.28 | 0.759[a] |
| Eastern hognose snake (*Heterodon platirhinos*) | 1.78 | 0.70 | 1.22 | 0.22 | 1.56 | 0.41 | 0.03 | 0.972[a] |
| Great Plains rat snake (*E. emoryi*) | 2.44 | 0.58 | 2.00 | 0.71 | 2.00 | 1.15 | 0.79 | 0.474[a] |
| Louisiana milk snake (*L. triangulum amaura*) | 0.56 | 0.34 | 0.56 | 0.24 | 0.44 | 0.18 | 0.12 | 0.890[b] |
| Northern Scarlet snake (*Cemophora coccinea copei*) | 0.78 | 0.36 | 1.33 | 0.55 | 0.78 | 0.66 | 1.16 | 0.346[a] |
| Prairie kingsnake (*L. calligaster*) | 1.00 | 0.29 | 0.56 | 0.24 | 1.22 | 0.43 | 1.32 | 0.302[a] |
| Redbelly snake (*Storeria occipitomaculata*) | 0.56 | 0.24 | 0.44 | 0.24 | 0.33 | 0.17 | 0.27 | 0.768[a] |
| Red milk snake (*L. triangulum syspila*) | 0.56 | 0.24 | 0.78 | 0.28 | 0.44 | 0.24 | 0.48 | 0.633[c] |
| Rough green snake (*Opheodrys aestivus*) | 0.56 | 0.29 | 0.22 | 0.15 | 0.11 | 0.11 | 0.77 | 0.485[c] |
| Southern copperhead (*Agkistrodon contortrix contortrix*) | 7.78 | 1.92 | 7.78 | 2.04 | 10.56 | 2.48 | 1.65 | 0.234[a] |
| Southern black racer (*Coluber constrictor priapus*) | 3.33A[d] | 0.73 | 7.33B | 1.34 | 9.44B | 2.08 | **9.03** | **0.004**[a] |
| Speckled kingsnake (*Lampropeltis getula holbrooki*) | 1.56 | 0.47 | 0.78 | 0.28 | 1.33 | 0.41 | 0.71 | 0.510[c] |
| Western ribbon snake (*T. proximus proximus*) | 0.44 | 0.18 | 1.22 | 0.46 | 0.89 | 0.35 | 1.16 | 0.345[a] |
| Western rat snake (*Elaphe obsoleta*) | 2.11 | 0.42 | 1.78 | 0.28 | 2.78 | 0.85 | 0.18 | 0.838[a] |
| Western pygmy rattlesnake (*Sistrurus miliarius streckeri*) | 2.11 | 0.26 | 2.00 | 0.67 | 2.78 | 0.55 | 1.49 | 0.265[c] |
| Yellow-bellied water snake (*Nerodia erythrogaster*) | 0.22 | 0.15 | 0.89 | 0.31 | 0.22 | 0.15 | 3.16 | 0.079[a] |
| Other snakes and unknown snake species | 1.00 | 0.41 | 1.22 | 0.40 | 0.78 | 0.32 | | |
| Lizards/Skinks (all species) | 46.78 | 6.05 | 44.44 | 6.54 | 36.22 | 2.90 | 3.24 | 0.075[a] |
| Broad-headed skink (*Eumeces laticeps*) | 11.11 | 1.49 | 9.78 | 2.10 | 9.22 | 1.74 | 1.31 | 0.307[a] |
| Fence lizard (*Sceloporus undulatus*) | 10.89A | 1.46 | 19.00B | 3.37 | 13.00AB | 1.9 | **5.70** | **0.018**[a] |
| Five-lined skink (*E. fasciatus*) | 5.44 | 0.84 | 5.33 | 0.97 | 5.56 | 1.29 | 0.06 | 0.938[a] |
| Ground skink (*Scincella lateralis*) | 16.11A | 4.56 | 9.33B | 2.05 | 6.78B | 1.05 | **7.98** | **0.006**[a] |
| Northern green anole (*Anolis carolinensis carolinensis*) | 2.22 | 1.30 | 0.11 | 0.11 | 0.33 | 0.24 | 2.81 | 0.100[c] |
| Six-lined racerunner (*Aspidoscelis sexlineatus*) | 0.67 | 0.29 | 0.56 | 0.34 | 0.11 | 0.11 | 1.49 | 0.264[b] |
| Southern coal skink (*E. anthracinus pluvialis*) | 0.11A | 0.11 | 0.11A | 0.11 | 0.67B | 0.24 | **4.58** | **0.033**[c] |
| Other and unknown species of lizard and skink | 0.22 | 0.15 | 0.22 | 0.15 | 0.56 | 0.24 | | |
| Turtles (all) | 0.67 | 0.24 | 1.44 | 0.38 | 0.89 | 0.35 | 1.36 | 0.293[c] |
| Three-toed box turtle (*Terrapene carolina triunguis*) | 0.56 | 0.24 | 1.44 | 0.38 | 0.78 | 0.32 | 2.61 | 0.115[b] |

Bold = significant difference among treatments at alpha = 0.05.

[a] Data were log-transformed ($\ln[x + 1]$).

[b] Data were transformed using $1/(x + 0.5)$.

[c] Analyses were conducted on ranks.

[d] Within rows, means with like capital letters were not significantly different.

likely adapted to this frequent disturbance. Prescribed burning often maintains the structure of fire-dependent vegetation for species adapted to these habitats (Russell et al., 1999), and species associated with fire-dependent habitats are likely behaviorally adapted to resist mortality by fire (Means and Campbell, 1982). In woodlands that were subjected to frequent fire, we found only minor changes in the herpetofaunal community during the 3-year interval between burns.

**Table 3**
Mean total captures per stand for each species of amphibian in nine restored pine woodlands compared during each year of a 3-year burn cycle (Year 1, Year 2, and Year 3) in the Ouachita Mountains of western Arkansas, 1999–2001. Stands were burned every 3 years in March or April of Year 1. Captures occurred during summer (April–September). Only species with ⩾ 8 captures and captured in at least six stands were compared. Probabilities (*P*) for each species were derived from ANOVA and significantly different means were compared using Tukey tests.

| Species | Year 1 | | Year 2 | | Year 3 | | *F* | *P* |
|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | SE | $\bar{x}$ | SE | $\bar{x}$ | SE | | |
| Amphibians (all) | 114.56A[c] | 37.29 | 52.78AB | 7.19 | 50.67B | 13.75 | **6.97** | **0.001**[a] |
| Anurans (all) | 112.44A | 36.09 | 51.44B | 7.07 | 49.00B | 13.02 | **7.65** | **0.007**[a] |
| Bronze frog (*Rana clamitans clamitans*) | 8.11 | 3.59 | 6.11 | 2.00 | 8.22 | 3.92 | 0.06 | 0.940[a] |
| Bullfrog (*R. catesbeiana*) | 2.78 | 1.05 | 1.78 | 0.40 | 3.22 | 1.76 | 0.09 | 0.916[a] |
| Dwarf American toad (*Bufo americanus charlessmithi*) | 82.78A | 30.64 | 31.44AB | 6.28 | 26.78B | 6.95 | **5.84** | **0.017**[a] |
| Eastern narrowmouth toad (*Gastrophryne carolinensis*) | 1.78 | 0.49 | 1.11 | 0.45 | 1.44 | 0.47 | 1.02 | 0.389[a] |
| Fowler's toad (*B. fowleri*) | 2.00A | 0.53 | 0.22B | 0.15 | 0.11B | 0.11 | **23.51** | **0.001**[b] |
| Gray treefrogs (*Hyla versicolor* and *H. chrysoscelis*) | 0.11 | 0.11 | 0.67 | 0.24 | 0.33 | 0.24 | 2.28 | 0.145[a] |
| Green frog (*R. clamitans melanota*) | 0.89 | 0.56 | 0.33 | 0.17 | 0.44 | 0.29 | 0.21 | 0.817[b] |
| Pickerel frog (*R. palustris*) | 4.89 | 1.18 | 4.00 | 0.88 | 2.56 | 0.85 | 2.15 | 0.159[a] |
| Southern leopard frog (*R. sphenocephala utricularius*) | 4.56 | 1.04 | 2.56 | 0.63 | 2.33 | 0.67 | 1.23 | 0.327[a] |
| Other and unknown anurans | 4.44 | 0.77 | 3.11 | 1.31 | 3.56 | 1.45 | | |
| Salamanders (all) | 2.12 | 1.29 | 1.33 | 0.44 | 1.67 | 0.76 | 0.01 | 0.988[a] |
| Central newt (*Notophthalmus viridescens louisianensis*) | 0.22 | 0.15 | 0.67 | 0.29 | 0.89 | 0.42 | 0.93 | 0.423[b] |
| Spotted salamander (*Ambystoma maculatum*) | 1.22 | 0.55 | 0.56 | 0.24 | 0.11 | 0.11 | 2.85 | 0.097[a] |
| Other and unknown salamanders | 0.78 | 0.66 | 0.11 | 0.11 | 0.67 | 0.33 | | |

Bold = significant difference among treatments at alpha = 0.05.

[a] Data were log-transformed (ln [$x$ + 1]).

[b] Analyses were conducted on ranks.

[c] Within rows, means with like capital letters were not significantly different.

**Table 4**
Mean total captures per stand for herpetofauna with significant effects of sampling year (1999–2011) captured in nine restored pine woodlands compared during each year of a 3-year burn cycle in the Ouachita Mountains of western Arkansas. Stands were burned every 3 years in March or April. Captures occurred during summer (April–September). Only species with > 8 captures and captured in at least six stands were compared. Probabilities (*P*) for each species were derived from ANOVA and significantly different means were compared using Tukey tests.

| Species | 1999 | | 2000 | | 2001 | | F | *P*[b] |
|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | SE | $\bar{x}$ | SE | $\bar{x}$ | SE | | |
| Reptiles (all) | 101.67A[a] | 8.78 | 76.44B | 4.41 | 55.78C | 3.17 | 20.03 | 0.001 |
| Snakes (all) | 42.56A | 6.45 | 37.33A | 3.56 | 23.56B | 1.80 | 7.84 | 0.007 |
| Louisiana milk snake | 0.78AB | 0.36 | 0.00B | 0.00 | 0.78A | 0.15 | 4.60 | 0.033 |
| Prairie kingsnake | 1.56A | 0.29 | 1.11A | 0.35 | 0.11B | 0.11 | 9.66 | 0.003 |
| Southern copperhead | 11.78A | 2.48 | 10.67A | 1.75 | 3.67B | 0.78 | 12.39 | 0.001 |
| Southern black racer | 8.56A | 1.89 | 8.22A | 1.60 | 3.33B | 0.89 | 9.91 | 0.003 |
| Lizards/skinks (all) | 57.56A | 6.13 | 38.56B | 2.56 | 31.33B | 2.34 | 21.73 | 0.001 |
| Ground skink | 19.22A | 3.81 | 8.22B | 1.32 | 4.78C | 1.19 | 34.66 | 0.001 |
| Fence lizard | 19.11A | 3.15 | 13.11AB | 1.82 | 10.67B | 1.89 | 7.88 | 0.007 |
| Five-lined skink | 5.89AB | 1.05 | 6.89A | 0.89 | 3.56B | 0.84 | 6.69 | 0.011 |
| Amphibians (all) | 107.33A | 38.15 | 59.11AB | 10.99 | 51.56B | 12.47 | 4.03 | 0.046 |
| Anurans (all) | 104.78A | 37.03 | 58.00AB | 10.90 | 50.11B | 11.69 | 4.23 | 0.041 |
| Dwarf American toad | 82.00A | 30.53 | 36.00AB | 7.75 | 23.00B | 5.97 | 7.22 | 0.009 |
| Fowler's toad | 0.11A | 0.11 | 1.22B | 0.46 | 1.00B | 0.53 | 10.97 | 0.002 |

[a] Within rows, means with like capital letters were not significantly different.

[b] See Tables 2 and 3 for transformations of data for each species or species group.

Fire-return intervals differ among various ecosystems. For example, Florida sand-pine scrub has long fire-return intervals and fires are often stand-replacing (e.g., Myers, 1985). However, relatively short fire-return intervals are fundamental to maintaining pine-woodland ecosystems. Means et al. (2004) suggested 1- to 3-year fire rotations were necessary to maintain the structure of fire-maintained ecosystems such as the longleaf-pine (*Pinus palustris*) woodlands of the southeastern US. Fire return intervals >10 years in these forests may result in replacement of herbaceous ground cover with shrubs and trees, and fire-return intervals of 5–12 years may result in a permanent shift in community composition (Means et al., 2004). Our study areas were burned every 3 years during the study and previously burned on 3–5 year intervals prior to the study. During the initial process of restoring these woodlands, midstory trees were felled, leaving abundant hardwood stumps with associated root stocks. Many of the woody stems in the understory were sprouts (coppice) from these stumps. It is unknown how long root stocks from these trees persist, but some stands restored >20 years prior still had persistent resprouting. Periodic fires top-killed these sprouts, but they typically regrew vigorously after fires. In these stands, dormant-season fire intervals >7 years may be too long to retain the open, herbaceous understory structure, and alternative treatments such as growing season burns or chainsaw felling may be necessary to reduce woody growth in the understory if fire return intervals are lengthened much beyond 5 years. Waldrop et al. (1992) found periodic burns every 3–7 years did not eliminate hardwood sprouting in the understory of loblolly pine (*Pinus taeda*) forests of the southeastern US, whereas annual summer burns killed the roost stock and eliminated most small (<2.5 cm) hardwoods (except for oaks and blackgum [*Nyssa sylvatica*]) in the understory. However, it is unknown how annual summer burns affect herpetofaunal communities.

Overstory and midstory structure of our nine woodlands was similar, and all had similar management histories. During the first

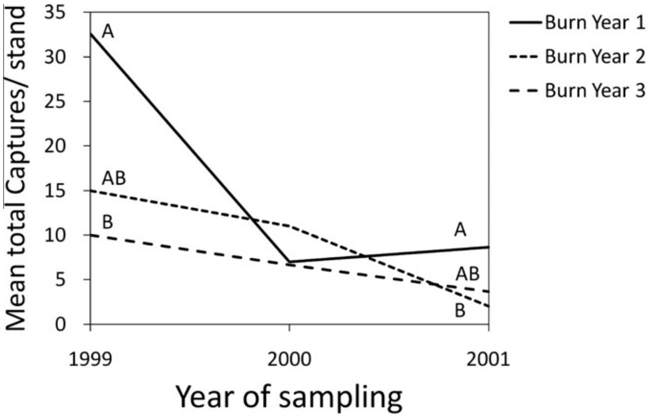

**Fig. 1.** Interaction between year of sampling (1999–2001) and year after burning for ground skinks captured in 9 restored pine woodlands during each of 3 years after burning (Burn Year 1, Burn Year 2, and Burn Year 3) in the Ouachita Mountains of western Arkansas. Stands were burned every 3 years in March or April of Year 1. Captures occurred during summer (April–September). For 1999 and 2001, like letters among the three burn years indicate no significant difference among treatments. No significant differences occurred among burn years in 2000.

year after a burn, stands had abundant forbs, but little woody vegetation in the understory and reduced amounts of leaf litter cover. By the third growing season after burning, a dense woody understory approximately 1 m high had developed. Furthermore, by the third growing season, leaf litter cover had increased. These changes in the understory during the 3-year burn cycle likely caused most of the differences in relative abundance of species we observed.

Reptile species may be more closely associated with characteristics of vegetation than to fire frequency (Lindenmayer et al., 2008), and some species of reptiles may be associated with differing fire intensities and periods after fire based on the amounts of ground-level vegetation retained (Braithwaite, 1987). Population declines may occur for some herpetofaunal species immediately after fires in other areas of the world (Patterson, 1984; Bamford, 1992; Friend, 1993); however, increases in reptile diversity often accompany prescribed fire in the southeastern US (Means and Campbell, 1982; Mushinsky, 1985; Moseley et al., 2003). Although others have found greater reptile abundance in burned stands compared to unburned stands (e.g., Greenberg and Waldrop, 2008; Perry et al., 2009), we found no difference in overall abundance of reptiles among the three post-burn years, and most species showed no significant response among the three post-burn years.

Studies suggest fire may benefit many lizards (Renken, 2006; Greenberg and Waldrop, 2008), and lizards appeared to be the group most affected by year after burn, with three of seven species showing significant responses to post-burn year. We found ground skinks were captured more often the first year after burning, fence lizards were captured more often the second year after burning, and coal skinks were captured most often the third year after burning. Greenberg et al. (1994) found that changes in habitat resulting from fire benefited some lizard species, but were unfavorable for others. Keyser et al. (2004) found fence lizards, ground skinks, and five-lined skinks (*Eumeces fasciatus*) were captured more often in burned versus unburned stands, and other studies have found fence lizards associated with burned forest (Litt et al., 2001; Greenberg and Waldrop, 2008). Our data suggest that ground skinks may benefit from the open, less dense understory found during the first year after fire. Little is known of the ecology of coal skinks (Hotchkin et al., 2000); they may inhabit both mesic and semiarid sites along streams to rocky hillsides, but they may have a strong affinity for mesic sites (e.g., Dundee and Rossman, 1996; Trauth et al., 2004). Thus, the more open and drier conditions of stands the first year after burning may have provided temporarily unfavorable conditions for this species. Nevertheless, in a related study, coal skinks capture rates did not differ between frequently burned woodlands and unburned mature forest (Perry et al., 2009).

Among snakes, only the southern black racer differed among the three post-burn periods, and their relative abundance was significantly lower in Year 1 stands. Similarly, Cavitt (2000) found a significantly lower abundance of southern black racers 1 year after wildfire in tall grass prairies of Kansas compared to unburned areas, and suggested this species may avoid crossing open areas with little ground-level cover. Further, he suggested a seasonal shift whereby southern black racers are abundant in unburned areas in spring and early summer, but moved into burned areas in late summer and fall when vegetation recovered from earlier burns. Although this species appears to respond negatively the first year after burning, we found no overall difference between the relative abundance of this species in pine woodlands subjected to frequent burning and mature, unmanaged forests where fire had been excluded (Perry et al., 2009).

Some snakes, including western worm snakes, redbelly snakes (*Storeria occipitomaculata*), and brown snakes are litter-dwelling species (Trauth et al., 2004). Given the decreased amount of leaf litter in these frequently burned stands, we expected their abundance to be fairly low. Among these species, only redbelly snakes were captured frequently enough for analysis, but we found no significant difference in capture rates among the three post-burn periods. Consequently, either enough litter was retained within stands to maintain this species the first growing season after burning or they inhabited burrows or other subterranean structures in lieu of dense litter. Often, not all litter is consumed during controlled burns in the eastern US (Kirkland et al., 1996; Ford et al., 1999; Floyd et al., 2002). In our study, the percent of ground covered by litter was only 6% less in Year 1 stands compared to Year 3 stands.

Overall relative abundance of amphibians and anurans was significantly greater in Year 1 stands than in Year 3 stands, mostly because captures of dwarf American toads (the most abundant amphibian) were three times greater in Year 1 stands compared to Year 3 stands. Other studies have found greater abundance of American toads in burned stands compared to unburned forests (e.g., Kirkland et al., 1996; Greenberg and Waldrop, 2008). Our data suggest this response is primarily the first year after burning and subsides in following years. American toads escape harsh environmental conditions by burrowing into the ground or entering burrows (e.g., Miller, 1909) and have toxic skin secretions that cause many predators to avoid them (e.g., Brown, 1974; Heinen, 1994). Furthermore, American toads may be ubiquitous across landscapes and occur in disturbed areas, farmland, and urban areas (e.g. Kolozsvary and Swihart, 1999; Trauth et al., 2004). Thus, these adaptations likely allow this species to tolerate open habitats with sparse cover immediately after the burns.

Aside from toads, capture rates did not differ among the three post-burn years for any other species of anuran. Greenberg et al. (1994) found frog occurrence in Florida sand-pine scrub appeared to be unaffected by silviculture treatments and burns. Studies suggest amphibian species richness decreases with increasing distance from aquatic sites where most amphibian reproduction occurs (e.g., Greenberg, 1993; Schurbon and Fauth, 2003). However, we found no significant correlation between abundance of any species and distance to permanent water sources, but we could not determine location and availability of temporary seasonal pools (Perry et al., 2009).

We found no difference in capture rates for all salamanders combined among the three post-burn years. Overall capture of salamanders was low, and central newts (*Notophthalmus viridescens louisianensis*) and spotted salamanders were the only species captured frequently. Capture rates among the three post-burn periods for spotted salamanders were just above significant ($P = 0.097$), suggesting they may have been captured more often in Year 1 stands. Micro-habitat variables (except for soil moisture) may not be helpful in explaining patterns of salamander relative abundance (Hyde and Simmons, 2001), and previous studies in the eastern US found no effect of fire on salamander abundance (Ford et al., 1999; Floyd et al., 2002; Keyser et al., 2004; Greenberg and Waldrop, 2008). However, salamander abundance estimates may be greatly affected by detectability and surface counts of many salamanders are believed to comprise only a small proportion of the total population (Smith and Petranka, 2000). For example, up to 95% of spotted salamanders may be located in small mammal burrows (Faccio, 2003). Alternatively, salamanders during moist periods may maximize time spent on the surface where prey is more abundant (Jaeger, 1980). Although relative abundance estimates of salamanders may have been biased by detectability issues. We are unaware of current mathematical methods for determining detectability with relatively low number of samples ($n = 9$ stands) and populations that were likely not closed.

Fourteen species or groups of species had significant effects of sampling year (1999–2001), including all reptiles combined, all snakes combined, all lizards, all amphibians, and all anurans. Nearly all species and species groups showed a marked decline in capture rates between the first year of sampling and the last year of sampling. Multiple reasons may have caused this decline. Average precipitation data from a nearby weather station (Mena, Arkansas) indicated the April–August period in the area was 28.4 cm above normal in 1999, 2.2 cm above normal in 2000, but 10.3 cm below normal in 2001. Consequently, the extremely wet summer of 1999, the near average precipitation of 2000, and the dry summer of 2001 may partially explain the response in herpetofauna to sampling years we observed. Captures typically increased dramatically after rain events and the lack of rain in 2001 may have contributed to reduced captures. Trapping effects may have also reduced captures of herpetofauna through the 3 years. Individuals may have become trap wise over the 3 years, resulting in reduced captures of individuals. Also, since most individuals were moved >50 m from the trap location after removal from traps, some individuals may have been displaced by these movements.

Burning is not a panacea for all species. Some species, such as plethodontid salamanders that do not have an aquatic stage, rely on soil moisture for reproduction and may not benefit from burning. For example, substantially fewer captures of slimy salamanders may occur in burned areas compared to unburned areas (Means and Campbell, 1982; Moseley et al., 2003; Perry et al., 2009). Thus, a mosaic of habitat structures should increase herpetofaunal diversity on a broader scale (Petraitis et al., 1989; Greenberg et al., 1994; Masters, 1996; McLeod and Gates, 1998; Russell et al., 1999). Landscape heterogeneity, which includes fire-adapted open forests and moist forests with less-frequent fire, likely contribute to a more diverse assemblage of reptiles and amphibians.

## 5. Conclusions

Open pine woodlands provide habitat for many species of wildlife (Thill et al., 2004), and maintaining these open woodlands requires frequent fires. We found only minor changes in the herpetofaunal community during the 3 years between successive fires in stands that were accustomed to frequent fires. Capture rates for only two of 36 species were lower the first year after fire, suggesting that the process of burning had few detrimental effects on the herpetofaunal community found in these areas. Capture rates for some species, especially toads and ground skinks were significantly greater the first few months after burning, suggesting the open understory conditions created initially by burning provided valuable habitat for some species. Nevertheless, not all species of herpetofaunal benefit from frequent burning, and some species such as the plethodontid salamanders likely benefit from retaining unburned areas, such as mesic sites, greenbelts, or unburned stands (e.g., Perry et al., 2009).

## Acknowledgments

We thank R. Buford, H. Williamson, T. Tanner, and students from Stephen F. Austin State University, Arkansas Tech University, and the University of Arkansas at Monticello for field assistance. We thank N. Koerth, D. Saenz, and K. Greenberg for helpful reviews. We also thank W. Montague and personnel of the Poteau-Cold Springs Ranger District of the ONF for their assistance locating sites and ensuring burns were completed on schedule. Funding was provided by the Southern Research Station and the ONF through the efforts of J. Guldin and L. Hedrick.

## References

Ash, A.N., 1997. Disappearance and return of plethodontid salamanders to clearcut plots in the southern Blue Ridge Mountains. Conserv. Biol. 11, 983–989.

Avery, T.E., Burkhart, H.E., 1994. Forest measurements, fouth ed. McGraw-Hill, New York, NY, USA.

Bamford, M.J., 1992. The impact of fire and increasing time after fire upon *Heleioporus eyrei*, *Limnodynastes dorsalis* and *Myobatrachus gouldii* (Anura: Leptodactylidae) in *Banksia* woodland near Perth, Western Australia. Wildl. Res. 19, 169–178.

Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J. Royal Stat. Soc. B 57, 289–300.

Bradford, D.F., 2005. Factors implicated in amphibian declines in the United States. In: Lannoo, M. (Ed.), Amphibian Declines: The Conservation Status of United States Species. University of California Press, Berkeley, CA, USA, pp. 915–925.

Braithwaite, R.W., 1987. Effects of fire regimes on lizards in wet-dry tropics of Australia. J. Trop. Ecol. 3, 265–275.

Brown, L.E., 1974. Behavioral reactions of bullfrogs while attempting to eat toads. Southwest. Nat. 19, 335–337.

Bukenhofer, G.A., Hedrick, L.D., 1997. Shortleaf pine/bluestem grass ecosystem renewal in the Ouachita Mountains. In: Wadsworth, K.G. (Ed.), Transactions of the 62nd North American Wildlife and Natural Resources Conference, March 14–18, Washington, DC, pp. 509–515.

Burgdorf, S.J., Rudolph, D.C., Conner, R.N., Saenz, D., Schaefer, R.R., 2005. A successful trap design for capturing large terrestrial snakes. Herpetol. Rev. 36, 421–424.

Cavitt, J.F., 2000. Fire and a tallgrass prairie reptile community: effects on relative abundance and seasonal activity. J. Herpetol. 34, 12–20.

Conover, W.J., Iman, R.L., 1981. Rank transformations as a bridge between parametric and nonparametric statistics. Am. Stat. 35, 124–129.

deMaynadier, P.G., Hunter Jr., M.L., 1995. The relationship between forest management and amphibian ecology: a review of the North American Literature. Environ. Rev. 3, 230–261.

Dundee, H.A., Rossman, D.A., 1996. The Amphibians and Reptiles of Louisiana. Louisiana State University Press, Baton Rouge, LA, USA.

Faccio, S.D., 2003. Post-breeding emigration and habitat use of the Jefferson and spotted salamanders in Vermont. J. Herpetol. 37, 479–489.

Floyd, T.M., Russell, K.R., Moorman, C.E., Van Lear, D.H., Guynn, D.C. Jr., Lanham, J.D., 2002. Effects of prescribed fire on herpetofauna within hardwood forests of the Upper Piedmont of South Carolina: A preliminary analysis. In: Outcalt, K.W. (Ed.), Proceedings of the Eleventh Biennial Southern Silviculture Research Conference. U.S. Forest Service, Gen. Tech. Rep. SRS-48, Asheville, NC, USA, pp. 123–127.

Ford, W.M., Menzel, M.A., McGill, D.W., Laerm, J., McCay, T.S., 1999. Effects of community restoration fire on small mammals and herpetofauna in the southern Appalachians. For. Ecol. Manage. 114, 233–243.

Friend, G.R., 1993. Impacts of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia: a review. Biol. Conserv. 65, 99–114.

Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S., Winne, C.T., 2000. The global decline of reptiles, déjà vu amphibians. Bioscience 50, 653–666.

Greenberg, C.H., 1993. Effects of high-intensity wildfire and silvicultural treatments on biotic communities of sand pine scrub. Ph. D. dissertation. University of Florida, Gainesville, FL, USA.

Greenberg, C.H., Leary, D.G., Harris, L.D., 1994. Effects of high-intensity wildfire and silvicultural treatments on reptile communities in sand-pine scrub. Conserv. Biol. 8, 1047–1057.

Greenberg, C.H., Waldrop, T.A., 2008. Short-term response of reptiles and amphibians to prescribed fire and mechanical fuel reduction in a southern Appalachian upland hardwood forest. For. Ecol. Manage. 255, 2883–2893.

Heinen, J.T., 1994. Antipredator behavior of newly metamorphosed American toads (*Bufo a. americanus*), and mechanisms of hunting by eastern garter snakes (*Thamnophis s. sirtalis*). Herpetologica 50, 137–145.

Hunter Jr., M.L., 1990. Wildlife, Forests, and Forestry: Principles of Managing Forests for Biological Diversity. Prentice Hall, Englewood Cliffs, NJ, USA.

Hotchkin, P.E., Camp, C.D., Marshall, J.L., 2000. Aspects of the life history and ecology of the coal skink, *Eumeces anthracinus*, in Georgia. J. Herpetol. 35, 145–148.

Houlahan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, A.H., Kuzmin, S.L., 2000. Quantitative evidence for global amphibian population declines. Nature 404, 752–755.

Hyde, E.J., Simmons, T.R., 2001. Sampling plethodontid salamanders: sources of variability. J. Wildl. Manage. 65, 624–632.

Jaeger, R.G., 1980. Microhabitats of a terrestrial forest salamander. Copeia 1980, 265–268.

Keyser, P.D., Sausville, D.J., Ford, W.M., Schwab, D.J., Brose, P.H., 2004. Prescribed fire impacts to amphibian and reptiles in shelterwood-harvested oak-dominated forests. Va. J. Sci. 55, 127–137.

Kirkland Jr., G.L., Snoddy, H.W., Amsler, T.L., 1996. Impacts of fire on small mammals and amphibians in a central Appalachian deciduous forest. Am. Midl. Nat. 135, 253–260.

Kolozsvary, M.B., Swihart, R.K., 1999. Habitat fragmentation and the distribution of amphibians: patch and landscape correlates in farmland. Can. J. Zool. 77, 1288–1299.

Kuehl, R.O., 2000. Designs of Experiments: Statistical Principles of Research Design and Analysis. Duxbury Press, Pacific Grove, CA, USA.

Langford, G.J., Borden, J.A., Major, C.S., Nelson, D.H., 2007. Effects of prescribed fire on the herpetofauna of a southern Mississippi pine savanna. Herpetol. Conserv. Biol. 2, 135–143.

Lindenmayer, D.B., Wood, J.T., MacGregor, C., Michael, D.R., Cunningham, R.B., Crane, M., Montague-Drake, R., Brown, D., Muntz, R., Driscoll, D.A., 2008. How predictable are reptile responses to wildfire? Oikos 117, 1086–1097.

Litt, A.R., Provencher, L., Tanner, G.W., Franz, R., 2001. Herpetofaunal responses to restoration treatments of longleaf pine sandhills in Florida. Restor. Ecol. 9, 462–474.

Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., 1996. SAS System for Mixed Models. SAS Institute, Inc., Cary, NC, USA.

Lorimer, C.G., 2001. Historical and ecological roles of disturbance in eastern North American forests: 9000 years of change. Wildl. Soc. Bull. 29, 425–439.

MacArthur, R.H., MacArthur, J.W., 1961. On bird species richness. Ecology 42, 594–598.

Masters, P., 1996. The effects of fire-driven succession on reptiles in spinifex grasslands at Uluru National Park, Northern Territory. Wildl. Res. 23, 39–48.

Masters, R.E., Engle, D.M., Robinson, R., 1993. Effects of timber harvest and periodic fire on soil chemical properties in the Ouachita Mountains. South. J. Appl. For. 3, 139–145.

McCallum, M.L., 2007. Amphibian declines or extinction? Current declines dwarf background extinction rate. J. Herpetol. 41, 483–491.

McLeod, R.F., Gates, J.E., 1998. Responses of herpetofaunal communities to forest cutting and burning at Chesapeake Farms, Maryland. Am. Midl. Nat. 139, 164–177.

Compilers: McNab, W.H., Avers, P.E., 1994. Ecological Subregions of the United States. U.S. Forest Service Administrative Publication WO-WSA-5, Washington, DC, USA.

Means, D.B., 2006. Vertebrate faunal diversity of longleaf pine ecosystems. In: Jose, S., Jokela, E.J., Miller, D.L. (Eds.), The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration. Springer, New York, NY, USA, pp. 157–213.

Means, D.B., Campbell, H.W., 1982. Effects of prescribed burning on amphibians and reptiles. In: Wood, G.W. (Ed.), Prescribed Fire and Wildlife in Southern Forests. The Belle W. Baruch Forest Science Institute, Georgetown, SC, USA, pp. 89–97.

Means, D.B., Dodd Jr., C.K., Johnson, S.A., Palis, J.G., 2004. Amphibians and fire in longleaf pine ecosystems: response to Schurbon and Fauth. Conserv. Biol. 18, 1149–1153.

Miller, N., 1909. The American toad (*Bufo lentiginosus americanus*, LeConte). II A study in dynamic biology. Am. Nat. 43, 730–745.

Moseley, K.R., Castleberry, S.B., Schweitzer, S.H., 2003. Effects of prescribed fire on herpetofauna in bottomland hardwood forests. Southeast. Nat. 2, 475–486.

Mushinsky, H.R., 1985. Fire and the Florida Sandhill herpetofaunal community: with special attention to responses of *Cnemidophorus sexlineatus*. Herpetologica 41, 333–342.

Myers, R.L., 1985. Fire and the dynamic relationship between Florida sandhill and sand pine scrub vegetation. Bull. Torrey Bot. Club 112, 241–252.

Patterson, G.B., 1984. The effects of burning-off tussock grassland on the population density of common skinks. New Zeal. J. Zool. 11, 189–194.

Perry, R.W., Rudolph, D.C., Thill, R.E., 2009. Responses of reptiles and amphibians to restoration of fire-maintained pine woodlands. Restor. Ecol. 17, 917–927.

Petraitis, P.S., Latham, R.E., Niessenbaum, R.A., 1989. The maintenance of species diversity by disturbance. Q. Rev. Biol. 64, 393–418.

Pilliod, D.S., Bury, R.B., Hyder, E.J., Pearl, C.A., Corn, P.S., 2003. Fire and amphibians in North America. For. Ecol. Manage. 178, 163–181.

Renken, R.B., 2006. Does fire affect amphibians and reptiles in eastern U.S. oak forests? In: Dickinson, M.B. (Ed), Fire in eastern oak forests: delivering science to land managers. U.S. Forest Service, Gen. Tech. Rep. NRS-P-1, Newton Square, PA, pp. 158–166.

Russell, K.R., Van Lear, D.H., Guynn Jr., D.C., 1999. Prescribed fire effects on herpetofauna: review and management implications. Wildl. Soc. Bull. 27, 374–384.

SAS Institute Inc., 2000. SAS/STAT User's Guide, Version 8 edition. SAS Institute Inc., Cary, NC, USA.

Schurbon, J.M., Fauth, J.E., 2003. Effects of prescribed burning on amphibian diversity in a southeastern U.S. National Forest. Conserv. Biol. 117, 1338–1349.

Semlitsch, R.D., Conner, C.A., Hocking, D.J., Rittenhouse, T.A.G., Harper, E.B., 2008. Effects of timber harvesting on pond-breeding amphibian persistence. testing the evacuation hypothesis. Ecol. Appl. 18, 283–289.

Sharitz, R.R., Boring, L.R., Van Lear, D.H., Pinder III, J.E., 1992. Integrating ecological concepts with natural resource management of Southern forests. Ecol. Appl. 2, 226–237.

Smith, C.K., Petranka, J.W., 2000. Monitoring terrestrial salamanders: repeatability and validity of area-constrained cover object searches. J. Herpetol. 34, 547–557.

Spetich, M.A., Perry, R.W., Harper, C.A., Clark, S.L., 2011. Fire in eastern hardwood forests through 14,000 years. In: Greenberg, C.H., Collins, B., Thompson, F.R., III (Eds.), Ecology and management of early successional habitats in the central hardwood region, USA. Springer, New York, NY, USA, pp. 41–58.

Thill, R.E., Rudolph, D.C., Koerth, N.E., 2004. Shortleaf pine-bluestem restoration for red-cockaded woodpeckers in the Ouachita Mountains: implications for other taxa. In: Costa, R., Daniels, S.J. (Eds.), Red-cockaded Woodpecker: Road to Recovery. Hancock House Publishers, Blaine, WA, USA, pp. 657–671.

Trainor, C.R., Woinarski, J.C.Z., 1994. Responses of lizards to three experimental fires in the savanna forests of Kakadu National Park. Wildl. Res. 21, 131–148.

Trauth, S.E., Robison, H.W., Plummer, M.V., 2004. The Reptiles and Amphibians of Arkansas. University of Arkansas Press, Fayetteville, AR, USA.

Van Lear D.H., Harlow R.F., 2002. Fire in the eastern United States: influence on wildlife habitat. In Ford W.M., Russell K.R., Moorman C.E. (Eds.), The role of fire in nongame wildlife management and community restoration: Traditional uses and new directions. U.S. Forest Service, Gen. Tech. Rep. NE-288, Newton Square, PA, USA, pp. 2–10.

Waite, T.A., Campbell, L.G., 2006. Controlling the false discovery rate and increasing statistical power in ecological studies. Ecoscience 13, 439–442.

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

Waldrop, T.A., White, D.L., Jones, S.M., 1992. Fire regimes for pine-grassland communities in the southeastern United States. For. Ecol. Manage. 47, 195–210.