

Available online at www.sciencedirect.com



Forest Ecology and Management

Forest Ecology and Management 255 (2008) 2883-2893

www.elsevier.com/locate/foreco

Short-term response of reptiles and amphibians to prescribed fire and mechanical fuel reduction in a southern Appalachian upland hardwood forest

Cathryn H. Greenberg^{a,*}, Thomas A. Waldrop^b

^a US Forest Service, Southern Research Station, Bent Creek Experimental Forest, Asheville, NC, 28806, United States ^b US Forest Service, Southern Research Station, Clemson, SC, 29634-0331, United States

Received 2 November 2007; received in revised form 25 January 2008; accepted 26 January 2008

Abstract

We compared the effects of three fuel reduction techniques and a control on the relative abundance and richness of reptiles and amphibians using drift fence arrays with pitfall and funnel traps. Three replicate blocks were established at the Green River Game Land, Polk County, North Carolina. Each replicate block contained four experimental units that were each approximately 14 ha in size. Treatments were prescribed burn (B); mechanical understory reduction (M); mechanical + burn (MB); and controls (C). Mechanical treatments were conducted in winter 2001–2002, and prescribed burns in March 2003. Hot fires in MB killed about 25% of the trees, increasing canopy openness relative to controls. Leaf litter depth was reduced in B and MB after burning, but increased in M due to the addition of dead leaves during understory felling. The pre-treatment trapping period was short (15 August-10 October 2001) but established a baseline for post-treatment comparison. Post-treatment (2002-2004), traps were open nearly continuously May-September. We captured a total of 1308 species of 13 amphibians, and 335 reptiles of 13 species. The relative abundance of total salamanders, common salamander species, and total amphibians was not changed by the fuel reduction treatments. Total frogs and toads (anurans) and Bufo americanus were most abundant in B and MB; however, the proximity of breeding sites likely affected our results. Total reptile abundance and Sceloporus undulatus abundance were highest in MB after burning, but differed significantly only from B. Mean lizard abundance in MB was highest in 2004 and higher than in other treatments, but differences were not statistically significant. Our results indicate that a single application of the fuel reduction methods studied will not negatively affect amphibian or reptile abundance or diversity in southern Appalachian upland hardwood forest. Our study further suggests that high-intensity burning with heavy tree-kill, as in MB, can be used as a management tool to increase reptile abundance - particularly lizards - with no negative impact on amphibians, at least in the short-term. Published by Elsevier B.V.

Keywords: Amphibians; Burn; Fire surrogate; Fuel reduction; Prescribed fire; Reptiles; Southern; Appalachians

1. Introduction

Species richness of amphibians and reptiles in the southern Appalachian Mountains rivals that in any other area of the United States (Kiester, 1971). In eastern hardwood forests, amphibians compose a substantial proportion of vertebrate biomass. Estimates of salamander biomass were similar to mouse and shrew biomass combined, and 2.6 times as great as breeding bird biomass, within the Hubbard Brook Experimental Forest in New Hampshire (Burton and Likens, 1975). Petranka and Murray (2001) estimated 18,486 individuals totaling 16.5 kg of salamanders per hectare at a southern Appalachian streamside site. Reptiles and amphibians are predators, and serve as prey for many vertebrate predators (Pough et al., 1987). Clearly, herpetofauna are an important component of biological diversity, and also play an important role in supporting the biological diversity of vertebrates.

More and more commonly, prescribed burning and mechanical understory reductions are being used in eastern hardwood forest as silvicultural tools for reducing fuels and the risk of wildfire (Pilliod et al., 2003), and for ecosystem restoration, oak regeneration, understory control, and wildlife conservation (Brawn et al., 2001). Yet, surprisingly little is known about how reptiles and amphibians are affected by prescribed burning or other fuel reduction methods, especially in eastern hardwood forest.

^{*} Corresponding author. Tel.: +1 828 667 5261x118; fax: +1 828 667 9097. *E-mail address:* kgreenberg@fs.fed.us (C.H. Greenberg).

Amphibians (Class Amphibia) and reptiles (Class Reptilia) are phylogenetically, physiologically, and ecologically distinct from one another, so their responses to habitat alterations would likely differ. Amphibians have permeable, moist skin that for many serves a respiratory function and increases their susceptibility to desiccation. In contrast, reptiles have dry, scaly skin that protects them from desiccation, and generally require warm temperatures (associated with higher light levels) for egg incubation and hatchling development (Deeming and Ferguson, 1991). Individual species within the two classes also widely differ in their ecology and life histories. For example, some amphibian species are fully aquatic, others are aquatic during breeding and larval development but terrestrial during most of their adult lives, and others, such as the woodland salamanders (Family Plethodontidae), are fully terrestrial (Pilliod et al., 2003).

Among the few studies of herpetofaunal response to fire, most have been conducted in ecosystems adapted to frequent fire, such as the pine woods of the southeastern coastal plain. Historically, lightning-caused fire controlled hardwood invasion in those ecosystems, thus maintaining suitable habitat for many species that require open conditions and bare ground (see Russell et al., 1999; Greenberg, 2002 for reviews). In contrast, fire in eastern upland hardwood forest was usually ignited by American Indians, and later by European settlers (Harmon, 1982; Lorimer, 1993; Brose et al., 2001). The frequency, extent, and intensity of burns varied spatially and temporally with topography, proximity to dense human populations, and drought (Delcourt and Delcourt, 1997; Guyette et al., 2006). To our knowledge, no reptile or amphibian species occurring in eastern hardwood forest requires post-fire conditions for its persistence, although evidence suggests that many tolerate it or possibly respond favorably to it, depending upon life history traits (Renken, 2006).

Response to various fire and mechanical fuel reduction treatments is likely to differ among taxa and among species that have evolved under different environmental conditions and fire regimes (Greenberg, 2002; Pilliod et al., 2003; Russell et al., 2004). Responses are also likely to correspond to the type and intensity of disturbance and changes in macro- and micro-habitat conditions such as leaf litter, shade, and thus ground-level temperature and moisture (DeMaynadier and Hunter, 1995; Pilliod et al., 2003).

Among the few studies that have been conducted in eastern upland hardwood forest, most suggest that prescribed fire does not result in substantial direct mortality or changes in amphibian abundance but may benefit reptiles, particularly lizards (Russell et al., 1999; Renken, 2006). Ford et al. (1999) reported no effect of high-intensity prescribed fire on woodland salamanders in the southern Appalachians. However, most prescribed fire in eastern hardwood forest does not eliminate canopy cover, coarse woody debris, or duff, which provide cover and ameliorate temperature fluctuations and moisture levels on the forest floor.

In contrast, several studies in the eastern hardwood forest suggest that heavy canopy removal for forest regeneration treatments (e.g., clearcuts or shelterwoods) can adversely affect local amphibian populations, especially populations of salamanders (see DeMaynadier and Hunter, 1995; Harpole and Haas, 1999; Russell et al., 2004). The response of reptiles to silvicultural reductions in canopy cover is less well studied; again, lizards in particular may increase in sites with reduced canopy cover (Greenberg, 2001; Russell et al., 2004). Canopy removal results in higher light levels, a warmer, drier microclimate, and reduced leaf litter cover. These changes could cause salamanders to desiccate but also facilitate movement and thermoregulation for many reptile species (DeMaynadier and Hunter, 1995; Russell et al., 2004; Renken, 2006). Clearly, land managers need more information about how prescribed burning and other fuel reduction methods affect both reptiles and amphibians so they can better manage for diverse herpetofaunal communities or populations of sensitive taxa while managing wildfire risk and achieving other forest management objectives.

As part of the multidisciplinary National Fire and Fire Surrogate study (NFFS) (Youngblood et al., 2005), we used a replicated experimental design to examine how reptile and amphibian communities and individual species respond to fuel reduction by prescribed burns, mechanical understory reduction, or mechanical treatments followed by burning. In this paper we examine differences in relative abundance of individual species, reptiles and amphibians, and species richness in the southern Appalachians in untreated controls and in three treatments for fuel reduction.

2. Study area and methods

2.1. Study area

Our study was conducted on the 5841-ha Green River Game Land (35°17'9"N, 82°19'42"W, blocks 1 and 2; 35°15'42"N, 82°17′27″W, block 3) in Polk County, North Carolina. The area is managed by the North Carolina Wildlife Resources Commission, and lies on the escarpment of the Blue Ridge Physiographic Province, near its interface with the South Carolina Piedmont. Soils were primarily of the Evard series (fine-loamy, oxidic, mesic, Typic Hapludults), which are very deep (>1 m) and well-drained in mountain uplands (USDA Natural Resources Conservation Service, 1998). There were also areas of rocky outcrops in steeper terrain. The upland hardwood forest was composed mainly of oaks (Quercus spp.) and hickories (Carya spp.). Shortleaf (Pinus echinata) and Virginia (P. virginiana) pines were found on ridgetops, and white pine (P. strobus) occurred in moist coves. Forest age within experimental units varied from 80 to 120 years. Predominant shrubs were mountain laurel (Kalmia latifolia) along ridge tops and on upper southwest-facing slopes, and rhododendron (Rhododendron maximum) in mesic areas. Elevations within treatment units ranged from approximately 505 to approximately 660 m. None of the sites had been thinned or burned for at least 50 years (Dean Simon, North Carolina Wildlife Resources Commission, pers. comm.).

2.2. Study design

Our experimental design was a randomized block design with repeated measures over years. We selected three study

areas (blocks) within the Game Land. Perennial streams border and (or) traverse all three replicate blocks. Blocks were selected on the basis of their capacity to accommodate four experimental units each, forest age, cover type, and management history, to ensure consistency in baseline conditions among the treatments. Minimum size of experimental units (four within each block) was 14-ha to accommodate 10-ha "core" areas, with 20-m buffers around each. Dirt roads or fire lines separated but did not traverse some of the experimental units, and wooded trails traversed some experimental units.

Three treatments and an untreated control (C) were randomly assigned within each of the three study blocks, for a total of 12 experimental units. Fuel reduction treatments were mechanical understory reduction (M), prescribed burn (B), and mechanical + burn (MB). Mechanical treatments were conducted during winter 2001-2002. The understory was reduced using chainsaws (with no heavy equipment), and included all mountain laurel, rhododendron, and other shrubs and trees >1.8 m tall and <10.0 cm in diameter at breast height (dbh). Cut fuels were left scattered onsite so that low or no piles remained. Prescribed burns were conducted in B and MB treatment units on March 12 or 13, 2003. One block was burned by hand ignition using spot fire and strip-headfire techniques. The other blocks were ignited by helicopter using a plastic sphere dispenser and a spot fire technique. The objective of all treatments was to reduce ladder fuels by substantially reducing the shrub layer.

Fire intensities varied within and among sites, but were generally moderate to high. Flame lengths of 1-2 m (214–965 kW/m by Byram's flame length index) (Brown and Davis, 1973) occurred throughout all burn units, but flame lengths reached up to 5 m (7073 kW/m) in localized spots where topography or intersecting flame fronts contributed to erratic fire behavior. Measured temperatures were generally below 120 °C on B sites but often exceeded 800 °C in MB sites due to a combination of higher fine woody fuel loading, lower fuel moisture, and topography in MB (Ross Phillips, U.S. Forest Service, pers. comm.). A detailed description of fire behavior in this study is given by Phillips et al. (2006).

2.3. Habitat measurements

Habitat variables were measured pre-treatment (2001) in all experimental units and re-measured during the growing season immediately post-treatment (2002 for M, and 2003 for C, B, and MB). Measured habitat variables included live tree and snag (≥ 10 cm dbh) densities, leaf litter and duff depths, coarse woody debris (≥ 1 m in length and ≥ 15 cm large-end diameter within transect), and canopy openness. Trees and snags (≥ 10 cm dbh) were measured within 10, 0.05-ha plots that were spaced systematically within each treatment. Percent cover of coarse woody debris was measured within 4 m × 20 m belt transects originating at gridpoints that were spaced at 50-m intervals throughout treatment areas. Depth of leaf litter and duff was measured at three locations along each of three randomly oriented, 15-m transects originating at grid points that were spaced at 50-m intervals throughout treatment areas.

We used a spherical densiometer to obtain a crude measure of percent canopy openness at breast height each summer (leaf on) beginning in 2002 (prior to canopy disturbance) at both herpetofaunal arrays within each experimental unit.

2.4. Herpetofaunal sampling

We established two drift fence arrays ≥ 100 -m apart in each experimental unit. Arrays were constructed with three 7.6-m sections of aluminum flashing positioned at approximately 120° angles (in a "Y" shape), with one 19-1 bucket buried at each section end such that its rim was flush with the ground surface, and a fourth pitfall shared by all three "arms" in the center of the "Y." Double-ended funnel traps were placed on both sides of each arm for a total of six funnel traps at each array. Wooden stakes were added for support. A moist sponge was placed in each bucket to provide moisture and cover for captured animals.

Arrays were open continuously and concurrently from 15 August to 10 October during 2001 (pre-treatment) to establish baseline conditions and to assess potential differences among (future) treatments prior to treatment implementation. Posttreatment (2002, 2003, and 2004), traps were open May-September with some exceptions (open 7 May–1 October 2002; open 5 May-2 July and 28 July-1 October 2003; and open 10 May-2 August and 20 August-1 October 2004). All traps were checked three times weekly. Reptiles and amphibians were identified, weighed, measured (snout-vent and total length), sexed, and marked by year and treatment by toe- or scale-(snakes) clipping. We captured two species of Plethodon (in the P. glutinosis and the P. jordani complexes, respectively) (Highton and Peabody, 2000), but combined them in our analyses because of occasional confusion between them during field identification and because of their similar ecological habits (Conant and Collins, 1998).

2.5. Statistical analyses

Our basic experimental design was a randomized block with four treatments, with repeated measures over years. However, because treatments were initiated incrementally in different years, a straightforward standard analysis was not possible. We therefore first used one-way ANOVA on pre-treatment (2001) species richness and natural log-transformed relative abundance (number of individuals captured in both drift fence arrays within a treatment unit, per 100 nights of trapping) data to test whether initial, pre-treatment differences in reptile or amphibian abundance existed among (future) treatments. We treated the incremental establishment of our study as three separate phases, with separate statistical analyses performed for each. Phase 1 analysis tested whether mechanical understory reduction affects reptiles or amphibians, and included data from 2001, prior to any fuel reduction treatments, and for 2002 when a mechanical understory reduction treatment was conducted in half of the experimental units. Phase 2 analysis compared effects of prescribed burns in experimental units that were untreated the previous year, prescribed burns in units that had undergone mechanical treatment the previous year, units that had undergone mechanical treatment the previous year and had no additional treatments since, and untreated units. Analysis of this phase included data from 2002, when half of the experimental units had undergone mechanical treatment and half were untreated, and from 2003 when prescribed burns had been conducted in half of the untreated units and in half of the units that had undergone mechanical treatment. Phase 3 analysis included data from 2003 to 2004, after all treatments had been implemented, and tested whether any of the three fuel reduction treatments (B, M, and MB) or controls (C) affected reptiles or amphibians over the 2-year period. Only species that were sufficiently common (\geq 15 individuals captured) during at least one of the years covered by each phase were included in statistical analyses.

2.5.1. Phases 1 and 2: Incremental application of fuel reduction treatments

We performed separate ANOVAs for phases 1 and 2. Each of these ANOVAs used data from 2 consecutive years to test for differential effects of treatments implemented between the 2 years. For each ANOVA, estimates of relative abundance or species richness were first natural-log transformed to reduce possible heteroscedasticity and to estimate effects on a multiplicative scale. We then subtracted the estimate for the first year from the second year for each experimental unit. The difference represents the relative increase or decrease in abundance (or species richness) between the 2 years. These differences were analyzed with a one-way ANOVA, followed by a Tukey multiple comparison procedure.

The ANOVA for phase 1 used data from 2001 (all pretreatment) and 2002 (mechanical treatment in two of the four units in each block), and thus the only comparison of interest was whether the response of herpetofauna in units that received mechanical treatment (C–M) differed from the response of herpetofauna in units that remained as controls (C–C). In our analyses we considered the two experimental units per block (two C–C and two C–M in each of the three blocks, in 2002) to be independent replicates because treatments were assigned randomly and most reptiles and amphibians use relatively small areas (Szaro, 1988). The ANOVA for phase 2 used data from 2002 and 2003, and four "treatments" were involved: was C and remained C (C–C), was M and remained M (M–M), was C and changed to B (C–B), and was M and changed to MB (M– MB). For both phases 1 and 2 we compared relative abundance and species richness of amphibians, reptiles, taxonomic orders or suborders (frogs and toads (Anura), salamanders (Caudata), lizards (Lacertilia), and snakes (Serpentes)), and commonly captured species between (phase 1) or among (phase 2) treatments.

2.5.2. Phase 3: Comparison of three fuel reduction treatments and controls, 2003–2004

We applied a two-way ANOVA with repeated measures over years to post-treatment data (2003–2004) to compare relative abundance and species richness of total amphibians and reptiles, and relative abundance of commonly captured taxa, among treatments and years, and to test for treatment \times year interactions. We used the Type III sum of squares and associated mean squares as the error term for treatment effects. We interpreted a significant treatment \times year interaction effect as a significant treatment effect indicating that year-to-year changes differed among the treatments. Post-hoc tests were performed using a Tukey multiple comparison procedure.

2.5.3. Habitat comparisons, pre- and post-treatment

We used one-way ANOVAs to test for among-treatment differences in measured habitat features for pre-treatment (2001) and post-treatment (2002 measurements for M; 2003 measurements for B, C, and MB) data. Canopy openness was also compared among treatments for 2002 (before canopy disturbance) and post-treatment (2003). Percentage data (shrub cover and canopy openness) was square-root arcsine transformed for ANOVAs. Post-hoc tests were performed using a Tukey multiple comparison procedure.

Table 1

Mean (\pm S.E.) number of pre- and post-treatment live trees (per ha), percent cover of coarse woody debris, duff and leaf litter depth (cm), and percent canopy openness, in three treatments: burned (B), mechanical understory felling (M), mechanical understory felling followed by burning (MB), and controls (C) (n = 3 each), Green River Game Land, Polk County, NC, USA

Habitat feature ^a	Measurement	Treatment				
		С	В	М	MB	
Live trees/ha	Pre-treatment Post-treatment	$\begin{array}{c} 566.0 \pm 10.6 \\ 550.7 \pm 15.0^{\rm A} \end{array}$	$\begin{array}{c} 568.7 \pm 29.3 \\ 539.3 \pm 30.0^{\rm A} \end{array}$	$\begin{array}{c} 602.0 \pm 18.1 \\ 588.0 \pm 11.0^{\rm A} \end{array}$	$\begin{array}{c} 506.7 \pm 33.8 \\ 379.3 \pm 43.5^{\rm B} \end{array}$	0.1662 0.0066
CWD (%)	Pre-treatment Post-treatment	$\begin{array}{c} 1.0\pm0.3\\ 0.9\pm0.3\end{array}$	$\begin{array}{c} 1.2\pm0.3\\ 1.2\pm0.3\end{array}$	$\begin{array}{c} 1.1\pm0.2\\ 1.0\pm0.2 \end{array}$	$\begin{array}{c} 1.7\pm0.7\\ 1.2\pm0.5\end{array}$	0.3998 0.8518
Leaf litter depth (cm)	Pre-treatment Post-treatment	$\begin{array}{c} 5.0\pm0.1\\ 4.2\pm0.5^{\mathrm{A}}\end{array}$	$\begin{array}{c} 4.8 \pm 0.3 \\ 0.9 \pm 0.1^{\rm B} \end{array}$	$\begin{array}{c} 5.0 \pm 0.2 \\ 5.5 \pm 0.2^{\rm C} \end{array}$	$\begin{array}{c} 5.1 \pm 0.3 \\ 0.5 \pm 0.1^{\rm B} \end{array}$	0.8955 <0.0001
Duff depth (cm)	Pre-treatment Post-treatment	$\begin{array}{c} 3.5\pm0.5\\ 3.5\pm0.6\end{array}$	$\begin{array}{c} 4.6\pm0.8\\ 3.6\pm0.3\end{array}$	$\begin{array}{c} 4.1\pm0.7\\ 5.4\pm1.0\end{array}$	$\begin{array}{c} 4.5\pm0.9\\ 3.0\pm0.4\end{array}$	0.1981 0.1871
Canopy openness (%)	Pre-treatment Post-treatment	$\begin{array}{c} 6.8 \pm 1.0 \\ 1.6 \pm 0.4^{\rm A} \end{array}$	$\begin{array}{c} 6.2 \pm 0.3 \\ 2.6 \pm 1.1^{\rm AB} \end{array}$	$\begin{array}{c} 8.3\pm1.2\\ 3.0\pm0.8^{AB} \end{array}$	$\begin{array}{c} 8.5 \pm 2.6 \\ 12.8 \pm 5.0^{\rm B} \end{array}$	0.5614 0.0280

^a Within each habitat feature and measurement (pre- or post-treatment), differences among treatments are denoted by different letters within rows.

3. Results

3.1. Habitat

Prior to treatment implementation, live tree density, percent cover of CWD, depth of the leaf litter and duff, and canopy openness did not differ among treatments (Table 1). Hot fires in MB killed approximately 25% of the trees within a few months of the burns (Table 1). Canopy openness was higher in MB than in C post-treatment, but did not differ from canopy openness in the other two fuel reduction treatments due to high variability among experimental units. Leaf litter depth was significantly lower (reduced by >80%) in both burned treatments (B and MB) after burning, but increased in M due to the addition of dead leaves during understory felling. None of the fuel reduction treatments had an immediate effect on duff depth or percent cover of CWD (Table 1).

3.2. Reptiles and amphibians

We captured a total of 1308 amphibians of 13 species and 335 reptiles of 13 species during the 4-year study period; three additional species were observed within the study area but never captured in traps, and were not included in analyses (Table 2). Because capture numbers were low, only a few species could be included in data analyses, and some could not be included in every phase of our study. Turtles were never included, and snakes were included only in phases 1 and 2.

Table 2

Annual and total number^a of amphibian and reptile captures (and recaptures) using drift fences with pitfall and funnel traps during 2001–2004, Green River Game Land, Polk County, NC, USA

Species	Year				
	2001 56 ^b	2002 147 ^b	2003 123 ^b	2004 126 ^b	452 ^b
Frogs and toads (Anura)	134 (11)	199 (15)	203 (3)	471 (7)	1007 (26)
American toads (Bufo americanus)	53 (4)	133 (4)	190 (3)	452 (7)	828 (18)
Gray treefrog (Hyla versicolor-chrysoscelis complex)	0 (0)	1 (0)	0 (0)	0 (0)	1 (0)
Green frog (Rana clamitans)	74 (7)	65 (1)	9 (0)	15 (0)	163 (8)
Pickerel frog (R. palustris)	7 (0)	4 (0)	0 (0)	3 (0)	14 (0)
Wood frog (R. sylvatica)	0 (0)	0 (0)	0 (0)	1 (0)	1 (0)
Salamanders (Caudata)	39 (1)	59 (0)	81 (3)	122 (0)	301 (4)
Northern dusky (Desmognathus fuscus)	0 (0)	0 (0)	1 (0)	0 (0)	1 (0)
Seal salamander (D. monticola)	0 (0)	0 (0)	1 (0)	2 (0)	3 (0)
Blackbelly salamander (D. quadramaculatus)	2 (0)	3 (0)	1 (0)	2 (0)	8 (0)
Blue Ridge two-lined (Eurycea wilderae)	2 (0)	0 (0)	7 (0)	6 (0)	15 (0)
Red-spotted newt (Nothphthalmus viridescens)	15 (1)	29 (0)	37 (2)	41 (0)	122 (3)
Plethodon spp. ^c	10 (0)	16 (0)	20 (0)	42 (0)	88 (0)
Northern red salamander (Pseudotriton ruber)	10 (0)	11 (0)	14 (1)	28 (0)	63 (1)
Lizards (Lacertilia)	24 (1)	107 (5)	48 (1)	61 (5)	240 (12)
Coal skink (Eumeces anthracinus)	2 (0)	6 (0)	3 (0)	0 (0)	11 (0)
Five-lined skink (Eumeces fasciatus)	13 (0)	61 (3)	30 (0)	42 (3)	146 (6)
Broad-headed skink (Eumeces laticeps)	0 (0)	17 (0)	3 (0)	1 (1)	21 (1)
Northern fence lizard (Sceloporus undulatus)	9 (1)	23 (2)	12 (1)	18 (1)	62 (5)
Snakes (Serpentes)	8 (0)	68 (0)	11 (0)	6 (0)	93 (0)
Copperhead (Agkistrodon contortrix)	1 (0)	1 (0)	1 (0)	0 (0)	3 (0)
Worm snake (Carphophis amoenus)	7 (0)	54 (0)	3 (0)	3 (0)	67 (0)
Black racer (Coluber constrictor)	0 (0)	1 (0)	×	0 (0)	1 (0)
Timber rattlesnake (Crotalis horridus)	×	2 (0)	×	0 (0)	2 (0)
Ringneck snake (Diadophis punctatus)	0 (0)	8 (0)	2 (0)	1 (0)	11 (0)
Black rat snake (Elaphe obsoleta)	_	×	×	×	×
Eastern hognose snake (Heterodon platyrhinos)	-	×	-	-	×
Northern water snake (Nerodia sipedon)	0 (0)	0 (0)	1 (0)	0 (0)	1 (0)
Northern redbelly snake (Storeria occipitomaculata)	0 (0)	0 (0)	1 (0)	0 (0)	1 (0)
Eastern garter snake (Thamnophis sirtalis)	0 (0)	2 (0)	3 (0)	2 (0)	7 (0)
Turtles (Testudinides)	1 (0)	1 (0)	0 (0)	0 (0)	2 (0)
Common snapping turtle (Chelydra serpentina)	-	-	×	×	×
Eastern box turtle (Terrapene carolina)	1 (0)	1 (0)	×	×	2 (0)
All amphibians	173 (12)	258 (5)	284 (6)	593 (7)	1308 (30)
All reptiles	33 (1)	176 (5)	59 (1)	67 (5)	335 (12)
Total	206 (13)	434 (10)	343 (7)	660 (12)	1643 (42)

 a × denotes sightings within the study area, but no captures in traps; sightings only noted if no captures.

^b Denotes the number of nights that both arrays were open.

^c Includes a species in the *P. glutinosis* and *P. jordani* complex, respectively.

Neither species richness of amphibians ($P_{trt} = 0.4547$) or reptiles ($P_{trt} = 0.6420$), nor the relative abundance of amphibians ($P_{trt} = 0.7668$), reptiles ($P_{trt} = 0.9106$), taxonomic orders or suborders ($P_{trt} \ge 0.3648$), and commonly captured species ($P_{trt} \ge 0.2509$) differed among (future) treatments during 2001 (pre-treatment).

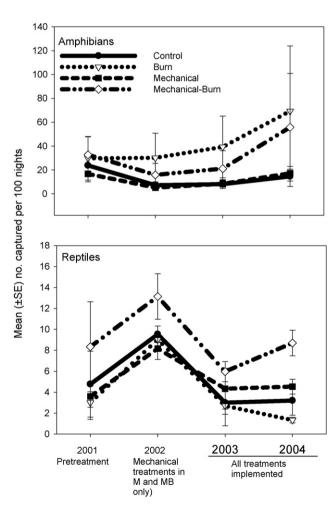
3.2.1. Phases 1 and 2

Mechanical understory reductions did not have a detectable effect on the relative abundance (Fig. 1) or species richness (Fig. 2) of total amphibians or reptiles. They did not have a detectable effect on the relative abundance of total anurans, salamanders, lizards, and snakes (Fig. 3). They did not have a detectable effect on the relative abundance of any tested species ($P_{trt} \ge 0.1008$) except green frogs (*R. clamitans*) ($P_{trt} = 0.0585$), which decreased in C–M relative to C–C (2001–2002). Overall, reptile captures increased by about 40% from 2001 to 2002 (Fig. 1), mostly due to dramatic increases in the relative abundance of worm snakes (*Carphophis amoenus*) (Table 2). However, the increase in worm snake abundance did

not appear to be related to implementation of the M treatment ($P_{trt} = 0.4035$). Similarly, there was no immediate, detectable response by reptiles or amphibians as a whole (Fig. 1), anurans, salamanders, lizards and snakes (Fig. 3), or any tested species ($P_{trt} > 0.1076$) (Fig. 4) to C–C, C–B, M–M, or M–MB (2002–2003).

3.2.2. Phase 3

Two-way ANOVA with repeated measures over years on post-treatment data (2003 and 2004) indicated that there were no differences in the relative abundance of total amphibians among treatments, but more were captured in 2004 than in 2003 (Table 3; Fig. 1). Amphibian species richness was higher in 2004 than in 2003, and a treatment \times year interaction effect indicated that change between the years was greater in M than in the other treatments (Table 3; Fig. 2). We found higher relative abundance of total anurans in both burn treatments (B and MB) than in the unburned treatments (M and C), and more in 2004 than in 2003 (Fig. 3). This effect was at least partially driven by American toads (*Bufo americanus*) (Table 2; Fig. 4);



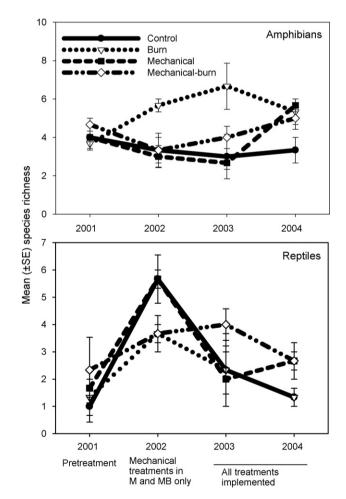


Fig. 1. Mean (\pm S.E.) relative abundance total amphibians and reptiles in three fuel reduction treatments: prescribed burn (B), mechanical understory reduction (M), mechanical + burn (MB), and controls (C) (n = 3 each), Green River Game Land, Polk County, NC, USA. Data for 2001 are pre-treatment; in 2002 only M treatments had been implemented (in M and MB); 2003–2005 data were collected after all treatments had been implemented.

Fig. 2. Mean (\pm S.E.) species richness of amphibians and reptiles in three fuel reduction treatments: prescribed burn (B), mechanical understory reduction (M), mechanical + burn (MB), and controls (C) (n = 3 each), Green River Game Land, Polk County, NC, USA. Data for 2001 are pre-treatment; in 2002 only M treatments had been implemented (in M and MB); 2003–2005 data were collected after all treatments had been implemented.

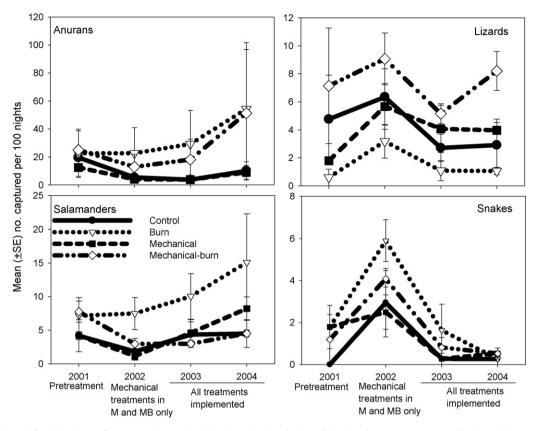


Fig. 3. Mean (\pm S.E.) relative abundance of anurans, salamanders, lizards, and snakes in three fuel reduction treatments: prescribed burn (B), mechanical understory reduction (M), mechanical + burn (MB), and controls (C) (n = 3 each), Green River Game Land, Polk County, NC, USA. Data for 2001 are pre-treatment; in 2002 only M treatments had been implemented (in M and MB); 2003–2005 data were collected after all treatments had been implemented.

treatment effects on anurans were not detected when American toads were removed from data analyses ($P_{trt} = 0.3119$; $P_{yr} = 0.5865$; $P_{trt \times yr} = 0.0761$). We did not detect differences in the relative abundance of total salamanders or any tested species among treatments. *Plethodon* spp. and northern red salamanders (*Pseudotriton ruber*) were more abundant in 2004 than in 2003, but relative abundance did not differ by year for total salamanders or red-spotted newt (*Notophthalmus viridescens*) efts.

Total reptiles (Table 3; Fig. 1) and fence lizards (*Sceloporus undulatus*) (Table 3; Fig. 4) were more abundant in MB than in B. The relative abundance of total lizards (Table 3; Fig. 3) and five-lined skinks (Table 3; Fig. 4) did not differ among treatments, but trends indicated an increase in MB for both species in 2004. Reptile species richness did not differ among the treatments (Table 3; Fig. 2). Snakes were not captured in sufficient numbers during 2003–2004 to be included in data analyses for phase 3.

4. Discussion

The general community composition of reptiles and amphibians was not changed by mechanical understory removal, prescribed burning, or both, at least in the shortterm. The relative abundance of most amphibian species was not changed by the fuel reduction treatments; a possible exception was American toads which were more abundant in burned (B and MB) than unburned (C and M) treatments. Kirkland et al. (1996) also reported a greater abundance of American toads on a burned than an unburned forest in Pennsylvania. In contrast, Keyser et al. (2004) reported no difference in the relative abundance of American toads between burned and unburned oak forest in the Virginia Piedmont. In our study, a large proportion of total (study-wide) American toad captures, mostly juveniles (<41 mm SVL), occurred in the same two of twelve experimental units each year, B (25-46%) and MB (28–39%), in a single study block. This suggests that there were breeding sites nearby. A large proportion of total green frog captures (all juveniles \leq 52 mm SVL) also occurred at the same two sites plus a few other sites. We believe that the proximity of breeding sites, successful recruitment of young (which varied each year), and juvenile dispersal distances influenced our capture rates of both American toads and green frogs far more than did the fuel reduction treatments and limit the conclusions we can draw regarding the treatment response of those species. This bias has been observed commonly in other studies of wetland-breeding amphibians (Greenberg, 2002). We caught relatively few individuals of other anuran species. Therefore, our results for "all anurans" were likely also heavily biased by the proximity of breeding sites for American toads and green frogs.

Salamanders and newts showed little numerical response to the fuel reduction treatments. This was somewhat surprising, as several micro- and macro-habitat conditions that mediate

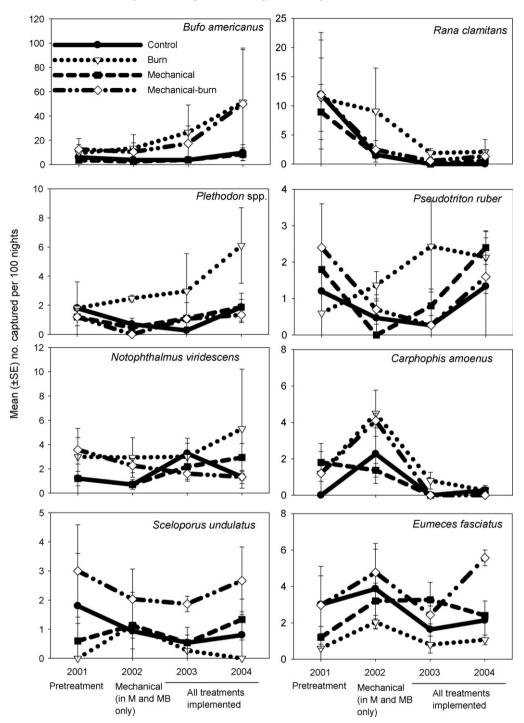


Fig. 4. Mean (\pm S.E.) relative abundance of commonly trapped species of reptiles and amphibians and reptiles in three fuel reduction treatments: prescribed burn (B), mechanical understory reduction (M), mechanical + burn (MB), and controls (C) (n = 3 each), Green River Game Land, Polk County, NC, USA. Data for 2001 are pre-treatment; in 2002 only M treatments had been implemented (in M and MB); 2003–2005 data were collected after all treatments had been implemented.

moisture and temperature at ground level, including leaf litter depth, live tree density, and canopy cover were dramatically reduced in MB (as was leaf litter depth in B). However, duff depth and percent cover of coarse woody debris did not differ among the treatments and may have provided sufficient cover and moisture for woodland salamanders. Further, salamanders may retreat underground and emerge at night to forage on the forest floor when temperatures are cooler and moisture levels are higher. Other studies in eastern upland hardwood forest also have found that prescribed fire does not affect salamander relative abundance (Ford et al., 1999; Floyd et al., 2002; Keyser et al., 2004). In the southern Appalachians (and in habitat somewhat similar to that in this study), high-intensity prescribed fire was not found to affect woodland salamanders, including Jordan's salamander (Ford et al., 1999). In the central Appalachians, Kirkland et al. (1996) captured more red-backed salamanders

Table 3

Results of two-way analysis of variance with repeated measures over years (RM ANOVA) for post-treatment (2003 and 2004) data on species richness and relative abundance (number captured per 100 nights that both arrays open) of common (\geq 30 individuals captured in during 2003 and 2004 combined) reptile and amphibian taxa captured in the three treatments: prescribed burn (B), mechanical understory reduction (M), mechanical + burn (MB), and controls (C), Green River Game Land, Polk County, NC, USA

	RM ANOVA (2003–2004)			Treatment effects ^A	Year effects ^A
	$P_{\rm trt}$ d.f. = 3,6	$P_{\rm yr}$ d.f. = 1,8	$P_{\rm trt \ \times \ yr}$ d.f. = 3,8		
Frogs and toads (Anura)	0.0286	0.0320	0.6059	$M^a C^a MB^b B^b$	2003 ^a 2004 ^b
American toad (Bufo americanus)	0.0378	0.0279	0.7237	M ^a C ^a MB ^b B ^b	2003 ^a 2004 ^b
Green frog (Rana clamitans)	0.1968	0.6022	0.1165		
Salamanders (Caudata)	0.2722	0.1157	0.6614		
Red-spotted newt (eft) (Notophthalmus viridescens)	0.9374	0.7996	0.5970		
Plethodon spp. (P. glutinosis and P. jordani complexes)	0.4887	0.0299	0.5605		$2003^{\rm a} \ 2004^{\rm b}$
Northern red salamander (Pseudotriton ruber)	0.2851	0.0205	0.1690		$2003^{a} \ 2004^{b}$
Total Amphibians (Amphiba)	0.1308	0.0038	0.8101		2003 ^a 2004 ^b
Amphibian richness	0.1112	0.0153	0.0233		$2003^{a} \ 2004^{b}$
Lizards (Lacertilia)	0.2147	0.8467	0.5244		
Five-lined skink (Eumeces fasciatus)	0.4064	0.2461	0.6233		
Northern fence lizard (Sceloporus undulatus)	0.0640	0.8838	0.6590	$B^a C^{ab} M^{ab} M B^b$	
Total reptiles (<i>Reptilia</i>)	0.0717	0.7200	0.8594	B ^a C ^{ab} M ^{ab} MB ^b	
Reptile richness	0.1029	0.5228	0.6002		

^A Where effects are significant, treatments and years are ordered from least to highest, and different letters among treatments or years indicate significant differences.

(*P. cinereus*) and slimy salamanders on burned than unburned sites, but in numbers too low to ascertain statistical significance.

Increased amphibian species richness on M in 2004 was suggested by a treatment × year interaction effect. However, increases did not involve the addition of any new species to M, but rather captures of the same species on more of the M experimental units, which increased mean species richness. Moreover, the M treatment units were not treated further after 2002, and thus an ecologically meaningful association between increased species richness and changes in habitat conditions between 2003 and 2004 is unlikely. Harpole and Haas (1999) reported no effect of understory reduction by herbicide on the relative abundance of salamanders in a southern Appalachian hardwood forest, but found fewer salamanders in sites with heavy canopy removal (e.g., clearcuts and shelterwoods).

Other studies in eastern upland hardwood forest suggest that reptiles are not measurably affected by prescribed fire (Floyd et al., 2002), or are positively affected by prescribed burning (Keyser et al., 2004) due to reduced leaf litter, more bare ground, and higher light levels that facilitate movement and thermoregulation (Russell et al., 1999; Renken, 2006). In the southern Appalachians, the abundance of total lizards, fence lizards, and five-lined skinks was higher in extended forest gaps with partial canopy cover than in forested controls, despite similar depths of leaf litter (Greenberg, 2001). Many studies do not report post-disturbance changes in habitat conditions or (in the case of prescribed burn studies) fire intensity, and this makes it difficult to interpret or compare their results.

In our study, high-intensity burns resulted in higher total reptile and fence lizard abundance; relative abundance of these taxa was highest in MB after burning, but differed significantly only from B. Although we did not detect a significant trend for lizards as a group, they were clearly important drivers for the significant differences detected for reptiles as a whole, as we captured relatively few snakes or turtles during phase 3. Further, relative abundance of the relatively common five-lined skink (*Eumeces fasciatus*) increased more in MB than in the other treatments by 2004, although the trend was not statistically significant. Hatchlings and juveniles of five-lined skinks and fence lizards were captured in both burned and unburned treatments, indicating that prescribed burning did not adversely affect lizard reproduction.

Causal factors for the differences we observed remain unclear. We found a higher abundance of reptiles in MB, where both leaf litter and canopy cover were reduced, than in B where leaf litter was reduced but canopy cover was not. This suggests that increased light may have been a greater positive influence on reptiles than reductions in leaf litter alone, although enhancement of visibility of ground-dwelling arthropod prey was likely similar for both burn treatments. Further, reptile abundance in burn treatments (B and MB) did not statistically differ from that in the unburned treatments (M and C) where leaf litter and canopy cover remained intact. Differences in arthropod prey availability were not a likely explanation for the differences we saw; neither species nor size of arthropods was determined, but relative abundance of total ground-dwelling macroarthropods did not differ among the treatments (Greenberg and Miller, 2007). Clearly, relationships between reptile abundance and specific habitat features, such as leaf litter and canopy cover, need further examination to determine if and how they influence the relative abundance of reptiles.

In our study, low treatment replication (n = 3 per treatment and control) and relatively low capture rates increased the likelihood that we did not detect some responses that did indeed occur (the likelihood of Type II error). Also, some response patterns can be difficult to interpret with limited replication, particularly for aquatic-breeding amphibians where proximity to breeding sites exerts a strong confounding influence (Greenberg, 2001). Nonetheless, we believe that our results for *Plethodon* spp. (no response) and reptiles (tendency to be higher in MB) reflect real trends, and our findings are corroborated by other studies in eastern hardwood forest.

Of notable interest was the dramatic increase in captures of both adult (\geq 180 mm SVL; 38%) and juvenile (<180 mm SVL; 62%) worm snakes in 2002 (54 captures) relative to other years (3–7 captures). Increases did not appear to be associated with treatments or precipitation. Also of note was the occurrence of coal skinks (*E. anthracinus*) on our study area; to the best of our knowledge, this species was previously unrecorded from Polk county (Palmer and Braswell, 1995).

5. Conclusions

Our results indicate that in southern Appalachian upland hardwood forest, a single application of the fuel reduction methods we studied does not negatively affect amphibian or reptile abundance or diversity. Our data further suggest that a one-time, high-intensity prescribed fire that kills trees and reduces canopy cover can be used as a management tool in upland hardwood forest to increase reptile abundance particularly lizards - without apparent adverse effects on amphibians, at least in the short-term. Herpetofaunal response to the MB treatment is likely to change over time as snags fall, light conditions change, leaf litter accumulates, and other habitat attributes and food resources (e.g., arthropod and fruit abundance) continue to change. Repeated fuel reduction treatments, such as multiple burns, and season of burn could affect responses differently than the treatments we report here. Further, herpetofaunal composition and communities shift across a moisture gradient, and in relation to proximity to water; hence, our results pertain to upland hardwood forests on drier sites within the southern Appalachians. In order to fully understand how fuel reduction treatments affect reptiles and amphibians at the community and species level, burn frequency and timing should also be studied, and post-treatment(s) sampling of both herpetofauna and habitat structure must continue for several years.

Acknowledgements

This is contribution number 146 of the National Fire and Fire Surrogate Research project. This research was funded by the Forest Service, U.S. Department of Agriculture, through the National Fire Plan. Although the authors received no direct funding for this research from the Interagency Joint Fire Science Program (JFSP), the research was greatly facilitated by the JFSP support of existing NFFS project sites. We thank J.D. Lanham for advice on drift fence array design, and J. Petranka for assistance with difficult identifications. J. Baker, A.L. Tomcho, J. Tomcho, D. Watts, V. Sudilovsky, T. Hayes, G. Graeter, P. Craig, S. Walter, and several volunteers for help in establishing drift fence arrays and (or) sampling herpetofauna. R. Phillips and others collected and provided habitat data. We thank the North Carolina Wildlife Resources Commission, especially D. Simon, for support, for permitting this study to be conducted on state Game Lands, and for conducting all fuel reduction treatments. W.M. Ford, A. Braswell, C. Moorman, and C.E. Matthews provided useful suggestions for improvements to an earlier version of this manuscript.

References

- Brawn, J.D., Robinson, S.K., Thompson III, A.R., 2001. The role of disturbance in the ecology and conservation of birds. Ann. Rev. Ecol. Syst. 32, 251–276.
- Brose, P., Schuler, T., Van Lear, D., Berst, J., 2001. Bringing fire back: the changing regimes of the Appalachian mixed-oak forests. J. For. 99, 30–35.
- Brown, A.A., Davis, K.P., 1973. Forest Fire Control and Use. McGraw-Hill, New York, New York, USA.
- Burton, T.M., Likens, G.E., 1975. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. Copeia 1975, 541– 546.
- Conant, R., Collins, J.T., 1998. Reptiles and Amphibians of Eastern/Central North America. Houghton Mifflin Company, New York, New York, USA.
- Delcourt, H.R., Delcourt, P.A., 1997. Pre-Columbian native American use of fire on southern Appalachian landscapes. Con. Biol. 11, 1010–1014.
- 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.
- Deeming, D.C., Ferguson, M.W.J., 1991. Physiological effects of incubation temperature on embryonic development in reptiles and birds. In: Deeming, D.C., Ferguson, M.W.J. (Eds.), Egg Incubation: It's Effects on Embryonic Development in Birds and Reptiles. Cambridge University Press, New York, New York, pp. 32–37.
- Floyd, T.M., Russell, K.R., Moorman, C.E., Van Lear, D.H., Guynn Jr., D.C., 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 11th Biennial Southern Research Conference. U.S. Forest Service General Technical Report SRS-48, Asheville, NC, pp. 123–127.
- Ford, W.M., Menzel, M.A., McGill, W.W., Laerm, J., McCay, T.S., 1999. Effects of a community restoration fire on small mammals and herpetofauna in the southern Appalachians. For. Ecol. Manage. 114, 233–243.
- Greenberg, C.H., 2001. Response of reptile and amphibian communities to canopy gaps crated by wind disturbance in the southern Appalachians. For. Ecol. Manage. 148, 135–144.
- Greenberg, C.H., 2002. Fire, habitat structure and herpetofauna in the southeast. 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 General Technical Report NE-288, Newtown Square, PA, pp. 91–98.
- Greenberg, C.H., Miller, S., 2007. Short-term response of shrews to prescribed fire and mechanical fuel reduction in a southern Appalachian upland hardwood forest. For. Ecol. Manage. 243, 231–236.
- Guyette, R.P., Dey, D.C., Stambaugh, M.C., Muzika, R., 2006. Fire scars reveal variability and dynamics of eastern fire regimes. In: Dickinson, M.B. (Ed.), Fire in Eastern Oak Forests: Delivering Science to Land Managers. U.S. Forest Service General Technical Report NRS-P-1, Newtown Square, PA, pp. 20–39.
- Harmon, M., 1982. Fire history of the westernmost portion of the Great Smoky Mountains National Park. Bull. Torrey Bot. Club 109, 74–79.
- Harpole, D.N., Haas, C.A., 1999. Effects of seven silvicultural treatments on terrestrial salamanders. For. Ecol. Manage. 114, 349–356.
- Highton, R., Peabody, R.B., 2000. Geographic protein variation and speciation in salamanders of the *Plethodon jordani* and *Plethodon glutinosus* complexes in the southern Appalachian Mountains with the description of four new species. In: Bruce, R.C., Jaeger, R.G., Houck, L. (Eds.), The Biology of Plethodontid Salamanders. Kluwer Academic/Plenum Publishers, New York, New York, pp. 31–93.

- Keyser, P.D., Sausville, D.J., Ford, M.W., Schwab, D.J., Brose, P.H., 2004. Prescribed fire impacts to amphibians and reptiles in shelterwood-harvested oak-dominated forests. Vir. J. Sci. 55, 159–168.
- Kiester, A.R., 1971. Species density of North American amphibians and reptiles. Syst. Zool. 20, 127–137.
- Kirkland Jr., G.L., Snoddy, H.W., Amsler, T.L., 1996. Impact of fire on small mammals and amphibians in a central Appalachian deciduous forest. Am. Midl. Nat. 135, 253–260.
- Lorimer, C.G., 1993. Causes of the oak regeneration problem. In: Loftis, D.L., McGee, C.E. (Eds.), Oak Regeneration: Serious Problems, Practical Recommendations. U.S. Forest Service General Technical Report SE-84, Asheville, NC, pp. 14–39.
- Palmer, W.M., Braswell, A.L., 1995. Reptiles of North Carolina. The University of North Carolina Press, Chapel Hill.
- Petranka, J.W., Murray, S.S., 2001. Effectiveness of removal sampling for determining salamander density and biomass: a case study in an Appalachian streamside community. J. Herpetol. 35, 36–44.
- Phillips, R.J., Waldrop, T.A., Simon, D.M., 2006. Assessment of the FARSITE model for predicting fire behavior in the southern Appalachian Mountains. In: Connor, K.F. (Ed.), Proceedings of the 13th Biennial Southern Silviculture Research Conference General Technical Report SRS-92, Asheville, NC, pp. 521–525.
- Pilliod, D.S., Bury, R.B., Hyde, E.J., Pearl, C.A., Corn, P.S., 2003. Fire and amphibians in North America. For. Ecol. Manage. 178, 163–181.
- Pough, R.H., Smith, E.M., Rhodes, D.H., Collazo, A., 1987. The abundance of salamanders in forest stands with different histories of disturbance. For. Ecol. Manage. 20, 1–9.

- 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 General Technical Report NRS-P-1. Newtown 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.
- Russell, K.R., Wigley, T.B., Baughman, W.M., Hanlin, H.G., Ford, W.M., 2004. Responses of southeastern amphibians and reptiles to forest management: a review. In: Rauscher, H.M., Johnsen, K. (Eds.), Southern Forest Science: Past, Present, and Future. U.S. Forest Service General Technical Report SRS-75. Asheville, NC, pp. 319–334.
- Szaro, R.C., 1988. The management of amphibians, reptiles and small mammals in North America: historical perspective and objectives. In: Szaro, R.C., Severson, K.E., Patton, D.R. (Eds.), Management of Amphibians, Reptiles, and Small Mammals in North America. U. S. Forest Service General Technical Report RM-166, Fort Collins, CO, pp. 1–2.
- USDA Natural Resources Conservation Service 1998. Soil Survey of Polk County, North Carolina. US Government Printing Office: 1998-432-697/ 60527/NCRS, Raleigh, NC, USA.
- Youngblood, A., Metlen, K., Knapp, E.E., Outcalt, K.W., Stephens, S.L., Waldrop, T.A., Yaussy, D., 2005. Implementation of the fire and fire surrogate study—a national research effort to evaluate the consequences of fuel reduction treatments. In: Peterson, C.E., Maguire, D.A. (Eds.), Balancing Ecosystem Values: Innovative Experiments for Sustainable Forestry. U.S. Forest Service General Technical Report PNW-635, Portland, OR, pp. 315–321.