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Research Article

Prescribed Fire and Timber Harvest Effects on Terrestrial Salamander Abundance, Detectability, and Microhabitat Use

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ABSTRACT Prescribed fire and timber harvest are anthropogenic disturbances that modify resource availability and ecosystem structure, and can affect wildlife both directly and indirectly. Terrestrial salamanders are effective indicators of forest health due to their high abundance and sensitivity to microclimatic conditions. Given their ecological importance, it is critical to understand how forest salamanders respond to management-related disturbances. We predicted that timber harvest and prescribed fire would decrease salamander abundance and availability, and increase salamander cover object use. We surveyed for southern red-backed salamanders (*Plethodon serratus*) over 9 sampling periods from 2010 to 2014 in a Missouri Ozark (USA) forest, and used binomial mixture models to estimate abundance and detectability in a large-scale Before-After, Control-Impact (BACI) experiment. Five replicate 5-ha units were randomly assigned to each treatment (prescribed burn, shelterwood harvest, midstory herbicide) and control. We compared abundance, surface activity, detectability, and microhabitat use among treatments. Abundance and surface activity decreased post-treatment in shelterwood, midstory, and burn units. Abundance estimates in midstory and burn units rebounded in the second post-treatment year but declined further in shelterwood harvest units. Overall, treatments had stronger effects on salamander availability than on actual abundance. We also found a higher proportion of salamanders under cover objects after prescribed fire, further illustrating the importance of accounting for imperfect detectability. Our findings foster a more robust understanding of the mechanisms underlying population-level responses to management practices, ultimately increasing our ability to manage terrestrial salamanders effectively. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS amphibian, forest management, hierarchical model, Missouri, N-mixture model, oak regeneration, Ozarks, partial harvest, *Plethodon serratus*, shelterwood.

Natural and anthropogenic disturbances affect ecosystems by modifying resource availability and community structure (Pickett and White 1985). The size, severity, and timing of disturbances greatly influence how wildlife populations are affected (Karr and Freemark 1985, White and Pickett 1985). Forest-associated wildlife populations are commonly exposed to management-related disturbances such as prescribed fire and timber harvest, which are used to achieve a variety of objectives. Prescribed fire is increasingly being employed to reintroduce fire as an ecosystem process, particularly in response to a century of fire suppression policies that led to increased fuel loads, more frequent and extensive wildfires in the western United States, and altered forest composition across the country (Pyne et al. 1996, Nowacki and Abrams 2008, Hanberry et al. 2013). Prescribed fire can decrease wildfire risk, reduce fuel loads, and restore fire-adapted ecosystems (Pilliod et al. 2003, Hanberry et al. 2013, Pausas and Keeley 2014). Commercial timber harvests are often implemented for the economic and practical benefits of wood, but trees are also cut for non-extractive purposes, such as ecosystem restoration, reducing the probability of wildfires, and creating wildlife habitat.

Amphibians and other wildlife can be affected by disturbances both directly (i.e., injury, mortality) and indirectly (i.e., disturbance-induced habitat changes). Animals may respond at an individual level to altered habitats in physiological, behavioral, or ecological ways that subsequently influence population-level dynamics such as survival rate and spatial distribution (Karr and Freemark 1985, Sutton et al. 2014). The relative impact of a disturbance is mediated not only by spatial and temporal factors but also the natural history and habitat of the affected organisms (Karr and Freemark 1985). Salamander responses to forest management practices are greatly influenced by their unique life-history characteristics.

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Terrestrial salamanders respire cutaneously, which makes them dependent on moisture (Spotila 1972, Gatz et al. 1975, Kleeberger and Werner 1982, Feder 1983) and limits their surface activity (Jaeger 1980, O'Donnell et al. 2014, Peterman and Semlitsch 2014). Terrestrial salamanders have small home ranges—typically just a few square meters—because of their limited movement capacity and high site fidelity (Kleeberger and Werner 1982, Ousterhout and Liebgold 2010). Salamanders are top vertebrate predators in forest-floor ecosystems and may have substantial effects on nutrient cycling and leaf litter decomposition (Burton and Likens 1975, Wyman 1998, Walton 2013, Best and Welsh 2014, Semlitsch et al. 2014). The tight linkages between terrestrial salamanders and their environment make them effective indicators of overall ecosystem health, and thus, ideal organisms for examining the impacts of forest disturbances (Welsh and Droege 2001, Davic and Welsh 2004, Welsh and Hodgson 2013).

Early investigations of wildlife responses to prescribed fire largely focused on terrestrial megafauna (Bendell 1974; Lyon et al. 1978, 2000). Much less is known about effects on amphibians, but available studies indicate that responses vary greatly among individuals, species, life-history strategies, and geographic regions (Russell et al. 1999, Bury et al. 2002, Pilliod et al. 2003). With prescribed fire, direct mortality of terrestrial salamanders is thought to be limited because they spend most of their time underground out of fire's path (Taub 1961, Russell et al. 1999, Petranka and Murray 2001, Bailey et al. 2004). However, many prescribed burns are conducted in spring and late fall, when terrestrial salamanders in many regions are most surface-active (Russell et al. 1999, Pilliod et al. 2003); thus, rates of direct mortality may vary with burn seasonality and geographic region. Indirect fire effects are thought to have more influence on terrestrial salamanders because they do not have the capability to emigrate as quickly or as far as many other terrestrial vertebrates (Kleeberger and Werner 1982, Ousterhout and Liebgold 2010). Salamanders may effectively become trapped in a fire-disturbed landscape, which could involve reduced prey availability, fewer cover objects, and decreased soil moisture (Russell et al. 1999, Pilliod et al. 2003). Prescribed fires generally decrease leaf litter and duff (i.e., decomposed organic material) depths, can combust or desiccate downed wood that salamanders use as refugia, and may lead to higher temperatures at ground level (Harmon and Franklin 1986, Bury et al. 2002, Pilliod et al. 2003, Cummer and Painter 2007, Matthews et al. 2010). Salamanders may respond by spending more time underground, which could reduce foraging and breeding opportunities and lead to decreased survival.

The relative importance of direct and indirect effects of prescribed fire on terrestrial salamanders is likely influenced by several factors, including seasonality, burn frequency, fire intensity, and historical fire regime (Pilliod et al. 2003). Several studies have found no effect of prescribed burns on terrestrial salamanders (e.g., Ford et al. 1999, 2010; Moseley et al. 2003; Schurbon and Fauth 2003; Keyser et al. 2004; Greenberg and Waldrop 2008). However, these conclusions are based on relative abundance measures (i.e., catch per unit effort) and do not account for potential differences in detectability between burned and unburned areas, which has been shown to change following wildland fires (Hossack and Corn 2007, Chelgren et al. 2011, Hossack et al. 2013). Additionally, prescribed fires differ in severity, which can greatly affect the magnitude of post-fire changes in the environment (Pilliod et al. 2003, Hossack and Pilliod 2011). In fact, Major (2005) found a negative relationship between fire severity and post-fire terrestrial salamander site occupancy. Unfortunately, fire severity is often not reported in wildlife studies (Renken 2006). For instance, although Keyser et al. (2004) and Greenberg and Waldrop (2008) found no difference in terrestrial salamander captures after prescribed fire, in both cases, fire did not consume the duff layer, which could have ameliorated negative effects of the burn.

In contrast to prescribed fire, impacts of timber harvest on amphibians have been more thoroughly studied; effects are predominantly negative, but the extent varies with amphibian species and the scale of harvest (Petranka et al. 1993, 1994; DeMaynadier and Hunter 1995; Semlitsch et al. 2009; Tilghman et al. 2012; Connette and Semlitsch 2013). Most adverse effects of timber harvest are due to post-harvest changes in salamanders' environments (i.e., indirect effects), not directly due to the harvest activity (DeMaynadier and Hunter 1995). Indirect effects of harvest can reduce survival of salamanders (Petranka et al. 1993, 1994; Homyack and Haas 2009), limit surface activity (Johnston and Frid 2002, Homyack et al. 2011, Hocking et al. 2013), and induce emigration from the harvested area (Ash and Bruce 1994, Semlitsch et al. 2008, Peterman et al. 2011), which have been expressed as the mortality, retreat, and evacuation hypotheses (Semlitsch et al. 2009). Many studies that have reported terrestrial salamander declines after timber harvest implicate higher ground temperatures and decreased soil moisture due to canopy cover removal (e.g., Petranka et al. 1993, 1994; DeMaynadier and Hunter 1995; Semlitsch et al. 2009; Tilghman et al. 2012; Homyack and Haas 2013). Several studies have shown ways to lessen or prevent salamander declines by limiting canopy cover removal via partial timber harvests or midstory removal with herbicide (Harpole and Haas 1999, McKenny et al. 2006, Semlitsch et al. 2009, Hocking et al. 2013, Homyack and Haas 2013) or retaining favorable microhabitats such as coarse woody debris (Rittenhouse et al. 2008, Kluber et al. 2009, Semlitsch et al. 2009). Generally, timber harvests can cause drier soil, loss and drying of leaf litter, and loss of fine woody debris—changes that decrease forests' ability to sustain salamander populations (Welsh and Droege 2001).

Discerning terrestrial salamander responses to forest management practices is essential for informing amphibian conservation and management strategies. Prescribed fire and timber harvest are used to accomplish many forest management objectives; in the eastern United States, they are often employed to encourage oak (*Quercus* spp.) or pine (*Pinus* spp.) regeneration. However, we do not have sufficient information about the effects of these disturbances on terrestrial salamander population dynamics and habitat use, especially in the Midwestern United States (but see Herbeck and Larsen 1999, Hocking et al. 2013). Considering the potential importance of terrestrial salamanders in ecosystems, it is critical to understand how they respond to disturbances. Our objective was to determine responses of southern red-backed salamanders (*Plethodon serratus*) to prescribed fire and timber harvest in a central hardwood forest. We examined salamander responses to 3 forest management practices in a randomized, large-scale Before-After, Control-Impact (BACI) experiment. We investigated changes in salamander abundance over 9 sampling periods, and explicitly accounted for potential differences in salamander detectability among the treatments. We also examined the effects of timber harvest and prescribed fire on terrestrial salamander microhabitat use. We expected salamander populations to decrease following timber harvest and prescribed fire treatments, but hypothesized that our ability to detect salamanders would increase after treatments were implemented. We predicted that salamanders would increase their use of pre-existing cover objects such as rocks and coarse woody debris in burned and harvested areas, and would decrease surface activity.

STUDY AREA

We conducted our study at the Sinkin Experimental Forest (Dent County, Missouri, USA; Fig. 1), located within the Current River Hills Subsection of the Ozark Highlands (Nigh and Schroeder 2002). The overstory was dominated by oaks—primarily white (*Quercus alba*), black (*Q. velutina*), scarlet (*Q. coccinea*), and northern red oak (*Q. rubra*)—as well as shortleaf pine (*Pinus echinata*) and hickory (*Carya* spp.; Kabrick et al. 2014). Understory species included spice bush (*Lindera benzoin*) and Carolina buckthorn (*Frangula caroliniana*). The mature (80–100-year-old) stands had not been harvested or thinned for at least 40 years.

Twenty 5-ha experimental units, each oriented on a slope covering a mesic-to-xeric moisture gradient, were separated by ≥10 m and delineated across our study area (Fig. 1). Five replicate units were randomly assigned to each treatment: 1)

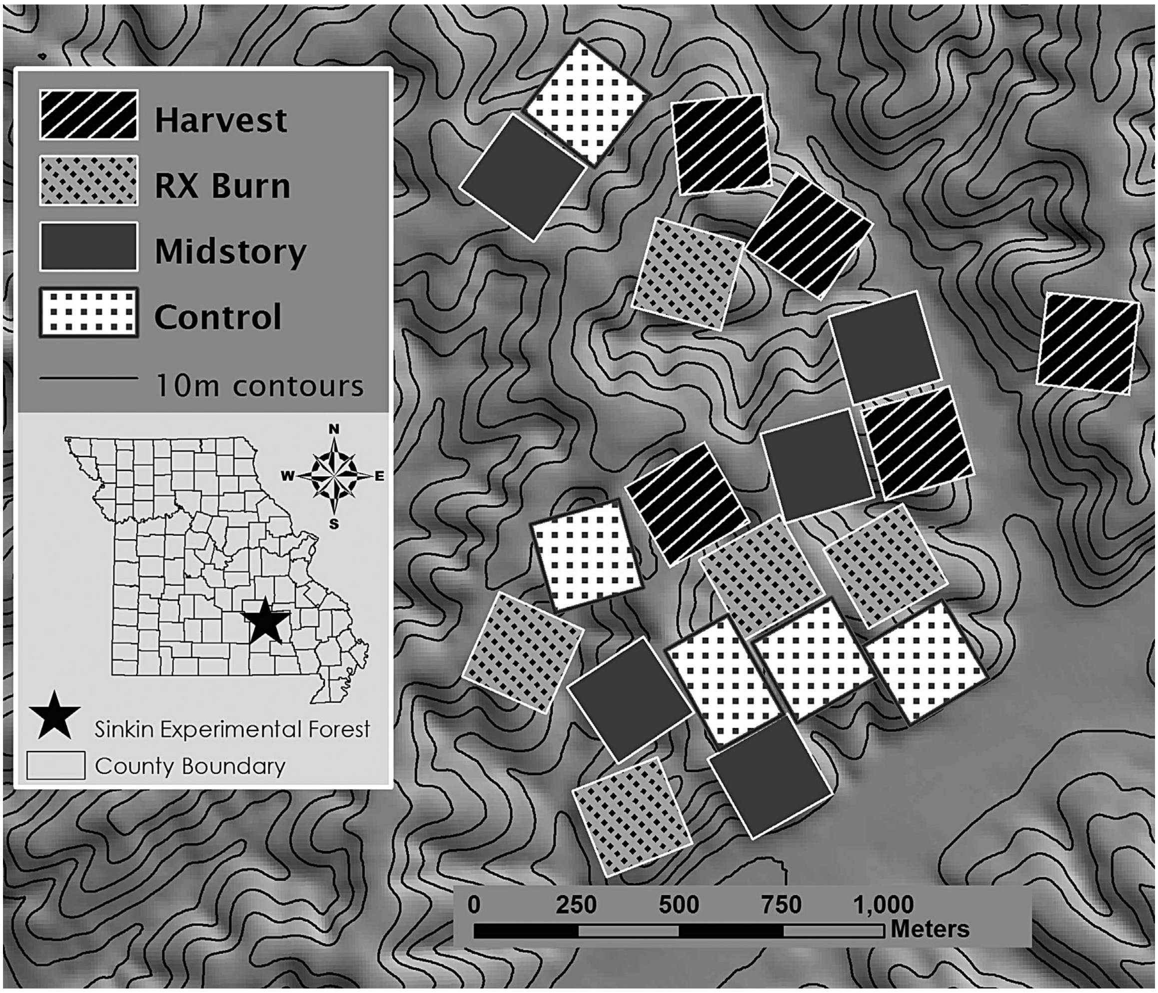

Figure 1. Arrangement of Regional Oak Study experimental units within the Sinkin Experimental Forest, Mark Twain National Forest, Dent County, Missouri, USA. Five replicate units were randomly assigned to each of 4 treatments: shelterwood harvest, prescribed (RX) burn, midstory herbicide, or control. We surveyed southern red-backed salamanders from 2010 to 2014.

prescription burn; 2) shelterwood harvest; 3) midstory herbicide; or 4) control. These treatments are part of the United States Department of Agriculture (USDA) Forest Service Regional Oak Study, which is investigating oak regeneration dynamics.

The midstory herbicide treatment was intended to decrease competition for young oak trees by killing midstory trees to reduce basal area by 25–30%. Garlon 3A herbicide at 50% strength was applied to non-oak midstory trees (5–25 cm dbh) via the hack-and-squirt method in fall 2011 (Loftis 1990). The initial application did not effectively kill all the treated stems, so a second application at full strength was applied in fall 2012. Midstory units will also be shelterwood-harvested in 8–10 years. The shelterwood treatment commercially harvested a portion of overstory trees, retaining 30–40% of original basal area to provide shadier conditions for oak seedlings (Brose et al. 1999). Harvesting was conducted in December 2011 and January 2012 (2 units), September and October 2012 (2 units), and January 2013 (1 unit); slash was left on site. All shelterwood-harvested units will also be prescription burned 3–5 years after harvest. All 5 units in the prescribed burn treatment were burned on 13 December 2012 via ground ignition. Fire temperatures were measured at ground level and 30 cm above ground using temperature-sensitive paint. Mean maximum fire temperature at ground level was 291° C (range 232–315° C) at lower slope positions and 312° C (range 232–371° C) at upper slope plots. At 30 cm above ground, lower slope mean maximum temperature was 168° C (range $93 \geq 537$° C); upper slope was 178° C (range 93–315° C). Five units were left untreated and served as controls.

METHODS

Sampling Design

We established 2 10-m × 10-m survey plots on each of the 20 5-ha experimental units ($n = 40$ sampling sites; Fig. 1). We conducted repeated surveys for southern red-backed salamanders 3–5 times each spring and fall from April 2010 to June 2014 (9 sampling periods, 39 surveys, $n = 1{,}560$ quadrats sampled). We thoroughly searched a 3-m × 3-m quadrat of each survey plot; 2 observers crawled through the quadrat, searching 1-m-wide transects with a small hand rake and flipping all natural cover objects encountered. We continually replaced leaf litter and cover objects, and ensured plots were reconstructed upon completion of each quadrat search. Each round of sampling lasted until we surveyed each plot once (2–4 days); we randomly determined search order of plots each round. For each plot, we recorded total salamanders captured, rocks (≥5 cm), woody cover objects, mean soil temperature, and mean leaf litter depth. We measured and recorded size (snout-vent length; SVL) and capture location (leaf litter, rock, woody cover) of each individual. We obtained rainfall and temperature data from the Sinkin Experimental Forest weather station (MSINM7). We obtained site-specific variables of slope (%) and Beers-transformed aspect (linear scale; southwest = 0, northeast = 2) from the Regional Oak Study. We handled all animals in accordance with the procedures approved by University of Missouri Animal Care and Use Committee (protocol no. 7403) and the Missouri Department of Conservation.

Statistical Analyses

We compared red-backed salamander raw counts (captures per plot) among treatments using a Poisson-distributed generalized linear mixed model (function glmer, package lme4, R version 3.1.1, www.r-project.org, accessed 10 Sep 2014) as a measure of salamander surface activity. We assessed treatment effects on leaf litter depth and soil temperature using linear mixed models (function lmer, package lme4, R version 3.1.1). We specified separate models for pre-treatment and post-treatment sampling periods to facilitate interpretation of results. For each model, we included treatment, sampling period, and a treatment × sampling period interaction as fixed effects and plot as a random effect. We tested for differences in counts, leaf litter depth, and soil temperature among treatments and sampling periods using Wald χ^2 tests (function Anova, package car, R version 3.1.1).

We calculated the proportion of salamander captures per microhabitat type (leaf litter, rock, woody cover) within each treatment and sampling period. We fit analysis of variance models to pre- and post-treatment log-transformed captures per microhabitat with treatment, microhabitat type, and a treatment × microhabitat interaction as fixed effects (function lm, package stats, R version 3.1.1).

We estimated red-backed salamander abundance by correcting for imperfect detection using a binomial mixture model, which can simultaneously estimate abundance and detectability (O'Donnell et al. 2015). The model is partitioned into 1) a state process that describes abundance as a result of ecological mechanisms; and 2) an observation process that produces spatial and temporal patterns in count data. Within the observation process, the availability parameter accounts for imperfect detection due to temporary emigration, and conditional capture probability accounts for false absences. We used a Bayesian approach to fit our model using JAGS (Plummer 2003, function jags, package R2jags, R version 3.1.1). We included covariates of slope, aspect, and treatments on abundance; time since rainfall, time of day, temperature, and treatments on availability; and leaf litter depth, woody cover object density, rock density, and treatments on conditional capture probability. We report the effect of a covariate if its Bayesian 95% credible interval did not overlap 0, or if ≥ 95% of its posterior distribution had the same sign (i.e., + or −) as its mean. We specified a normal prior (mean = 0.9, SD = 0.25) for the conditional capture probability intercept, and uninformative prior distributions for all other parameters. We standardized all covariates to promote Markov chain Monte Carlo convergence. We ran 3 chains for 200,000 iterations, discarded the first 150,000 as burn-in, and thinned the remaining samples by 1 in 10 to obtain 5,000 simulations for analysis. We confirmed convergence using the Gelman-Rubin statistic (R-hat < 1.01; Gelman and Hill 2007) and performed posterior predictive checks (Bayesian P-value) to assess model fit adequacy (Kéry and Schaub 2012).

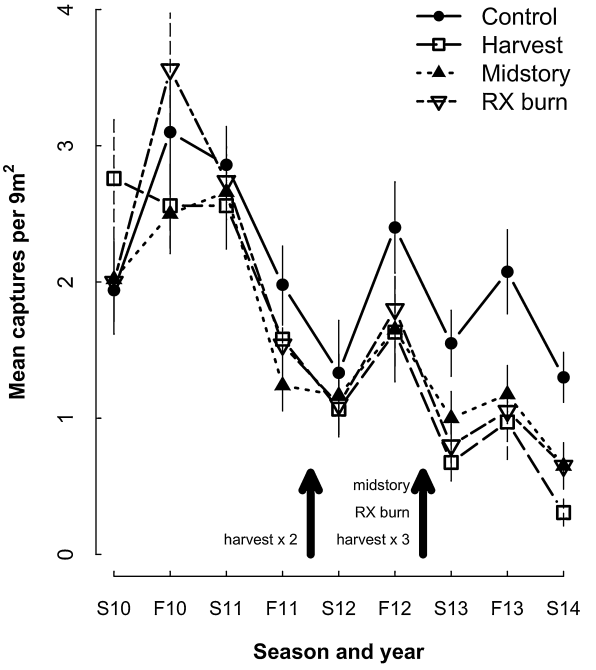

Figure 2. Variation among sampling periods in mean captures of southern red-backed salamanders per plot (± SE) across 4 treatments in Dent County, Missouri, USA from 2010 to 2014. We completed surveys during spring (S) and fall (F) of each year (indicated by last 2 digits of the year). The first arrow represents harvest of 2 units; the second arrow represents timing of harvest of the 3 remaining units, prescribed (RX) burns, and midstory herbicide treatments.

RESULTS

Surface Activity and Abundance

Prior to treatments, salamander surface activity (mean counts) varied among sampling periods, from 1.59 (fall 2011) to 2.93 (spring 2010) salamanders per 9-m^2 plot ($\chi_5^2 = 169.18$, $P \leq 0.001$; Fig. 2). The average difference between the highest and lowest per-treatment mean counts was 26.8% for the first 4 sampling periods, but there was no consistent relationship among the treatments ($\chi_3^2 = 1.30$, $P = 0.73$; Fig. 2). After all treatments were implemented, the mean difference between the highest and lowest mean counts was 62.0%, with controls consistently higher than the other treatments. Relative to controls, counts decreased by 58.4% in shelterwood, 49.0% in prescribed burn, and 36.7% in midstory herbicide units after treatments. In addition to differences among treatments ($\chi_3^2 = 14.34$, $P = 0.002$), surface activity continued to vary among sampling periods ($\chi_2^2 = 25.30$, $P \leq 0.001$) but the relationship among treatments did not vary (treatment × sampling period, $\chi_6^2 = 4.12$, $P = 0.66$).

Mean per-plot abundance (accounting for imperfect detection) varied among sampling periods but did not vary consistently among treatments prior to implementation (Table 1). Each of the 4 treatments had the highest mean abundance in 1 of the first 4 sampling periods. Following treatments, mean abundance was lowest in shelterwood harvest units and highest in control units (Table 1). Bayesian 95% credible intervals (CRI) overlapped in most pairwise contrasts, but the extent varied among treatments (Table 1). The greatest difference between control and a treatment occurred in spring 2014; mean abundance in shelterwood harvests was 50.2% lower than controls (Table 1). Mean abundance in midstory herbicide and prescribed burn units treatments was lower than controls in fall 2013 (30.4% and 24.3%, respectively), but the differences lessened by spring 2014 (Table 1). Treatments had stronger effects on salamander availability (i.e., probability of being exposed

Table 1. Mean abundance (per 9-m^2 plot) and percent difference (vs. control) of southern red-backed salamanders per treatment in Sinkin Experimental Forest, Dent County, Missouri, 2010–2014.

	Treatment			
Season and year	Control	Shelterwood harvest	Midstory herbicide	Prescribed burn
Spring 2010	7.71 (4.9, 13.2)[a]	8.62 (6.8, 12.9) +11.8%	7.11 (5.0, 12.2) −7.8%	7.16 (4.2, 12.2) −7.1%
Fall 2010	7.36 (6.0, 10.7)	7.34 (5.2, 11.9) −0.3%	6.68 (4.9, 11.1) −9.2%	8.96 (7.5, 12.3) 21.7%
Spring 2011	5.40 (4.6, 8.3)	6.11 (4.7, 9.3) 13.1%	6.76 (5.5, 10.3) 25.2%	6.37 (5.0, 9.4) 18.0%
Fall 2011[b]	4.87 (4.2, 7.5)	4.07 (3.2, 7.2) −16.4%	3.88 (2.7, 7.0) −20.3%	4.74 (3.5, 7.8) −2.7%
Spring 2012[c]	4.05 (2.9, 7.4)	3.01 (2.0, 6.9) −25.7%	3.48 (2.2, 7.2) −14.1%	3.21 (2.0, 6.8) −20.7%
Fall 2012[d]	5.29 (4.4, 8.5)	4.47 (3.3, 8.4) −15.5%	5.20 (3.9, 9.0) −1.7%	4.03 (3.2, 7.4) −23.8%
Spring 2013[e]	3.04 (2.5, 5.6)	2.17 (1.5, 5.2) −28.6%	3.30 (2.3, 7.0) +8.6%	2.56 (1.6, 5.9) −15.8%
Fall 2013	5.75 (4.2, 10.0)	4.85 (2.3, 10.4) −15.7%	4.00 (2.6, 8.2) −30.4%	4.35 (2.7, 9.0) −24.3%
Spring 2014	3.21 (2.7, 5.7)	1.60 (0.9, 4.5) −50.2%	2.71 (1.6, 6.4) −15.6%	2.98 (1.6, 6.9) −7.2%

[a] Values in parentheses represent Bayesian 95% credible intervals.
[b] First midstory herbicide application applied during fall 2011 sampling period.
[c] 2 of 5 shelterwood units harvested.
[d] 3 of 5 shelterwood units harvested; second midstory herbicide application.
[e] All treatments fully implemented.

Table 2. Mean effect (Bayesian 95% credible intervals) of treatments on southern red-backed salamander availability and abundance in Sinkin Experimental Forest, Dent County, Missouri, 2013–2014.

	Effect on availability				**Effect on abundance**			
	Control	**Shelterwood harvest**	**Midstory herbicide**	**Prescribed burn**	**Control**	**Shelterwood harvest**	**Midstory herbicide**	**Prescribed burn**
Spring 2013	−0.39	−1.02	−1.21	−1.47	0.23	−0.09	0.36	0.078
	(−2.6, 2.2)	(−2.9, 1.6)	(−2.9, 1.1)	(−2.9, 1.3)	(−2.5, 2.7)	(−2.8, 2.4)	(−2.4, 2.8)	(−2.7, 2.6)
Fall 2013	−0.27	−1.86	−1.18	−1.33	0.45	0.29	0.13	0.20
	(−2.6, 2.2)	(−2.9, 0.30)	(−2.9, 1.1)	(−2.9, 0.8)	(−2.4, 2.8)	(−2.6, 2.7)	(−2.7, 2.6)	(−2.7, 2.6)
Spring 2014	0.30	−1.40	−1.73	−1.79	0.41	−0.32	0.25	0.34
	(−2.1, 2.5)	(−2.9, 1.6)	(−2.9, 0.7)	(−2.9, 0.4)	(−2.2, 2.8)	(−2.8, 2.2)	(−2.4, 2.7)	(−2.3, 2.7)

to sampling) than they did on abundance (Table 2). Aspect was also a strong predictor of abundance (mean effect [CRI]; 0.181 [0.079, 0.282]), whereas time since rainfall (−0.345 [−0.616, −0.082]), soil temperature (−1.603 [−1.891, −1.333]), and time of day (−0.203 [−0.438, 0.028]) highly influenced availability.

Habitat Conditions and Use

Mean soil temperature varied among sampling periods from a low of 14.9° C (spring 2010) to a high of 20.0° C (fall 2010) before treatments were implemented (Fig. 3; $\chi_5^2 = 184.60$, $P \leq 0.001$). In the first 4 sampling periods, the mean difference between the lowest and highest temperature per treatment was 5.7%; in the last 3 sampling periods (after all treatments implemented), the mean difference was 16.6%. Soil temperature differed among both treatments ($\chi_3^2 = 10.24$, $P = 0.017$) and sampling periods ($\chi_2^2 = 22.47$, $P \leq 0.001$) following treatment. Mean post-treatment soil temperature was higher in both shelterwood harvest (+2.58° C) and midstory herbicide (+1.62° C) treatments relative to controls; mean soil temperature in prescribed burn units did not differ from controls.

Mean leaf litter depth ranged from 1.98 cm (fall 2011) to 2.52 cm (spring 2011) prior to treatments (sampling period: $\chi_5^2 = 129.49$, $P \leq 0.001$; Fig. 4) but did not differ among treatments. Post-burn leaf litter depth decreased in prescribed burn units for 2 sampling periods following prescribed burn, averaging 0.57 cm in spring 2013 (63.7% lower than other treatments) and 0.58 cm in fall 2013 (57.7% lower than other treatments). In spring 2014, mean leaf litter depth in prescribed burn plots was only 8.7% lower than controls (Fig. 4). The treatment × sampling period interaction ($\chi_6^2 = 42.15$, $P \leq 0.001$) explained differences in mean leaf litter depth post-treatments.

We found higher proportions of salamanders in leaf litter than under rocks or woody cover prior to treatments ($F_{2,\,60} = 43.02$, $P \leq 0.001$; Fig. 5), but relative microhabitat

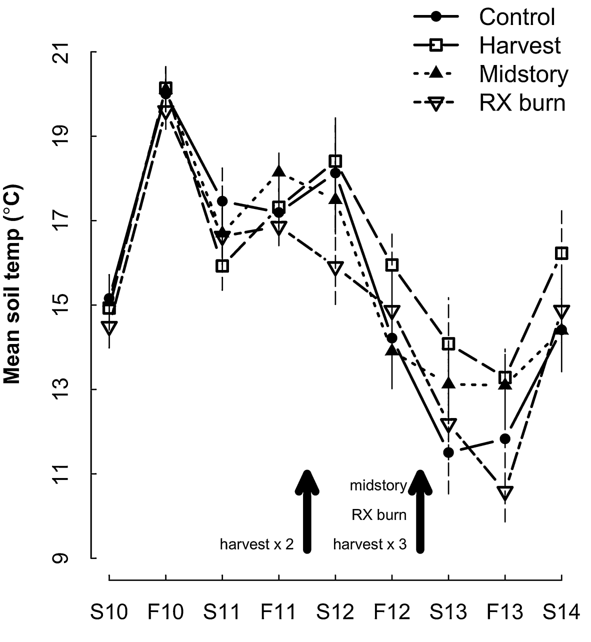

Figure 3. Mean (± SE) soil temperature of survey plots per sampling period across 4 treatments in Dent County, Missouri, USA from 2010 to 2014. We completed surveys during spring (S) and fall (F) of each year (indicated by last 2 digits of the year). The first arrow represents harvest of 2 units; the second arrow represents timing of harvest of the 3 remaining units, prescribed (RX) burns, and midstory herbicide treatments.

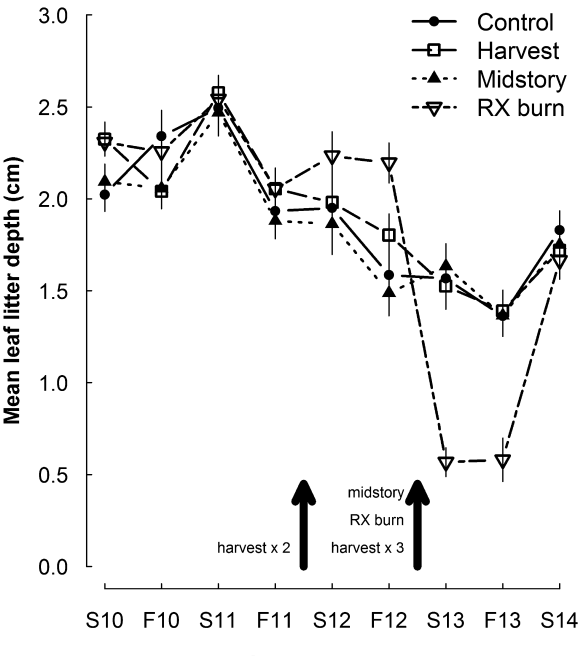

Figure 4. Mean leaf litter depth (± SE) within sampling plots across 4 treatments in Dent County, Missouri, USA from 2010 to 2014. We completed surveys during spring (S) and fall (F) of each year (indicated by last 2 digits of the year). The first arrow represents harvest of 2 units; the second arrow represents timing of harvest of the 3 remaining units, prescribed (RX) burns, and midstory herbicide treatments.

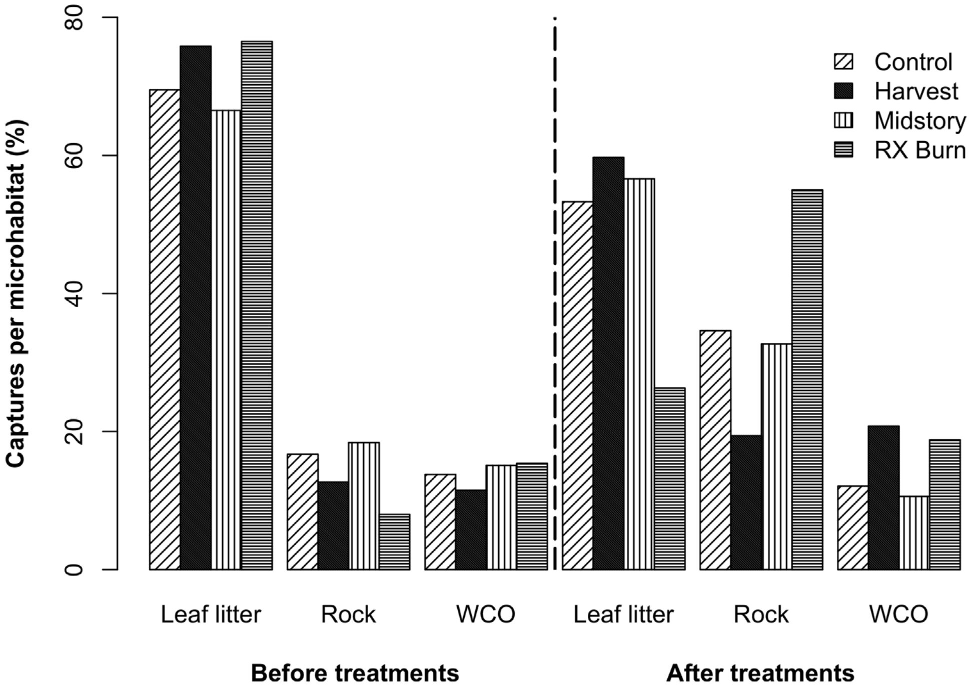

Figure 5. Frequency of southern red-backed salamander captures per treatment (harvest, midstory herbicide, prescribed [RX] burn) in 3 microhabitat types—leaf litter, rocks, and woody cover objects (WCO)—in Missouri, 2010–2014. Bars represent percent of pre- or post-treatment captures within each microhabitat.

use did not differ among treatments (treatment × microhabitat, $F_{6,\ 60} = 0.540$, $P = 0.78$). Following treatment implementation, captures differed among treatments ($F_{3,\ 24} = 8.08$, $P \leq 0.001$) and microhabitats ($F_{2,\ 24} = 14.18$, $P \leq 0.001$). Additionally, the relative use of microhabitat differed among treatments ($F_{6,\ 24} = 2.12$, $P = 0.088$); relative capture frequency in prescribed burn units was higher under cover objects (73.8% of captures) than within leaf litter (26.3% of captures), whereas capture frequency remained highest in leaf litter in shelterwood harvest, midstory herbicide, and control treatments (mean = 56.5%; Fig. 5).

DISCUSSION

Our findings indicate that red-backed salamanders were most adversely affected by shelterwood harvests but were also negatively affected by midstory herbicide and prescribed burn treatments. Lower post-treatment capture rates in shelterwood, midstory, and burn units reflect reduced surface activity in response to these forest management practices (Fig. 2). Abundance estimates corrected for imperfect detection also generally decreased in all treatments the year following implementation; estimates in midstory herbicide and prescribed burn units recovered slightly in the second year, but estimates in shelterwood harvest units decreased further (Table 1).

In shelterwood harvest units, lower salamander surface activity was likely due to higher soil temperatures and drier leaf litter. Although some overstory trees remained after harvest, substantial canopy gaps were created, which led to harsher microhabitat conditions for salamanders overall. We saw the largest control versus treatment discrepancy in abundance in shelterwood harvest units in the third sampling period after harvests were completed, which indicates that microhabitat conditions likely worsened over time. In contrast, the shrinking differences between control and both midstory herbicide and prescribed burn units in estimated abundances in spring 2014 (Table 1) indicate quicker recovery of favorable microhabitat conditions in those treatments.

Decreased surface activity in the prescribed burn treatment may have reflected the drastic decline in leaf litter depth following the burn (Fig. 4). Leaf litter is an important resource for terrestrial salamanders: it affords cover from predators, reduces soil desiccation, and provides ideal foraging opportunities due to high prey abundance in leaf litter (Fraser 1976, Jaeger 1980). Notably, salamanders were still less active in leaf litter in spring 2014 after leaf litter depth had seemingly recovered. We suspect this is partly due to the condition of the leaf litter layer—though it was present, it did not appear to retain moisture as well as litter that was further fragmented and decomposed. Those salamanders that were surface active following prescribed burn were more frequently captured under cover objects such as coarse woody debris and rocks (Fig. 5), which were often the only moist microhabitat available in burned areas.

We did not expect the decrease in surface activity in midstory herbicide plots, as microhabitat conditions did not appear to differ greatly from control plots. However, soil temperatures were slightly higher in midstory plots, which may explain the difference in activity. Higher temperatures increase the amount of energy needed for salamanders to maintain homeostasis (Gifford and Kozak 2012). Therefore, salamanders may retreat further underground to avoid high temperatures and the associated increase in energetic demand (Homyack et al. 2011).

The changes in salamander microhabitat use we observed after the prescribed fire illustrated the importance of accounting for variable and imperfect detectability of wildlife. Several studies have found differences in capture probabilities after fire (Bury et al. 2002, Chelgren et al. 2011, Hossack et al. 2013). We did not find a substantial effect of treatment on conditional capture probability—that is, given a salamander was exposed to sampling, our probability of capturing it did not differ among treatments. This was likely due to the comprehensive nature of our sampling method, but we posit that conditional capture probability could vary greatly between treatments if the sampling method was less intensive. Tilghman et al. (2012) found that studies using passive sampling techniques (e.g., pitfall traps) were likely to report weaker effects of timber harvest than those using active sampling methods. We also stress that sampling method can influence conclusions; for instance, finding more salamanders in pitfall traps in a given area may not truly reflect higher abundance. Instead, it may indicate that salamanders are attempting to evacuate or disperse from an area to escape poor habitat conditions (Semlitsch et al. 2008, Peterman et al. 2011).

Accounting for imperfect detection allowed us to increase understanding of the mechanisms behind the broad patterns we observed. Our modeling results indicated that terrestrial salamanders reduced their activity in response to both prescribed burn and timber harvest, but their abundance did not change drastically in the short term. We observed a trend of abundance progressively decreasing in harvested areas, which may become a stronger trend with longer-term data. Reduced probability of availability, presumably due to salamanders spending more time underground, could cause a lag in detecting population trends. Lower levels of surface activity could indicate a behavioral avoidance of increased physiological stress, which also reduces potential foraging time. These indirect consequences of disturbance could take time to manifest into detectable changes in abundance.

MANAGEMENT IMPLICATIONS

We encourage forest managers to consider management practices that limit canopy removal where there is interest in minimizing impacts on salamanders because it is likely the ultimate cause of increased temperatures and decreased moisture in harvested areas. Increased temperatures and decreased moisture may limit the ability of salamanders to be surface-active, which reduces foraging and breeding opportunities. Retaining coarse woody debris in harvested areas could also provide important microhabitat for salamanders, perhaps increasing their capacity to remain surface-active. Managers may also want to consider limiting prescribed burns during periods of high salamander surface activity to minimize direct mortality. Although timber harvest more adversely affected terrestrial salamanders in our study than prescribed burning, we note that all prescribed burns occurred in December, which is a period of low salamander activity. Burns that occur during breeding events or emergence from hibernation could be more detrimental and cause higher direct mortality. Additionally, burns that promote herbaceous understory vegetation could help ameliorate the drier and more variable environmental conditions that typically follow prescribed burns. We suggest terrestrial salamander monitoring surveys following disturbances sample the leaf litter and not just cover objects. We found minimal differences in salamander use of woody cover objects between treatments, but large differences in leaf litter use. Including all potential microhabitats in sampling protocols yields a more complete understanding of microhabitat use and limits potential post-management observation biases.

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