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Prescribed fire alters surface activity and movement behavior of a terrestrial salamander

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Abstract

Prescribed fire has become a commonly used forest management tool for reducing the occurrence of severe wildfires, decreasing fuel loads and reestablishing the historic ecological influences of fire. Investigating population-level wildlife responses to prescribed fire is important for evaluating the effects of fire management on animals, but in order to predict and simulate wildlife responses to potential management actions, mechanistic studies that elucidate individual-level responses are also necessary. We used radio-frequency identification to investigate individual-level responses of western slimy salamanders *Plethodon albagula* to prescribed fire. We compared the salamander home-range sizes [minimum convex polygons (MCP)], movement behaviors, and activity levels before and after prescribed fire using a randomized block experiment. We initiated the study at three plots in 2011, and added two new plots in 2012. We captured, tagged and released ≥38 salamanders at each plot from May 2011–May 2012 (total $N = 205$). We recorded 918 total recaptures of 142 unique salamanders; 31% of tagged salamanders were never recaptured. Across all years and treatments, only 14% of relocations were surface-active (i.e. visually confirmed) salamanders; the others were underground. Following prescribed fire, the surface-active proportion of recaptures was nearly seven times greater in control versus burned areas, which indicates that *P. albagula* respond to post-prescribed fire conditions by spending more time belowground. We did not find evidence of direct mortality of salamanders from fires; the proportion of known-alive individuals did not differ between treatments. Maximum daily displacement was 43.3% higher among burn-area than control-area salamanders, and MCP varied in a similar pattern; this may indicate salamanders were attempting to find more hospitable microenvironments or other resources, such as prey. Together, these individual-level observations corroborate our findings from a population-level study of a congeneric terrestrial salamander and contribute to our understanding of the behavioral mechanisms underlying population dynamics.

Introduction

Fire is a key driver of ecosystem composition and function, but fire regimes have shifted over the last century due to human population growth and changes in forest management practices (Pyne, Andrews & Laven, 1996; Pausas & Keeley, 2009). These changes – particularly fire suppression policies – have caused combustible forest material ('fuel') buildups that have increased wildfire frequency and extent in some ecosystems, and have produced continental-scale changes in forest composition (e.g. increased tree density, shifts in species dominance and reduced diversity; Pyne *et al.*, 1996; Nowacki & Abrams, 2008; Hanberry, Kabrick & He, 2013). In response, prescribed fire has become a commonly used forest management tool for reintroducing or managing fires in many fire-adapted systems, allowing for greater control of fuel loads where necessary, and integrating the ecological influences of fire (Pilliod *et al.*, 2003; Hanberry *et al.*, 2013; Pausas & Keeley, 2014).

Despite the importance of wildlife to ecosystem health, there is a considerable lack of information about faunal responses to prescribed fire. Because the effects of prescribed fire on wildlife remain unclear (and likely differ considerably among taxa), many decisions about fire management have been weighted toward predicted vegetation responses (Lyon *et al.*, 2000; Driscoll *et al.*, 2010). Investigating population-level wildlife responses to prescribed fire is important for evaluating the effects of fire management on animals. However, to increase our ability to predict and simulate wildlife responses to potential management actions, mechanistic studies

that elucidate individual-level responses are essential (Driscoll *et al.*, 2010).

Amphibians are ideal for examining effects of prescribed fire – they are especially sensitive to changes in microhabitat, yet the diversity of life-history strategies within this taxon yields a variety of expected responses to fire (Russell, Van Lear & Guynn, 1999; Bury, Major & Pilliod, 2000; Pilliod *et al.*, 2003). Terrestrial woodland salamanders (family Plethodontidae) are ecologically important animals that comprise large amounts of biomass (Burton & Likens, 1975*a*; Semlitsch, O'Donnell & Thompson, 2014), are important for nutrient cycling (Burton & Likens, 1975*b*; Davic & Welsh, 2004; Semlitsch *et al.*, 2014), and are key predators in forest-floor ecosystems (Wyman, 1998; Walton, 2013; Best & Welsh, 2014).

Because terrestrial salamanders are largely fossorial, direct mortality and injury of these organisms due to fire likely is rare (Taub, 1961; Bailey, Simons & Pollock, 2004). However, plethodontid salamanders may be especially sensitive to fire-induced habitat changes, including reduction in woody debris and leaf litter that provide refugia and foraging opportunities (Fraser, 1976; Russell *et al.*, 1999; Pilliod *et al.*, 2003). Terrestrial salamanders lack the physical capacity to disperse long distances to find new habitat conditions (Ousterhout & Liebgold, 2010; Liebgold, Brodie & Cabe, 2011); thus, their persistence is closely linked with immediate microclimatic conditions and microhabitat availability (Peterman & Semlitsch, 2013; O'Donnell, Thompson & Semlitsch, 2014). Plethodontid salamanders also have particularly small home ranges relative to most vertebrates; they often spend their entire lives in areas <15 m^2 (Merchant, 1972; Kleeberger & Werner, 1982). In contrast to more mobile vertebrates that can easily disperse from altered habitats, terrestrial salamanders may exhibit subtler behavioral responses to prescribed fire. They may spend more time belowground due to drier surface conditions and reduced cover object abundance, or may expand foraging areas because of decreased prey availability (due to leaf litter reductions) and increased energetic requirements (e.g. Homyack, Haas & Hopkins, 2011). Higher metabolic costs could trigger a decrease in the amount of energy available for processes such as growth and reproduction, or could increase the amount of food that salamanders require (Homyack *et al.*, 2011). These seemingly minor changes in salamander activity and energy needs could substantially affect overall population dynamics through increased emigration or decreased survival and fecundity (Sears, 2005; Homyack *et al.*, 2011), thus warranting further investigation.

We used radio-frequency identification (RFID) to investigate individual-level responses of western slimy salamanders *Plethodon albagula* to prescribed fire. We implanted salamanders with uniquely coded passive integrated transponder (PIT) tags and located them $\leq$30 cm belowground with a portable reader/antenna system. PIT-telemetry minimizes habitat disturbance from repeated surveys. We compared salamander home range sizes, movement behaviors, and activity levels before and after prescribed fire using a randomized block experiment. We predicted that salamanders would decrease surface activity following prescribed fire, but would expand their home ranges if foraging activity increased to compensate for increased energy requirements or decreased prey availability. We also expected salamanders in burned areas to move to control areas if they were close to the burn periphery, and little direct mortality of salamanders from prescribed fire. We suggest that individual behavioral responses to prescribed fire would improve our understanding of population-level patterns of salamander responses to fire and other disturbances, such as canopy or understory removal.

Materials and methods

Study site

We conducted our study within the 1425-ha Daniel Boone Conservation Area (DBCA), Warren County, in east-central MO, USA (Fig. 1). DBCA lies in the Outer Ozark Border subsection of the Ozark Highlands, and consists of rugged hills covered with mature (80–100 years old) oak-hickory (*Quercus-Carya*) forest (Nigh & Schroeder, 2002). Seasonal (April–September) temperatures taken from a nearby weather station ranged from -5.1 to 43°C, and mean annual precipitation was 990.9 mm.

Field methods

We initiated a pilot study at three replicate plots (PR2, CN2 and EGG) in May 2011, and added two new plots (CN5 and

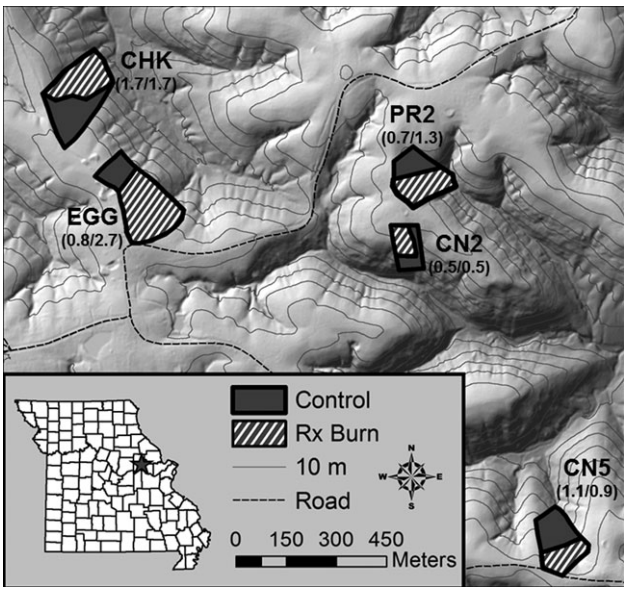

Figure 1 Location of study plots within Daniel Boone Conservation Area, Warren County, MO, USA. Each plot was divided into two subplots containing equal numbers of passive integrated transponder-tagged *Plethodon albagula*; one subplot in each plot was randomly assigned the prescribed (RX) burn treatment. Numbers in parentheses represent area (ha) of control/burned portion of each plot.

CHK) in April 2012 (Fig. 1). In March 2013, we split each plot into two subplots that contained approximately equal numbers of previously recaptured salamanders. We randomly assigned one subplot per replicate to the prescribed burn treatment, and left the other subplot in each replicate as an unburned control. On 4–5 April 2013, we conducted prescribed burns on all plots via ground ignition. At ignition, air temperatures ranged from 10.6 to 14.4°C, relative humidity was 30–42% and winds were very light. Flame heights were ≤0.3 m, except in a few patches of accumulated leaf litter, and ≥95% of the area of each subplot was burned. Fine fuel (leaf litter, fine woody debris) consumption was ≥75% in all plots.

We used PIT-tag telemetry to compare salamander home ranges and activity patterns before and after prescribed fire. To conduct telemetry observations, we first collected adult and large juvenile *P. albagula* by searching under rocks and woody cover objects – including some remnant coverboards from a previous study (Hocking *et al.*, 2013). We captured, tagged and released at least 38 *P. albagula* at each of the five plots from 21 May 2011–13 May 2012 (total $N = 205$; Table 1).

We flagged initial capture locations, placed salamanders in individual containers containing wet leaf litter, and transported animals to the University of Missouri for PIT-tag implantation. We anesthetized salamanders in a 1% solution of tricaine methanesulfonate (MS-222) buffered with sodium bicarbonate (as in Peterman & Semlitsch, 2006). Once salamanders were anesthetized (5–10 min), we measured snout-vent length (SVL) and used a sterile scalpel to make a 3-mm incision ~5 mm anterior to the right hind limb. We then inserted a PIT tag just under the skin and gently pushed it forward ~5 mm from the incision. Salamanders with SVL 41–51 mm received an HPT9 PIT tag (9.0 × 2.12 mm, 0.08 g; Biomark, Boise, ID, USA); those measuring 52–75 mm SVL received an HPT12 PIT tag (12.5 × 2.03 mm, 0.115 g; Biomark). HPT9 and HPT12 tags do not substantially differ in maximum detection distance (Ousterhout & Semlitsch, 2013). Salamanders' skin secretions immediately sealed incisions shut, so sutures were not needed. We rinsed salamanders in deionized water and allowed them to recover on wet leaf litter. We returned each salamander to its point of capture within 1–3 days.

Table 1 Total captures and recapture frequency of *Plethodon albagula* at Daniel Boone Conservation Area, Warren County, MO, USA from 2011 to 2014

	Plots					
	PR2	CN2	EGG	CN5	CHK	Total
Total *P. albagula* tagged	39	38	49	39	40	**205**
No. not recaptured	14	22	6	8	13	**63**
Percent not recaptured (%)	36	58	12	21	32	**31**
No. with ≥1 recapture	25	16	43	31	27	**142**
Percent with ≥1 recapture (%)	64	42	88	79	68	**69**
Total recaptures	110	69	422	149	168	**918**
No. visually confirmed	14	31	42	32	5	**124**
Percent visually confirmed (%)	13	45	10	21	3	**14**

We conducted 29 surveys in the 2011 pilot season (3 June–1 November) to identify peak detection periods. Detection was <5% from mid-July to mid-September; thus, we maximized our survey efforts from mid-April to June in subsequent years. We completed 12–16 surveys per plot from 17 April to 8 September 2012, 7–13 per plot from 7 April to 31 July 2013 and 8–10 per plot from 15 April to 9 July 2014. We attempted to conduct surveys in optimal detection conditions – following rain events and in morning hours. For each individual, we searched an ~30 m^2 area centered on the point-of-capture flag (and the most recent relocation flag, when applicable). We performed these searches by slowly walking in three 1-m wide concentric circles while scanning the ground with a portable RFID system (FS-2001F-ISO reader, BP portable antenna; Biomark). We placed a marked flag at each new detection location, searched the immediate vicinity by hand, and noted whether the detected salamander was visually confirmed (i.e. within the leaf litter or under a cover object, collectively defined as 'surface-active') or not (i.e. underground).

Analysis

For each relocated individual, we measured the distance and bearing from the point-of-capture flag to each recapture flag. We converted these points to X and Y coordinates (relative to point-of-capture), which we used to determine utilized spatial area and distance between successive detections. We could not use GPS locations due to the small spatial scale of salamander movements. For each individual, we divided each intercapture distance by time (days) since the last relocation to determine mean daily displacement. We defined 'maximum daily displacement' as the highest rate per individual. We calculated minimum convex polygons (MCP) for individuals with ≥5 detections using the 'adehabitatHR' package in R (Calenge, 2006; R Core Team, 2014). If the final position of an individual was the same location as ≥1 consecutive previous detections, we only included the first detection in that location in our analyses. We compared MCP area, maximum daily displacement, recapture frequency and recapture status (underground vs. surface-active) between treatments (burn vs. control) and treatment stages (pre vs. post) by fitting linear mixed models in the 'lme4' package in R (R Core Team, 2014) and testing differences via Wald χ^2 tests (ANOVA function, 'car' package in R). We specified site or salamander ID as random effects in each model, and used a Gaussian error distribution and identity link function. We compared post-treatment proportions of known-alive salamanders in burn and control using an analysis of variance model in R (R Core Team, 2014).

Results

We recorded 918 total recaptures of 142 *P. albagula* (69%); 63 *P. albagula* (31%) of the 205 tagged salamanders were never recaptured (Table 1). The proportion of salamanders recaptured ranged from 42–88% per site (mean = 69%; Table 1). Nearly half of all recaptures ($n = 422$; 46%) occurred at a single site – EGG. Across all seasons and both

treatments, we visually confirmed that 14% of detected salamanders were surface-active (Table 1). Prior to prescribed burns, the proportion of surface-active salamander recaptures did not differ between treatments ($\chi_1^2 = 0.12$, $P = 0.73$; Table 2). Following prescribed burns, the surface-active proportion of recaptures was nearly seven times higher in control areas than burned areas ($\chi_1^2 = 3.55$, $P = 0.06$; Table 2). The total number of recaptures did not substantially differ between treatments before or after prescribed burns (Table 2).

Following prescribed burns, we found no difference between treatments in the proportion of salamanders known alive ($F_{1,8} = 0.24$, $P = 0.64$). We relocated 28 unique salamanders in burned areas in 2013, which represented 50.1% of a possible 55 that were detected in 2012 (year prior to burns). In control areas, we relocated 26 salamanders in 2013 – 44.8% of the 58 we relocated in 2012.

The pre-burn maximum daily displacement was 13.1% higher among control salamanders (mean ± SE; 50.4 ± 7.9 cm day^{-1}) than burn salamanders (43.8 ± 5.2 cm day^{-1}; Fig. 2). Following prescribed burns, the maximum daily displacement was 43.3% higher among burn-area (30.2 ± 8.6 cm day^{-1}) than control-area salamanders (17.1 ± 4.3 cm day^{-1}; Fig. 2). Statistically, maximum daily displacement differed between pre- and post-treatment stages ($\chi_2^2 = 10.7$, $P = 0.001$), but did not differ between treatments ($\chi_2^2 = 0.009$, $P = 0.92$) or the treatment stage interaction ($\chi_2^2 = 2.47$, $P = 0.116$).

Overall, the mean MCP was 1.81 m^2 ($N = 89$), and 90% of MCPs were ≤3.8 m^2 (Fig. 3). We had relatively few salamanders with ≥5 pre- and post-burn recaptures ($N_{burn} = 9$; $N_{control} = 7$; Fig. 4), but we found that MCP varied among treatments and stages in a similar pattern to maximum daily displacements. In burned plots, the pre- and post-burn MCP means were 1.16 and 1.58 m^2, respectively; however, the median MCP decreased after prescribed burn (Table 3). In control plots, both mean and median MCP values decreased from pre-treatment to post-treatment (Table 3).

Table 2 Position of *Plethodon albagula* relocations within each treatment before (2011–2012) and after (2013–2014) prescribed fire at Daniel Boone Conservation Area, Warren County, MO, USA

	2011–2012		2013–2014	
	(pre)Burn	Control	(post)Burn	Control
No. surface-active	47	40	5	32
Percent surface-active (%)	12.9	12.2	4.3	28.8
No. underground	317	288	110	79
Total no. relocations	364	328	115	111

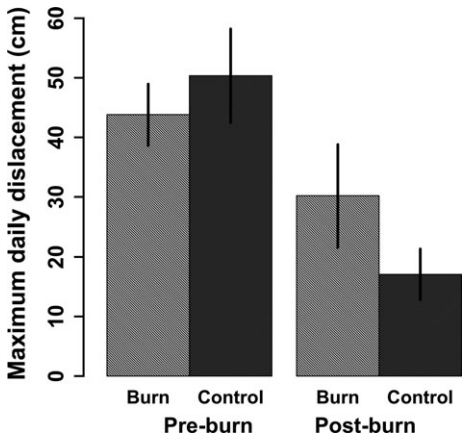

Figure 2 Pre- and post-treatment comparison of maximum daily displacement (mean ± SE) of *Plethodon albagula* salamanders in burned and control plots at Daniel Boone Conservation Area, Warren County, MO, USA from 2011 to 2014.

Discussion

Following prescribed fire, we found a substantial decrease in surface activity among salamanders in burned areas, which indicates that *P. albagula* respond to post-prescribed fire conditions by spending more time belowground. Forest-floor conditions following the prescribed fires were rarely suitable for terrestrial salamanders to actively forage due to leaf litter combustion. Leaf litter returned following leaf fall in fall/winter 2013, but it did not seem to hold moisture in 2014, as it did not contain a decomposed duff layer. Leaf litter is critical for terrestrial salamanders because it buffers soil from desiccation and contains abundant invertebrate food resources (Fraser, 1976; Jaeger, 1980). We did not find evidence of direct mortality of salamanders from prescribed fires, as the post-burn proportion of known-alive individuals did not differ between

Table 3 Minimum convex polygon measurements (m^2) of *Plethodon albagula* across treatments and stages at Daniel Boone Conservation Area, Warren County, MO, USA from 2011 to 2014

		Minimum	Median	Mean	Maximum
Burn ($n = 9$)	Pre	0.06	0.38	1.16	4.63
	Post	0.0	0.29	1.58	10.25
Control ($n = 7$)	Pre	0.0	0.31	0.54	2.17
	Post	0.0	0.035	0.24	1.11

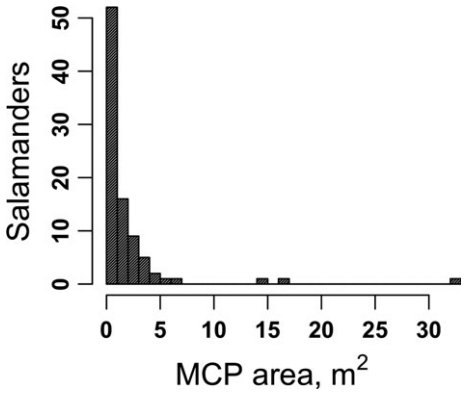

Figure 3 Frequency distribution of minimum convex polygon (MCP) values from *Plethodon albagula* at Daniel Boone Conservation Area, Warren County, MO, USA from 2011 to 2014.

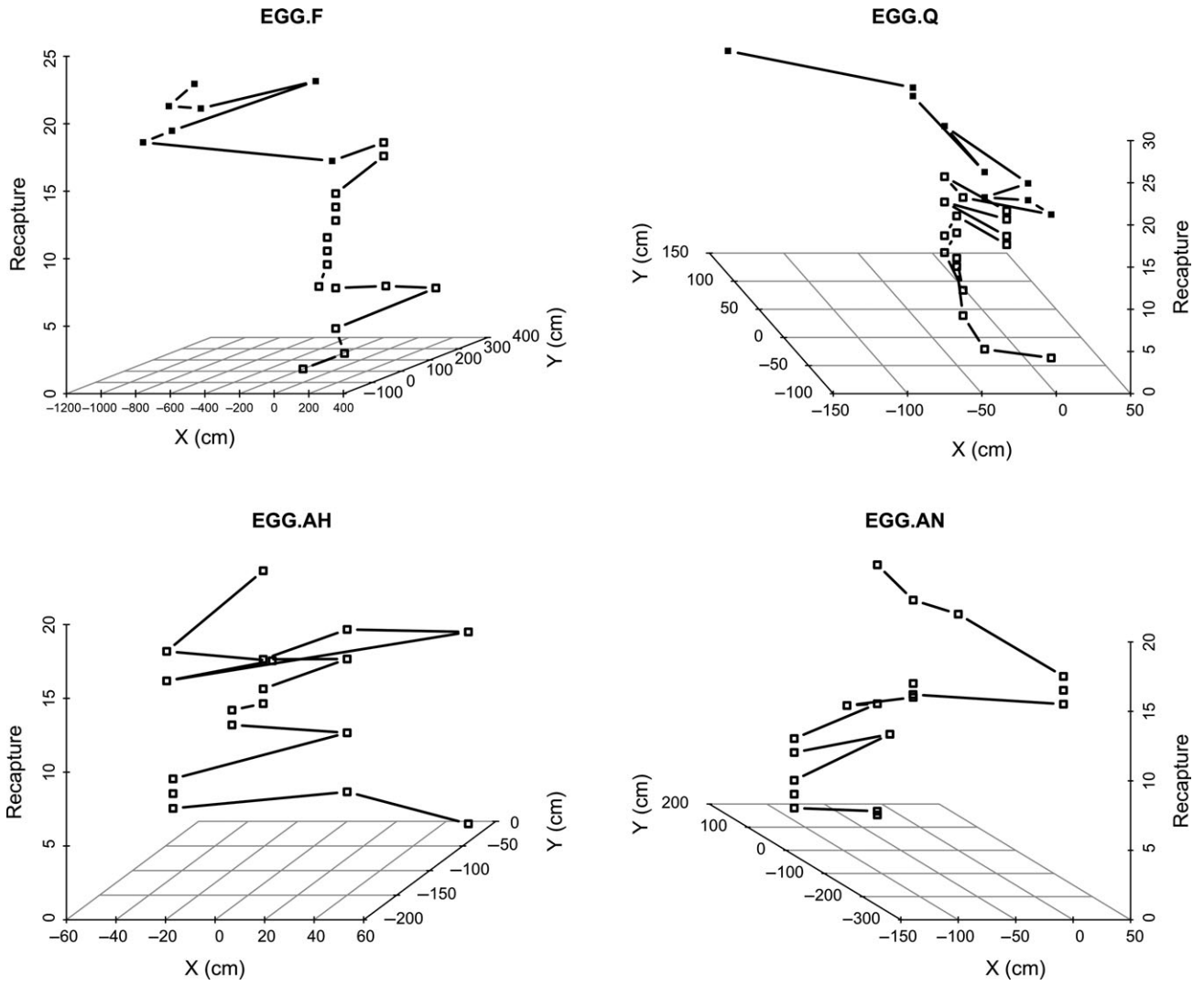

Figure 4 Three-dimensional representations of select individual salamander movements over time. Individuals 'EGG.F' and 'EGG.Q' were from burn treatments; open squares represent pre-burn captures, closed squares represent post-burn captures. Individuals 'EGG.AH' and 'EGG.AN' were in unburned areas. Longer distance post-burn movements were observed in individuals 'EGG.F' and 'EGG.Q'.

treatments. The lack of direct mortality was expected – the early April burns occurred just after snow melt, which coincides with a period of low salamander surface activity.

Together, these individual-level observations of salamanders retreating belowground corroborate our findings from a population-level study of a congeneric terrestrial salamander, *P. serratus* (O'Donnell, Thompson & Semlitsch, 2015*a*). *P. serratus* individuals are smaller bodied than *P. albagula*, but have similar reported home ranges sizes and general behavioral responses. In that study, we found that availability probability (i.e. surface activity) decreased following prescribed burns, but abundance (corrected for imperfect detection) did not decrease, indicating that salamanders are responding behaviorally rather than dying. However, we found that both surface activity and abundance decreased following timber harvest (O'Donnell *et al.*, 2015*a*). Our findings indicate that the behavioral mechanisms of terrestrial salamander responses may differ between disturbance types (i.e. prescribed fire vs. timber harvest).

Though it appears that terrestrial salamanders can largely avoid direct consequences of prescribed fire, behavioral responses to post-fire micro-environmental conditions could affect salamander populations in ways that are not yet apparent. Terrestrial salamanders have narrow moisture and temperature tolerances; they primarily forage within leaf litter on the forest floor, but must use cover objects (i.e. woody debris, rocks) or retreat below ground when surface conditions are sub-optimal to conserve water and energy (Spotila, 1972; Homyack *et al.*, 2011; Peterman & Semlitsch, 2013, 2014). If salamanders substantially decrease their surface activity, it is possible that populations may decline due to reductions in foraging and breeding opportunities (Homyack *et al.*, 2011), though further behavioral studies are required.

We detected a trend of longer maximum daily displacements in burned areas (Fig. 4), which may indicate attempts by salamanders to search for more hospitable microenvironments. Increased movement could also be a response to an overall reduction in invertebrate prey. Though we did not measure prey availability in this study, prescribed fire has been shown to decrease invertebrate abundance (Verble-Pearson & Yanoviak, 2014). While we observed increases in movement metrics among salamanders in burned areas, neither the total number of recaptures nor minimum number of known-alive salamanders decreased in burned areas. Thus, we do not believe that salamanders made extensive efforts to disperse from burned areas. It is possible that some salamanders emigrated horizontally out of survey areas, but we believe that most non-detections occurred because salamanders were deep enough underground that the portable RFID system could not detect them. Plethodontid salamanders use underground retreats extensively, and some are known to lay eggs >1 m underground (Camp, 1988; Petranka, 1998).

Our finding that only 14% of all relocations were surface-active salamanders is consistent with many other studies of plethodontid salamander surface availability (Taub, 1961; Bailey *et al.*, 2004; O'Donnell, Thompson & Semlitsch, 2015*b*). PIT-telemetry allowed us to confirm that most salamanders did not emigrate from their pre-burn home area. This approach is well suited for long-term tracking of fossorial plethodontid salamanders with small home ranges, as PIT tags last ≥10 years, can be detected underground, and allow movement estimation at fine scales. The individual-level data contribute to our understanding of mechanisms underlying population dynamics measured at larger scales, which is critical for managers to effectively simulate various management scenarios and promote suitable post-management habitat conditions. Currently, fire regime design is influenced more by predicted vegetation responses than by predicted wildlife responses, as the former have been more widely studied (Driscoll *et al.*, 2010). We found that an early season prescribed fire conducted prior to peak salamander surface activity did not seem to cause direct salamander mortality. When minimizing adverse effects of fire on terrestrial salamanders or other amphibians is important, we encourage avoiding prescribed burn applications during seasons of peak surface activity (terrestrial salamanders) or breeding migrations of pond-breeding amphibians, as this may limit direct mortality. We saw evidence of salamander behavioral responses to post-fire conditions – particularly in reduced surface activity. Prescribed burns that foster rapid regeneration of herbaceous vegetation could provide a mechanism for moisture retention near the forest floor, which is a crucial requirement for terrestrial salamanders that often depend on leaf litter and duff layers for foraging and moisture.

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