



Effects of experimental forest management on a terrestrial, woodland salamander in Missouri

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ABSTRACT

Successful multi-use planning for forested landscapes requires an understanding of timber management effects on wildlife species. Lungless, woodland salamanders depend on forested habitats and are sensitive to changes in temperature and moisture associated with many forestry practices. Additionally, woodland salamanders are territorial and have relatively low vagility, making it unlikely that they can successfully migrate to more favorable habitat when the surrounding forest is harvested. Therefore, we examined the abundance of the Western Slimy Salamander, *Plethodon albagula*, in an experimentally manipulated forest in central Missouri. We used artificial cover object searches to compare salamander abundance in three replicate treatments that were clear-cut then burned to reduce maple regeneration, clear-cut and not burned, partially harvested, and un-manipulated control forest. We captured a total of 300 Western Slimy Salamanders between April 2007 and September 2011. We found significantly fewer salamanders in the burn and clear-cut treatments compared with the partial and control treatments. We also found a lower proportion of juveniles and had fewer recaptures in the burn and clear-cut than in the partial and control treatments. Consistent with other studies of woodland salamanders, our results suggest that for at least the first 7 years post-harvest, clear-cutting is detrimental to woodland salamander populations. This initial reduction in abundance combined with the further reduced proportion of juveniles may have longer lasting effects even as the forest regenerates. Finally, it appears that timber harvest resulting in limited canopy thinning may be compatible with maintaining populations of Western Slimy Salamanders in Missouri.

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1. Introduction

Management of both public and private forest land increasingly involves planning for multiple uses such as recreation, timber production, watershed management, and maintenance of biodiversity and wildlife habitat. Effectively balancing ecological sustainability with complex economic and social objectives requires an understanding of how both management decisions (intensity, timing, and spatial arrangement of harvesting) and species biology (vagility, degree of habitat specialization, and tolerance of changes in local microclimate) influence the long-term dynamics of plant and animal populations.

Although changes in habitat structure and microclimate may promote habitat generalists and early successional species (Wallendorf et al., 2007; McDermott and Wood, 2009), there is evidence from a wide range of taxa that intensive timber harvesting has a negative influence on abundance of forest-dependent species

(deMaynadier and Hunter, 1995; McLachlan and Bazely, 2001; Decocq et al., 2004; Augenfeld et al., 2008). The resulting shifts in forest community composition may persist for many years after harvesting (McLachlan and Bazely, 2001; Homyack and Haas, 2009). Although short-term population declines of forest-dependent species may be acute, the ecological sustainability of timber harvesting practices should be assessed by the long-term responses of plant and animal populations to these disturbance events.

Management of forests for timber production may cause long-lasting changes in habitat and microhabitat characteristics. Changes in habitat and vegetation, including patterns of host-plant occurrence, can explain shifts in the abundance and species composition of Lepidopteran communities (Summerville and Crist, 2002). Clear-cutting is also known to cause increased air and soil temperature, higher wind speeds, and larger fluctuations in temperature (Keenan and Kimmins, 1993; Brooks and Kyker-Snowman, 2008). Leaf litter depth and decomposition rates may also be influenced by timber harvesting (Ash, 1995; Li et al., 2009). These changes in microhabitat may drive declines in many soil microinvertebrates (Blair and Crossley, 1988; Donegan et al.,

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2001). Intensive timber harvesting can also result in soil compaction, changes in soil chemical properties, and erosion if harvesting on a slope subject to heavy rains or snowmelt (Keenan and Kimmins, 1993). Creation of temporary logging roads may be an additional source of soil compaction with long-term impacts on species distributions (Semlitsch et al., 2007). Cumulatively, these changes in habitat characteristics may limit the repopulation of early-successional timber cuts by forest-dependent species.

Plethodon salamanders are ectothermic vertebrates which, unlike most other North American amphibians, circumvent an aquatic larval stage and undergo direct development from egg to terrestrial juvenile. These salamanders can be extremely abundant predators in forest ecosystems of the eastern United States (Burton and Likens, 1975; Bailey et al., 2004) and provide an important link between the “green” and “brown” food webs by consuming both herbivorous above-ground invertebrates as well as detritivorous leaf-litter and soil invertebrates (Petranka, 1998). As a result of their top-down role in regulating invertebrate populations (Wyman, 1998; but see Homyack et al., 2010), these salamanders may also influence rates of leaf litter decomposition and carbon storage (Wyman, 1998).

All salamanders in the family Plethodontidae lack lungs and have cutaneous respiration that requires moist skin for gas exchange. As a result, changes in temperature and moisture conditions associated with timber harvest may fall outside of the narrow tolerance of many Plethodontid species (Spotila, 1972). Even small increases in temperature could represent a considerable metabolic cost associated with the occupation of early-successional timber cuts (Homyack et al., 2011). Although only a temporary form of habitat loss, timber harvesting may reduce terrestrial salamander abundance for decades (Petranka et al., 1993; Ash and Bruce, 1994; Ash, 1997; Herbeck and Larsen, 1999). Therefore, there is a need to investigate the dynamics of populations persisting in early-successional timber cuts in order to better understand the processes underlying the slow recoveries of populations.

Understanding the effects of different forest management practices on salamanders, especially different harvest levels, can help inform practical decisions when balancing wildlife conservation and economic gains from silviculture. Currently much of the evidence for forestry effects on amphibians, especially on Plethodontids, is from the Pacific Northwest (e.g. Biek et al., 2002; Johnston and Frid, 2002; Vesely and McComb, 2002; Karraker and Welsh, 2006) and southern Appalachian Mountains (e.g. Petranka et al., 1993, 1994; Harpole and Haas, 1999; Knapp et al., 2003; Homyack and Haas, 2009). In contrast, there is a paucity of information on the effects of forest management practices on woodland salamanders in the midwestern United States (but see Herbeck and Larsen, 1999; Renken et al., 2004), which is characterized by hotter, drier summers. Here we present the results of a 5-year study examining the effects of experimental forest management practices on the Western Slimy Salamander, *Plethodon albagula*, in central Missouri. Specifically, we examined the effects of a range of forestry practices on (1) local abundance, (2) population age structure, and (3) body condition of salamanders. We also examined recapture rates of salamanders across treatments, as these could reflect fundamental differences in detectability, immigration, survival, or abundance, thereby influencing population dynamics and recovery.

2. Methods

2.1. Study area

Our study was conducted within the 1425-ha Daniel Boone Conservation Area (DBCA) in central Missouri. The DBCA is located in the upper Ozark Plateau and is characterized by rolling hills

dominated by secondary growth (80–100 year old) oak-hickory forest (*Quercus-Carya*). We established four experimental forest treatments at each of four sites in 2004–2005. Sites were located at least 2 km from one another. Four silvicultural treatments were randomly applied at each site: two clear-cuts, a partial-cut, and an un-manipulated control. The partial-cut was designed to promote rapid growth of the remaining oak trees by thinning the canopy of undesirable species to approximately 60% stocking density. In February 2007, one of the clear-cut treatments at each site was burned. Post-harvest burns are of local management interest as a technique to reduce invasive maple (*Acer* spp.) colonization and promote oak (*Quercus* spp.) regeneration. The treatment quadrants are approximately 2.1 ha in size and are centered around an amphibian breeding pond. Although the spatial arrangement of treatments was designed to test for effects on pond-breeding amphibians (e.g. Hocking and Semlitsch, 2007; Semlitsch et al., 2008, 2009), the experimental design also provides an appropriate platform to test for effects of forest management on terrestrial, woodland salamanders.

2.2. Sampling

In April–May 2006, we placed artificial cover objects (ACOs) at three of four experimental arrays due to property boundaries near the edge of the fourth site. Within each treatment, we placed ACOs in two transects, each spanning 110 m. These transects ran from the adjacent forest 50 m beyond the treatment edge to 50 m into each treatment. Eleven ACO locations were spaced at 10-m intervals within each transect (Fig. 1; 264 total ACO locations for all three sites). At each ACO location we placed one wooden and one carpet ACO of equal area. Since carpet was not used by slimy salamanders (Scheffers et al., 2009) and deteriorated after 18 months, we only used data associate with wooden ACOs for this study. Wooden ACOs were untreated pine boards measuring $\sim 90 \times 30 \times 2.5$ cm. We also limit our comparison to treatment effects and therefore only use data from ACOs located 10–50 m within the treatments. We began checking ACOs during the first spring after the burn treatments were applied (2 years post-harvest). Thus, the first year of our study represents the first year post-burn and the third year after the clear-cut and partial-cut treatments

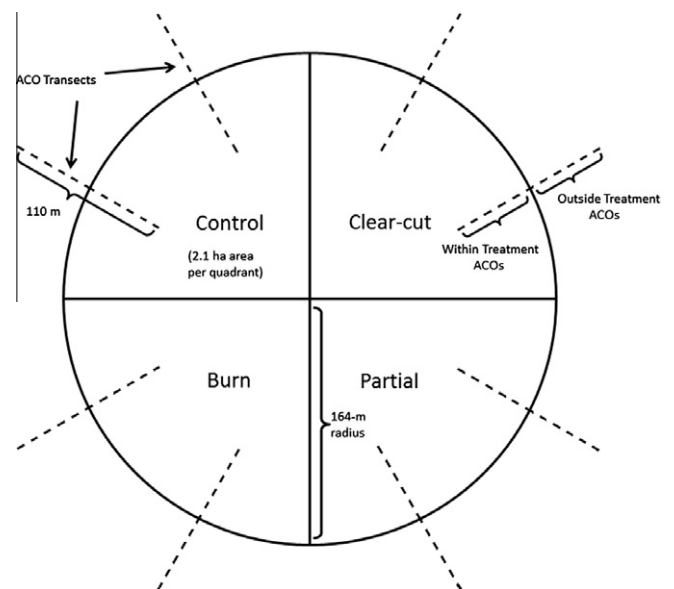


Fig. 1. Schematic of experimental forest manipulations depicting layout of ACO transects.

were applied. We checked the ACOs in spring, summer, and fall of 2007 and 2008, fall of 2009, and spring and fall of 2010 and 2011. We did not check the transects more frequently than once every 7 days to avoid bias from intense sampling (Marsh and Goicochea, 2003). We marked all captured *P. albagula* by clipping two toes to provide a batch mark. Additionally, we weighed all animals using a 20 g Pesola spring scale (± 0.1 g) and measured snout-to-vent length (SVL) to the nearest 1 mm using a ruler. We designated animals <56 mm SVL as juveniles unless sexual characteristics were present (Trauth et al., 2004; Milanovich et al., 2006).

2.3. Analysis

We attempted to account for the differences in the probability of detection among treatments using the Dail–Madsen model (Dail and Madsen, 2011). The Dail–Madsen model assumes an open population between primary sampling periods by estimating survival and recruitment (Dail and Madsen, 2011). This is a generalization of previous hierarchical models for repeated counts, such as the N-mixture model, which require population closure (Royle, 2004; Royle and Dorazio, 2006, 2008). We compared 14 models with various covariates for abundance, detection, survival, and recruitment (Table 1) allowing abundance to change between each survey. This resulted in 36 primary periods with a single secondary sample per primary period from 2007 to 2011). All models were compared using Akaike's Information Criterion adjusted for small sample size (AIC_c). The models based on 36 primary periods had difficulty dividing the variance associated with treatment between the four latent variables. Therefore, we excluded summer sampling in further detection analyses and considered spring and fall samples from each year as primary periods. This resulted in 7 primary periods with 1–8 secondary samples per primary period. This method also presented challenges in parameter estimation; therefore, we

tried two additional approaches. First we combined data into open canopy (burn and clear-cut) and closed canopy (partial-cut and control) treatments to see if this helped stabilize the models. When this did not improve model fit, we reduced captures to presence–absence data and used the equivalent open-population occupancy colonization–extinction model (Mackenzie et al., 2002; MacKenzie et al., 2006). This resulted in unacceptable model fit; therefore, we used a traditional analysis to compare counts across treatments (described below). All hierarchical models were fit using maximum likelihood estimation in the R package unmarked (Fiske and Chandler, 2011).

For the traditional analysis assuming equal, unbiased detection probabilities, we used an analysis of variance (ANOVA) to test for significant differences in salamander total captures among silvicultural treatments. The total number of captures in each of 12 experimental units was square-root transformed to meet the assumption of homoscedasticity. Following significant ANOVA results, we used Tukey's Honestly Significant Differences Test to test for significant differences in all pairwise comparisons. We also performed a *post hoc* contrast to compare the mean of the two open-canopy treatments (clear-cut, burn) with the two closed-canopy treatments (partial, control). We used residuals from ordinary least squares regression of log-transformed body mass on log-transformed length (SVL) as an index of body condition (Schulte-Hostedde et al., 2005). We then compared body condition of *P. albagula* across silvicultural treatments by averaging body condition for each experimental unit and testing for treatment effects with a one-way ANOVA. To test for differences in population age structure among treatments, we performed a Fisher's Exact Test of the null hypothesis of a random association between lifestage (juvenile vs. adult) and canopy cover (closed vs. open). Salamanders were classified as juveniles if they were less than 55 mm in SVL (Trauth et al., 2004). We also used a Fisher's Exact Test to

Table 1
Models of salamander captures compared using the Dail–Madsen method to estimate abundance, recruitment, survival, and detection probability for all observations (36 primary periods) and just spring and fall sampling periods (7 primary periods with 1–8 secondary samples). We also compare the equivalent models of occupancy, colonization, extinction, and detection probability. Models include the effects of site, experimental forestry treatment (Trt), distance from the treatment edge in meters (Dist), mean temperature ($^{\circ}$ C) on each sampling day (MeanT), the quadratic effect of mean daily temperature (MeanT²), and the amount of rain (cm) during the 5 days preceding sampling (Rain5day). Models with the lowest AIC_c value are marked with an asterisk. AIC_c values are only comparable within a column. All Dail–Madsen models were compared with Poisson (P), Zero-Inflated Poisson (ZIP), and Negative Binomial (NB) distributions. Values from the best (lowest AIC_c) distribution are presented and noted parenthetically.

Model	Abundance/occupancy	Recruitment/colonization	Survival/extinction	Detection
1	Site + Trt + Dist + Trt * Dist	Site + Trt + Dist + Trt * Dist	Site + Trt	Trt + MeanT + MeanT ² + Rain5day
2	Site + Trt + Dist + Trt * Dist	Trt	Trt	Trt + MeanT + MeanT ² + Rain5day
3	Site + Trt + Dist + Trt * Dist	Trt	Intercept only	Trt + MeanT + MeanT ² + Rain5day
4	Site + Trt + Dist + Trt * Dist	Intercept only	Trt	Trt + MeanT + MeanT ² + Rain5day
5	Site + Trt + Dist + Trt * Dist	Intercept only	Intercept only	Trt + MeanT + MeanT ² + Rain5day
6	Site + Trt	Trt	Trt	Trt + MeanT + MeanT ² + Rain5day
7	Site + Trt	Trt	Intercept only	Trt + MeanT + MeanT ² + Rain5day
8	Site + Trt	Intercept only	Trt	Trt + MeanT + MeanT ² + Rain5day
9	Site + Trt	Intercept only	Intercept only	Trt + MeanT + MeanT ² + Rain5day
10	Site + Trt	Intercept only	Intercept only	MeanT + MeanT ² + Rain5day
11	Site + Trt	Intercept only	Intercept only	Trt + MeanT + MeanT ²
12	Trt	Intercept only	Intercept only	Trt
14	Trt	Trt	Trt	Trt
Model	All observations	Spring/fall	Occupancy	
1	Inestimable	Inestimable	1544.0*	
2	Inestimable	Inestimable	1576.5	
3	Inestimable	Inestimable	1574.3	
4	Inestimable	Inestimable	1591.9	
5	Inestimable	1588.2 (NB)	1596.3	
6	2077.5 (NB)	Inestimable	1630.4	
7	2071.5 (NB)*	1598.4 (P)	1574.3	
8	Inestimable	1598.7 (NB)	1569.6	
9	Inestimable	1593.2 (NB)*	1750.5	
10	Inestimable	1681.1 (NB)	1744.5	
11	Inestimable	1597.0 (NB)	1750.5	
12	Inestimable	1618.4 (P)	1573.4	
14	Inestimable	1626.8 (ZIP)	1573.6	

examine the association between the recapture status of individuals (recaptured vs. not recaptured) and canopy cover (closed vs. open). A critical α value of 0.05 was used to test the significance of all statistical tests.

3. Results

We captured a total of 300 slimy salamanders from April 2007 to September 2011. Of these, 197 were unique individuals, 92 were recaptures, and the remaining 11 escaped before they could be checked for markings. We only captured 22 individuals in the burn and 11 in the clear-cut treatments. This represents 11% of total captures between the two treatments in 2160 coverboard searches. Given the large number of searches with zero captures and low, variable detection probability, the hierarchical models were unable to partition the variance between the four latent variables (Tables 1 and 2). Therefore, using ANOVA, we found a significant difference in salamander captures among treatments ($F_{3,8} = 4.03, P = 0.05$). Across three sites, we captured the greatest total number of salamanders across years in the control (mean captures \pm SE = 46.7 ± 11.1), followed by the partial-cut (42.3 ± 20.2), burn (7.3 ± 4.4), and clear-cut treatments (4.0 ± 2.0), respectively (Fig. 2). Although we found an overall treatment effect, we failed to detect significant pairwise differences between treatments at

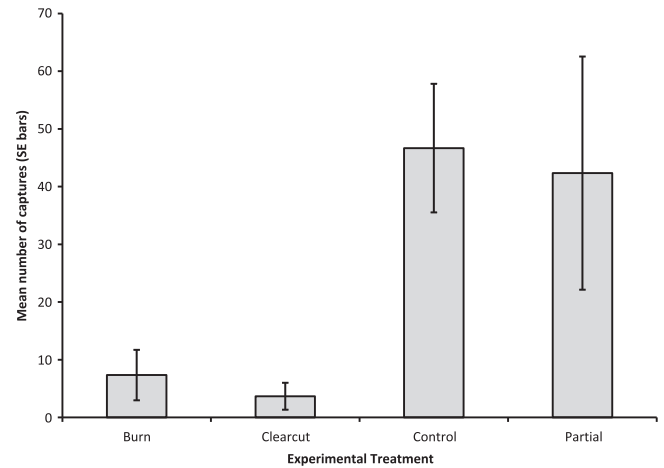


Fig. 2. Salamander captures differ by treatment (ANOVA: $P = 0.05$). Data are from three sites, with salamander captures pooled across years.

the $\alpha = 0.05$ level using Tukey's HSD Tests. The greatest mean difference was between the control and clear-cut treatments (Tukey's HSD Test: $P = 0.07$). This trend was not significant despite a nearly 12 times greater number of captures in the control treatment,

Table 2
Maximum likelihood parameter estimates for the three best models determined by AIC_c comparison.

Occupancy model 1				All observations model 7			Spring/fall model 5		
Predictor	Estimate	SE	P	Estimate	SE	P	Estimate	SE	P
<i>Initial occupancy</i>				<i>Abundance</i>			<i>Abundance</i>		
Intercept	-29.49	69.83	0.673	-2.862	0.926	0.002	-1.242	0.483	0.010
Site2	29.38	69.79	0.674	0.692	0.866	0.424	1.467	0.469	0.002
Site3	14.58	24.87	0.558	-0.694	1.225	0.571	1.327	0.472	0.005
Burn	-17.65	294.1	0.952	-8.894	60.40	0.883	-0.821	1.009	0.415
Clear-cut	36.39	338.0	0.914	0.001	1.000	0.999	0.350	0.688	0.611
Partial	28.61	72.49	0.693	0.406	0.913	0.657	0.191	0.373	0.609
Distance	-0.012	0.062	0.850				-0.524	0.254	0.040
Burn * Dist	-0.531	278.7	0.998				-1.043	0.778	0.180
CC * Dist	1.129	264.8	0.997				0.339	0.571	0.553
Partial * Dist	-0.380	0.726	0.600				0.346	0.343	0.313
<i>Colonization</i>				<i>Recruitment</i>			<i>Recruitment</i>		
Intercept	-3.093	0.563	<0.001	-1.904	0.092	<0.001	-0.370	7.620	0.961
Site2	0.653	0.415	0.116	-1.891	0.262	<0.001			
Site3	1.579	0.397	0.000	-2.338	0.379	<0.001			
Burn	-0.360	0.740	0.626	-0.111	0.133	0.403			
Clear-cut	2.609	2.123	0.219						
Partial	0.216	0.718	0.763						
Distance	-0.002	0.015	0.914						
Burn * Dist	-0.069	0.028	0.014						
CC * Dist	0.008	0.062	0.898						
Partial * Dist	-0.025	0.022	0.248						
<i>Extinction</i>				<i>Apparent survival</i>			<i>Apparent survival</i>		
Intercept	-1.134	0.572	0.048	-22.7	1439.0	0.987	-2.250	79.70	0.978
Site2	-1.140	0.649	0.079						
Site3	-0.186	0.626	0.767						
Burn	3.400	0.925	0.000						
Clear-cut	33.57	330.28	0.919						
Partial	0.407	0.660	0.538						
<i>Detection</i>				<i>Detection</i>			<i>Detection</i>		
Intercept	18.64	13.19	0.158	6.179	4.585	0.178	-1.565	0.195	<0.001
Burn	11.81	224.1	0.958	-0.666	1.682	0.692	-2.000	0.320	<0.001
Clear-cut	-2.911	0.541	<0.001	-3.705	1.889	0.050	-2.627	0.420	<0.001
Partial	0.291	0.373	0.434	0.068	0.827	0.935	-0.023	0.214	0.915
MeanT	-2.906	1.989	0.144	-0.547	13.09	0.967	-0.473	0.116	<0.001
MeanT ²	0.107	0.075	0.152	-3.829	7.233	0.597	0.521	0.127	<0.001
5-Day Rain	-1.197	0.765	0.117	0.331	0.319	0.301	0.202	0.085	0.017
				<i>Dispersion</i>			<i>Dispersion</i>		
				10.6	350.0	0.976	1.860	1.470	0.206

likely due to a lack of statistical power from using study plots as our unit of analysis. A *post hoc* contrast between closed- and open-canopy treatments was highly significant ($t = 3.40$, $P < 0.01$). In each year of our study, salamanders were captured in every treatment; however, the relative frequencies of captures occurring in each treatment remained fairly consistent over the course of our 5-year study (Fig. 3).

Body condition of *P. albagula* was consistent among treatments (Fig. 4) and we found no statistically significant relationship between body condition and silvicultural treatment ($F_{3,7} = 0.06$, $P = 0.98$). The proportion of juveniles differed significantly between closed- and open-canopy (Fisher's Exact Test: $P = 0.02$), with juveniles representing 52% of salamanders captured in the control and partial-cut treatments ($N = 267$) and only 33% in the clear-cut and burn treatments ($N = 43$). We also detected a significant association between recaptures and silvicultural treatment (Fisher's Exact Test: $P < 0.01$). Recaptured animals represented approximately 35% of captures in the closed-canopy treatments ($N = 259$) but only 3% of salamander captures in the open-canopy treatments ($N = 31$).

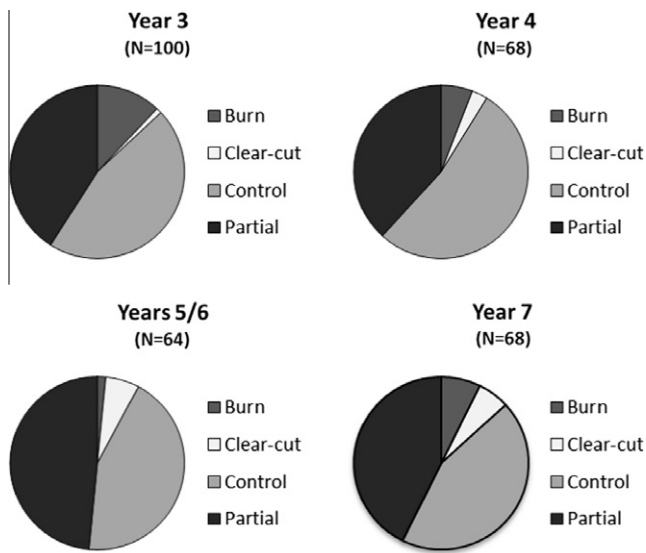


Fig. 3. Total salamander captures by treatment. Our study began in the third year following clear-cutting when experimental burn treatments were applied.

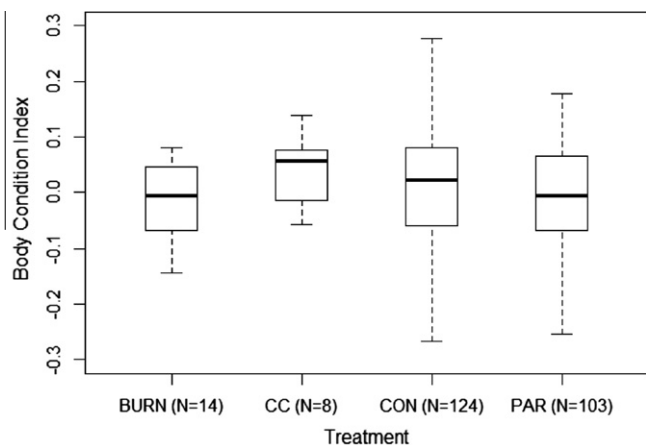


Fig. 4. Relative body condition (\pm SE) of *Plethodon albagula* individuals in four experimental forest treatments. Body condition (size-corrected mass) was calculated as the residuals of OLS regression of log SVL and log mass.

4. Discussion

4.1. Salamander abundance

Our study examined the dynamics of *P. albagula* populations for 5 years following large-scale experimental forest manipulations. Consistent with previous studies assuming equal detection of woodland salamanders among forest types (e.g. Petranka et al., 1994; Ash, 1997; Herbeck and Larsen, 1999; Knapp et al., 2003), we found that salamander captures were significantly reduced immediately following clear-cut logging. The extreme differences in captures among treatments suggest that even significant differences in detection among treatments would not change the general conclusions from the traditional analysis. Both our experimental clear-cut and burn treatments involved complete canopy removal, and these treatments demonstrated reduced salamander abundance compared to the partial-cut and control treatments. Furthermore, there was no apparent increase in salamander abundance in either of these treatments over the course of our study (Fig. 3). These results are consistent with the findings of Herbeck and Larsen (1999), who compared salamander abundance across stand age classes in the Missouri Ozarks. In their study, very few salamanders were found in recent regeneration-cut sites (<5 years old) compared with older forest stands. As part of the Missouri Ozark Forest Ecosystem Project (MOFEP), Renken and colleagues (Renken et al., 2004) did not detect any differences in woodland salamander captures among sites with even-aged (clear-cut), uneven-aged (select and group cut), and un-harvested control treatments at the landscape scale. In the MOFEP study, even-aged management treatments largely involved forest thinning with just 10–15% of the total area being clear-cut. These management activities resulted in an overall decline in canopy cover of just 13% relative to un-managed forest. The results of their study likely differ from ours because we examined only the effects of harvesting on local populations while the results of the MOFEP study represented salamander abundance at a broader landscape level. Similarly, Hawkes and Gregory (2012) did not detect a reduction in salamander abundance following clear-cut logging in the Pacific Northwest, although they did find a reduction in Coast Tailed Frogs (*Ascaphus truei*). Future studies should examine how regional and environmental differences exacerbate or ameliorate the effects of logging on salamander abundance and why these effects vary across species.

While we found reduced abundance of salamanders in treatments involving full canopy removal, salamander abundance in our partial-cut treatments was nearly as high as in our control stands. These results suggest that canopy thinning without timber removal or heavy machinery is potentially compatible with maintaining healthy populations of large-bodied lungless salamanders in the Midwest region. This is supported by the findings of Renken et al. (2004), who demonstrated that salamander abundance was not significantly reduced relative to un-managed forest in landscapes with extensive thinning. In spite of these results, studies have shown that timber extraction involving less intensive alternatives to clear-cutting can still have strong negative effects on terrestrial salamanders (but see Sattler and Reichenbach, 1998). A previous study showed that thinning with heavy machinery and timber removal reduced the abundance of Western Red-backed Salamanders (*Plethodon vehiculum*), in the Pacific Northwest, where forestry effects may differ from those in the Midwest due to climate, forest types, soil types, and other regional differences (Grialou et al., 2000). Morneau et al. (2004) captured significantly fewer Eastern Red-backed Salamanders (*Plethodon cinereus*) under coverboards in shelterwood harvests (=50% canopy removal) than in un-cut control forest in Canada. In this case, these differences in abundance were short-lived (<5 years) as canopy cover filled

in rapidly following these cuts (Morneault et al., 2004). Finally, an extensive comparison of silvicultural alternatives found that all harvest techniques involving canopy removal resulted in reduced salamander abundance or no change in abundance but none reduced abundance more than clear-cutting (Harpole and Haas, 1999; Knapp et al., 2003; Homyack and Haas, 2009). In our study, canopy thinning likely had less of an impact on terrestrial salamanders because it did not include marketable timber removal but rather left the girdled undesirable trees standing as snags or on the ground as coarse woody debris. The moist microclimate provided by woody debris could potentially mitigate the effects of reduced canopy cover (Moseley et al., 2004). Additionally, heavy machinery was not used to remove the timber in our partial-cut treatment, potentially leading to less soil compaction than when timber is removed during the thinning process (e.g. Grialou et al., 2000).

Due to the apparent sensitivity of woodland salamanders to silvicultural practices of a wide range of intensities, it is critical that research focus on the process behind the apparent declines and limited recovery of salamander populations in the years post-harvest. Proposed mechanisms for the initial declines in salamander abundance are direct mortality (e.g. Petranka et al., 1993; Petranka et al., 1994), decreased activity and increased refuge use resulting in lower detection probability (e.g. Johnston and Frid, 2002), or dispersal away from timber cuts (e.g. Reichenbach and Sattler, 2007; Peterman et al., 2011). These hypotheses have been summarized as (1) mortality, (2) retreat, or (3) evacuation, and these hypotheses are not mutually exclusive (Semlitsch et al., 2008). The use of relative abundance data does not allow us to differentiate between mortality, retreat underground (lower detection probability), or emigration away from the clear-cuts. However, we found no evidence of *P. albagula* dispersing away from the clear-cuts (RDS unpublished data – 16 enter, 12 leave 2005–2007), although we did find *Ambystoma* salamanders emigrating off of the clear-cuts (Semlitsch et al., 2008). We found a greater proportion of recaptures in the control and partial treatments compared with the clear-cut and burned treatments, which could indicate higher mortality in inhospitable habitat. Alternatively, lower capture and recapture rates may be due to reduced activity at the ground surface, thereby reducing our probability of detecting salamanders. In our study, the magnitude of the difference in salamander captures between closed and open-canopy treatments as well as the fact that we captured salamanders in artificial refuges instead of using counts that depended on surface activity suggest that there were large differences in salamander abundance due to canopy removal. Furthermore, in the only study using mark-recapture techniques to estimate terrestrial salamander abundance independent of detection probability, the decline in estimated abundance was more severe than the decline in apparent abundance from surface counts following clear-cutting (Sattler and Reichenbach, 1998).

While mark-recapture would be useful for answering particular questions, it is too time intensive for large-scale, replicated determination of abundance across sites. Hierarchical models of abundance provide the potential for comparing abundance across the landscape while accounting for detection probability (Royle and Dorazio, 2006, 2008; Dail and Madsen, 2011). However, in our study the low capture rate, especially in the burn and clear-cut treatments, prevented reliable use of hierarchical modeling to account for potential bias in detection probability. Future studies would benefit from explicit design for analysis in a hierarchical framework that includes detection probability (e.g. N-mixture, Dail–Madsen, colonization–extinction, etc.). These models require a large number of spatially replicated sites, even more than the more specific N-mixture models due to the greater number of latent variables (possibly 200+ sites). Additionally, our models probably suffered from relatively low detection and low abundance. Future studies would benefit from techniques

that increase detection probability (e.g. multiple ACOs per site, nighttime surveys when animals are active, etc.) and abundance (e.g. larger survey areas).

4.2. Body condition

Due to the difficulty in separating survival, dispersal, and detection probability from abundance data, amphibian body size and body condition have been used as alternative metrics of habitat quality (Knapp et al., 2003; Karraker and Welsh, 2006; Todd and Rothermel, 2006). For instance, Todd and Rothermel (2006) found that both survival and mean body size of southern toads, *Bufo terrestris*, were reduced in clear-cuts in spite of there being no difference in relative abundance between treatments. Karraker and Welsh (2006) examined differences in body condition of two terrestrial salamanders across forestry treatments and found that one species, *Ensatina eschscholtzii*, demonstrated significantly higher body condition in un-thinned forest but did not differ between clear-cut and thinned forest sites. Knapp et al. (2003) found that gravid *Desmognathus ochrophaeus* were of lower body condition in harvested treatments. In contrast, neither *Plethodon elongatus* (Karraker and Welsh, 2006) nor gravid *P. cinereus* (Knapp et al., 2003) demonstrated a relationship between forest harvesting and body condition. Similarly, our results show that body condition of a congeneric species, *P. albagula*, did not differ among treatments. Because increased temperature is likely to increase energetic costs for terrestrial salamanders, it has been proposed that post-harvest survival could entail increased energetic allocation to basic maintenance at the expense of growth and reproduction (Homyack et al., 2011). Although body condition did not differ among treatments, reproduction could be reduced in recent clear-cuts because maintaining body condition is more energetically costly at higher temperatures. Energy that would otherwise be devoted to reproduction (e.g. developing eggs) might be required for maintaining body condition in clear-cuts. This would result in important changes in population age structure and a decrease in population growth rates that would be expected to cause further reductions in salamander abundance over time.

4.3. Population age structure

In our study, we also found significantly fewer juvenile salamanders in open-canopy clear-cut treatments. Previous studies of the effects of timber harvesting on population structure of terrestrial salamanders have produced inconsistent results. Although two studies found a smaller proportion of juveniles in existing clear-cuts (Sattler and Reichenbach, 1998; Ash et al., 2003), other studies have either shown the opposite trend (deMaynadier and Hunter, 1998; Welsh et al., 2008) or inconsistency among species (Homyack and Haas, 2009). Although little is known about dispersal in woodland salamanders, one study has found male-biased dispersal of juvenile red-backed salamanders, *P. cinereus* (Liebgold et al., 2011). *P. cinereus* colonizing experimental habitat patches in an open field also tended to be smaller individuals (Marsh et al., 2004). Given that small individuals should be over-represented as colonizers of early-successional habitat, our results would indicate that either juvenile survival or surface activity are reduced relative to adults in open-canopy treatments. If reduced surface activity translates into a reduction in foraging opportunities, this process could still be important in limiting individual growth and future reproduction.

4.4. Conclusions and implications

Although timber harvesting may provide habitat for a number of early-successional species, forest management which seeks to

sustain healthy populations of forest-dependent species should account for the length of time required for species recovery following harvesting. This is complicated by the fact that projected recovery times of plant and animal populations often appear to be taxa-specific and may depend on species life history. A number of studies have shown that understory herbaceous plant diversity may either increase (e.g. Roberts and Zhu, 2002; Scheller and Mladenoff, 2002) or show no change (e.g. Ford et al., 2000; Gilliam, 2002) relative to un-harvested forest. However, this is often due to the increased success of shade-intolerant species in recent timber cuts, while a number of sensitive late-successional plants may become reduced or absent (Moola and Vasseur, 2008). Furthermore, many of the understory plant species most sensitive to timber harvest can be typified by limited seed dispersal and intrinsically low rates of growth or reproduction (reviewed in Moola and Vasseur, 2008). For species that are highly vagile or have a high intrinsic rate of increase, the recovery of populations following local-scale disturbance may proceed rapidly when habitat becomes suitable. For instance, densities of some forest-interior bird species in regenerating clear-cuts may approximate densities in control forest within 20–25 years of harvesting (Thompson et al., 1992; McDermott and Wood, 2009). The abundance of forest floor microinvertebrates may initially be reduced following timber harvest (Blair and Crossley, 1988; Donegan et al., 2001) but has been shown to recover rapidly to pre-harvest levels within 20 years (Heneghan et al., 2004). As a result, it is clear that several factors may limit the rate of species recovery, such as the rate at which habitat suitability is restored following harvesting, the intrinsic rate of increase of a species, and the density and dispersal ability of potential colonizers. Thus, a better understanding of population dynamics and factors limiting species recovery in early-successional habitat may allow management practices to be optimized. Poor dispersers may require re-introduction or smaller harvest areas may allow for faster re-colonization. In addition, less intensive forest management practices such as canopy thinning or partial harvest (50% or less) may have less severe impacts on species (Semlitsch et al., 2009). We found that salamander abundance in our partial-cut treatment was comparable to our control treatment, suggesting that limited canopy thinning without timber removal may have little impact on terrestrial salamander abundance, even in the first years after thinning.

Projected recovery times for terrestrial salamanders range from 20 to 70 years in the southern Appalachians (Petranka et al., 1993; Ash, 1997; Homyack and Haas, 2009). Our study indicates that *P. albagula* populations in central Missouri are greatly reduced in abundance following clear-cutting and are characterized by an age structure skewed towards the adult life-stage. This current bottleneck at the juvenile life-stage may be an important factor in limiting population growth in upcoming years. Low juvenile survival in early-successional habitat would also suggest that juvenile dispersers should be less effective in contributing to current population growth.

Although numerous studies have demonstrated that the apparent abundance of terrestrial salamanders declines in response to timber harvest (e.g. Petranka et al., 1993; Ash, 1997; Homyack and Haas, 2009; but see Hawkes and Gregory, 2012), just a single study has used mark-recapture methods to validate the use of relative abundance data to assess changes in salamander abundance following timber harvest (Sattler and Reichenbach, 1998). Because this study was un-replicated, future research applying mark-recapture techniques would be valuable in clarifying the full effects of timber harvest on salamander abundance and population age structure. Additionally, behavioral studies may elucidate the relative importance of reduced activity and dispersal as causes of perceived declines in salamander populations. Such approaches may also determine whether animals persisting on young timber cuts

are colonizers or survivors from pre-harvest populations. This would be helpful in determining whether the recovery of salamander populations is limited only by the progress of forest succession and restoration of favorable microclimates or whether re-colonization rate or survival of dispersers are still inadequate to promote rapid population growth for many years.

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