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Effects of timber harvest on survival and movement of stream salamanders in a managed forest landscape

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Abstract. With escalating anthropogenic alteration of landscapes worldwide, managed forests are increasingly important as providers of ecosystem services and wildlife habitat. Therefore, it is crucial to maintain a balance between producing forest products and biodiversity conservation. Several studies have reported negative effects of forest management on terrestrial plethodontid salamanders, but fewer have focused on stream-dwelling species or evaluated mechanisms for shifts in their abundance (e.g., mortality vs. movement). We used a before–after–control–impact design to examine the effects of clear-cut harvesting on a semi-aquatic stream-breeding salamander endemic to the Ouachita Mountains, *Desmognathus brimleyorum*. We conducted a three-year capture–mark–recapture (CMR) study at three streams within a managed pine (*Pinus* spp.) landscape in west-central Arkansas, USA. Loblolly pine (*Pinus taeda*) stands surrounding two of the streams were clear-cut (leaving a 14–21 m wide forested buffer on each side of the stream) midway through the study; the third stream served as a control site and remained unharvested. We estimated apparent survival using open CMR models and compared salamander movement over time and between harvested and control streams. Overall, our models revealed seasonal and temporal variation in salamander survival and abundance, but little evidence for strong immediate effects of timber harvesting on post-metamorphic salamanders within two years postharvest. However, there was increased salamander movement at sites where forest harvest occurred. Our results suggest that streamside buffers of at least 14–28 m on either side of a stream are effective for minimizing immediate effects of forestry activities on juvenile and adult stream-dwelling salamanders, when timber harvest occurs in the winter months. These results will inform management decisions aimed at conserving biodiversity and ecosystem integrity in managed forest landscapes while also filling a critical gap in the knowledge of stream salamander demographic parameters.

Key words: Arkansas; before–after–control–impact; capture–mark–recapture; *Desmognathus brimleyorum*; Interior Highlands; Ouachita Dusky Salamander; Ouachita Mountains; streamside management zone.

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INTRODUCTION

Privately owned forests managed for timber production have become a common land cover in many parts of the world, including the southern United States. There are currently over 32 million acres of planted pine (*Pinus* spp.) stands in the southeastern United States (Fox et al. 2007), accounting for almost half of the world's planted forests (Allen et al. 2005). These large tracts of pine forest have ecological value (see Ninan and Inoue 2013) and can help alleviate pressures from urban and agricultural development on ecosystem services, including wildlife.

However, it is necessary to understand how periodic forest disturbances (e.g., clear-cutting, thinning, and site preparation) affect wildlife populations. With a clear understanding of mechanisms driving relationships between forestry practices and wildlife population dynamics, we can seek to balance economic, social, and ecological value of working forests.

Most private, working pine forests in the southern United States are managed under an even-aged management regime, where an entire stand is harvested and/or planted at the same time (Miller et al. 2009, Demarais et al. 2017). Even-aged management practices (such as clear-cutting) can cause physical changes to forest ecosystems including temporarily reduced canopy cover, increased soil temperatures, nutrient loss, and soil disturbance (Bormann et al. 1968, Keenan and Kimmins 1993, Brooks and Kyker-Snowman 2008). These alterations in abiotic conditions can influence wildlife population dynamics. For example, reduced canopy cover, soil compaction, and increased temperatures may increase desiccation risk for many amphibian species, reducing their survival within harvested stands (e.g., Rothermel and Luhring 2005, Rittenhouse et al. 2008). Further, mobile species may leave disturbed areas in search of areas that better meet physiological and life-history needs (Peterman et al. 2011).

In sustainably managed forests, indicator species (usually chosen for their sensitivity or ecological influence) often are used to assess how environmental changes affect ecosystem function and biodiversity (Wiens et al. 2008). Salamanders have been touted as meaningful indicator species because they can be sensitive to environmental stressors due to their complex life histories and cutaneous respiration (Vitt et al. 1990, Southerland et al. 2004). In addition, salamanders may also have a substantial effect on ecosystem function (Davic and Welsh 2004). For example, in many systems, salamander biomass exceeds all other vertebrate groups (Vitt et al. 1990), thus providing a vital energy resource to predators (Burton and Likens 1975, Milanovich and Peterman 2016). Conversely, salamanders are also predators, and may exert top-down control on invertebrate prey, potentially indirectly affecting decomposition rates and carbon storage within forest landscapes (Wyman 1998, Best and Welsh 2014, but see Homyack et al. 2010). Lastly, the life-history patterns of many salamander species facilitate transfer of matter and energy between aquatic and terrestrial systems (Davic and Welsh 2004), further underscoring their importance in ecosystem function at landscape scales. Although stream salamanders are often abundant in headwater systems and are directly affected by changes in water quality (Southerland et al. 2004), the effects of anthropogenic stressors on stream-associated salamander species are understudied and their use as indicators is hindered by lack of demographic and population data (Homyack and Kroll 2014).

Numerous studies investigating the effect of clear-cut harvesting on fully terrestrial salamander species (e.g., *Plethodon* spp.) have observed declines in abundance postharvest with potentially long recovery periods of a decade or more (Petranka et al. 1994, deMaynadier and Hunter 1995, Tilghman et al. 2012, Connette and Semlitsch 2013). Notably, the influence of clear-cutting on stream-associated salamanders is more variable. For example, studies have found variation in response of stream salamander species to timber harvest and management; some species exhibit short-term positive and negative responses to harvest (Jackson et al. 2007, Pollett et al. 2010). The disparity in responses may reflect regional differences resulting from local climate, variation among stream sites (including presence and size of riparian buffers), and life-history differences among species (Bury and Corn 1988, Perkins and Hunter 2006, Jackson et al. 2007, Peterman and Semlitsch 2009, Tilghman et al. 2012). Differentiating among these potential mechanisms requires broadscale studies that span various ecoregions, forest types, and management regimes, as well as demographic studies that investigate the mechanisms driving observed effects. To date, studies of the effects of timber harvest on stream salamanders have been conducted almost exclusively in the Pacific Northwest and Appalachian Mountain ecoregions, and most studies have focused primarily on changes in salamander occupancy or abundance (e.g., Petranka and Smith 2005, Crawford and Semlitsch 2007, 2008, Moseley et al. 2008, Kroll 2009, Peterman et al. 2011). Less research has examined the possible mechanisms for observed declines, such as changes in survival, reproduction, growth, or movement, leaving a major gap in our understanding of stream salamander conservation in managed forests (but see Homyack and Haas 2009, Semlitsch et al. 2009, Connette et al. 2015).

To better understand the effects of forest harvest on stream salamanders, and the demographic mechanisms driving those effects (i.e., changes in survival or movement), we conducted a capture–mark recapture (CMR) study, using a before–after–control–impact (BACI) design, to assess short-term effects of clear-cut harvesting on the Ouachita Dusky Salamander (*Desmognathus brimleyorum*), a common stream salamander endemic to the understudied Ouachita Mountains ecoregion of Arkansas and Oklahoma. Specifically, we monitored three streams in managed timber stands (one control and two before–after sites) from May 2014 to October 2016 and examined changes in (1) relative abundance, (2) apparent survival, and (3) individual movements along the stream channel associated with a harvesting event. We hypothesized that the relative abundance of *Desmognathus* salamanders would decline after harvest and that this reduction would coincide with either reduced apparent survival or increased individual movement, indicating displacement or abandonment of the study site. Both possible effects (reduced survival and increased movement) would cause decreased numbers of individuals captured during stream surveys either through direct mortality or emigration from study sites.

METHODS

Sampling design

We implemented a BACI design at three headwater streams in a managed forest landscape within the Ouachita Mountains of west-central Arkansas to assess the short-term effects of timber harvesting on stream-dwelling salamander populations (Fig. 1). Specifically, we conducted intensive capture–mark–recapture of salamanders at one reference (unharvested) site and two before–after sites (hereafter referred to as "control," "BA1," and "BA2") that were clear-cut-harvested during the study. We conducted salamander surveys at each site in March, June, and October from June 2014 until October 2016 for the control and BA1 sites and from March 2015 until October 2016 for the BA2 site. During each sampling month, we surveyed each stream on three nights, approximately one week apart. Timber harvesting occurred at BA1 in January 2015 and at BA2 in January 2016 (Fig. 1). The intensity of data collection necessary to rigorously estimate demographic parameters prevented us from including greater replication at the site level.

Study sites

We selected sites based on similar stream size, morphology, and silvicultural history. All three sites were first order, headwater streams located within 16 km of each other in the Little Missouri Watershed in northeast Howard County, Arkansas, USA, at elevations from 190 to 300 m above sea level (Fig. 1). The study area was owned and managed by Weyerhaeuser Company. Intensive forest management in the region often includes even-aged management of loblolly pine (*Pinus taeda*). Forest stands are clear-cut-harvested at 30–35 yr, followed by site-specific applications of mechanical and/or chemical site preparation to promote growth and survival of planted seedlings. During the rotation, forest stands may receive fertilizers, be thinned from about 435 trees per acre to 125–185 trees per acre, and be subject to pruning, based on local site conditions. Each study stream drained a small watershed (0.41–1.15 km^2) within an even-aged, mature (29–35 yr old) loblolly pine stand and had a 14–21 m forested riparian buffer (i.e., streamside management zone, SMZ) on each side of the stream. The forested area within the SMZ is retained during harvesting events as part of forestry BMPs and not controlled for overstory species. The SMZs at the control and BA2 sites were dominated by an overstory of oak (*Quercus* spp.) and hickory (*Carya* spp.) with an understory of cedar (*Juniperus virginana*) and American holly (*Ilex opaca*). The SMZ overstory at BA1 site was dominated by loblolly pine with an understory of American holly, musclewood (*Carpinus caroliniana*), and hop hornbeam (*Ostrya virginiana*). At each site, we delineated a 200-m in-stream transect for salamander surveys. Due to the short length of the stream with surface flow within the harvested stand at the BA1 site, this stream transect extended past the previously harvested stand boundary (i.e., 100 m in clear-cut,

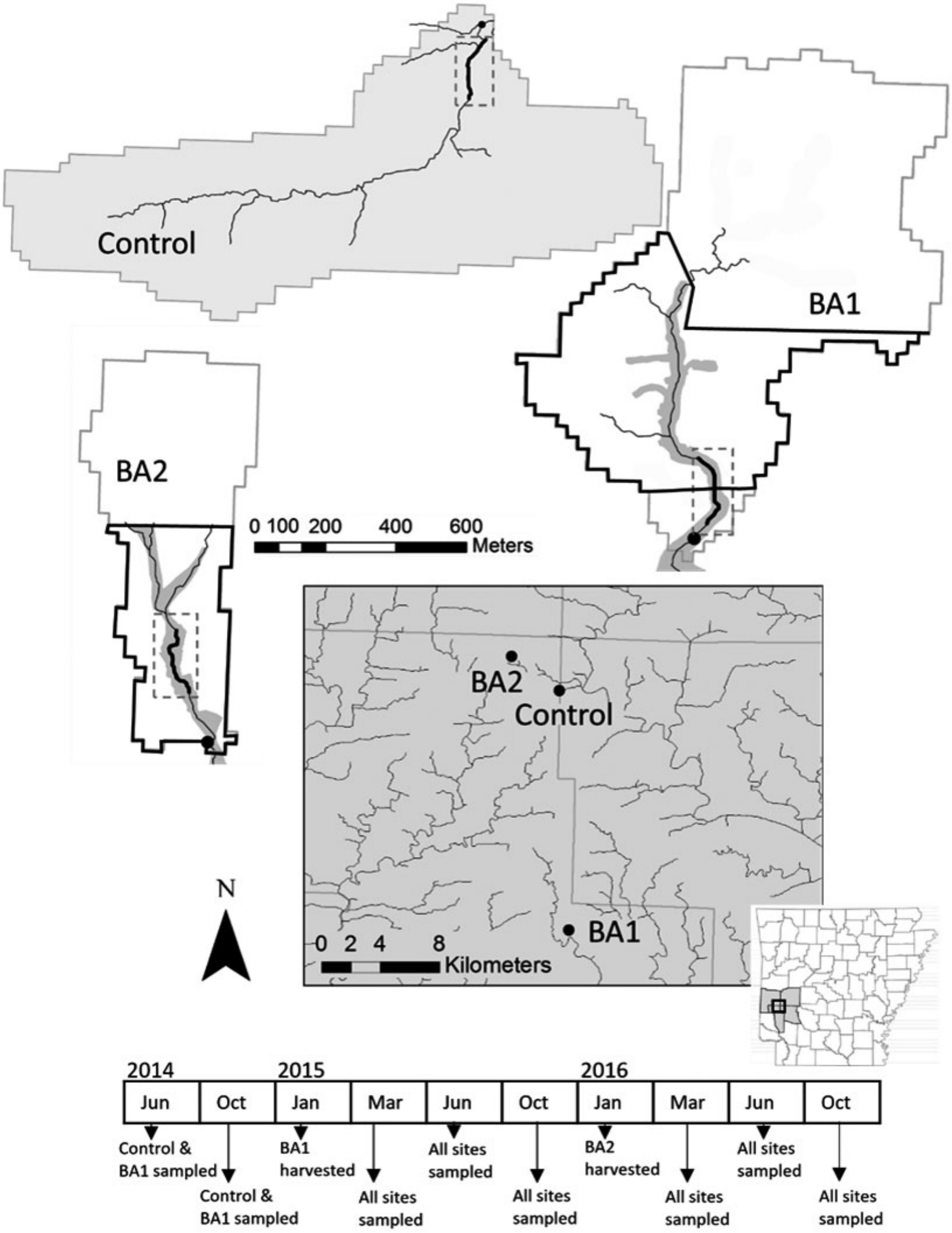

Fig. 1. Map of study sites and timeline of timber harvest and sampling schedule. All three sites are in the Little Missouri Watershed in northeast Howard County, Arkansas, USA. The watershed of each stream is outlined in gray. Approximate extent of riparian buffers (SMZs) around each stream (thin black lines) is shaded in gray. Stream transects (200 m) where salamanders were sampled are bolded and enclosed in a dashed box. For the before–after sites, the harvested section of the watershed is outlined in black.

100 m downstream in the adjacent unharvested 12-yr-old stand; Fig. 1), allowing us to assess movement out of the harvested section. Our decision to have the BA1 stream transect to span the stand boundary was made after the June 2014 surveys; therefore, only half the BA1 transect was surveyed in June 2014. The BA1 and BA2 stands were clear-cut in January 2015 and January 2016, leaving behind a 14 m and a 21 m SMZ, respectively, on each side of the stream. Several large pine trees were removed from the SMZ during the harvesting of the BA1 site to promote hardwood regeneration in the riparian area; this practice aligns with Arkansas BMPs (Arkansas Forestry Commission 2002).

Survey methods

Each nighttime sampling event consisted of a thorough visual search of the streambed for the length of each transect. Surveys were not time-constrained but continued until the entire 200-m transect had been thoroughly searched (average effort = 10.6 person-hours per sampling event). We carefully turned rocks and other cover objects to detect salamanders and captured them using dip nets; each capture location was marked with a numbered survey flag, so animals could be returned to their exact capture location. We placed each salamander in a separate 4 oz container for transport. Our study focused on the most common salamander species in the area, *D. brimleyorum*, and we excluded larval individuals from capture due to difficulties marking them because of small size. The following day, we anesthetized each salamander by placing them in a solution of 1 g Orajel (Del Pharmaceuticals, Uniondale, New York, USA; Cecala et al. 2007) per liter of conditioned tap water and measured mass (g), total length (mm), and snout–vent length (mm; SVL). We then individually marked salamanders using subcutaneous injection of four colors (pink, orange, blue, and yellow) of visible implant elastomer (VIE; Northwest Marine Technologies, Shaw Island, Washington, USA; Grant 2008) at up to six marking locations (posterior to each limb and anterior to each hind limb) using a 0.5-mL Micro-Fine Insulin Syringe (28 gauge/0.35 mm). We considered recently metamorphosed individuals (less than a year since metamorphosis, ≤45 mm SVL) as juveniles. Elastomer marks are retained well without a decline in readability (Heemeyer et al. 2007) for at least three years (J. Guzy and K. Halloran, *unpublished data*). However, we avoided marking juveniles at the positions anterior to each hind limb because the integument layer here is thin and marks tend to fall out or end up in the body cavity and thus migrate (J. Guzy and K. Halloran, *personal observation*). We identified first-year individuals based on mean growth rate of known marked metamorphs and an obvious break in body size distributions, creating a first-year growth threshold of 45 mm SVL. We considered individuals >45 mm SVL at the time of capture as adults. We generally returned all salamanders to their capture location within 2 d, but occasionally held salamanders for up to 5 d to avoid releasing them during high flow events. Upon release, we measured each salamander's capture location to the nearest 1 cm along the 200-m transect using a laser distance meter (Fluke 414D Laser Distance Meter; Fluke Corporation, Everett, Washington, USA). More specifically, the transect was subdivided into 10-m sections numbering from 1 (downstream) to 20 (upstream) to increase the precision of laser distance readings (i.e., all measurements <10 m distance). When salamanders were returned, their position along the transect was recorded relative to the section where they were captured (e.g., 3.52 m upstream of Section 6 marker, corresponding to a position along the stream of 63.52 m from the downstream end of the 200-m transect).

Data analysis

We analyzed CMR data using open population models because our primary objective was to estimate survival. However, open population models do not allow for comprehensive evaluation of factors influencing detection and thus do not provide reliable estimates of abundance (Pollock et al. 1990). As an alternative to model-generated estimates of abundance, we used count data from area-constrained searches to compare salamander relative abundance over time within sites. Specifically, we examined the effect of timber harvesting on salamander abundance by comparing the number of unique individuals captured at each site during each sampling season (spring, summer, and fall for each year). We accounted for potential confounding factors influencing our count-based abundance estimates by (1) excluding recaptures within the same season and (2) comparing estimates across years within seasons and sites.

We estimated salamander survival across sampling seasons at each site using full-likelihood open Cormack-Jolly-Seber (CJS) models in Program MARK 6.0 (White and Burnham 1999). For CJS models, we collapsed encounter histories within the same sampling season, yielding eight samples for the control site, eight samples (two before harvest and six after harvest) for the BA1 site, and six samples (three before harvest and three after harvest) for the BA2 site. We evaluated a series of candidate models for each site that allowed capture probability (p) and apparent survival (φ) to vary based on hypothesized patterns of variation related to natural (i.e., season) and harvest-related factors (Tables 1, 2). Specifically, we first held φ constant and evaluated models where p varied by time or season. Once we determined the best parameterization for p, we included that parameterization in subsequent models examining hypothesized variation in survival. Likewise, for each site, we evaluated models that represented relevant patterns of temporal variation in survival: (1) constant, φ held constant across all time intervals for each site; (2) time variation, φ allowed to vary fully over time (i.e., different for each interval); (3) winter variation, φ held constant across spring/summer (April–June) and summer/fall intervals (July–October), but allowed to differ over winter (November–March); (4) seasonal variation, φ different among seasons, but held constant across years; and (5) harvest variation (only for before/after sites), φ in preharvest intervals allowed to differ from all postharvest intervals. We evaluated support for models using the Akaike information criterion (AIC; Akaike 1973) adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). We evaluated goodness of fit of the most parameterized model at each site using the median $\hat{c}$ method and subsequently adjusted AIC_c values to account for overdispersion of our data (QAIC_c; White and Burnham 1999). We ranked QAIC_c weights to determine the strength of evidence for each model and assumed models with higher weights and lower QAIC values were better able to explain variation in data and minimize over-parameterization. To account for model selection uncertainty, we used model averaging to generate p and φ estimates that were weighted based on the support of each model (Burnham and Anderson 2002).

Movement

We used location history of individuals to assess salamander movement in two ways: (1) We compared net movement (i.e., distance between furthest upstream and furthest downstream capture locations) across the forest harvesting interval between control and harvested sites and (2) compared the mean linear distance (m) traveled upstream or downstream per day before and after timber harvest between sites. To determine how timber harvest affected net salamander movement at each before–after site, we subtracted the first known location of each individual after timber harvest from the last known location before timber harvest. Because capture locations were measured from downstream to upstream along the transect, negative distances represented downstream movement. For a direct (i.e., not confounded in time) comparison to the control site, net movement at the control site was determined for the same time interval as each before–after sites' forest harvesting events.

We calculated the mean distance traveled per day for each individual by subtracting the position of the recapture location from the previous capture location (m). Because this value could be negative for downstream movements, we took the absolute value of the distance and divided it by the elapsed time interval (days). We then averaged across all salamanders to get mean distance traveled per day. For the BA1 site, we calculated before-harvest mean movement distance per day using location data during June 2014–October 2014 and after-harvest mean distance using data from March 2015 to June 2015 (i.e., locations from the six sampling nights immediately before and six after harvest). For the BA2 site, before and after time intervals ranged from March 2015 to October 2015 and March 2016 to October 2016, respectively (nine sampling nights before and nine after). We calculated the mean distance per day at the control site for all four intervals for direct comparison. We performed robust ANOVAs in R version 3.3.3 (R Core Team 2017) using the raov function of the Rfit package (Kloke and Mckean 2012) to examine the effects of time

Table 1. Parameterization of capture probability (p) in a priori candidate models designed to evaluate support for hypothesized patterns of temporal variation in *Desmognathus brimleyorum* vital rates at three sites from June 2014 to October 2016.

Model	Capture probability (p)	June	October	March	June	October	March	June	October
1	Constant (.)	1	1	1	1	1	1	1	1
2	Time (t)	1	2	3	4	5	6	7	8
3	Seasonal (s)	1	2	3	1	2	3	1	2
4	Winter (w)	1	1	2	1	1	2	1	1

Notes: Numbers within the table represent parameters within each model, with the same numbers indicating parameters that were equal. The hypotheses we investigated include fully time-varying p (Model 2), seasonally varying p (Model 3), and winter-varying p (Model 4).

Table 2. Parameterization of apparent survival (φ) in a priori candidate models designed to evaluate support for hypothesized patterns of temporal variation in *Desmognathus brimleyorum* vital rates at three sites from June 2014 to October 2016.

Model	Apparent survival (φ)	July–October	November–March	April–June	July–October	November–March	April–June	July–October
a	Constant (.)	1	1	1	1	1	1	1
b	Time (t)	1	2	3	4	5	6	7
c	Seasonal (s)	1	2	3	1	2	3	1
d	Winter (w)	1	2	1	1	2	1	1
e	Harvest (h)	1	1/2†	1/2†	2	2	2	2

Notes: Numbers within the table represent parameters within each model, with the same numbers indicating parameters that were equal. The hypotheses we investigated include fully time-varying φ (Model b), seasonally varying φ (Model c), winter-varying φ (Model d), and harvest-varying φ (Model e).

† We adjusted the parameterization of φ in the harvest model to reflect the time of harvest for each site. BA1 was harvested in January 2015, and BA2 was harvested in January 2016.

(before vs. after harvest), site (control vs. before–after sites), and the interaction of time and site on mean distance moved per day, which was not normally distributed. The functions in the Rfit package are used to calculate rank-based estimators (nonparametric, robust alternatives to least-squares estimators; Kloke and Mckean 2012). The raov function is a rank-based analysis for the main effects (time and site) and their interactions using an algorithm described in Hocking (1985).

RESULTS

Relative abundance

At the control site, we had 1987 captures of *D. brimleyorum* over eight seasonal samples (24 sampling nights), representing 1030 individual salamanders. At the BA1 site, we had 659 captures of *D. brimleyorum* over eight seasonal samples, representing 361 individual salamanders. At the BA2 site, we had 1894 captures of *D. brimleyorum* over six seasonal samples (18 sampling nights), representing 1062 individuals. All three sites had a similar total proportion of recaptures (43–48%). At all three sites, captures during area-constrained searches were lowest in March and highest in July (Fig. 2). In general, the number of adult individuals captured increased over the three-year study at all sites (Fig. 2). The numbers of juveniles (recruitment) were more variable and were highest in 2014 at the control site and in 2015 at both before–after sites. At the before–after sites, there was no obvious reduction in salamander captures following harvest of the surrounding stand (Fig. 2). Captures of adults at the BA1 site increased substantially following harvest in 2015 and 2016 (Fig. 2b), and captures were similar to preharvest capture rates at the BA2 site following harvest in 2016 (Fig. 2c). Relatively few newly metamorphosed juvenile salamanders were captured at the BA1 site (37% of captures) in 2016, 1.5 yr after harvesting, compared with 2014 (88% of captures), before harvest (Fig. 2b).

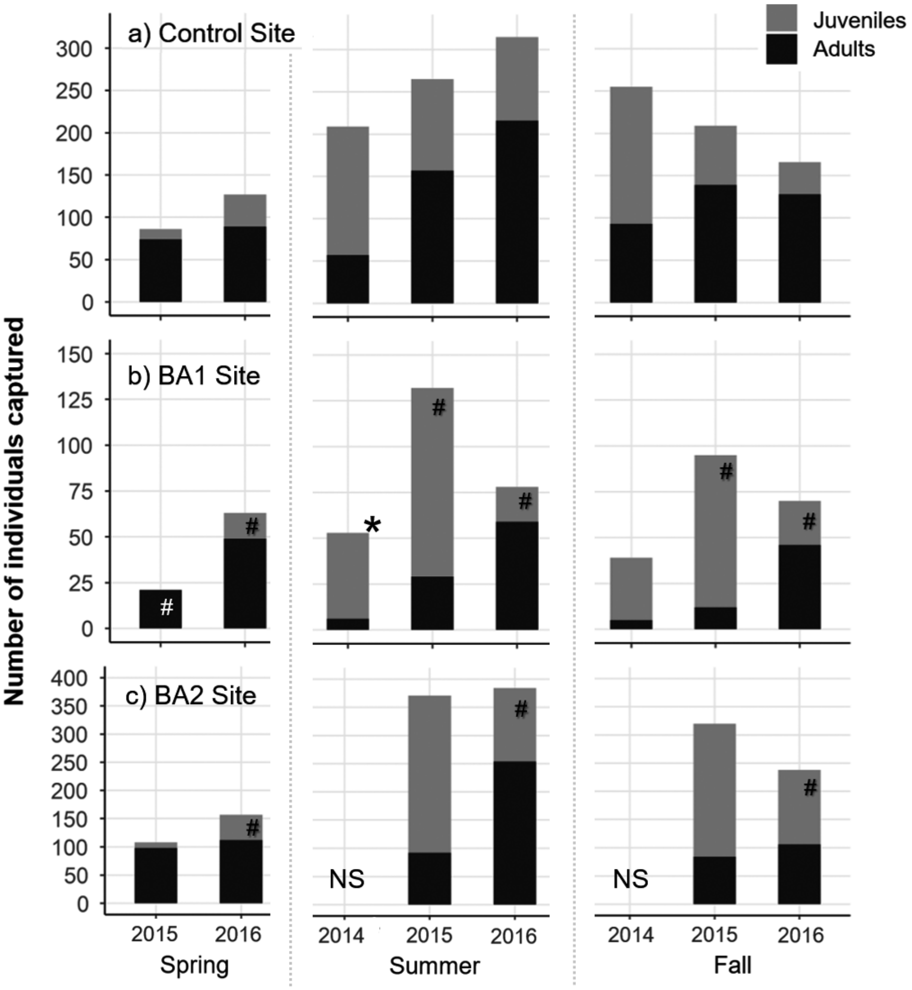

Fig. 2. Number of individual *Desmognathus brimleyorum* captured by seasonal sampling interval during area-constrained searches at the three CMR sites in the Ouachita Mountain region of Arkansas, USA, grouped by season. # indicates postharvest intervals at the before–after sites. Note that the BA2 site was not sampled in 2014 (NS). * indicates only half of BA1 site (100 m) was surveyed in summer 2014.

Capture probability

Analysis of capture/recapture data for both the control and BA2 sites favored models where individual capture probability (p) was fully time-varying (Table 3; Model 2). For the BA1 site, model selection favored a scenario where capture probability differed between the winter period and the rest of the year (Model 4). Individual capture probabilities at the control site and BA2 site were variable (16–52%), but always lowest during winter (November–March) sampling periods. Additionally, p estimates at the control and BA2 were consistently higher in 2016 (mean = 47%, April–October) than in 2015 (mean = 31%, April–October). Individual capture probabilities at the BA1 site were estimated as 19% (CI: 13–27%) during the winter sampling period and 38% (CI: 30–46%) during the rest of the year.

Apparent survival

A model where apparent survival (φ) was fully time-varying was favored at the control site (Table 3; Model 2b). This model generated φ estimates ranging from 49% to 97% with apparent survival being lowest (49%) between the first and

Table 3. Model selection results for the Cormack-Jolly-Seber analysis of capture–recapture data for *Desmognathus brimleyorum* at three sites.

Model	Parameterization	$QAIC_c$	$\Delta QAIC_c$	Model weight	K
Control site					
2b	φ(t), *p*(t)	2683.531	0	0.943	13
2c	φ(season), *p*(t)	2689.809	6.278	0.041	10
2a	φ(.), *p*(t)	2692.381	8.851	0.012	8
2d	φ(winter), *p*(t)	2694.003	10.472	0.005	9
3a	φ(.), *p*(season)	2707.827	24.297	0.000	4
4a	φ(.), *p*(winter)	2720.897	37.366	0.000	3
BA1 site					
4e	φ(harvest), *p*(winter)	817.874	0	0.946	4
4b	φ(t), *p*(winter)	824.499	6.625	0.034	9
4a	φ(.), *p*(winter)	829.910	12.035	0.002	3
4d	φ(winter), *p*(winter)	831.603	13.729	0.001	4
3a	φ(.), *p*(season)	831.841	13.967	0.001	4
4c	φ(season), *p*(winter)	833.597	15.723	0.000	5
2a	φ(.), *p*(t)	838.008	20.134	0.000	8
BA2 site					
2a	φ(.), *p*(t)	1501.104	0	0.456	6
2d	φ(winter), *p*(t)	1502.771	1.667	0.198	7
2e	φ(harvest), *p*(t)	1502.999	1.895	0.177	7
2c	φ(season), *p*(t)	1504.173	3.069	0.098	8
2b	φ(t), *p*(t)	1505.715	4.611	0.045	9
3a	φ(.), *p*(season)	1507.139	6.035	0.022	4
4a	φ(.), *p*(winter)	1511.065	9.961	0.003	3

Notes: Models were constructed by varying capture–recapture probability (*p*) and survival (φ) by time (t), season, winter (i.e., November–March), or harvest. (.) refers to parameters held constant. Models are listed in decreasing order of support using the quasi-Akaike information criterion, corrected for small sample size and data overdispersion ($QAIC_C$). Abbreviations are $QAIC_c$, quasi-Akaike information criteria, corrected for sample size and overdispersion; Δ $QAIC_c$, difference in $QAIC_c$ relative to the top model; *K*, number of parameters in the model.

second and between the fifth and sixth (60%) sampling intervals, and relatively high (mean = 82.5%) over all other intervals (Fig. 3a). A harvest-varying model was favored at the BA1 site (φ before harvesting is different from φ after harvesting; Table 3; Model 4e). Under this model, survival was estimated to be 29% (CI: 16–49%) between preharvest intervals (July–October 2014) and 73% (CI: 67–79%) between postharvest intervals (Fig. 3b). Model selection for the BA2 site showed equivocal support for models that represented constant (Model 2a), winter-varying (Model 2d), and harvest-varying (Model 2e) survival (ΔQAICc < 2; Table 3), with the constant φ model yielding a survival estimate of 69% (CI: 65–73%) between sampling events. This translates to an average annual survival rate of 33%. Parameter estimates from the fully time-varying model support this pattern: Survival was relatively uniform throughout the study with no indication of a change in survival following harvest (Fig. 3c).

Movement

In general, individual salamanders had a net movement <20 m and exhibited a slight upstream movement bias (Fig. 4). A few individuals, however, moved relatively large distances—up to 164 m. More specifically, 35% of individuals at the control site had a net movement less than or equal to 4 m over each of the intervals we examined (Fig. 4a, c). The before–after sites, however, showed a higher proportion of individuals (90% and 81%, respectively) with net movements >4 m between preharvest and postharvest surveys. There also was a slight downstream movement bias at the BA2 site, but there was no evidence of downstream movement out of the harvested area (Fig. 4d).

Overall, mean distance an individual traveled per day increased at both experimental sites following timber harvest (Fig. 5). We observed a postharvest increase in mean distance traveled per day of 72% and 39% at BA1 and BA2, respectively (Fig. 5). In contrast, mean distance moved

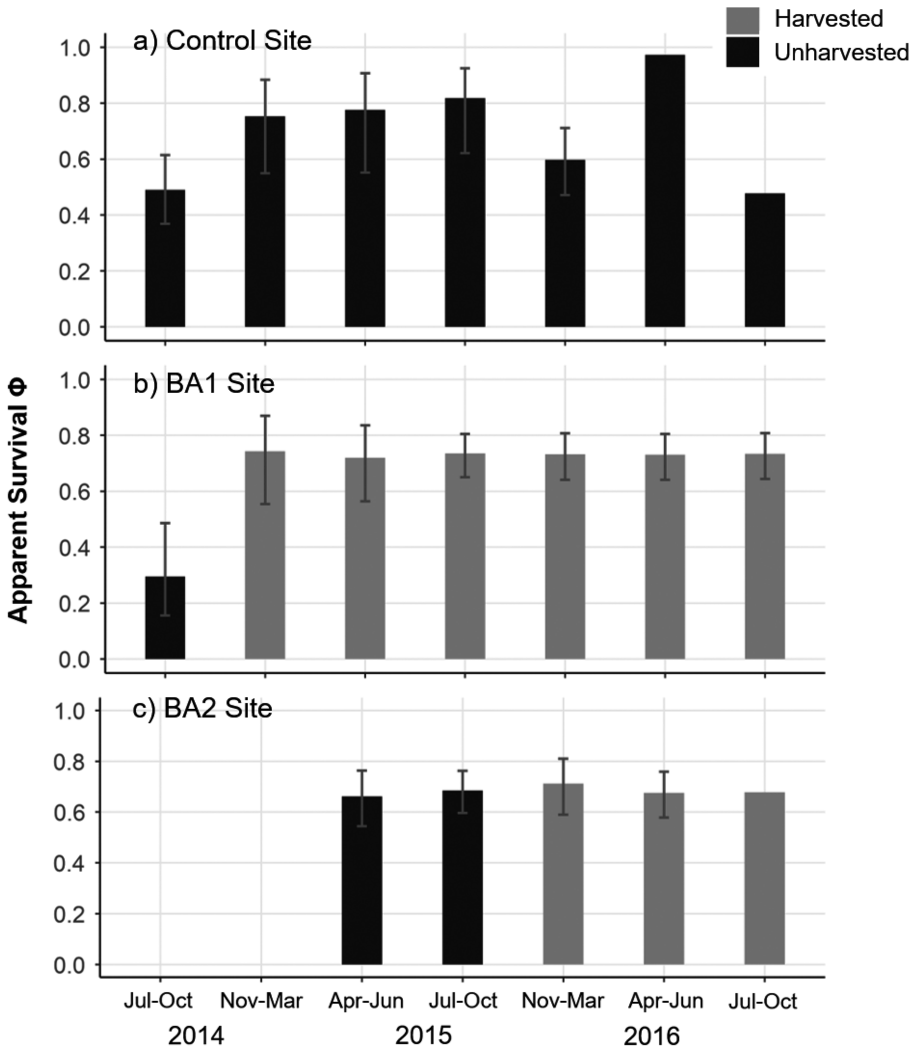

Fig. 3. Model-averaged apparent survival of *Desmognathus brimleyorum* by sampling interval at the three sites in the Ouachita Mountain region of Arkansas, USA. Gray bars indicate postharvest intervals at the before–after sites. Error bars represent 95% confidence intervals. Because of low capture rates in the spring, the survival rate at the control site for the second April–June interval is nonsensical, but is likely high.

per day was similar across all intervals at the control site (Fig. 5). For both BA1 and BA2, a significant increase in movement following harvest relative to the same time interval at the control site was reflected in a significant site-by-time interaction (BA1 $F = 13.62$, df = 1, $P < 0.01$; BA2 $F = 22.10$, df = 1, $P < 0.01$).

Discussion

Our three-year mark–recapture study fills a critical gap in the knowledge of stream salamander vital rates in managed forest environments, and took place in an understudied biodiversity hotspot, the Ouachita Mountains ecoregion of the Interior Highlands. Across three before–after–control–impact stream sites, we had a remarkable 4540 captures representing 2453 individual *D. brimleyorum*, providing important insight into the effects of clear-cut harvesting on a semi-aquatic stream-breeding salamander. We documented seasonal and temporal variation in survival and abundance along with increased salamander movement postharvest. However,

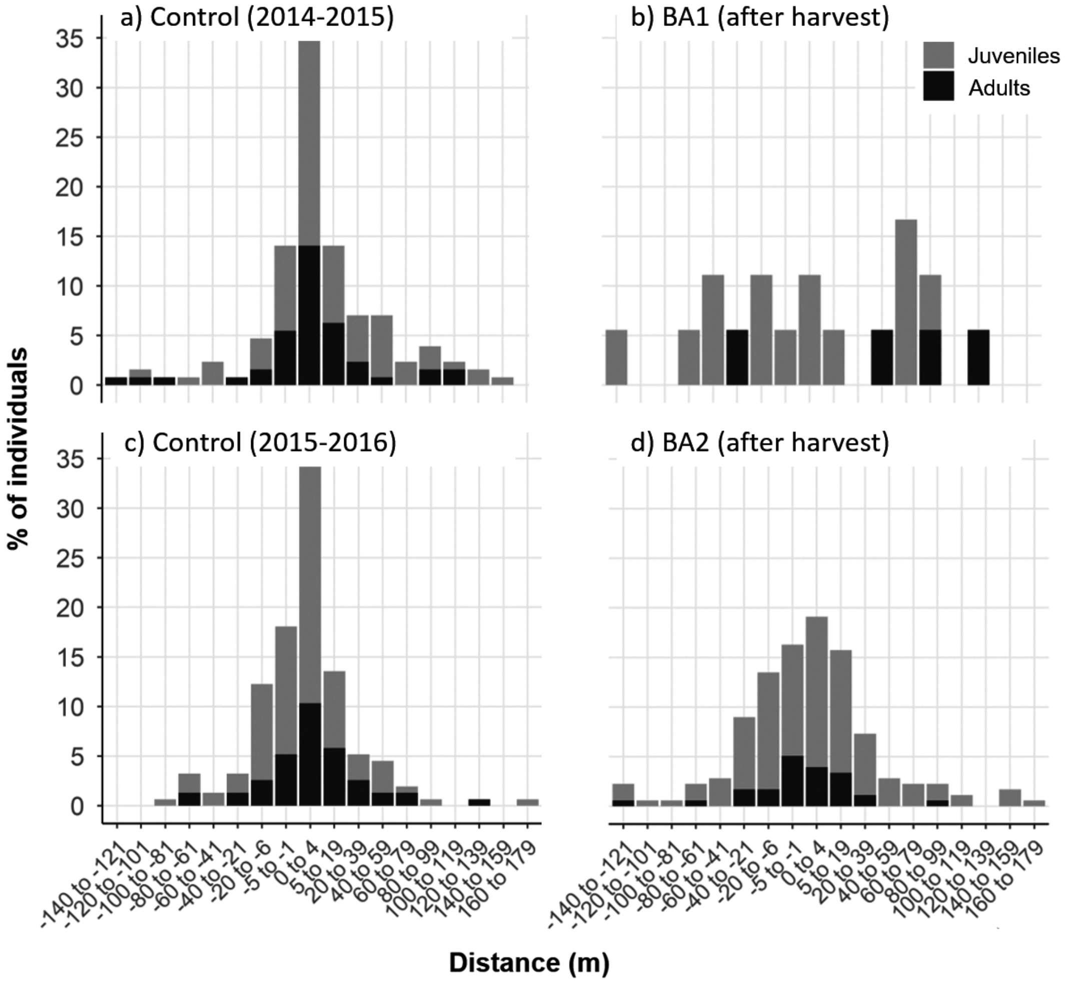

Fig. 4. Net movement of individual adult and juvenile *Desmognathus brimleyorum* within three streams in the Ouachita Mountain region of Arkansas, USA, over time intervals during which harvesting occurred at the before–after sites. Movement distances for before–after sites (b and d) were calculated by subtracting the first known location after timber harvest from the last known location before the harvesting event. Movement distances for salamanders at the control site (a and c) over the same time intervals are provided for comparison. Negative distance measures indicate downstream movement.

we found little evidence for strong immediate effects of timber harvesting on post-metamorphic salamanders within two years after clear-cutting occurred during the inactive season (i.e., winter months). We provide support that streamside buffers of at least 14–28 m on either side of a stream help minimize immediate effects of timber harvest on juvenile and adult stream-dwelling salamanders.

Contrary to our hypotheses, our BACI study did not reveal evidence of a negative effect from upland timber harvest on relative abundance or apparent survival of post-metamorphic stream-associated salamanders 1–2 yr postharvest. Variation in relative abundance among sites was seasonal, with captures lowest in the spring, highest in the summer, and moderate in the fall. This pattern is best explained by the individual capture probability estimates produced in the top CJS models (where capture probability was lowest during winter). Lower capture probability in winter was likely driven by temporary

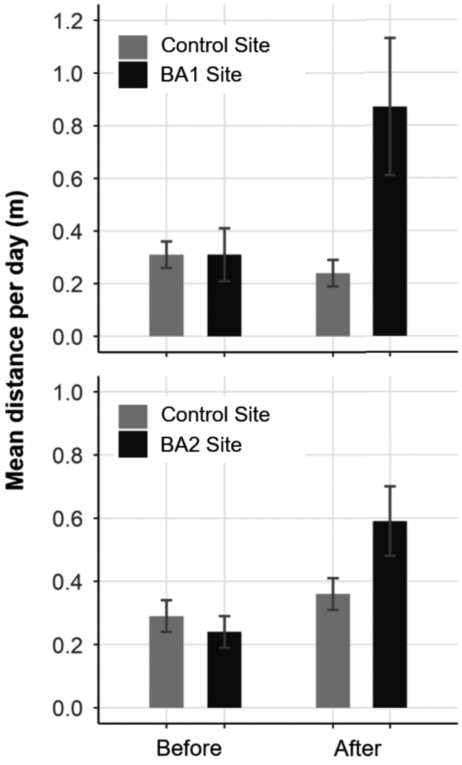

Fig. 5. Average distance traveled per day (±1 SE) by *Desmognathus brimleyorum* pre- and post-timber harvest at three streams in the Ouachita Mountain region of Arkansas, USA. For comparison, before and after distances at the control site were calculated using the same time intervals as the experimental sites, even though no harvesting occurred.

emigration of individuals into places where they were not available for capture, such as subterranean retreats. Typically, the surface activity of *Desmognathus* salamanders is lowest in the cooler and drier months (Ashton 1975, Orser and Shure 1975, Petranka 1998). In a thorough examination of *D. brimleyorum* population parameters using robust design analysis of this dataset, Halloran (2017) reported that conditional capture probability was generally constant over time and seasonal variation in salamander captures was driven by relatively high rates of temporary emigration in winter. While the relative abundance of juveniles varied annually, relative abundance of adult individuals within a season increased over time at all sites. This change in relative abundance may have been driven by favorable environmental conditions during our study period. Indeed, all three years (2014–2016) of our study were considered wet for this region, receiving 10.82, 38.05, and 15.32 cm of precipitation greater than the annual average (137.34 cm), respectively (NOAA Weather Station, Newhope, Arkansas, USA).

Apparent survival at all three sites remained remarkably constant throughout our study, although there was some variation over time at the control site. A CJS model with a timber harvesting effect on survival was only supported at the BA1 site and that model suggested survival was higher postharvest compared with the July—October 2014 preharvest interval. High survival postharvest could reflect a change in food availability. Increased macroinvertebrate abundance may alleviate competition for food resources and/or individual territories, thus increasing salamander survival, as aquatic macroinvertebrates make up a substantial portion of *D. brimleyorum* diets (Means 2005). Aquatic macroinvertebrate abundance may increase postharvest as a result of reduced canopy cover and increased detrital input (Murphy et al. 1981, Rempel and Carter 1986, Kiffney et al. 2004, Jackson et al. 2007). However, apparent survival was also low during the July–October 2014 interval at the control site, suggesting that high survival after 2014 at the BA1 site may have been partially attributable to favorable climatic conditions in those years or other factors.

Consistent relative abundance and survival estimates across sites contradict the conclusions of other studies investigating effects of timber harvest on salamanders, many of which report evidence of negative effects of clear-cutting (Perkins and Hunter 2006, Crawford and Semlitsch 2008, Tilghman et al. 2012, etc.). For example, studies report considerable reductions in terrestrial plethodontid salamander abundance immediately following a clear-cut (Petranka et al. 1993, Reichenbach and Sattler 2007). However, stream-breeding salamanders (*Desmognathus ocoee* and *Eurycea wilderae*) may recover from a disturbance more rapidly than terrestrially breeding species (e.g., *Plethodon* spp.; Connette and Semlitsch 2013), and in general, studies focused on stream-associated species have had variable results (see review by Kroll [2009]). For example, Jackson et al. (2007) found that clear-cutting had no effect on torrent salamanders (*Rhyacotriton* spp.) and giant salamander (*Dicamptodon* spp.) abundance can increase within streams surrounded by harvested areas without a riparian buffer (Bury and Corn 1988, Pollett et al. 2010). Other studies of *Desmognathus* salamanders in Appalachian streams suggest long-term partial cutting may suppress abundance, possibly because of short-term increases in sediment entering streams, embedding rocks, and reducing available habitat (Moseley et al. 2008). For *Desmognathus* in our study, a riparian buffer of 14–21 m on both sides of the stream may have ameliorated potential negative effects of upland harvesting, as observed for other stream salamanders (e.g., Stoddard and Hayes 2005, Perkins and Hunter 2006, Maigret et al. 2014).

Although we did not detect an effect of harvesting on either relative abundance or apparent survival of post-metamorphic salamanders, their movement patterns changed following harvesting of uplands. Throughout our two-year experiment, salamanders at the control site exhibited behavior consistent with movement patterns in undisturbed streams, including small movements with a slight upstream bias (Barthalmus and Bellis 1972, Lowe 2003, Grant et al. 2010). Meanwhile, salamanders at both before–after sites increased movement distance in both directions after harvesting events. One possible mechanism of increased in-stream movement is increased water velocity during storm events within harvested watersheds. Clear-cut watersheds in the Ouachita Mountains have increased annual water yields compared with unharvested watersheds (Miller et al. 1988, Stednick 1996), and increased velocity may displace salamanders (e.g., Barrett et al. 2010). However, because we did not observe a downstream bias in salamander movement, displacement seems unlikely to drive the pattern we observed. Instead, increased salamander movement may reflect shifts in refugia quality or other disturbance that prompts salamanders to move greater distances and/or more frequently than typical. Although treatment streams in our study had riparian buffers, they were relatively narrow (14–21 m) and selective harvesting of large pine trees at the streambank did occur at both sites, particularly at BA1, where the SMZ was narrower and where we observed the greatest postharvest movements by salamanders. Selective thinning within the SMZ along the streambank may have disturbed salamanders by destabilizing the banks and creating canopy gaps that may have influenced salamander movement. Other studies have demonstrated that displaced stream salamanders were 86% less likely to return to their capture location when required to cross gaps in the stream canopy as short as 13 m (Cecala et al. 2014). Our results indicate that substantial changes to in-stream salamander dispersal may occur, even with a riparian buffer. Further investigation is necessary to determine whether these altered movement patterns affect salamander body condition, reproductive success, population connectivity, and/or survival on longer timeframes. Increased dispersal may increase energetic costs and territorial disputes, indirectly affecting long-term survival and/or reproduction (e.g., Keen and Reed 1985, Schmidt et al. 2007). Alternatively, at the population level, increased dispersal may facilitate metapopulation dynamics or alleviate perils of small population size through increased gene flow.

Although we did not detect a harvesting effect on abundance or survival of post-metamorphic salamanders up to 2 yr post-treatment, a delayed response may have occurred after our study ended. For example, altered movement patterns may have caused a lagged reduction in salamander survival, where survival is stable immediately following a disturbance, but decreases over time from indirect effects that manifest later. In the same landscape, Guzy et al. (2019) observed that stream salamander abundance was lowest in forest stands 5–10 yr postharvest, suggesting that time-lagged effects on survival or recruitment may occur in our study system. Here, we observed decreased abundance of newly metamorphosed individuals at BA1 in the second year; these individuals were the first cohort to hatch after harvest. *Desmoganthus brimleyorum* deposit eggs between late June and July (Means 1975), eggs hatch in October (Chaney 1958; J. Guzy and K. Halloran, *personal observation*), and metamorphosis occurs between May and June (Means 1975; J. Guzy and K. Halloran, *personal observation*); time to metamorphosis is thought to take approximately 1 yr (Means 1974). Thus, if the harvesting event affected reproductive potential or egg or larval survival, reductions in juvenile recruitment would not be apparent for at least a year (depending on the season of harvesting). However, because we did not target eggs or larvae as study metrics, further population monitoring is needed to determine whether population demography exhibits delayed responses to harvest.

The timing of harvest events may also influence the magnitude of response in stream salamander vital rates. At both before–after sites, harvesting occurred in January, when *D. brimleyorum* adults were relatively inactive and after eggs had hatched in the fall (Means 2005). Further, our research occurred during years with high spring and summer precipitation, including several high flow events. Whether or not the season that forest harvesting occurs influences salamanders is not known. For example, we do not know whether indirect effects on in-stream habitat components from harvesting would have been stronger if harvesting occurred in the active season (April–November). Further research is needed to understand relationships among the timing and frequency forestry-related disturbances (site preparation, thinning, harvest, etc.) and salamander population recovery and persistence (Homyack and Kroll 2014).

We did not observe negative effects of upland harvest on relative abundance and apparent survival of post-metamorphic *D. brimleyorum* for up to 2 yr postharvest, when disturbance occurred in winter. Given the prevalence of literature documenting the benefits of intact forest to salamanders (e.g., Semlitsch and Bodie 2003, Crawford and Semlitsch 2007, Olson et al. 2007, Connette et al. 2016, Guzy et al. 2019), we suggest that our results were likely driven by riparian buffers at our sites. Thus, our results add to the literature and suggest that buffers of at least 14 m on each side of a stream have the potential to mitigate negative effects of forest harvest on juvenile and adult stream salamanders. Although it was beyond the scope of this study, future work comparing sites with minimal buffers to those with wide buffers (e.g., >50 m; Guzy et al. 2019) and incorporating other demographic metrics such as body condition and reproductive success will further inform what role riparian buffers play in supporting salamander populations (e.g., Homyack 2010). Timber harvesting changed the movement patterns of juvenile and adult *D. brimleyorum* in the stream, but it is unclear whether this will have long-term ramifications for population or community dynamics and studies examining effects downstream of harvested areas may be important. We recommend long-term salamander population monitoring within riparian buffers of harvested forest stands to evaluate the potential for delayed responses that affect abundance or vital rates. More broadly, our research contributes to a growing body of evidence indicating that with inclusion of riparian buffers managed forest landscapes across North American can support viable populations of stream salamanders and other semiaquatic wildlife.

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