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Population Dynamics of Ouachita Dusky Salamanders (*Desmognathus brimleyorum*) in a Managed Forest Landscape

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biology

by

Kelly Halloran University of Vermont Bachelor of Science in Environmental Science, and Wildlife and Fisheries Biology, 2012

December 2017 University of Arkansas

This thesis is approved for recommendation to the Graduate Council.

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Abstract

With anthropogenic alteration of landscapes increasing world-wide, managed forests are increasingly important as providers of ecosystem services including habitat for numerous wildlife species. It is crucial to maintain a balance between timber production and conservation of biodiversity on managed landscapes. Salamander populations can play key roles in the function and diversity of temperate forest ecosystems. Several studies have reported negative effects of forestry on terrestrial plethodontid salamanders, but less research has focused on stream-dwelling species, evaluated mechanisms driving observed shifts in abundance, or described the dynamics of populations residing in managed forests. Using a Before-After-Control-Impact design, we examined the effects of clearcut timber harvesting on a streamdwelling salamander endemic to the Ouachita Mountains, Desmognathus brimleyorum. We specifically focused on two possible mechanisms of salamander abundance shifts, survival and movement. We conducted a capture-mark-recapture (CMR) study at three streams within intensely managed pine forests in west-central Arkansas from May 2014-October 2016. The pine stands surrounding two of the streams were harvested following state Best Management Practices (BMPs) (leaving a 28-42 m wide forested stream buffer) in January 2015 and 2016, respectively. We also explored effects of seasonal, site, and age variation on the capture probability, recapture probability, temporary emigration, abundance, and apparent survival of D. brimleyorum with robust design CMR models. Overall, our models provided evidence for seasonal and temporal variation in salamander survival and abundance, but little evidence for strong immediate effects of timber harvesting. However, there was increased salamander movement at the sites where harvesting occurred. The results of this study will help inform

management decisions aimed at conserving biodiversity and ecosystem integrity in landscapes managed for timber production.

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Introduction

Due to rapidly increasing human populations, much of the world's natural landscapes have been altered to meet human needs (Foley et al. 2005), and remaining reserves of unaltered land are often insufficient to preserve biodiversity (Westman 1990; Wilcove 1989). Forests managed for timber production, being relatively similar to unaltered landscapes, may be managed for both biodiversity and product, augmenting natural biodiversity reverses (Hansen 1991; Harris 1984). Managed forests have become a dominant form of land use in the United States, with over 32 million acres of pine plantations in the southeastern United States (Fox et al. 2007). These large tracts of pine forest have ecological value (see Ninan and Inone 2013) and can alleviate the pressures of urban and agricultural development for many wildlife populations. However, managed forests differ in many ways from historic forest types and are subject to disturbances such as clearcutting, thinning, mechanical site preparation, and chemical treatment which, in turn, shape vegetation characteristics and wildlife populations residing in these timber stands and the ecosystem services they provide. With a clear understanding of wildlife population dynamics in plantations managed for timber, we can maximize the value of managed forests as wildlife habitat.

Salamanders are often proposed as indicators of ecosystem health for disturbed habitats such as managed timber forests (Southerland et al. 2004). Salamanders are particularly sensitive to environmental stressors due to their complex life histories and cutaneous respiration that make them vulnerable to pollutants and microhabitat changes (Vitt et al. 1990). Salamanders also have a substantial impact on ecosystem function (Davic and Welsh 2004). 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). Salamanders are also predators

themselves, exerting top-down controls on invertebrate primary consumers, and potentially indirectly affecting decomposition rates of leaf litter and carbon storage (Best and Welsh 2014; Wissinger et al. 1998; Wyman 1998). Lastly, the life history patterns of many salamander species facilitate the transfer of matter and energy between aquatic and terrestrial habitats (Davic and Welsh 2004). While stream salamanders are directly affected by changes in water quality and are often abundant in headwater systems (Southerland et al. 2004), the effects of anthropogenic stressors on stream-associated salamander species and their role in aquatic ecosystems are understudied.

Numerous studies investigating the effects of clearcut timber harvest on salamander species have observed declines in salamander abundance post-harvest with potentially long recovery periods (Connette and Semlitsch 2013; Kroll 2009; Petranka et al. 1994; Tilghman et al. 2012). Relatively few studies have examined possible mechanisms, such as changes in survival, reproduction, growth, or movement, that drive these declines (but see Connette et al. 2015; Semlitsch et al. 2009). Furthermore, limited conclusions about salamander populations in managed forests can be gleaned because abundance estimates were generally based on raw count data without accounting for factors that influence detection probability (Mazerolle et al. 2007; Schmidt 2004). Bailey et al. (2004) recommends the use of robust design capture-mark-recapture (CMR) models to investigate parameters affecting detection probability and generate less biased estimates of salamander abundance and survival. Similarly, Maigret et al. (2014) proposed the use of Before-After-Control-Impact (BACI) experimental designs to assuage variation due to site dissimilarities in studies examining the effects of timber harvest on stream salamanders. As the name implies, BACI studies use both before and after data at impacted sites, allowing those sites to be compared over time and to control sites (McDonald et al. 2000).

In this thesis, I present two manuscripts focused on the population biology of

Desmognathus brimleyorum, a common, but understudied, stream-associated salamander endemic to the Ouachita Mountains of west-central Arkansas, in intensively managed pine forests. In the first manuscript, I used a BACI design to examine effects of timber harvest on salamander relative abundance. I also evaluated two mechanisms potentially driving changes in relative salamander abundance: apparent survival and movement. In the second manuscript, I used robust design CMR models to explore the effects of seasonal, site, and age variation on estimates of *D. brimleyorum* capture and recapture probability, temporary emigration, abundance, and apparent survival. This is the first study to rigorously describe stream salamander populations in forests managed for timber production using robust design methods. Understanding population vital rate and life history parameters in managed forests may help inform future assessment, monitoring, and conservation of stream-associated salamander populations.

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Chapter 1:

Effects of Timber Harvest on the Survival and Movement of the Ouachita Dusky Salamander (*Desmognathus brimleyorum*) in Managed Forests.

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Abstract

With anthropogenic alteration of landscapes increasing world-wide, managed forests are increasingly important as providers of ecosystem services and wildlife habitat. Therefore, it is crucial to maintain a balance between timber production and biodiversity conservation. Several studies have suggested negative effects of forestry on terrestrial plethodontid salamanders, but fewer have focused on stream-dwelling species or evaluated mechanisms driving observed shifts in abundance (e.g., mortality vs. movement). Using a Before-After-Control-Impact design, we examined the effects of clearcut timber harvesting on a stream-dwelling salamander endemic to the Ouachita Mountains, Desmognathus brimleyorum. We conducted a capture-mark-recapture study at three streams within intensely managed pine forests in west-central Arkansas from May 2014-October 2016. The pine stands surrounding two of the streams were harvested (leaving a 28-42 m wide forested buffer) in January 2015 and 2016, respectively. The third stream served as a control site and remained unharvested. We estimated salamander survival and movement over the course of two years and compared rates of change between the harvested and control streams. Overall, our models show seasonal and temporal variation in salamander survival and abundance, but little evidence for strong immediate effects of timber harvesting. However, there was increased salamander movement at the sites where harvesting occurred. Our results suggest that streamside buffers of at least 28 m are an effective method for minimizing effects of forestry activities on stream-dwelling salamanders. The results of this study will help inform management decisions aimed at conserving biodiversity and ecosystem integrity in landscapes managed for timber production.

Introduction

Forests intensively managed for timber production have become a pervasive land cover in many parts of the world, including the southern United States. There are currently over 32 million acres of pine plantations in the southeastern United States (Fox et al. 2007), accounting for almost half the of the world's industrial timber plantations (Allen et al. 2005). These large tracts of pine forest have ecological value (see Ninan and Inone 2013) and alleviate the pressures of urban and agricultural development for many wildlife populations. However, it is necessary to understand how major periodic forestry disturbances (e.g. clearcutting, thinning, and site preparation) affect wildlife populations using managed stands and the ecosystem services these populations provide. With a clear understanding of mechanisms driving relationships between forestry practices and wildlife population dynamics we can maximize the value of managed forests as wildlife habitat.

Most of the pine forests in the southern United States are the result of even-aged timber management, where an entire stand is harvested and/or planted at the same time producing forests where most trees are the same age. Even-aged management practices (such as clearcutting) cause considerable physical changes to forest ecosystems including reduced canopy cover, increased soil and water temperatures, nutrient loss, sedimentation, and soil compaction (Borman et al. 1968; Brooks and Kyker-Snowman 2008; Keenan and Kimmins 1993). These alterations in abiotic conditions can influence wildlife population dynamics. For example, reduced canopy cover, soil compaction, and increased temperatures may cause dehydration in many animal species, reducing the survival of those species within the harvested stand. Mobile species may leave a disturbed area in search of another stand that better meets their physiological and life history needs.

In sustainable forest management, the success of a few indicator species (usually chosen for their sensitivity or ecological influence) are often used to assess how these physical changes are affecting overall ecosystem function and biodiversity (Wiens et al. 2008). Salamanders are often proposed as such indicator species because they are particularly sensitive to environmental stressors due to their complex life histories and cutaneous respiration (Southerland et al. 2004; Vitt et al. 1990). Salamanders also have a substantial impact on ecosystem function (Davic and Welsh 2004). 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). Salamanders are also predators themselves, and have been suggested to exert top-down control on invertebrate prey, indirectly affecting decomposition rates and carbon storage (Wyman 1998). Lastly, the life history patterns of many salamander species facilitate the transfer of matter and energy between aquatic and terrestrial habitats (Davic and Welsh 2004). While stream salamanders are directly affected by changes in water quality and are often abundant in headwater systems (Southerland et al. 2004), the effects of anthropogenic stressors on streamassociated salamander species and their role in aquatic ecosystems are understudied.

Numerous studies investigating the effect of clearcut timber harvest on fully terrestrial salamander species (e.g., *Plethodon* spp.) have observed declines in salamander abundance post-harvest with potentially long recovery periods (Connette and Semlitsch 2013; deMaynadier and Hunter 1995; Petranka et al. 1994; Tilghman et al. 2012). Relatively few studies have examined possible mechanisms, such as changes in survival, reproduction, growth, or movement, that drive these declines (but see Connette et al.2015; Semlitsch et al. 2009). The observed effects of clearcutting on stream-associated salamanders are more variable. For example, Pollett et al. (2010) found that timber harvest had a negative impact on *Rhyacotriton cascadae* abundance but

a positive impact on *Dicamptodon* spp. abundance. This disparity is likely a result of variation between stream sites (especially the presence and size of riparian buffers) and the life histories of studied species (Bury and Corn 1988; Jackson et al. 2007; Peterman and Semlitsch 2009; Perkins and Hunter 2006). Maigret et al. (2014) proposed the use of Before-After-Control-Impact (BACI) experimental designs to assuage variation due to site dissimilarities in studies examining the effects of timber harvest on stream salamanders. As the name implies, BACI studies use both before and after data at impacted sites, allowing those sites to be compared over time and to control sites (McDonald et al. 2000).

In this study, we conducted a capture-mark recapture (CMR) study, using a BACI design, to assesses the effect of clearcut timber harvesting on *Desmognathus brimleyorum*, a common stream-associated salamander endemic to the Ouachita Mountains of west-central Arkansas. Specifically, we monitored three streams in managed timber stands (one control and two beforeafter sites) from May 2014-October 2016 and examined changes in 1) relative abundance 2) apparent survival, and 3) movement along the stream channel associated with a harvesting event. By estimating vital rates, in addition to relative abundance, we evaluated possible mechanisms for changes in salamander abundance resulting from timber harvest. Based on previous studies of salamanders and timber harvest, we hypothesized that relative abundance of *Desmognathus* salamanders would be lower after a harvesting event and that this reduction would coincide with either a reduction in survival or an increase in movement. Both possible effects (reduced apparent survival and increased movement) would cause decreased numbers of individuals captured during stream surveys either through direct mortality or emigration out of the study area.

Methods

Sampling Design

We implemented a BACI design at three headwater streams on timber holdings in the Ouachita Mountains of west-central Arkansas to assess the 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, each stream was surveyed on three nights, approximately one week apart. Timber harvesting occurred at BA1 in January 2015 and at BA2 in January 2016 (Fig. 1).

Study Sites

We selected sites based on similar stream size, morphology, and silvicultural history. All three sites were 1st order, headwater streams located within 16 km of each other in the Little Missouri Watershed in northeast Howard County, Arkansas, USA at elevations from 190-300 m above sea level (Fig. 1). Each study stream drained a small watershed (0.41-1.15 km²) within an even-aged, mature (29-35 years old) loblolly pine (*Pinus taeda*) stand. Each stream also had a streamside management zone (SMZ) serving as a riparian buffer, ranging between 28-50 m wide (total width including stream). The forested area within the SMZ is retained during harvesting events and not controlled for overstory species. The SMZ at the Control and BA2 sites were dominated by oak (*Quercus* spp.) and hickory (*Carya* spp.) in the overstory and cedar (*Juniperus*

virginana) and holly (*Ilex opaca*) in the understory. The SMZ of the BA1 site was dominated by loblolly pine in the overstory and holly, musclewood (*Carpinus caroliniana*) and hophornbeam (*Ostrya virginiana*) in the understory. At each site, we delineated a 200 m stream transect for salamander sampling. At the BA1 site, this transect spanned the stand boundary (100 m in clear-cut, 100 m downstream in the adjacent unharvested 12 yr-old stand), allowing us to assess movement out of the harvested section. The BA1 and BA2 stands were clear-cut in Jan 2015 and Jan 2016, leaving behind a 28 m and a 42 m SMZ, respectively. A number of large pine trees were removed from the SMZ during the harvesting of the BA1 site (this practice is permissible under Arkansas Best Management Practices) (Arkansas Forestry Commission 2002).

Survey Methods

Each night-time sampling event consisted of a thorough visual search of the streambed for the length of each transect. Surveys were not time-constrained, but rather were continued until the entire 200 m transect had been thoroughly searched (average effort was 10.6 person-hours per sampling event). We carefully turned rocks and other cover objects to detect salamanders and captured them using dip nets. We placed each salamander in a separate container that corresponded to a flag placed in the stream marking the capture location of each individual. We excluded larval *Desmognathus* and other salamander species from capture. The following day we processed captured salamanders by recording body metrics (mass, total length, snout-vent length (SVL), external parasite count, and any other distinguishing features) and marking each new individual with a unique identification mark using subcutaneous injection of visible implant elastomer (VIE; Northwest Marine Technologies, Shaw Island, WA; Grant 2008). We anesthetized each salamander prior to processing 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. Any recently metamorphosed individuals (less than a year since metamorphosis, 45 mm SVL or under) were labeled as juveniles. We identified first-year animals based on the average growth rate of known metamorphs and an obvious break in body size distributions, creating a first-year growth threshold of 45 mm SVL. Individuals > 45 mm SVL at time of capture were considered adults. We generally returned all salamanders to their exact capture location within 2 days after capture, but occasionally salamanders were held up to 5 days to avoid releasing them into a flooded stream 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).

Data Analysis

We assessed our CMR data using open population models because our primary parameter of interest was survival. However, open population models do not allow for comprehensive evaluation of factors influencing detection and thus do not provide reliable estimates of abundance. As an alternative to model-generated estimates of abundance, we used count data to compare salamander relative abundance over time. Specifically, we assessed 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 affecting our count-based abundance estimates: 1) excluding recaptures within the same season, and 2) comparing estimates across years within seasons and sites. We then estimated salamander survival between sampling seasons at each site using open Cormack-Jolly-Seber (CJS), full-likelihood models in Program MARK 6.0 (White and Burnham 1999). For our CJS models, we collapsed encounter histories within the same sampling season,

yielding 8 samples each for the Control and BA1 sites, and 6 samples for the BA2 site. We structured CJS models in MARK by varying capture probability (p) and apparent survival (ϕ) over different time intervals. First, keeping φ constant, we evaluated models where p was held constant, varied fully by time, varied by season (but held constant across years), and varied by winter (winter p (Nov-Mar) different from the rest of the year). Once we determined the best parameterization for p, we included that parameterization in subsequent models examining variation in survival. 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 (Apr-Jun) and summer/fall intervals (Jul-Oct), but allowed to differ over winter (Nov-Mar); 3) 'Seasonal Variation': φ different among seasons, but held constant across years; 4) 'Harvest Variation' (only for Before/After sites): φ in pre-harvest intervals allowed to differ from all post-harvest intervals. Model selection was based on Akaike Information Criterion (AIC; Akaike 1974) adjusted for small samples sizes (AICc; Burnham and Anderson 2002). We evaluated the goodness-of-fit of the most parameterized model at each site using the median \hat{c} method and subsequently adjusted AICc values to account for overdispersion of our data (QAICc) (White and Burnham 1999). We ranked QAICc 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 without over-parametrizing. To account for model selection uncertainty, we used model averaging to generate p and φ estimates that were weighted by the support of each model (Burnham and Anderson 2002).

We used the location history of individuals to assess salamander movement in two ways: 1) we compared net movement over the harvesting interval between sites and 2) we compared the mean distance traveled per movement event before and after timber harvest between sites. To determine how timber harvest affects net salamander movement, we subtracted the first known location of each individual after timber harvest from the last known location before timber harvest at each before-after site. For a direct time comparison, net movement at the Control site was calculated around each of the before-after sites' harvesting events. We calculated mean distance traveled per movement of each individual by summing the absolute value of all their movements in a specified time period and then dividing by the number of movement events during that time. For the BA1 site, we calculated before harvest mean movement distance using location data from Jun 2014-Oct 2014 and after harvest mean distance using data from Mar 2015-Jun 2015, thus using data from the six sampling nights immediately before and after harvest. For the BA2 site, the before and after time intervals ranged from Mar 2015-Oct 2015 and Mar 2016-Oct 2016 respectively (9 sampling nights before and after). We calculated mean distance per movement at the Control site for all four time intervals for direct temporal 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 (before vs. after harvest), site (control vs. before-after site), and the interaction of time and site on mean distance moved per individual, 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 1,987 captures of D. brimleyorum over 8 seasonal samples (24 sampling nights), representing 1,030 individual salamanders. At the BA1 site, we had 659 captures of *D. brimleyorum* over 8 seasonal samples, representing 361 individual salamanders. At the BA2 site, we had 1,894 captures of *D. brimleyorum* over 6 seasonal samples (18 sampling nights), representing 1,062 individuals. All three sites had a similar proportion of recaptured individuals (43-48%). At all three sites, capture rates were lowest in the spring (March) and highest in the summer (July). In general, the number of adult individuals increased over the three-year study at all sites (Fig. 2). 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 harvesting of the surrounding stand. In fact, captures of adults at the BA1 site increased substantially following harvest in 2015 and 2016 (Fig. 2b), and capture rates were similar to, or greater than, pre-harvest capture rates at the BA2 site following harvest in 2016 (Fig. 2c). However, relatively few newly metamorphosed juvenile salamanders were captured at the BA1 site in 2016, 1.5 years after harvesting (Fig. 2b).

Capture Probability

CJS analysis of capture/recapture data for both the Control and BA2 sites favored models where individual capture probability (p) was fully time varying (Table 1). For the BA1 site, model selection favored a model where capture probability differed between the winter period and was the rest of the year. Individual capture probabilities at the Control Site and BA2 site

were variable (16-52%), but were always lowest during the winter (Nov-Mar) sampling periods. Additionally, *p* estimates at the Control and BA2 were consistently higher in 2016 (averaging 47% from April-Oct) than 2015 (averaging 31% from April-Oct). 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 1). This model generated φ estimates ranging from 49-97% with apparent survival being lowest between the first and second (49%) and between the fifth and sixth (60%) sampling intervals and relatively high (mean 82.5%) over all other intervals (Fig. 3). A harvest-varying model was favored at the BA1 site (φ before harvesting is different from φ after harvesting) (Table 1). Under this model, survival was estimated to be 29% (CI 16-49%) between pre-harvest intervals (July-Oct 2014) and 73% (CI 67-79%) between post-harvest intervals (Fig. 3). Model selection for the BA2 site showed equivocal support for models that represented constant, winter-varying, and harvest-varying survival (Δ QAICc < 2; Table 1); with the constant φ model yielding a survival estimate of 69% (CI 65-73%). Parameter estimates from the fully timevarying model support this pattern: survival was relatively uniform throughout the study with no indication of a change in survival following harvest.

Movement

We examined movement of recaptured salamanders at our three CMR sites to assess the influence of timber harvest on the direction and magnitude of salamander movement (Fig. 4, 5). In general, individuals had a net movement <20 m and exhibited a slight upstream movement

bias. 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 greater than 4 m between pre-harvest and post-harvest 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, the mean distance an individual traveled per movement event increased at both experimental sites following timber harvest (Fig. 5). We observed a post-harvest increase in mean distance traveled per movement of 108% and 29% at BA1 and BA2, respectively. For BA1, a significant increase in movement following harvest relative to the same time interval at the control was reflected in a significant site x time interaction (F=9.753, df=1, p=0.002). Although BA2 also exhibited a trend for increased movement following harvest, only a site effect on movement was significant (F=16.91, df=1, p=0.000).

Discussion

Contrary to our hypotheses, timber harvest did not have an immediate negative effect on relative abundance or apparent survival of *D. brimleyorum* at either of our before-after sites. Variation in relative abundance among sites appeared to be highly seasonal (lowest in the spring, highest in the summer, and moderate in the fall). This pattern is best explained by the capture probability estimates produced in the top CJS models (where capture probability was lowest in the winter). Low capture probability in winter was likely driven by temporary emigration of individuals into habitats where they are not available for capture, such as subterranean retreats. Many *Desmognathus* salamanders are less active and move below the stream surface during

cooler and dryer months (Ashton 1975; Orser and Shure 1975; Petranka 1998). In their thorough examination of *D. brimleyorum* population parameters using robust design analysis of this dataset, Halloran et al. (2018, in prep.) found that conditional capture probability was generally constant over time and that seasonal variation in salamander captures was driven by relatively high rates of temporary emigration in winter. While relative abundance of juveniles varied annually, the relative abundance of adult individuals within a given season increased over time at all sites. This change in relative abundance may be driven by favorable environmental conditions. Indeed, all three years (2014-2016) of our study were considered wet years for this region, receiving 10.82 cm, 38.05 cm, and 15.32 cm of precipitation over the annual average (137.34 cm), respectively (NOAA weather station in Newhope, AR).

Apparent survival at all three sites remained remarkably constant throughout the 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 that survival was greater post-harvest than in the Jul-Oct 2014 pre-harvest interval. High survival post-harvest could reflect a change in food availability. Aquatic macroinvertebrate abundance may increase post-harvest as a result of reduced canopy cover and increased detrital input (Jackson et al. 2007; Kiffney et al. 2004; Murphy et al. 1981; Rempel and Carter 1986). 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). However, it should be noted that apparent survival was also low during the Jul-Oct 2014 interval at the Control site. This suggests that high survival after 2014 at the BA1 site may be partially attributable to favorable climatic conditions in those years.

Annually consistent relative abundance and survival estimates contradict the conclusions of most studies investigating the effects of timber harvest on salamanders, many of which suggest a negative effect of clearcutting (Crawford and Semlitsch 2008; Perkins and Hunter 2006; Tilghmen et al. 2012, etc.). For example, Petranka et al. (1993) and Reichenbach and Sattler (2007) observed considerable reductions in terrestrial plethodontid salamander abundance immediately following a clearcut event. However, as Kroll (2009) shows in his review of studies from the Pacific Northwest, studies focused on stream-associated species have had variable results. For example, Jackson et al. (2007) found that clearcutting had no effect on torrent salamanders (*Rhyacotriton spp.*) and Pollet et al. (2010) and Bury and Corn (1988) found that giant salamander (*Dicamptodon spp.*) abundance increased in areas that experienced timber harvest. Furthermore, Connette and Semlitsch (2013) suggest that stream-breeding salamanders (*Desmognathus ocoee* and *Eurycea wilderae*) are able to recover from a harvesting event faster than their terrestrial-breeding counterparts.

Much of the variability in studies focused on responses of stream-associated salamanders to forestry is a reflection of the range of management practices employed around streams located within commercially harvested timber stands. For example, streamside management zones (SMZs, also referred to as stream buffers) are often designated to preserve stream water quality while the surrounding area is harvested. However, the size of SMZs and the activities permissible within them (such as road crossings and selective timber extraction) are variable from stream to stream and region to region. As SMZs have become a common forest management practice and are now required by law in some states, the number of studies investigating the influence of these buffers on stream-associated salamanders has increased (Maigret et al. 2014; Perkins and Hunter 2006; Stoddard and Hayes 2005). Most of these studies

agree that riparian buffers are an effective way to reduce the negative impacts of harvesting on salamanders (but see Pollett et al. (2010) with respect to *Dicamptodon spp.*), although the minimum effective buffer size is still debated. For example, Peterman and Semlitsch (2009) concluded that 18 m wide SMZs were ineffectual at preserving larval salamander abundance while larval abundance in streams with 60 m wide SMZs did not differ significantly from uncut reference sites. Vesely and McComb (2002) suggest that SMZ greater than 40 m wide are needed to maintain salamander abundance. Arkansas Best Management Practices for water quality protection recommend SMZs of 20-50 m (dependent on bank slope class) for non-ephemeral streams (Arkansas Forestry Commission 2002). The SMZ widths in this study ranged from 28-50 m which are common sizes for streams in timberlands in the Ouachita Mountain region. SMZs of this size are perhaps large enough that the abundance and survival of a strongly aquatic species such as *D. brimleyorum* would be largely unaffected by timber harvesting events. Further investigation is needed to determine if smaller SMZs can maintain D. brimleyorum populations and make threshold width recommendations. Additionally, we are unable to make conclusions about the SMZ requirements of other stream salamander species, as their tolerance to disturbance and riparian habitat requirements may differ from *D. brimleyorum*.

Although we did not detect an effect of harvesting on either relative abundance or apparent survival, salamander movement patterns changed during the harvesting event. Throughout the study, salamanders at the control site exhibited behavior consistent with observed movement patterns in undisturbed streams: small movements, with a slight upstream bias (Barthalmus and Bellis 1972; Grant et al. 2010). Meanwhile, salamanders at both beforeafter sites showed an increase in movement distance in both directions after harvesting events. This result differs from that of Chelgren and Adams (2017) who found that in-stream movement

of *Dicamptodon tenebrosus* had an inverse relationship with timber harvest intensity. While no other studies have assessed in-stream movement, Johnston and Frid (2002) and Peterman et al. (2011) found no significant changes in the terrestrial movement patterns of stream salamanders when a 40-60 m SMZ was retained. One possible mechanism behind increased in-stream movement is increased water velocity during storm events as a consequence of a harvested watershed. Segev and Blaustein (2014) found that greater movements of Salamandra infraimmaculata were associated with increasing water velocity. While clearcut watersheds in the Ouachita Mountain region have increased annual water yields over unharvested watersheds, significant differences in stormflow or peakflow conditions have not been recorded for this region (Miller et al. 1988; Stednick 1996). Our results indicate that substantial changes to instream salamander dispersal may occur, even when a 28-42 m SMZ is retained around the stream. Further investigation is necessary to determine if these altered movement patterns will have a lasting effect on salamander body condition, reproductive success, and survival. Increased dispersal may expose individuals to higher energetic costs and more frequent territorial disputes, indirectly affecting long-term survival and/or reproduction (Keen and Reed 1985; Schmidt et al. 2007).

Although we didn't detect a harvesting effect on abundance or survival 1-2 years postharvest, we cannot rule out the possibility of a time lagged response. For example, altered movement patterns could potentially drive a lagged reduction in salamander survival, where salamander survival is stable immediately following a harvesting event, but then decreases overtime due to secondary factors. Guzy et al. (2018, in prep.) observed that stream salamander abundance is lowest in stands 5-10 years post-harvest, suggesting that time-lagged effects on survival or recruitment may occur in our study system. In this study, we observed decreased

abundance of newly metamorphosed individuals at the BA1 site in 2016. The salamanders that metamorphosed at the BA1 site in 2016 are the first cohort to hatch after the harvesting event. Thus, if the harvesting event affected reproductive potential or egg survival, reductions in juvenile recruitment would not be apparent for at least a year (depending on the season of harvesting). Further population monitoring is needed to determine if time-lagged effects will occur at these sites.

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 are relatively inactive and after their eggs have hatched in the fall (Means 2005). Furthermore, harvesting at our sites occurred during years with relatively high spring and summer precipitation. Further research is necessary to determine if salamanders are adversely affected if harvesting occurs when they are highly active (April-November) and/or their resources and mobility are limited by drought conditions. Lastly, the timing and frequency of future logging-related disturbances (site preparation, thinning, harvest, etc.) will likely influence salamander population recovery and persistence.

We found that SMZs of 28 m or larger effectively avoided negative effects of timber harvest on *D. brimleyorum* relative abundance and apparent survival up to 2 years post-harvest, when mechanical timber removal occurred in the winter months. Timber harvesting changed the movement patterns of juvenile and adult *D. brimleyorum* in the stream, but it is unclear if this will have long-term ramifications. We recommend long-term salamander population monitoring in the SMZs of harvested timber stands to evaluate the mechanisms of possible time-lagged responses and longstanding population viability. However, we cautiously suggest that, provided

with adequate SMZs, intensely managed forests can support viable, dense populations of stream salamanders.

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Figures and Tables

Table 1. Model selection results for Cormack-Jolly-Seber analysis of capture-recapture data for *D. brimleyorum* at three sites. Models were constructed by varying capture/recapture probability (p) and survival (φ) by time (t), season, winter, or harvest ("." refers to parameters held constant). Models are listed in decreasing order of support using Quasi-Akaike Information Criterion, corrected for small sample size and data overdispersion (QAICc).

Model	QAICc	ΔQAICc	Model Weight	K
Control Site				
$\phi(t), p(t)$	2683.531	0	0.943	13
$\varphi(\text{season}), p(t)$	2689.809	6.278	0.041	10
φ(.), p(t)	2692.381	8.851	0.012	8
$\varphi(\text{winter}), p(t)$	2694.003	10.472	0.005	9
$\varphi(.), p(season)$	2707.827	24.297	0.000	4
$\varphi(.), p(winter)$	2720.897	37.366	0.000	3
BA1 Site				
φ(harvest), p(winter)	817.874	0	0.946	4
$\varphi(t)$, p(winter)	824.499	6.625	0.034	9
$\varphi(.), p(winter)$	829.910	12.035	0.002	3
$\varphi(\text{winter}), p(\text{winter})$	831.603	13.729	0.001	4
$\varphi(.), p(season)$	831.841	13.967	0.001	4
φ(season), p(winter)	833.597	15.723	0.000	5
φ(.), p(t)	838.008	20.134	0.000	8
BA2 Site				
φ(.), p(t)	1501.104	0	0.456	6
φ(winter), p(t)	1502.771	1.667	0.198	7
φ (harvest), p(t)	1502.999	1.895	0.177	7
$\varphi(\text{season}), p(t)$	1504.173	3.069	0.098	8
$\varphi(t), p(t)$	1505.715	4.611	0.045	9
$\varphi(.), p(season)$	1507.139	6.035	0.022	4
$\varphi(.), p(winter)$	1511.065	9.961	0.003	3

 $QAIC_c$ = Quasi-Akaike Information Criteria, corrected for sample size and over-dispersion; $\Delta QAIC_c$ = difference in QAICc relative to the top model; K = Number of parameters in the model.


Figure 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 grey. Approximate SMZs around each stream (thin black lines) are shaded in grey. 200 m stream transects 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.







Summer

■ Adults ■ Juveniles

Spring

Figure 2. Number of individual *D. brimleyorum* captured by seasonal sampling interval at the three CMR sites in the Ouachita Mountain region of Arkansas, USA, grouped by season. Dotted bars indicate post-harvest intervals at the before-after Sites. *Only the harvested half of BA1 Site was surveyed in summer 2014.

Fall



c) BA2 Site



Figure 3. Model-averaged apparent survival by sampling interval at the three sites in the Ouachita Mountain region of Arkansas, USA using Cormack-Jolly-Seber models. Hatched bars indicate post-harvest intervals at the before-after Sites. Error bars represent 95% confidence intervals. Because of low captures rates in the spring, the survival rate at the Control Site for the second Apr-Jun interval is nonsensical, but is likely high.



Figure 4. Net movement of individual adult and juvenile *D. 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 & 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 & c) over the same time intervals are provided for comparison. Negative distance measures indicate downstream movement.



Figure 5. Average individual *D. brimleyorum* mean distance traveled per movement event (+/-1 standard error) pre- and post-timber harvest for 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.

Appendix



Office of Research Compliance

MEMORANDUM

TO: J.D. Willson

- FROM: Craig N. Coon, Chairman Institutional Animal Care and Use Committee
- DATE: April 4, 2014
- SUBJECT: IACUC APPROVAL Expiration date: March 31, 2017

The Institutional Animal Care and Use Committee (IACUC) has APPROVED protocol 14032: "Occupancy and habitat relationships of stream-associated salamanders in intensively managed forests of the Ouachita Mountains ecoregion"

In granting its approval, the IACUC has approved only the protocol provided. Should there be any changes to the protocol during the research, please notify the IACUC in writing (via the Modification form) prior to initiating the changes. If the study period is expected to extend beyond March 31, 2017 you must submit a new protocol. By policy the IACUC cannot approve a study for more than 3 years at a time. Annually the IACUC will request a report on the status of the protocol.

The IACUC appreciates your cooperation in complying with University and Federal guidelines for involving animal subjects.

CNC/aem

cc: Animal Welfare Veterinarian

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Chapter 2:

Population biology of Ouachita Dusky Salamanders (*Desmognathus brimleyorum*) in a Managed Forest Landscape.

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Abstract

Salamander populations can play a key role in the function and diversity of temperate forest ecosystems. However, the population parameters of salamanders residing in forests managed for timber production are generally unknown. We conducted a capture-mark-recapture (CMR) study at three streams within intensely managed pine forests in the Ouachita Mountain region of Arkansas from March 2015-October 2016. Specifically, we used robust design CMR models to explore the effects of seasonal, site, and age-class variation on the capture probability, recapture probability, temporary emigration, abundance, and apparent survival of a stream salamander, Desmognathus brimleyorum. We found evidence of significant seasonal variation in temporary emigration rates, which were lowest in late spring and highest in the winter months. Our estimates of mean salamander density (1.31 individuals/m², adjusted to account for temporary emigration and conditional capture probability) and apparent survival (46%) were comparable to those of other *Desmognathus* species. This suggests that streams in forests managed for evenaged timber production can support viable, dense populations of salamanders comparable to those in protected forests. Understanding the dynamics of such populations may help inform future assessment, monitoring, and conservation of stream-associated salamanders.

Introduction

Due to rapidly increasing human populations, much of the world's natural landscapes have been altered to meet human needs (Foley et al. 2005), and remaining reserves of unaltered land are often insufficient to preserve biodiversity (Westman 1990; Wilcove 1989). Forests managed for timber production, with similarities to unaltered landscapes, may be managed for both biodiversity and production of commodities, augmenting natural biodiversity reserves (Hansen 1991; Harris 1984). Managed forests have become a dominant form of land use in the

United States, with over 32 million acres of pine plantations in the southeastern United States (Fox et al. 2007). These large tracts of pine forest have ecological value (see Ninan and Inone 2013) and can alleviate the pressures of urban and agricultural development for many wildlife populations. However, managed forests differ in many ways from historic forest types and are subject to disturbances such as clearcutting, thinning, mechanical site preparation, and chemical treatments to control competing vegetation. Although many studies have investigated the immediate impact of these disturbances on wildlife abundance, few studies have described the population biology of wildlife species residing in intensively managed forests, which limits our ability to understand and predict changes in response to novel disturbances. With a clear understanding of wildlife population dynamics in plantations managed for timber, we can maximize the value of managed forests as wildlife habitat.

Salamanders are important contributors to biodiversity in forested habitats and have substantial impact on ecosystem function (Davic and Welsh 2004). In many forested systems, salamander biomass exceeds all other vertebrate groups (Vitt et al. 1990), thus providing a vital energy resource to higher trophic levels (Burton and Likens 1975). For example, Davic and Welsh (2004) recorded salamander densities of up to 14.7 individuals/m² (9.75 g/m²) in a North Carolina stream. Salamanders are also important macroinvertebrate predators, and may exert topdown controls on primary consumers, with potential indirect effects on macroinvertebrate diversity and decomposition rates (Best and Welsh 2014; Wissinger et al. 1998; Wyman 1998). Lastly, the life history patterns of many salamander species facilitate the transfer of matter and energy between aquatic and terrestrial habitats (Davic and Welsh 2004). Most of the studies evaluating the functional role and abundance of salamanders have focused on relatively undisturbed forest habitats. Little is known about the roles and abundance of salamanders in

managed systems. Furthermore, the abundance and ecological function of stream-breeding salamanders are understudied compared to their terrestrial- and pond-breeding counterparts.

Most studies that have examined salamanders in managed forests focus on effects of forestry, lending little insight into the characteristics of salamander populations in managed landscapes or their variation over space and time (see reviews Kroll 2009; Tilghman et al. 2012). Limited conclusions about salamander population dynamics in managed forests can be gleaned from these impact studies because abundance estimates were generally based on raw count data without thoroughly accounting for factors that influenced detection probability (Mazerolle et al. 2007; Schmidt 2004). Salamanders spend most of their time under cover objects or in underground refugia, inaccessible to researchers (Bailey et al. 2004b). Because of their cryptic and elusive nature, surface counts of salamanders are often small and variable and may not be representative of overall abundance or trends in abundance over time (Smith and Petranka 2000). Furthermore, the surface activity of many salamanders is highly dependent on season or climatic conditions, making surface counts temporally variable (Hyde and Simons 2001; Petranka 1998).

Capture-Mark-Recapture (CMR) methods (where individuals are captured, marked, released alive, and then recaptured on a later survey) are often used to estimate population parameters because many CMR analytical models allow for the estimation of capture probability, reducing bias in abundance and vital rate estimates (Schmidt 2004). Robust design (Pollock 1982; Kendall et al. 1997) is a particularly useful CMR approach because it allows for the estimation of both temporary emigration (the probability that an individual is alive but temporarily unavailable for capture, i.e. outside the sampled area) and conditional capture probability (the probability that an individual will be captured given that it is available for capture) (Bailey et al. 2004b). This is accomplished by nesting frequent secondary sampling

periods where population closure is assumed within widely spaced primary sampling periods where the population is considered open (Kendall et al. 1997). Accounting for temporary emigration allows for more confident, unbiased abundance and survival estimates and increased insight into life history processes (Mazorolle et al. 2007). For example, Bailey et al. (2004b) estimated that nearly 90% of Plethodonid salamanders were unavailable for capture at any given time. Without accounting for temporary emigration, any abundance estimates for the salamanders in Bailey et al. (2004b)'s system would be exaggerated while survival rates may be underestimated.

In this study, we employed robust design CMR methods to describe the population biology of *Desmognathus brimleyorum*, a common, but understudied, stream-associated salamander endemic to the Ouachita Mountains of west-central Arkansas, in intensively managed pine forests. We conducted intensive CMR surveys of D. brimleyorum at three headwater streams over two years. Using robust design CMR models, we explored the effects of season, site, and age on estimates of *D. brimleyorum* capture and recapture probability, temporary emigration, abundance, and apparent survival. We hypothesized that survival and temporary emigration would vary by season because salamander surface activity, and thus presumed mortality risk, is usually seasonal. We also hypothesized capture probability and temporary emigration would vary among sites, as availability of refugia is likely site-dependent (assuming salamanders utilizing refugia are unavailable for capture or more difficult to capture). Finally, we hypothesized that abundance would be site-varying as resource availability, and thus salamander carrying capacity, is site-dependent. This is the first study to rigorously describe stream salamander populations in forests managed for timber production using robust design methods. Understanding the dynamics of such population parameters in managed forests may

help inform future assessment, monitoring, and conservation of stream-associated salamander populations.

Methods

Study Sites

We conducted intensive capture-mark-recapture (CMR) sampling at three headwater streams on intensively managed pine landscapes on the Athens Plateau (Woods et al. 2004), the southern foothills of the Ouachita Mountains in west-central Arkansas (hereafter referred to as sites 1, 2, and 3). We selected sites based on similar stream size, morphology, and timber management 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. Each study stream drained a small watershed (0.41-1.15 km²) within a mature even-aged (29-35 years at the start of our study), loblolly pine (Pinus taeda) plantation. Each site had similar timber management history with the stand being harvested approximately every 35 years. The stands surrounding sites 1 and 2 were harvested during our 2-year study while the mature stand at site 3 remained intact. A concurrent study found that the harvesting events at sites 1 and 2 had minimal effects on the stream salamander survival and relative abundance (Halloran et al. 2018, in prep.), so we did not explicitly examine the effects of timber harvest on demographic parameters in this study. Each stream had a 28-50 m wide streamside management zone (SMZ) buffer (total width including stream: site 1-28 m, site 2-42 m, site 3-50 m). The forested area within the SMZ was retained during harvesting events. The SMZ at site 2 and 3 were dominated by oak (Quercus spp.) and hickory (Carya spp.) in the overstory and cedar (Juniperus virginana) and holly (Ilex opaca) in the understory. The SMZ of site 1 was dominated by loblolly pine in the overstory and holly, musclewood (*Carpinus caroliniana*) and hophornbeam (*Ostrya virginiana*) in the

understory. At each site, we delineated a 200 m stream transect for the CMR sampling area. The elevation along transects ranged from 190-300 m above sea level.

Salamander Sampling

We sampled salamanders under a robust design framework where sampling events were clustered through the length of the study (Fig. 1). We surveyed each stream one night a week for three weeks (secondary periods) in March, June, and October (primary periods) from March 2015 through October 2016. We assumed populations were closed to birth/death and permanent immigration/emigration between secondary periods (weeks) and were open to gains and losses of individuals between primary periods (seasons). This allowed us to estimate abundance within primary periods and apparent survival between primary periods.

Each night-time sampling event consisted of a thorough visual search of the streambed for the length of each transect. The average number of observers was 2.5 with an average effort of 10.6 person-hours per sampling event. We carefully turned rocks and other cover objects to uncover salamanders and captured them using dip nets. We placed each salamander in a separate container that corresponded to a flag placed in the stream marking the capture location of each individual. We excluded larval *Desmognathus* and other salamander species from capture. The following day, we recorded body metrics [mass, total length, snout-vent length (SVL), and any other distinguishing features] and uniquely marked each individual with subcutaneous injection of visible implant elastomer (VIE; Northwest Marine Technologies, Shaw Island, WA; Grant 2010). Any recently metamorphosed individuals (< 1 year since metamorphosis, \leq 45 mm SVL) were considered juveniles. We identified first-year animals based on the average growth rate of known metamorphs and an obvious break in body size distributions, creating a first-year growth threshold of 45 mm SVL. Individuals > 45 mm SVL at time of capture were considered adults.

We generally returned all salamanders to their exact capture location within 2 days after capture, but occasionally held them up to 5 days to avoid releasing them into a flooded stream.

Data Analysis

We assessed D. brimleyorum population parameters using full-likelihood, robust design models in Program MARK 6.0 (White and Burnham 1999). To avoid small sample sizes, we combined capture data across all three sites into a single encounter history and included site as a covariate in model selection. We structured models by systematically varying conditional capture probability (p), conditional recapture probability (c), temporary emigration (γ) , apparent survival (ϕ) , and individuals not encountered (f0), in that order. To avoid over-parameterization, we held p and c constant within each primary sample, thus assuming p and c were constant across weeks, but could vary across seasons. More general models with fully time-varying p and c are possible, but generally failed to converge. First, we created two constant models where p=c and $p\neq c$ to test behavioral responses to capture. Then, while holding other parameters constant, we evaluated models where p varied by primary period (t) and site. Once we determined the best parameterization for p, we included that parameterization in subsequent models that sequentially allowed c, γ , φ , and f0 to vary by t and site. When parameterizing γ , we created models that varied in type of temporary emigration as well as time and site effects. Specifically, we created models with no temporary emigration ($\gamma'=1$, $\gamma''=0$), random temporary emigration ($\gamma'=\gamma''$), and Markovian temporary emigration ($\gamma'_k = \gamma'_{k-1}, \gamma''_k = \gamma''_{k-1}$) where: 1) γ' is the probability of being unavailable for capture in a primary sampling session given that the individual is alive and wasn't available for capture in the previous sampling session, 2) γ " is the probability of being unavailable for capture in a primary sampling session given that the individual was alive and was available for capture in the previous session, and 3) k is the primary sampling occasion (Kendall

et al. 1997). We based model selection on Akaike Information Criterion (AIC; Akaike 1973) adjusted for small samples size (AICc; Burnham and Anderson 2002). We also explored seasonal and annual variation of population parameters, but excluded these models from our final model selection due to lack of support. To account for model selection uncertainty, we used model averaging to generate estimates that were weighted by the support of each model (Burnham and Anderson 2002). We calculated superpopulation size (N_{super}, the total number of individuals including those unavailable for capture) for each primary sampling session by dividing the estimated abundance of available individuals (\hat{N}) by the ratio of available individuals (1- γ) (Bailey et al. 2004b).

Once our initial model selection was completed, we completed a separate analysis to evaluate variation among salamander age classes (juvenile vs. adult) in *p*, *c*, γ , and φ . Age was not included in our original model set due to the large number of alternative models required to test every parameter permutation of time, site, type of temporary emigration, and age. Instead, we began our age-analysis with a model that included time effects where they were supported in our primary model selection (all parameters except *p*), but did not consider site effects (to avoid overparameterization). Next, we systematically applied age-effects to each population parameter. We parameterized age models by assigning each individual a cohort covariate ("2015", "2016", and "Adult"). Cohort names referred to the year in which each individual metamorphosed, if known. We could not determine age of individuals over 45 mm SVL at first encounter and thus, we labeled those individuals as "Adults" collectively. When creating models with age-varying parameters, we allowed individuals less than a year since metamorphosis to differ from adults and older cohorts, which were set equal. All juvenile cohort parameter rates were fixed to 0 until the time interval when those individuals metamorphosed and were recruited into the sampled

population. No juvenile parameters were estimated during all April-June primary intervals and March secondary intervals because, by that time, all metamorphosed individuals were greater than 1 year old and their size class can no longer be differentiated from adults.

Results

We captured 3,858 salamanders representing 2,111 individuals over 54 nights from March 2015-October 2016. At all three sites, capture rates were highest during the summer primary sample and lowest during the spring primary sample. Captures were highest at site 2 (n=1,896), followed by site 3 (n=1,415), and site 1 (n=547). Model selection indicated the model that allowed φ to vary by time and site, γ was random and varied by time, p varied by site, c varied by time, and f0 varied by time and site had the strongest support [φ (t,site), γ (random,t), p(site), c(t), f0(t,site), model weight= 0.741, Table 1].

Capture and Recapture Probability

A constant model that allowed for a behavioral response to capture $(p \neq c)$ was supported over a constant model without a behavioral response (p=c) ($\Delta AIC_c=4.049$, Table 1). A model where *p* varied by site but was constant over time was most supported. However, the effect of site on *p* was weak, as indicated by nearly equivocal support for the second ranked model where *p* was constant across sites ($\Delta AIC_c=2.099$, model weight=0.259). Model averaged *p* was estimated as 12.4% (CI 9.6%-15.9%) at site 1, 11.9% (CI 9.9%-14.1%) at site 2, and 14.3% (CI 11.7%-17.4%) at site 3 (Fig. 2a). A site effect on *c* was not supported, although *c* varied over time. Model averaged *c* increased steadily from 15.3% (CI 10.9%-20.9%) in March 2015, to 30.9% (CI 27.6%-34.4%) in Jun 2016, before dropping to 23% (19.7%-26.6%) in October 2016 (Fig. 2b).

Temporary Emigration

Our null model where no individuals are unavailable for capture was not supported $(\Delta AIC_c=20.954, \text{ model weight}=0.000)$. Our top model included random temporary emigration that varied across primary samples. Estimates of γ were highly seasonal, with all individuals available for capture ($\gamma = 0$) during the April-June primary intervals, moderate γ (12.6-17.1%) in the July-October interval, and high γ (38.3%) during the winter (November-March) (Fig. 3a).

Abundance

Surface population (\hat{N} , or the abundance of individuals available for capture) ranged from a minimum of 60 (CI 35-86) within the stream transect at site 1 in Mar 2015 to a maximum of 1207 (CI 994-1419) at site 2 in Jun 2016 (Fig. 3b). Estimates of \hat{N} showed strong seasonal variation, with highest salamander abundance in during the June sampling session and lowest abundance during the March sampling session. Examination of the superpopulation size estimates (N_{super} , calculated from \hat{N} and γ) revealed that much of the seasonal change in \hat{N} is due to high γ rates in the winter primary intervals (Fig.3c). Superpopulation size estimates yield an average salamander density of 1.46 salamanders per m of stream at site 1, 5.14 salamanders/m at site 2, and 3.21 salamanders/m at site 3 (averaging 1.31 individuals per m² across all sites assuming an average stream width of 2.5 m).

Apparent Survival

A model where φ varied by time and site was supported. There were no clear seasonal or site patterns in the φ estimates, although φ estimates at site 1 were the most variable (45.7%-93.7%) (Fig. 4). Estimates of φ ranged from 57.3% to 92.4% at site 2 and 65.8% to100% at site

3. Average apparent survival per primary period was 77% across all sites. This extrapolates to an annual survival rate of approximately 46%.

Age Effects

Models that incorporated age and time effects for c, γ , and φ were favored over models that applied age and time effects separately, although variation among juveniles and adults for most parameters was not strong. A model with age-varying p was favored over constant p, although p estimates for juveniles were not significantly different from p estimates for adults (Fig. 5a). Estimates of c were generally higher for juveniles (mean 27.1%) than adults (mean 21.3%) in intervals where both ages were present (Fig. 5b). However, adult γ values (mean 32.9%) were consistently higher than juvenile γ (mean 25.1%) estimates, although this was also not significant (Fig. 5d). Although the estimates of φ differed by age class and time interval, no clear pattern was apparent (Fig. 5c).

Discussion

Salamanders play a key role in the ecosystem function and diversity of temperate forest systems. However, salamanders are often cryptic, making it difficult to accurately estimate demographic parameters. In this study, we used intensive mark-recapture to examine three populations of a little studied stream salamander, *D. brimleyorum*, residing in forests managed for timber production. Our model selections supported time-varying conditional recapture probability (*c*) and temporary emigration (γ). Conditional capture probability (*p*) was constant over time but varied by site. Lastly, survival (φ) and surface abundance (\hat{N}) varied by both time and location.

Our models yielded an average *D. brimleyorum* density of 3.27 individuals per m of stream (approximately 1.31 individuals per m²), across all sites and seasons and adjusted for temporary emigration. This density estimate is comparable to within-stream salamander densities reported in less disturbed Appalachian forests (Table 2). Salamander density at site 2 was nearly four times greater than density at site 1, suggesting that salamander density is highly dependent on local environmental conditions and may vary substantially between locations. Across all three sites, salamander density was lowest in March (mean 0.96 per m²) and highest in June (mean 1.53 per m²). One possible explanation for this pattern is the seasonal timing of salamander recruitment. Larval *D. brimleyorum* typically metamorphose in May, bolstering summer density (Means 2005). Adult and juvenile individuals then die or permanently emigrate throughout the year producing the lowest salamander density in spring, immediately before the next recruitment event.

Our *Desmognathus* density estimates suggest that streams in managed forests can support populations similar in size to those in relatively undisturbed habitats. This underscores the value of managed forests for providing wildlife habitat for stream-associated amphibians. Furthermore, we observed *Eurycea multiplicata* in the stream and *Plethodon glutinosis, Plethodon serratus, Pethodon caddoensis, Ambystoma maculatum,* and *Hemidactylium scutatum* in the surrounding riparian area, providing further evidence that managed forests can support a diverse salamander community. Our study streams are surrounded by delineated SMZs (28-50 m wide) that are not harvested with the rest of the timber stand to protect water quality, which is standard practice under Arkansas Forestry Best Management Practices (Arkansas Forestry Commission 2002). Many studies report the negative effects of timber harvest on salamanders residing in harvested areas (see reviews Kroll 2009; Tilghman et al. 2012), thus the value of managed forests may be reduced if these riparian buffers are not present.

Our study also revealed variation in detection and vital rate parameters that are important for accurate assessment of salamander populations in managed forests in the future. Our pestimates (averaging 12.9%) were lower than those recorded in other studies examining Plethodonid salamander populations using robust design. Bailey et al. (2004b), Bunderman and Liedgold (2012), and Price et al. (2012b) report average p estimates near 30%. Bailey et al. (2004b) noted different p values between species groups and Bailey et al. (2004c) observed that p was influenced by local vegetation and elevation. Therefore, differences in life history and site conditions may account for our lower p estimates. We also observed site variation in p, further supporting the theory that p is dependent on local conditions. Both Bailey et al. (2004b) and Price et al. (2012b) observed temporal variation in p, although both studies had more sampling events per year and were thus more likely to detect seasonal variations in p.

While our *p* estimates were relatively low, our *c* estimates (averaging 22.2%) were substantially higher compared to other robust design salamander studies [Bailey et al. (2004a) reports a mean of 7%, Buderman and Liedgold (2012) reports a mean of 4%, Price et al. (2012b) reports a mean of 8%]. These studies suggested that comparatively low recapture probability in Plethodonid salamanders was due to a negative behavioral response to being captured and handled. In contrast, we observed that the probability of recapture was always higher than the probability of initial capture. As we captured individuals by hand without the use of bait or traps, we think a trap-happy response, where an individual actively seeks recapture, is unlikely. It is possible that *c* is influenced by time of previous release. For example, there may be an adjustment period after release where individuals are more likely to be moving near the surface

of the stream (perhaps searching for their prior refuges) and, thus, more obvious to researchers, when the stream is resampled 4-7 days later.

Similar to other studies on plethodonid salamanders (Bailey et al. 2004c; Bunderman and Liedgold 2012; and Price et al. 2012b), our model selection favors γ estimates that are random (independent of previous availability) and temporally varying. This suggests that the availability of individual salamanders is strongly dependent on season and environmental conditions. Salamanders can remain in refugia (unavailable for capture) for extended periods, only emerging when weather conditions are favorable (Ashton 1975; Petranka 1998). In our study, estimated γ was close to zero in the spring (Apr-Jun), suggesting that this is a time of high surface activity. This result is congruent with Price et al. (2012b), where γ rates for *D. fuscus* were lowest in May and June. This also suggests that \hat{N} estimates made during these months would be close to N_{super}, possibly negating the need for accounting for γ in the spring of a given year when generating point population estimates. Meanwhile, our γ estimates were highest during the winter (Nov-Mar) when salamander activity is assumed to be the lowest. The seasonal nature of our γ estimates support the conclusions of other studies: failure to account for temporary emigration (particularity during some seasons) can result in misleading conclusions about abundance or change in abundance over time (Bailey et al. 2004b; Mazorolle et al. 2007).

While temporal variation of γ was supported, our γ estimates (mean 13.6%) were considerably lower than other studies. Bailey et al. (2004c) reports a mean γ of 87% and Price et al. (2012b) reports a mean of 73%. Our relatively small γ estimates may be due to favorable climate conditions during the years of our study. For example, all three years (2014-2016) of our study were considered wet years for this region, receiving 10.82 cm, 38.05 cm, and 15.32 cm of precipitation over the annual norm respectively (NOAA weather station in Newhope, AR). Price

et al. (2012a) found that γ rates were twice as high in drought conditions, suggesting salamander modify behaviors in response to environmental conditions. Another possible explanation for our small γ estimates is that the habitats (loose rock substrate and relatively few embedded cover objects) of our streams are more amenable to thorough searching than those in other studies.

Our model selection favored models where φ varied by site and primary interval, however estimated φ were consistently high across all sites and seasons, averaging 77% per primary interval (46% mean annual survival). This is the first rigorous estimate of postmetamorphic *D. brimleyorum* survival. In his study, Organ (1961) reports annual survival rates ranging from 11%-57% for five species of *Desmognathus* (*D. quadramaculatus*, *D. monticola*, *D. fuscus*, *D. ochrophaeus*, *D. wrighti*). Danstedt (1975), Price et al. (2012a), and Price et al. (2012b) report *D. fuscus* annual survival rates of 23.8%-42.6%, 24.7%-69.4%, and 3.6%-21.6% respectively. Our φ estimates are within the range of those reported for other *Desmognathus* species, although they are comparatively high. Similar to our analysis, Price et al. (2012b) found strong support for site-specific φ . *Desmognathus brimleyorum* maintained high survival rates following clearcut harvesting of the forest stands surrounding two streams, suggesting that streamside buffers provide adequate habitat to support population maintenance for this species (Halloran et al. 2018, in prep.).

We found little support for the effect of age class (juvenile vs. adult) on any of our demographic parameters, as evidenced by overlapping confidence intervals and inconsistent trends. In contrast to our results, Danstodt (1975) reports a significant difference in annual survival rate between *D. fuscus* individuals under 3 years of age (8.4%-13.9%) and individuals over 2 years of age (23.8%-42.6%), although his study included larval individuals in the under 3 years age class. Similarly, Bunderman and Liegold (2012) found evidence that γ varies with age

class in *P. cinereus* (two classes: juvenile- <35 mm SVL, adult- >35 mm SVL). However, Bunderman and Liegold (2012) found no evidence for an age class effect on encounter probability. In contrast, Peterman et al. (2008)'s model selection for *D. quadramaculatus* favored constant capture probability for individuals under 70 mm SVL and temporally and spatially variable capture probability for individuals over 70 mm SVL. Based on our observations, *D. brimleyorum* grow rapidly and reach sexually maturity within 2-3 years after hatching; whereas many other large-bodied *Desmognathus* species require 3-7 years to reach sexual maturity (Petranka 1998). It is possible that the lack of a prominent age effect on these parameters is driven by the rapid growth of *D. brimelyorum* at our sites. More data and finer age classes with a stringent identification protocol are needed to fully evaluate the effects of age on the parameters estimated in this study.

In this study, we characterized three stream salamander populations in intensively managed timberlands. Our estimates of salamander density and survival were comparable to estimates reported for other *Desmognathus* species in relatively undisturbed forests. This suggests that streams in forests managed for even-aged timber production are able to support viable, dense populations of salamanders. These populations are likely having a substantial effect on ecosystem function in managed forests, including the energetic support of other species of wildlife. While our estimates of temporary emigration were lower than previous salamander studies, we observed strong seasonal variation, underscoring the need to account for both temporary emigration and factors influencing conditional capture probability when investigating demographic parameters of stream salamanders.

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Figures and Tables



Figure 1. Robust design annual sampling schedule at three sites. One rotation represents one calendar year. Population is considered closed (dark gray) between secondary samples (approximately one week apart) and open (light gray) between primary samples (at least two months apart).

Table 1. Model selection results for robust design analysis of capture-recapture data for *D. brimleyorum* at three forested stream sites. Models were constructed by varying capture probability (p), recapture probability (c), survival (ϕ), temporary emigration (γ), and number of individuals not encountered (f0) by time (t) and site ("." refers to parameters held constant). Models are listed in decreasing order of support using Akaike Information Criterion, corrected for small sample size (AICc).

Model	AICc	ΔAIC _c	Model Weight	K
$\varphi(t,site), \gamma(random,t), p(site), c(t), f0(t,site)$	-11936.364	0	0.741	46
φ (t,site), γ (random,t), p(.), c(t), f0(t,site)	-11934.265	2.099	0.259	44
φ (t,site), γ (markovian,t,site), p(site), c(t), f0(t,site)	-11919.311	17.053	0.000	60
φ (t,site), γ (no movement), p(site), c(t), f0(t,site)	-11915.410	20.954	0.000	42
φ (t,site), γ (random,.), p(site), c(t), f0(t,site)	-11913.365	22.999	0.000	43
φ (t,site), γ (random,site), p(site), c(t), f0(t,site)	-11909.270	27.095	0.000	45
φ (t,site), γ (random,t,site), p(site), c(t), f0(t,site)	-11896.331	40.033	0.000	53
φ (t,site), γ (markovian,t,site), p(site), c(t), f0(.)	-11545.513	390.851	0.000	41
φ (site), γ (markovian,t,site), p(site), c(t), f0(.)	-11542.072	394.293	0.000	40
$\varphi(t), \gamma(markovian, t, site), p(site), c(t), f0(.)$	-11540.605	395.759	0.000	41
$\varphi(.), \gamma(markovian, t, site), p(site), c(t), f0(.)$	-11539.750	396.614	0.000	38
$\varphi(.), \gamma(random, t, site), p(site), c(t), f0(.)$	-11536.339	400.025	0.000	26
$\varphi(.), \gamma(\text{markovian,t}), p(\text{site}), c(t), f0(.)$	-11511.411	424.954	0.000	20
$\varphi(.), \gamma(random,t), p(site), c(t), f0(.)$	-11511.161	425.204	0.000	16
$\varphi(.), \gamma(random, site), p(site), c(t), f0(.)$	-11442.588	493.777	0.000	14
$\varphi(.), \gamma(random,.), p(site), c(t), f0(.)$	-11400.883	535.482	0.000	12
$\varphi(.), \gamma(random,.), p(site), c(t,site), f0(.)$	-11398.435	537.929	0.000	24
$\varphi(.), \gamma$ (no movement), p(site), c(t), f0(.)	-11379.601	556.764	0.000	11
φ(.), γ(random,.), p(site), c(.), f0(.)	-11370.950	565.415	0.000	7
$\varphi(.), \gamma(random,.), p(site), c(site), f0(.)$	-11367.054	569.311	0.000	9
φ(.), γ(random,.), p(t,site), c(.), f0(.)	-11193.656	742.708	0.000	21
φ(.), γ(random,.), p(.), c(.), f0(.)	-11142.672	793.692	0.000	5
$\varphi(.), \gamma(random, .), p=c(.), f0(.)$	-11138.624	797.741	0.000	4
$\varphi(.), \gamma(random, .), p(t), c(.), f0(.)$	-11028.632	907.733	0.000	9

 AIC_c =Akaike Information Criteria, corrected for sample size and over-dispersion; ΔAIC_c = difference in AICc relative to the top model; K = Number of parameters in the model.



Figure 2. Model-averaged conditional a) capture probability and b) recapture probability by sampling interval at the three sites using robust design models. Error bars represent 95% confidence intervals.











Figure 4. Model-averaged estimates of apparent survival of *D. brimleyorum* by sampling interval at the three sites using robust design models. Error bars represent 95% confidence intervals. Because of low capture rates in the spring, the survival rate at site 3 for the second Apr-Jun interval is nonsensical, but is likely high.



Figure 5. Estimates of a) conditional capture probability, b) conditional recapture probability, c) apparent survival, and d) temporary emigration for juvenile (less than one year post metamorphsis) and adult groups by sampling interval at all sites using robust design models. Error bars represent 95% confidence intervals.

Citation	Species	Methods	Locality	Habitat Type	Density (m ⁻²)
Bush et al. 2017	D. monticola	Closed-capture CMR	Benton Co., AR	Spring-fed stream	14.5*
Camp & Lee 1996	D. quadramaculatus	Jolly-Seber CMR	Habersham Co., GA ⁺	Spring-fed stream	1.41
Crawford & Peterman 2013	D. monticola, D. ocoee, D. quadramaculatus	Jolly-Seber CMR	Macon Co., NC ⁺	Wet rock face	14.69
Davic & Welsh 2004	D. quadramaculatus	-	Macon Co., NC ⁺	Spring-fed stream	1.73
Hall 1977	D. fuscus, D. ochrophaeus	Jolly CMR	Tioga Co., PA ⁺	Stream and surrounding seeps	1.9
Huheey & Brandon 1973	D. ochrophaeus	Lincoln-Petersen, Jolly, and Schnable CMR	Macon Co., NC ⁺	Wet rock face	3.0- 19.0
Peterman et al. 2008	D. quadramaculatus	Closed-capture CMR	Macon Co., NC ⁺	Spring-fed stream	1.13
Petranka & Murray 2001	D. carolinensis	Removal sampling	Buncombe Co., NC	Riparian old growth forest	1.07
Petranka & Murray 2001	D. wrighti	Removal sampling	Buncombe Co., NC	Riparian old growth forest	0.67
Spight 1967	D. fuscus	Count-based	Orange Co., NC	Spring-fed stream	1.42
Tilley 1980	D. ochrophaeus	Jolly-Seber CMR	Macon Co., NC ⁺	Wet rock face	5.8-6.9
This study	D. brimleyorum	Robust Design CMR	Howard Co., AR	Stream, runoff- fed	1.31

Table 2. Summary of published density estimates for *Desmognathus* salamanders.

* Introduced population, may not reflect density in natural range; ⁺Public land (National or State Parks/Forests)

Appendix



Office of Research Compliance

MEMORANDUM

TO: J.D. Willson

- FROM: Craig N. Coon, Chairman Institutional Animal Care and Use Committee
- DATE: April 4, 2014
- SUBJECT: IACUC APPROVAL Expiration date: March 31, 2017

The Institutional Animal Care and Use Committee (IACUC) has APPROVED protocol 14032: "Occupancy and habitat relationships of stream-associated salamanders in intensively managed forests of the Ouachita Mountains ecoregion"

In granting its approval, the IACUC has approved only the protocol provided. Should there be any changes to the protocol during the research, please notify the IACUC in writing (via the Modification form) prior to initiating the changes. If the study period is expected to extend beyond March 31, 2017 you must submit a new protocol. By policy the IACUC cannot approve a study for more than 3 years at a time. Annually the IACUC will request a report on the status of the protocol.

The IACUC appreciates your cooperation in complying with University and Federal guidelines for involving animal subjects.

CNC/aem

cc: Animal Welfare Veterinarian

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Conclusion

This thesis presents two studies that investigate the population biology of a stream salamander endemic to the Ouachita Mountain region of Arkansas, *Desmognathus brimleyorum*. The objective of the first study was to examine the effects of timber harvest on *D. brimleyorum* populations and investigate possible mechanisms driving harvest-related abundance change. We found that SMZs of 28 m or larger effectively avoided negative effects of timber harvest on *D. brimleyorum* relative abundance and apparent survival up to 2 years post-harvest, when mechanical timber removal occurred in the winter months. However, timber harvesting changed the movement patterns of *D. brimleyorum* in the stream and it is unclear if these changes will have long-term ramifications. We recommend long-term salamander population monitoring in the SMZs of harvested timber stands to evaluate the mechanisms of possible time-lagged responses and longstanding population viability.

The objective of the second study was to estimate vital rate and capture probability parameters of *D. brimleyorum* in managed forests, specifically assessing seasonal, site, and age variation in estimates of capture probability and recapture probability, temporary emigration, abundance, and apparent survival. Our estimates of salamander density and survival varied by season and site and were comparable to estimates reported for other *Desmognathus* species in relatively undisturbed forests. This suggests that streams in forests managed for timber production are able to support viable, dense populations of salamanders. These populations are likely having a substantial effect on ecosystem function in managed forests, including the energetic support of other species of wildlife. While our estimates of temporary emigration were lower than pervious salamander studies, we saw a distinct pattern of seasonal variation,
underscoring the need to account for both temporary emigration and conditional capture probability when investigating demographic parameters of stream salamanders.