INDIVIDUAL, POPULATION AND LANDSCAPE-SCALE

EFFECTS OF TIMBER HARVEST ON THE

RED-LEGGED SALAMANDER (*PLETHODON SHERMANI*)

A Dissertation Presented to the Faculty of the Graduate School

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Doctor of Philosophy

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by

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dissertation entitled:

INDIVIDUAL, POPULATION AND LANDSCAPE-SCALE

EFFECTS OF TIMBER HARVEST ON THE

RED-LEGGED SALAMANDER (*PLETHODON SHERMANI*)

Presented by Grant M. Connette,

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TABLE OF CONTENTS

4. USE OF AUXILIARY PIT-TAG TELEMETRY DATA TO ESTIMATE SURVIVAL

OF A TERRESTRIAL SALAMANDER FOLLOWING TIMBER HARVEST

5. LIFE HISTORY AS A PREDICTOR OF SALAMANDER RECOVERY RATE

FROM TIMBER HARVEST IN SOUTHERN APPALACHIAN FORESTS

6. SUMMARY

LIST OF TABLES

Chapter 5.

LIST OF FIGURES

Chapter 5.

Appendix B.

INDIVIDUAL, POPULATION AND LANDSCAPE-SCALE EFFECTS OF TIMBER

HARVEST ON THE RED-LEGGED SALAMANDER (*PLETHODON SHERMANI*)

ABSTRACT

Habitat loss and alteration are widely recognized as major threats to global

biodiversity and the vulnerability of animal species to these disturbance processes can

depend on the behavioral responses of individuals to modified landscapes. In response to

a changing environment, individuals may either attempt to adapt to changing conditions

or disperse to new habitat. At the local scale, the emigration of individuals or changes in

activity patterns could lead to reduced counts of animals in ecological studies. At broader

spatial scales, organismal movement may enable population rescue or reestablishment

after disturbance and maintain demographic connectivity among populations. These

complex mechanisms underlying the perceived abundance and distribution of species

often requires a careful deconstructing of demographic trends and sampling variation in

ecological data.

Lungless salamanders (Family Plethodontidae) are extremely abundant in many

forest and headwater stream ecosystems of eastern North America. These salamanders

breathe across their moist skin surface, making them sensitive to fluctuations in

temperature and moisture conditions. Thus, changes in habitat characteristics are known

to have a considerable effect on populations of these salamanders. However, studies

identifying the behavioral or demographic causes of declines as well as patterns of long-

term recovery are critically needed.

My dissertation research combined behavioral, population and landscape-scale

studies to identify the effects of timber harvest on a lungless woodland salamander (*Plethodon shermani*). The primary objectives of my research were to 1) to describe the short- and long-term effects of timber harvest on salamander abundance and 2) to determine the behavioral or demographic processes dictating the abundance and distribution of salamanders at both local and landscape scales.

To characterize baseline population dynamics of the salamander, *P. shermani*, I conducted a 5-year capture-mark-recapture study which revealed substantial annual variation in survival, recruitment, and population size under natural conditions. Initial results suggest that differences in recruitment and over-winter survival might be responsible for the lower abundances of terrestrial salamanders in logged areas at the end of this study. In an experimental translocation of salamanders into a timber cut and nearby forest habitat, I found that salamanders respond to differences in habitat quality by altering their movement behavior. This type of behavioral shift might help mitigate the risk of sustaining activity in recently logged forest. In an additional study, I tracked salamanders using a PIT-tag telemetry system in order to identify mortality, rather than emigration or reduced activity, as the likely cause for perceived declines in salamanders immediately following timber harvest. Finally, in a series of landscape-scale surveys, I found that salamander abundance was positively correlated with forest age (i.e., years since harvest), that full population recovery can require greater than 100 years, and that populations of species with greater movement ability may recover faster due to immigration of individuals from surrounding forest. Collectively, these studies identify key behavioral and demographic processes responsible for observed changes in salamander populations and suggest specific strategies for conservation and management.

Chapter 1

INTRODUCTION

Habitat loss and alteration are widely recognized as major threats to global

biodiversity and the vulnerability of species to these disturbance processes can be highly

dependent upon the behavioral responses of individuals to modified landscapes

(Schtickzelle and Baguette 2003, Fahrig 2007). In response to a changing environment,

individuals may either attempt to adapt to changing conditions or disperse to new habitat

(Duckworth 2009, Quintero and Wiens 2013). At the local scale, the emigration of

individuals or changes in activity patterns could lead to reduced counts of animals

(Semlitsch et al. 2008). At broader spatial scales, organismal movement may enable

population rescue or reestablishment after disturbance and maintain spatially-structured

populations (Hanski 1998, Eriksson et al. 2014). These complex mechanisms underlying

the perceived abundance and distribution of species often requires a careful

deconstructing of demographic trends and sampling variation in ecological data (e.g.,

MacKenzie et al. 2006).

Timber harvest is thought to be one of the most important forms of anthropogenic

disturbance in North America (Burton et al. 1999). Due to high domestic demand for

timber products (Shifley 2006) and growing interest in woody biomass as an alternative

energy source (Berndes et al. 2003), forest-management objectives increasingly represent

a balance between the socioeconomic demand for timber and ecological sustainability.

Timber harvest may cause significant changes to forest ecosystems, such as soil

compaction, reduced canopy cover, increased wind exposure, higher air temperatures, and changes in decomposition rates of leaf litter (Keenan and Kimmins 1993, Ash 1995, Brooks and Kyker-Snowman 2008). These changes can have varying effects on the abundance of organisms. For early-successional species, silviculture may be an important tool for creating habitat where land management has historically suppressed natural disturbances, such as fire or flooding (Brawn et al. 2001). In contrast, timber harvest may cause the loss or degradation of habitat for sensitive forest-dependent species (Thompson et al. 1992; deMaynadier & Hunter 1995; McLachlan & Bazely 2001).

Lungless salamanders (Family Plethodontidae) are extremely abundant in many forest and headwater stream ecosystems of eastern North America (Bailey 2004, Peterman et al. 2008). They may also be ecologically important as consumers of invertebrates (Wyman 1998, but see Homyack et al. 2010) and as a supply of energy and nutrients for higher trophic levels (Burton and Likens 1975). These salamanders breathe across their moist skin surface, making them sensitive to fluctuations in temperature and moisture conditions (Spotila 1972, Feder 1983). Thus, changes in habitat characteristics often have a considerable effect on populations of these salamanders. Numerous studies have reported a negative short-term response of plethodontid salamander abundance to timber harvest (reviewed by Tilghman et al. 2012), yet most do not attempt to establish the ultimate fate of individuals. Several studies have suggested that observed declines in salamander counts are at least partially explained by mortality (Petranka 1993, Homyack and Haas 2009), decreased activity and increased refuge use (Johnston and Frid 2002), or dispersal away from harvested areas (Ash and Bruce 1994, Reichenbach and Sattler 2007, Peterman et al. 2011). These possible responses of amphibians to timber harvest have

been summarized as: 1) mortality, 2) retreat and 3) evacuation (Semlitsch et al. 2008).

These hypotheses are not mutually exclusive and clearly underscore the importance of

accounting for behavior in studies of amphibian responses to land use. Specifically,

emigration behavior can reduce relative counts and negatively bias survival estimates

while decreased surface activity would also result in reduced counts of salamanders in

harvested areas. Furthermore, the long-term recovery of salamander populations

following timber harvest is poorly understood. Relative abundance in harvested areas is

thought to remain well below that of mature forest even through 10–15 years of forest

regeneration (Ash 1997, Reichenbach and Sattler 2007, Homyack and Haas 2009).

Projected recovery times have either been extrapolated from long-term monitoring or

estimated from cross-sectional studies of various stand age classes, and results of these

projections are highly disparate (20–100 years; Petranka 1993, Ash 1997, Crawford and

Semlitsch 2008, Welsh et al. 2008). Because of the uncertainty of these estimates and the

high variability of terrestrial salamander counts among sites (e.g., Dodd and Dorazio

2004), studies identifying the behavioral or demographic causes of declines as well as

patterns of long-term recovery are critically needed.

The primary objectives of my dissertation research are: 1) to describe the short-

and long-term effects of timber harvest on plethodontid salamander abundance and 2) to

determine the behavioral or demographic processes dictating the abundance and

distribution of salamanders at both local and landscape scales. In Chapter 2, I present the

results of a 5-year capture-mark-recapture study which characterizes baseline population

dynamics of the salamander *Plethodon shermani* and identifies demographic mechanisms

responsible for initial differences in abundance between harvested and unharvested

forest. In Chapter 3, I describe an experimental translocation study which examined the ability of salamanders to recognize and respond to differences in habitat quality. In Chapter 4, I present a study which combined "PIT-tag telemetry" and visual resighting of animals in order to discriminate between mortality and behavioral explanations (i.e., emigration or reduced activity) as likely causes for perceived declines in salamander counts following timber harvest. Finally, in Chapter 5, I describe a study which used spatially- and temporally-replicated salamander counts to identify the relationship between salamander abundance and forest age. In addition, this study identifies immigration as an important component of post-harvest population growth for species with migratory life histories.

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LOCAL POPULATIONS OF A WOODLAND SALAMANDER (*PLETHODON SHERMANI*) SHOW CONSIDERABLE VARIATION IN POPULATION SIZE, APPARENT SURVIVAL AND RECRUITMENT

Abstract

An accurate understanding of population growth and contributing demographic parameters is highly important in many ecological studies as well as for species monitoring and management efforts. Although plethodontid salamanders are widely believed to exist in stable populations with high individual survival and relatively stable recruitment, few multi-year mark-recapture studies have been conducted to estimate key demographic parameters for populations of these salamanders. We report initial results from an ongoing mark-recapture study of the red-legged salamander, *Plethodon shermani*, which provide a detailed summary of population dynamics of this species over a five-year period (2009–2013). We repeatedly visited 16 (25 x 25m) survey plots on the Nantahala National forest of western North Carolina and recorded 13,816 total captures of 11,580 unique individuals across all sites and years. We found substantial spatial and temporal variation in population size, with estimated densities ranging from 0.22 – 2.16 salamanders per m^2. Monthly apparent survival probability was variable but generally high over the summer active season while recruitment was considerably higher from 2011-2012 and 2012-2013 than in previous years. We also used growth interval data from recaptured individuals to estimate age at maturity of 2-3 years for males and 3+ years for

females. We believe this ongoing study will provide important baseline data on the population ecology of terrestrial plethodontid salamanders and will enable a better understanding of the demographic consequences of habitat alteration.

Introduction

Changes in population size are of critical interest in the fields of ecology, wildlife management and conservation biology (Lebreton, Pradel & Clobert 1993; Ricklefs & Miller 2000; Williams, Nichols & Conroy 2002), yet abundance is often difficult to estimate directly due to factors such as imperfect detection and uneven spatial distributions of organisms (Decesare *et al.* 2012). Furthermore, changes in local abundance or density may exhibit time lags following habitat change (Brooks, Pimm & Oyugi 1999; Harju *et al.* 2010) or fail to reflect habitat quality due to immigration or the spatial segregation of territorial species (Van Horne 1983). As a result, understanding population growth often requires the estimation of contributing demographic rates as well as their spatial and temporal variability. In many cases, species life history can determine whether population growth is more strongly tied to survival or recruitment (Gaillard, Festa-Bianchet & Yoccoz 1998; Sæther & Bakke 2000). Generally, population growth of long-lived, slow maturing species with low fecundity is particularly susceptible to changes in survival (Sæther & Bakke 2000; Schmidt, Feldmann & Schaub 2005).

The majority of woodland salamanders (genus *Plethodon*) are relatively long-lived, slow maturing, and less fecund, compared to most pond-breeding amphibians (Petranka 1998). Woodland salamanders are often considered to be useful indicators of forest health due to their longevity, high densities, sensitivity to disturbance and

populations which are believed to be relatively stable (Welsh & Droege 2001). Although a number of studies have estimated densities of plethodontids using mark-recapture techniques (e.g., Semlitsch 1980; Petranka & Murray 2001; Bailey, Simons & Pollock 2004a; Peterman, Crawford & Semlitsch 2008; Buderman & Liebgold 2012), few multi-year studies have resulted in estimates for survival or recruitment (but see Lee *et al.* 2012; Price *et al.* 2012). Instead, the high survival of individuals has previously been inferred from population size-frequency histograms under an assumption of stable population size among years (Hairston 1983). Although this assumption may be supported by the relatively low variability of salamander counts reported from several studies (Hairston 1983; Smith & Petranka 2000; Welsh & Droege 2001), recent work has identified high annual variability in the number of juveniles sampled (Buderman & Liebgold 2012; Connette, Crawford & Peterman 2014). As a result, studies directly estimating key population parameters such as survival, recruitment and time to maturity are critically needed to appropriately characterize the stability of plethodontid salamander populations and associated demographic rates.

The objective of this study is to empirically determine major components of the population dynamics of the red-legged salamander, *Plethodon shermani*, based on analysis of five years of capture-mark-recapture data from sixteen survey plots. Specifically, we seek to obtain accurate estimates for 1) time to maturity, 2) survival, 3) recruitment and 4) abundance of this species. We also examined how land use effects such as timber harvest might affect key components of salamander population dynamics. For half of our survey plots, our sampling window spans a recent two-aged regeneration

timber harvest and allows initial insight into the potential effects of this partial harvest strategy on salamander populations.

Methods

Study Site

Our study was conducted on the Nantahala National Forest in Clay County, North Carolina, U.S.A. The study area is located along a ridgeline at approximately 1200m in elevation and is dominated by mixed hardwoods (predominantly *Quercus, Carya, Liriodendron*). In 2009, we established four (25 x 25m) capture-mark-recapture plots at each of four forest stands scheduled for commercial timber harvest as part of a U.S. Forest Service management project (Fig. 1). All harvest areas were 11−16 hectares in size and separated by a distance of less than 2.5 km. At each harvest area, our survey plots were divided among the following four treatments: 1) 65m into a harvest area, 2) 10m into a harvest area, 3) 10m outside a harvest area and 4) a control 250m from the nearest harvest area. Timber was harvested during late May and early June of 2011 at one harvest area and during the fall and spring of 2013 at the remaining three harvest areas. Timber was cut according to a two-aged regeneration harvest procedure which will create forest stands with interspersed trees of two distinct age classes by retaining approximately 20 square feet basal area of overstory trees during the current harvest operations.

Field Methods

From 2009−2013, we performed a total of 11−13 area-constrained searches of each plot during the summer active season (May−August). We conducted all surveys

between 21:30 and 05:45 EST. During each survey, 2 observers (occasionally 3)

conducted an area-constrained search of the entire plot. These exhaustive searches

generally lasted 1–2 hours. We hand-captured all salamanders that were encountered

visible on the ground surface but did not disturb natural cover objects. We then marked

each salamander's capture location with a numbered survey flag and placed them in a

sealable plastic bag with moist leaf litter. We conducted surveys at 1–4 plots per night

and then transported all salamanders to the Highlands Biological Station (~ 40 km away)

where they were housed in an environmental chamber at 10°C to limit their metabolism.

We subsequently anesthetized salamanders in a 500mg/L solution of MS-222 buffered

with sodium bicarbonate according to published procedures (Peterman & Semlitsch

2006) and uniquely marked salamanders with visual implant elastomer (Northwest

Marine Technologies, Shaw Island, WA, U.S.A.). We also measured the mass and snout-

vent length (SVL) of each individual prior to returning them to within 5m of their

individual capture location, usually by the second night after capture (range: 1–4 nights

post-capture).

Data Analysis

 *Population Size and Survival.—*We used individual capture history data from our

capture-mark-recapture surveys to generate a detailed summary of *P. shermani*

population dynamics over a five-year period for each of our 16 survey plots. We

independently analyzed data for each survey plot using the superpopulation formulation

(Schwarz & Arnason 1996) of the Jolly-Seber model (Jolly 1965; Seber 1965). We used

program MARK (White & Burnham 1999) to fit models using Markov chain Monte

Carlo (MCMC) simulation, with uninformative priors assumed for all parameters. We calculated the mean and 95% credible intervals for all model parameters based on posterior summaries of 20,000 MCMC iterations after an initial burn-in of 20,000 iterations.

To identify temporal patterns in apparent survival, as well as any initial effects of timber harvest, we considered a single model structure where survival varied among all survey periods. Recruitment was constrained to occur only between summer active seasons because all first-year juveniles have likely entered the population by early summer, regardless of their availability for capture. Based on previous research (Connette & Semlitsch 2013, 2014), we assumed that individual detection probability would vary primarily as a function of rainfall. Thus, we fit the model with rainfall over the three days prior to each survey as a covariate for detection probability.

Individual Growth.—We used growth interval data from recaptured individuals (excluding post-harvest captures) to estimate the expected growth trajectory and time to maturity for *Plethodon shermani*. We fit a von Bertalanffy growth curve using a hierarchical modeling approach that accommodates natural variation in growth as well as measurement error in capture-recapture data (Eaton & Link 2011). We conducted a Bayesian analysis of this growth model in the program JAGS (Plummer 2003) using the R2JAGS package (Su & Yajima 2014) in program R (R Core Team 2012). We assigned uninformative uniform priors to all model parameters. Because brood sites and recently hatched individuals have never been found for this species, we used the mean size of hatchlings observed in the month of May (18.08 mm) as the starting size (age 0) of the

growth curve. We then generated estimates for age at maturity for males using two different size thresholds: the size of the smallest male showing mental gland development (43.1 mm) and the size of the first male above the 5th percentile of SVL for individuals showing mental gland development (48.4 mm). Similarly, we derived two estimates for age at maturity in females using both the size of the smallest gravid female observed (49.4 mm) and the size of the first female above the 5th percentile of SVL for gravid females (51.8 mm). We generated posterior summaries for model parameters from 500,000 iterations of three parallel Markov chains following a burn-in of 500,000 iterations. These posterior samples were then thinned at a rate of 1/20 and convergence was assessed using the Gelman-Rubin statistic (Gelman & Hill 2007).

Results

We recorded 13,816 total captures of 11,580 salamanders during our five-year mark-recapture study. Recapture rates averaged 21% during plot surveys and occasionally reached greater than 40% by the end of the 2013. Most captures were of *P. shermani* (N=11,948; 2,093 recaptures), followed by *Desmognathus ocoee* (N=1,219), *Eurycea wilderae* (N=481), *P. serratus* (N=60), *D. wright* (N=41), *D. aeneus* (N=28), *Notophthalmus viridescens* (N=26), *Gyrinophilus porphyriticus* (N=3), and *D. monticola* (N=2).

Population Dynamics

Population size of *Plethodon shermani* (Fig. 2) ranged from 138 to 1,350 at individual survey plots and at certain times during our study. This corresponded to a

range of densities of 0.22 – 2.16 individuals per m^2. The mean point estimate for all plot-survey combinations was 552 individuals, or a mean density of 0.88 individuals per m^2. Relative counts of salamanders captured showed a positive correlation with mean population size estimates across plots (Fig. 3).

Mean monthly apparent survival probability during the summer active season (June-July and July-August intervals) was estimated at 0.92 ± 0.06 (mean $\pm$ 1 SD) across all plots for all pre-harvest surveys. Mean apparent survival for the approximately 10-month overwinter period (August – June) was estimated to be 0.67 ± 0.12 (mean $\pm$ 1 SD) pre-harvest. By combining these overwinter and summer survival probabilities (i.e., 0.92^2 x 0.67), we obtained an estimated apparent survival of 0.57 annually across all individuals in the population (juvenile and adult). We also calculated per-capita recruitment, f, as the ratio of the estimated number of new entries into the population, B, and the population size, N, at the previous survey; $f_t = B_t/N_{t-1}$. Recruitment varied considerably among sites within years, but was considerably higher on average in 2011 – 2012 and 2012 – 2013 (0.99 ± 0.81; mean $\pm$ 1 SD) than in the two previous years (0.38 ± 0.37; mean $\pm$ 1 SD). Finally, the three-day rainfall total prior to a survey was a highly significant predictor of individual detection probability in the independent analysis for each survey plot, with detection probability predicted to vary from 0.027 – 0.247 across the observed range of rainfall.

Survey plots which had timber harvested according to a two-aged regeneration method generally exhibited pre-harvest apparent survival and recruitment rates which were similar to un-harvested plots. Apparent survival during the summer active season remained fairly constant from pre- to post-harvest in all plots (Fig. 4). In contrast, over-

winter survival increased considerably from pre- to post-harvest across all plots with the largest increases coming in un-harvest plots (Fig. 5). Similarly, per-capita recruitment increased on average from the pre- to post-harvest period but with the largest increases occurring in un-harvested plots (Fig. 6). Although estimated population sizes in harvested plots did not show severe declines following timber harvest, point-estimates for population size of the two un-harvested plots exceeded the two harvested plots at each of our four harvest units by the final survey of 2013 (Fig. 3).

Individual Growth

Across all years, we captured just 16 gravid female *P. shermani*, with these observations generally occurring in early summer sampling. Thus, we believe that females at our study location likely brood eggs belowground throughout the summer and into the fall. First-year juveniles (hatchlings) are then observed above-ground beginning in the spring. Using typical hatchling body size in June to represent an Age 0 individual, we estimate time to maturity of 1.69 years for males (95% CRI: 1.59 – 1.79) based on the body size of the smallest male with mental gland development or 2.38 (CRI: 2.25 – 2.52) for the 5th percentile of males showing mental glands. Similarly, estimated time to maturity was 2.53 (CRI: 2.38 – 2.68) based on the body size of the smallest gravid female and 3.02 (CRI: 2.85 – 3.19) for the 5th percentile of gravid females. This suggests that males could reach maturity by their second or third summer, while females should reach maturity by their third summer at the earliest. Individuals are predicted to reach an average body size of 35.5mm by the end of their first year, 45.7mm by the end of their second year, 51.7mm by the end of their third year, and 55.2mm by the end of their

fourth year (Fig. 7). Expected asymptotic size was estimated at 60.3mm (CRI: 58.7 – 61.8). Because model-based age prediction will often be limited for individuals approaching asymptotic body size (Eaton & Link 2011), we could not reliably estimate longevity from observed body size data alone. However, a number of individuals first captured in 2009 at greater than the expected asymptotic body size were recaptured in 2013, suggesting a likely minimum age of 5-6 years at first capture and an age of at least 10-11 years in 2013.

Discussion

Understanding population growth is a key focus of wildlife management and conservation efforts. In many cases, this requires the estimation of demographic rates (e.g., survival, recruitment) as well as their spatial and temporal variability. Although a number of studies have estimated densities of plethodontid salamanders using mark-recapture techniques (e.g., Semlitsch 1980; Petranka & Murray 2001; Bailey, Simons & Pollock 2004a; Peterman, Crawford & Semlitsch 2008; Buderman & Liebgold 2012), few multi-year studies have been conducted to identify population growth trends or to characterize variability in critical demographic rates (but see Lee *et al.* 2012; Price *et al.* 2012; Zipkin *et al.* 2013).

The results of our mark-recapture study indicated a high baseline level of spatial and temporal variation in population size, apparent survival and recruitment rates of the red-legged salamander, *P. shermani*. Although survival estimates derived from mark-recapture studies typically represent underestimates in the presence of permanent emigration of individuals from a study area (Lebreton *et al.* 1992), the extent of this

problem depends on the scale of animal movements in relation to the size of the study

area (Marshall *et al.* 2004; Schmidt, Schaub & Steinfartz 2007; Zimmerman, Gutiérrez &

Lahaye 2007). Terrestrial salamanders of the genus *Plethodon* are typically assumed to

undertake extremely short dispersal movements (~ 8m; Liebgold, Brodie III & Cabe

2011) and maintain small, stable home ranges (Madison & Shoop 1970; Kleeberger &

Werner 1982; Nishikawa 1990). Thus, we believe that apparent survival estimates

generated in this study are likely not substantially lower than true survival and entry (i.e.,

recruitment) probabilities derived from mark-recapture analyses are more likely to reflect

local reproduction than immigration of individuals from surrounding areas.

Our results indicate that monthly survival was variable but that survival

probabilities were higher on average during the overwinter period (0.97) than during the

summer active season (0.92). Although desiccation may be an important source of

mortality during the summer, Schmidt et al. (2007, 2014) suggested that lower survival of

amphibians during the active season might indicate the influence of biotic processes such

as competition and predation on individual survival, whereas survival during the inactive

period would likely be limited by abiotic factors such as winter severity. Active season

survival, therefore, could be further modulated by weather conditions which impact

ground surface activity and potential foraging time (Peterman *et al.* 2013). Although

longer time series would be needed for definitively identifying the effects of rainfall on

survival, we note that monthly apparent survival during the active season was

considerably higher (0.96 ± 0.04; mean ± 1 SD) in un-harvested plots during two years

with high summer rainfall, 2010 and 2013, than in two years, 2011 and 2012, with

relatively low rainfall (0.89 ± 0.08; mean ± 1 SD). Just one survey was completed at 14

of 16 plots in 2009, so active season survival estimates could not be calculated for this year. Per capita recruitment also varied considerably among years and study plots (see also Buderman & Liebgold 2012). In particular, an atypically wet year prior to our 2013 field season (~ 282 cm rainfall from 1 June, 2012 to 31 May, 2013) corresponded with extremely high recruitment, especially in un-harvested areas (1.53 ± 1.22 per-capita; mean ± 1 SD). Furthermore, this difference in recruitment between harvested and un-harvested plots appeared to an important driver of the overall higher abundance estimates in un-harvested plots at the end of our study.

Although over-winter survival and recruitment tended to be lower in harvested plots, our initial results fit with a broader tendency for salamander abundance to decline less following partial harvest than after clearcutting (Semlitsch et al. 2009; Tilghman, Ramee & Marsh 2012), when terrestrial salamanders may completely disappear from harvested areas (Ash 1997). Because terrestrial plethodontid salamanders extensively use below-ground retreats or natural cover objects (Grover, 2006, Petranka & Murray, 2001, Taub, 1961) and show extreme variation in detection probability (Bailey, Simons & Pollock 2004b; Dodd Jr. 2004; Buderman & Liebgold 2012; Connette & Semlitsch 2013; Peterman & Semlitsch 2013), the results of our mark-recapture study should ultimately confirm that timber harvest generates a difference in abundance between harvested and un-harvest plots while identifying the demographic processes responsible. Furthermore, we have previously found evidence in this system that detection probability initially increases following timber harvest (Connette & Semlitsch 2014), providing additional evidence that lower abundances are not simply due to a reduced probability of encountering individuals.

Management Implications

Population demographic rates may be more immediately affected by habitat change than population size (Brooks, Pimm & Oyugi 1999), making them particularly useful for early identification of environmental stressors (Todd 2006). Because an accurate understanding of demographic processes often requires extensive mark-recapture effort or spatially- and temporally-replicated count surveys (Williams, Nichols & Conroy 2002; Zipkin *et al.* 2013), time and resources are frequently devoted to monitoring a subset of possible species which are believed to be effective indicators of habitat quality or ecosystem function (Wiens *et al.* 2008; Caro & Girling 2010). These indicator species may be preferred for monitoring due to their large populations, ease of sampling, sensitivity to environmental conditions and well known life histories (Caro & O'Doherty 1999). Although plethodontid salamanders are considered useful indicators of forest health (Welsh & Droege 2001), most baseline studies on their population dynamics are limited in inference due to the use of relative counts to assess demographic trends. Our 5-year mark-recapture study represents an important case study and reveals the complex dynamics of *P. shermani* populations that exhibited considerable variation in population size, apparent survival and recruitment through time. Time to maturity is likely 2-3 years in males and 3+ years in females, with some individuals likely living to greater than 10 years of age. Although mean annual survival is relatively low, suggesting high turnover, future stage-structured analyses may elucidate differences in survival rates among age classes.

Acknowledgements

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Figure 1. Map indicating the locations of timber harvest units and 25 x 25m salamander

mark-recapture plots on the Nantahala National Forest, North Carolina, U.S.A.
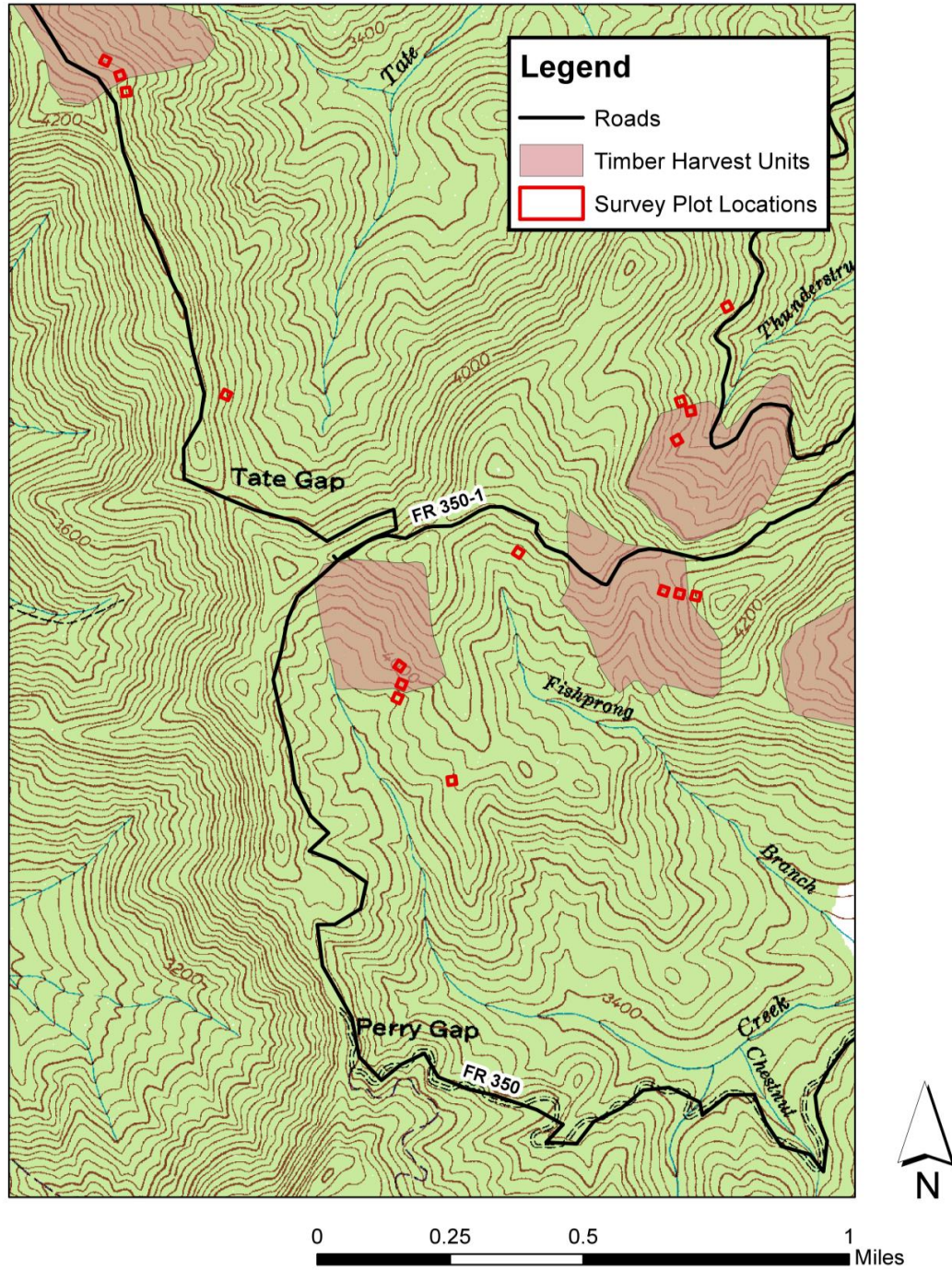
Figure 2. Estimated abundance of *Plethodon shermani* through time at 16 mark-recapture plots. Population size estimates for each plot are based on an independent analysis of a Jolly-Seber model with fully time-dependent survival and recruitment constrained to occur between summer active seasons. Black arrows indicate the date at which plots at the center and edge of a harvest unit had timber removed according to a two-aged regeneration method.
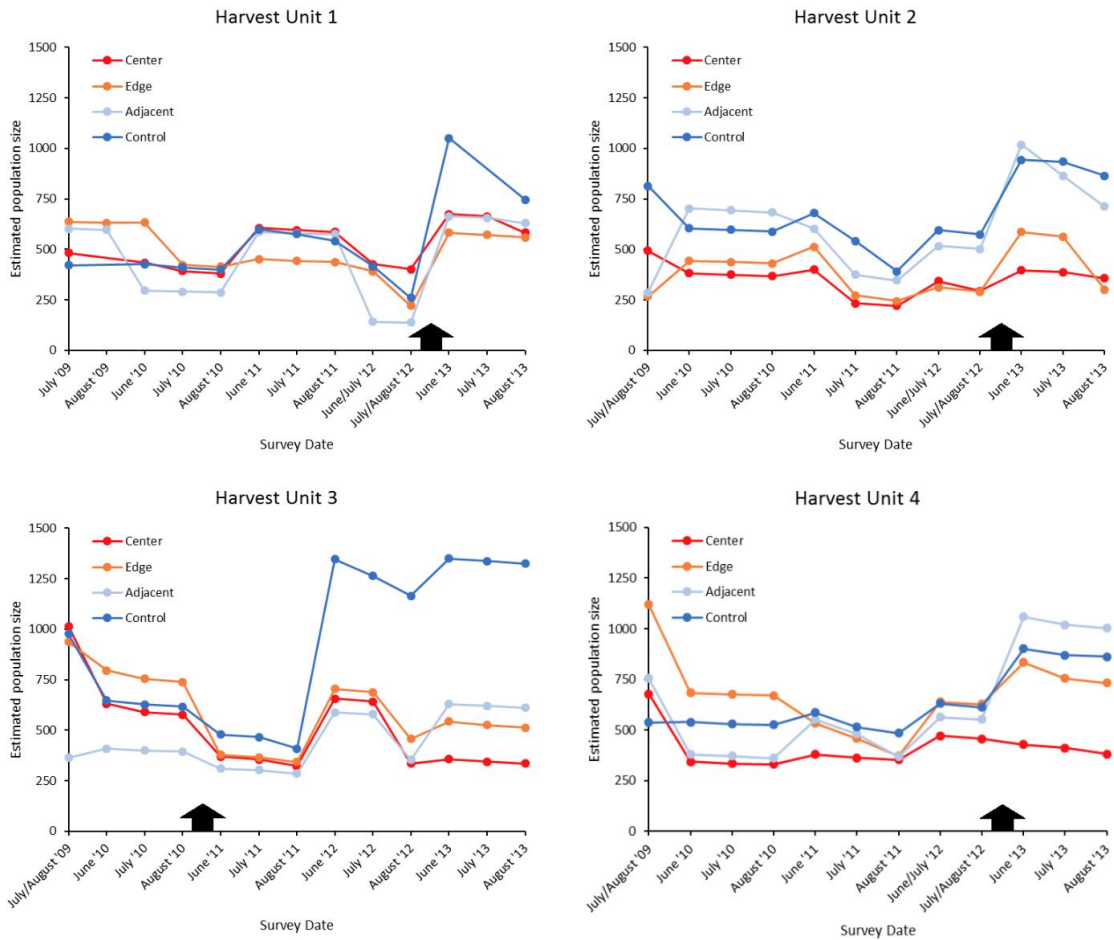
Figure 3. Correlation between the mean number of individuals collected and the mean estimated population size for each survey plot based on mark-recapture analysis.
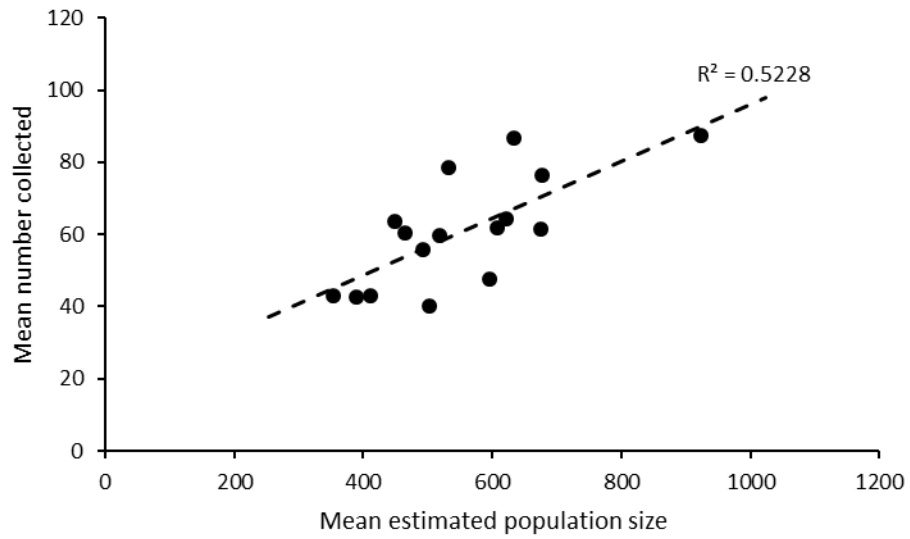
Figure 4. Estimates for summer monthly apparent survival probability. Treatment points represent averages across all harvested plots (center and edge of harvest area; N=8). Control points represent averages across all un-harvested plots (adjacent to harvest area and control; N=8). Error bars represent the standard errors of plot-specific point estimates.
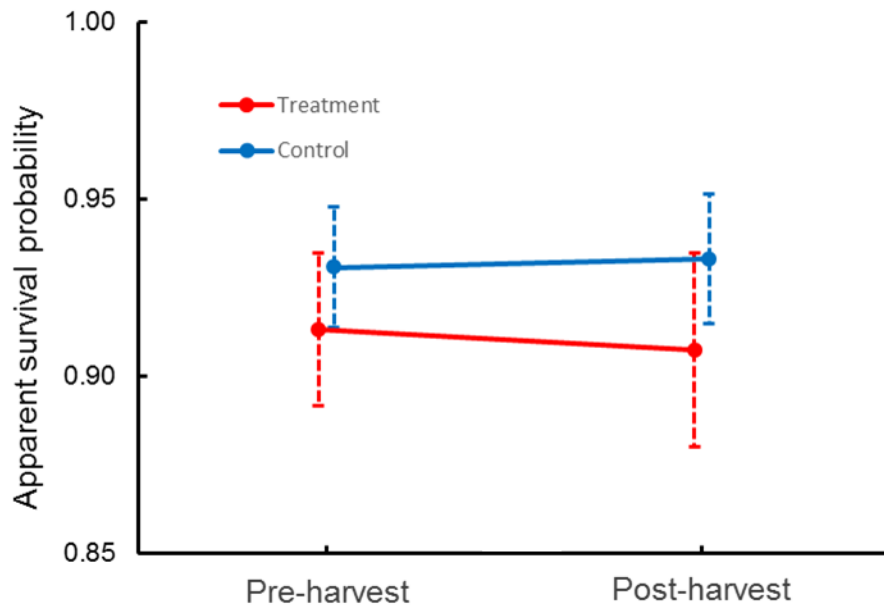
Figure 5. Estimated apparent survival probability across the entire over-winter period (~ 10 months between active season sampling). Treatment points represent averages across all harvested plots (center and edge of harvest area; N=8). Control points represent averages across all un-harvested plots (adjacent to harvest area and control; N=8). Error bars represent the standard errors of plot-specific point estimates.
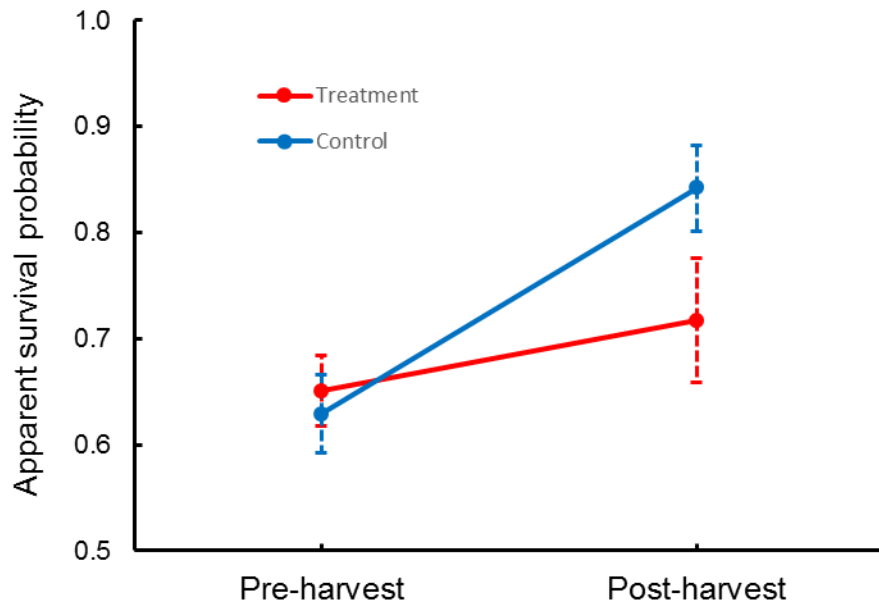
Figure 6. Estimated per-capita recruitment between summer active seasons. Treatment points represent averages across all harvested plots (center and edge of harvest area; N=8). Control points represent averages across all un-harvested plots (adjacent to harvest area and control; N=8). Error bars represent the standard errors of plot-specific point estimates.
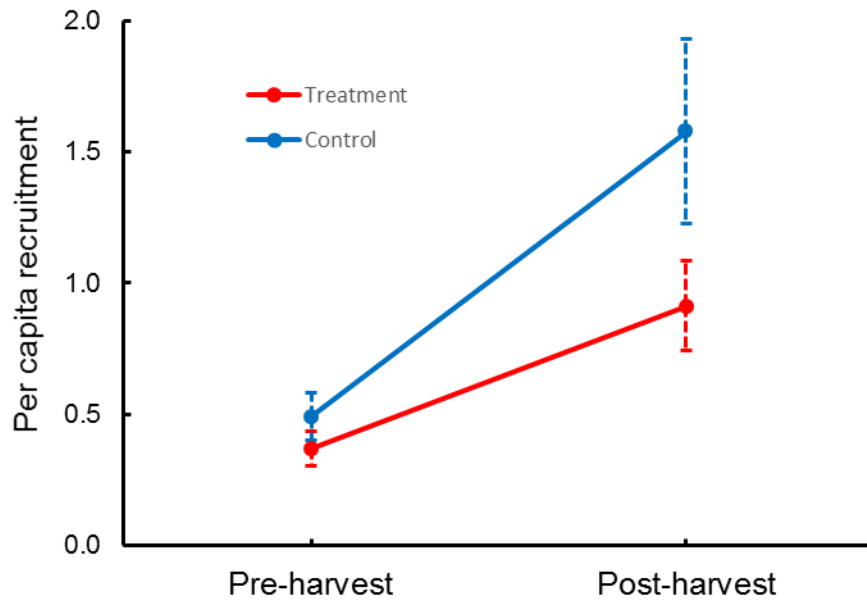
Figure 7. The black line indicates the expected growth curve of red-legged salamanders, *Plethodon shermani*. Gray lines indicate 35 simulated growth trajectories which illustrate the estimated level of variation in growth among individuals.
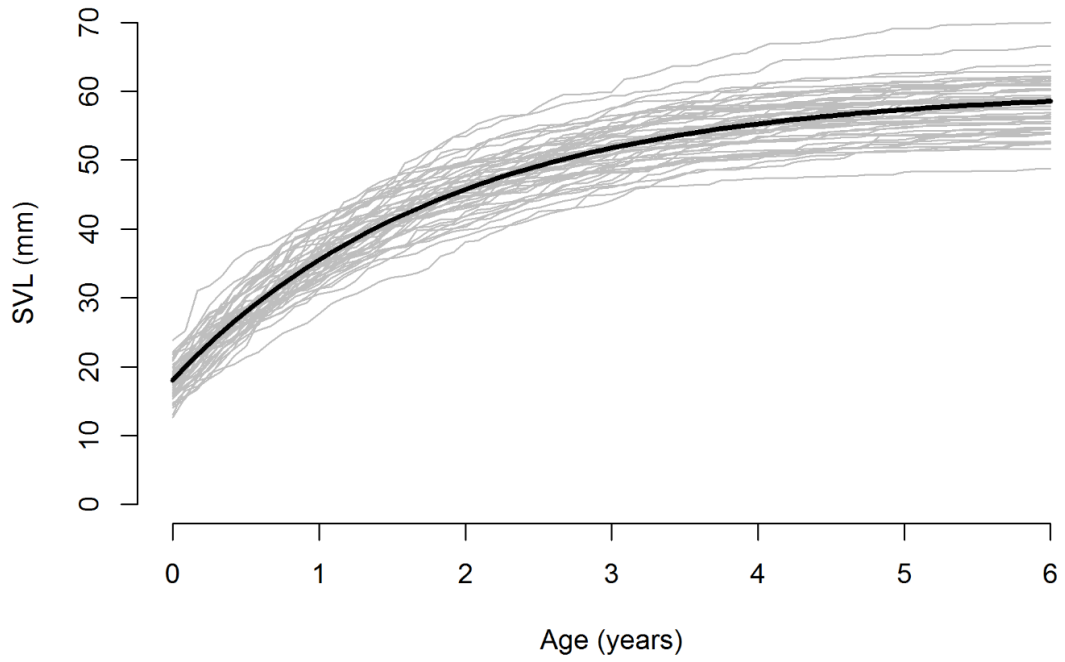
Chapter 3

CONTEXT-DEPENDENT MOVEMENT BEHAVIOR OF WOODLAND

SALAMANDERS (*PLETHODON*) IN TWO HABITAT TYPES

Abstract

Animal movement is critical to the maintenance of functional connectivity at the

landscape scale and can play a key role in population persistence and metapopulation

dynamics. The permeability of habitat to animal movement may vary as a result of either

differential mortality, physical resistance, or simply the behavioral responses of

organisms to perceived habitat quality. Understanding how and when animal movement

behavior varies among habitat types is critical for identifying barriers to dispersal and

predicting species distributions in relation to landscape features. We conducted an

experimental translocation study and compared the movement success and behavioral

strategies of plethodontid salamanders in both forest and open-canopy habitat. We found

that individuals in closed-canopy forest oriented more strongly towards their home ranges

and moved significantly farther on their release night. In spite of the clear differences in

movement paths, the ultimate movement success of homing salamanders did not appear

to vary with habitat type. Our study contributes to a growing body of literature suggesting

the importance of recognizing the context dependence of animal movement behavior.

Because the movement rates of displaced salamanders were significantly reduced in

open-canopy, dispersal rates of plethodontid salamanders in open-canopy habitat are likely lower than in control forest. Further mechanistic studies focusing on habitat-specific movement behavior and survival costs will be valuable for effectively identifying and mitigating barriers to animal movement.

Introduction

"Functional connectivity" describes the extent of movement across a landscape resulting from both the spatial arrangement of landscape features (such as high-quality habitat patches) and the actual movement behavior of organisms in response to the landscape (Kindlmann and Burel 2008). Thus, the behavioral responses of individuals to habitat boundaries and to the perceived quality of the inter-patch matrix can be important determinants of landscape-scale movement patterns (Baguette and Van Dyck 2007). The matrix between high-quality habitat patches may vary greatly in the extent to which it facilitates or impedes animal movement (Ricketts 2001). This can occur when there are true differences in energetic cost or mortality risk associated with movement (e.g., Belichon et al. 1996, Rothermel 2002) or when movement strategy and frequency are influenced by the behavioral responses of individuals to the inter-patch matrix. Individuals of many species show inter-patch movement behavior (e.g., Ferreras 2001, Haynes and Cronin 2006) or responses to habitat boundaries (e.g., Schtickzelle and Baguette 2003, Stevens et al. 2006) which vary with landscape composition. For instance, animals may avoid crossing habitat boundaries or exhibit movement paths that vary in movement rate or straightness depending on the matrix habitat type (Haynes and Cronin 2006). Such context-dependent behavior can result in different probabilities of inter-population movement across different intervening habitat types. As a result, the dynamics

of spatially structured populations may be very sensitive to the behavioral responses of individuals to perceived risk while moving (Revilla and Wiegand 2008). The importance of understanding animal movement behavior has become increasingly apparent as species are faced with the alteration, loss, or fragmentation of their habitat (Fahrig 2007). Recently, species conservation and management efforts have begun to recognize the importance of maintaining or improving connectivity (Beier et al. 2008). In order to predict species responses to landscape structure, many classes of models have been used to quantify the influence of landscape features on functional connectivity. These include individual-based movement models (e.g., Walters 2007, Revilla and Wiegand 2008), least-cost path analysis (e.g., Larkin et al. 2004), graph theory (e.g., Urban and Keitt 2001, Minor and Lookingbill 2010), and circuit theory (e.g., McRae and Beier 2007). A commonality of these models is that different habitat types must be assigned appropriate resistance values, which represent the degree to which they facilitate or impede the movement of organisms. Because observing natural movement behavior can be difficult (Ims and Yoccoz 1997), many studies rely heavily on expert opinion to estimate landscape resistance values (Zeller et al. 2012). This clearly highlights the need for empirical studies of animal movement behavior in matrix habitat (Knowlton and Graham 2010, Zeller et al. 2012). Because the movement behavior of organisms may differ with habitat type, an understanding of how and when species exhibit context-dependent movement behavior will be critical for recognizing and mitigating threats to regional species persistence.

Little is known about dispersal behavior in woodland salamanders (genus *Plethodon*) and, although they are believed to have limited dispersal ability (Liebgold et

al. 2011), they have previously been found to traverse up to 55 m in the process of colonizing high-quality habitat patches isolated in open field (Marsh et al. 2004). These species are fully terrestrial and spend the majority of their time below ground or beneath cover objects, emerging on moist nights to forage on small invertebrates (Petranka 1998). All salamanders in the genus *Plethodon* are lungless and depend on maintaining a moist skin surface for cutaneous respiration, making them highly sensitive to warm, dry conditions which put them at increased risk of desiccation (Spotila 1972). As a result, these forest-dependent salamanders may experience greater risk while moving in open-canopy habitat and, as ectotherms, a greater metabolic cost to surface activity at warmer temperatures (Homyack et al. 2011). Although we are not easily able to study natural dispersal behavior in *Plethodon*, translocation experiments allow insight into their movement distances, movement rates, and behavioral decisions in response to different landscape features (Bélisle 2005, Knowlton and Graham 2010). We conducted experimental displacements to determine whether woodland salamanders (genus *Plethodon*) exhibit context-dependent movement behavior in response to habitat quality. Using homing success as an indicator of landscape resistance, we also sought to quantify the potential for open-canopy habitat to function as a barrier to movement in these forest-dependent salamanders.

Methods

Study site and species

The present study was conducted in the Nantahala National Forest of southwestern North Carolina, approximately 10 km east of Hayesville (34.9997ºN,

83.6193ºW). The area consists primarily of mixed deciduous forest at an elevation of approximately 830 m. Our research was conducted at the site of a 2008 timber cut, during which a basal area of 20 square feet of scattered overstory trees was retained. In this study, we examined the movement behavior of salamanders of the genus *Plethodon*. Terrestrial plethodontids are ideal for displacement studies because they typically maintain stable territories in terrestrial habitat and are capable of homing to these territories following experimental translocation (Madison and Shoop 1970, Kleeberger and Werner 1982, Ousterhout and Liebgold 2010). Several studies have indicated that olfactory cues likely contribute to the homing ability of *Plethodon* salamanders (Madison 1969, Madison and Shoop 1970). Our study area was located 1.1 km NWW and 1.7 km NE of two localities of similar elevation where *P. shermani* and *P. chattahoochee* are known to hybridize. Therefore, salamanders used in our study were assumed to be hybrids of these species and typically showed coloration intermediate between *P. shermani* and *P. chattahoochee*.

Collection of animals

We captured 52 large *Plethodon* salamanders in a 6 m x 60 m collection area in the forest alongside a timber harvest plot. This rectangular collection area was arranged parallel to the edge of the harvested area at a distance of 4–10 m from the forest edge. We captured salamanders by hand during nighttime surveys between 15 June and 25 July 2010 and marked their capture locations with numbered flags. We collected salamanders on the day of a rainfall event and only captured individuals that exceeded 40 mm in snout–vent length (SVL) in order to restrict our sampling to individuals that were most

likely sexually mature or approaching maturity. Overall, individuals ranged in size from 40.3 to 72.0 mm SVL. We transported all salamanders ~ 70 km to the Highlands Biological Station in Highlands, NC. We implanted all individuals with 12.5-mm passive integrated transponder (PIT) tags (TX1411SST; Biomark, Boise, ID, USA) on the following day (Connette and Semlitsch 2012). On the second night after capture, we returned all salamanders to the field for experimental release. Prior to release, we allowed all salamanders a minimum recovery period of 32 h after any stress which may have been associated with handling and PIT tag implantation.

Experimental displacement

We sought to assess the context dependence of salamander behavior as well as the resistance of open-canopy habitat to movement. We displaced salamanders into a recent timber cut and into forest habitat as a control condition and compared both homing success and characteristics of salamander movement paths in these two habitat types. We randomly assigned an equal number of salamanders to either of our two treatments: a 35-m displacement into the timber cut (N=26) or a 35-m displacement further into the control forest (N=26). Because salamanders were initially captured 4–10 m from the edge of the timber cut, all individuals displaced 35 m in the direction of the timber cut had to cross at least 25 m of open-canopy habitat in order to return to their initial capture location. Our random assignment of individuals resulted in 13 known males and a mean SVL (± 1 SD) of 63.1 ± 5.5 mm in our open-canopy treatment group compared to 9 known males and a mean SVL of 60.2 ± 7.6 mm in our control treatment group. We measured the displacement distance for each salamander relative to their unique capture

location to ensure that each salamander was released exactly 35 m from their presumed home range. This distance was selected to fall within the range over which con-generics have proven successful at homing to their territories following experimental displacement (Madison and Shoop 1970, Marsh et al. 2004). Furthermore, typical dispersal distances are likely less than 10 m (Liebgold et al. 2011), indicating that salamanders are unlikely to have prior experience with areas 35 m away from their capture sites.

We performed all salamander releases across five nights, with release cohorts ranging in size from 6 to 20 individuals. To ensure that conditions were somewhat hospitable to movement but not uniformly wet, salamander cohorts were always captured on rainy days and experimentally released two nights later. We released each salamander at a unique bearing from its home range in order to control for the possibility of directional biases in salamander movement due to unforeseen weather or microclimatic gradients. The bearing from each salamander's release location to its home range varied from 147° to 201° in the timber cut (mean=171) and from 311° to 24° in the control forest (mean=0). This also ensured that each individual experienced a different set of microhabitat conditions between its release location and its home range.

We used fluorescent powder (e.g., Rittenhouse and Semlitsch 2006, Ousterhout and Liebgold 2010) to track the initial movement behavior of a subset of 42 salamanders. For these individuals, we coated the tail and posterior half of the body with fluorescent powder prior to release. We then placed each individual under a 4-inch diameter clay pot at their release site and allowed them a 5-minute recovery period after handling. A researcher with a dim ultraviolet light then slowly lifted each clay pot and carefully left the area, to minimize effects on the salamander's behavior. We performed all salamander

40

releases shortly after dark, typically staggered between 21:30 and 23:00 EST. After

allowing 3 h of uninterrupted movement, we returned with an ultraviolet light and located

each salamander's powder trail. We used survey flags and colored paper clips to mark the

final location of each powdered salamander as well as any turns of greater than 2° along

the trail. When we were unable to locate salamanders, we used the last detected point on

the trail as the endpoint of a salamander's movement path. We later returned during the

day to map the movement path of each salamander by recording the distance and bearing

between each turn of the salamander's movement trail.

PIT telemetry

To evaluate salamander homing success through our treatments, we conducted

PIT telemetry surveys of the 6 m x 60 m collection area using an FS-2001F-ISO reader

and a BP portable antenna (Biomark, Boise, ID, USA). In total, we performed 15 surveys

from 18 June 2010 to 7 July 2011. We conducted surveys on the first and third night after

each release as well as opportunistically on wet nights when we expected increased

salamander activity on the ground surface. To further increase the probability of detecting

these nocturnal salamanders at or near the surface, we conducted each survey between

21:30 and 1:00 EST. Because release nights were staggered throughout the summer of

2010, the number of opportunities to detect salamanders differed by release cohort

(range: 5–15 surveys). However, salamanders within release cohorts were evenly divided

between the two displacement treatments. During each survey, a single observer

systematically scanned the entire ground surface within the 6 m x 60 m collection area and recorded the PIT tag identification of any salamanders detected. For the purpose of analysis, a salamander detected within the collection area at any point during the PIT telemetry surveys was counted as a homing success.

Data analysis

From powder trails obtained on release nights, we calculated the initial orientation of each salamander as the bearing from the release point to the final point of each salamander's movement path. We then performed a separate V test (Durand and Greenwood 1958) for each treatment group in order to determine whether salamanders in each habitat type showed a significant tendency to orient their movement towards their initial capture location. This test evaluates whether a set of bearings are randomly distributed with respect to a predicted direction.

We calculated the total distance travelled by each salamander as the sum of all straight-line movements between turns along its powder trail. We then used a one-way analysis of variance (ANOVA) to compare the total distance travelled by salamanders between treatment groups. For this analysis, we excluded data from a single individual which was identified as an outlier in order to meet the distributional assumptions of the model. Because the total distance travelled was confined to a standardized 3-h time period, our discussion of these results generalizes differences in movement distances by referring to them as movement rates.

Path straightness was calculated for each salamander as the total distance travelled divided by the salamander's net displacement (straight-line distance between the

two endpoints of its movement path). Because path straightness values for each individual were on a bounded 0–1 scale, we performed a one-way ANOVA with a binomial error structure to compare path straightness between our two treatment groups. Finally, we used a G-test to compare the homing success of salamanders moving through forest and the timber harvest plot.

This research was conducted under a North Carolina Wildlife Resources Commission collection permit (10-SC00405) and according to approved IACUC protocols at the University of Missouri (protocol #6144) and the Highlands Biological Station. All statistical analyses were performed in program R (R Development CoreTeam 2012).

Results

To determine whether salamanders moving through a forest exhibited fundamentally different behavior from those moving through a timber harvest plot, we characterized individual movement behavior according to orientation, path straightness, and total distance travelled. Salamanders displaced into forest appeared to show strong orientation towards their home range (V-test, $r=0.43$, $p<0.01$), while those displaced into the timber cut did not (V-test, $r=0.20$, $p<0.11$; Fig. 1). The movement paths of individuals travelling through forest did not differ in straightness from individuals moving through the timber harvest plot ($F_{1,39}=1.39$, $p=0.25$). Fluorescent powder tracking also allowed us to determine that salamanders in the forest moved significantly farther (5.44 ± 3.23 m, mean ± 1 SD) during their initial 3 h of movement than salamanders displaced into the timber harvest (3.15 ± 3.10 m) ($F_{1,38}=14.08$, $p<0.001$). However, the longest movement

path recorded was of a salamander in the timber harvest which was found on the ground surface at the end of a 15.5 m movement trail. After removing this path as an outlier, the mean movement distance of the remaining salamanders released in the timber cut was just 2.51 ± 1.48 m (Fig. 2). No other salamander released in the timber harvest moved more than 5 m, compared to 52% (11 of 21) of salamanders displaced into the forest.

Of the 52 salamanders implanted with PIT tags prior to experimental displacement, 35 individuals (67.3%) were eventually detected within the forested collection area along the boundary of the timber harvest plot. There was no significant difference in return success between habitat types (G=0.09, p=0.92) and a majority of animals in both treatment groups successfully returned to the vicinity of their initial capture locations. Across all PIT telemetry surveys, 69.2% of salamanders (18 of 26) were detected after successfully returning through the timber cut and 65.4% (17 of 26) were detected following movement through the forest. Detection rates were fairly low during PIT telemetry surveys, ranging from 5% on the night after the first cohort was released to a maximum of 36.5% of possible animals detected (mean ± 1 SD: 24.2 ± 11.8%). During these surveys, tagged animals were seldom detected on the ground surface. Although our relatively low detection rates during PIT telemetry surveys limited our ability to compare return rates through our two habitat treatments, more individuals displaced into forest were detected back in the collection area on the first and third nights following their release. Four of five individuals detected within the collection zone on the first night after release had returned through forest. Five out of eight individuals known to have returned by the third night after release moved through the forest (Fig. 3).

Discussion

Animal movement is critical to the maintenance of functional connectivity at the landscape scale and can play a key role in population persistence and metapopulation dynamics. The permeability of habitat to animal movement may vary as a result of either differential mortality, physical resistance, or simply the behavioral responses of organisms to perceived habitat quality. Understanding how and when animal movement behavior varies among habitat types is likely critical for identifying and limiting barriers to dispersal.

We exploited the homing ability of terrestrial salamanders to examine their movement success and behavioral strategies in relation to habitat type. We found that salamanders in forest and open-canopy habitat differed in several fundamental aspects of their movement behavior. Following displacement, salamanders in closed-canopy forest initially oriented more strongly towards their home ranges and moved farther during the first 3 h after their release than salamanders moving through the timber harvest plot. In spite of these behavioral differences, the ultimate movement success of homing salamanders did not appear to vary with habitat type.

Although translocation studies do not fully simulate natural dispersal behavior, they do provide valuable insight into the costs of movement in different habitat types as well as the influence of landscape features on movement behavior (Knowlton and Graham 2010). Such studies are particularly valuable for species such as terrestrial salamanders, for which observations of natural dispersal events are difficult to obtain. A previous study which used return rates of translocated salamanders to estimate dispersal costs in open-field habitat found no difference in return rates between forest and open-field habitat

(Marsh et al. 2004). Furthermore, salamanders were found to colonize artificial habitat patches in an open-field matrix of non-habitat, suggesting that fields did not provide a complete barrier to dispersal in a forest-dependent salamander species. In contrast, roads have been shown to reduce habitat permeability for several amphibian species compared to forest interior, suggesting that they act as partial barriers to movement (Gibbs 1998, Marsh et al. 2005). We found no reduction in the final movement success of homing salamanders in spite of the fact that canopy removal has been shown to increase air and soil temperature, temperature fluctuations, and wind speeds (Keenan and Kimmins 1993, Brooks and Kyker-Snowman 2008). Furthermore, the substrate in our timber harvest plot was primarily bare dirt or a thin layer of leaf litter and was unlikely to provide many suitable refuges or a favorable microclimate.

The use of PIT telemetry enabled us to confirm that at least 65%–69% of individuals were successful at homing following a 35 m displacement while indicating that homing success did not differ by treatment. This was a far higher known success rate than would have been obtained had we relied on surface recaptures as an index of return rates (e.g., 8–18%; Marsh et al., 2004). The high rate of homing success and the lack of a difference between forest and open-canopy habitat in our study indicate that timber harvest plots may not present severe barriers to movement for large-bodied *Plethodon* or that the physiological costs of movement are sub-lethal and do not reduce homing success. Alternatively, the reduced movement rates of individuals in open-canopy habitat may have represented a short-term strategy for reducing desiccation risk, potentially compensating for the elevated risk of movement in this habitat type.

Several studies have found that the movement rates of amphibians increase with the presumed "risk" of habitat. In our study, individuals moving through the area of a recent timber harvest tended to move much shorter distances than salamanders in nearby forest habitat. This behavioral response of terrestrial *Plethodon* to open-canopy habitat contrasts with that of wood frogs, *Lithobates sylvatica*, which showed elevated movement rates while dispersing out of clear-cuts (Rittenhouse and Semlitsch 2009). Rosenberg et al. (1998) found that a terrestrial salamander, *Ensatina eschscholtzii*, tended to show higher movement velocities, and a decreased probability of settling, on bare ground than on leaf litter substrate. *Plethodon metcalfi* also showed a similar tendency to increase their movement rate on asphalt, gravel, or bare ground substrates compared to grass and leaf litter substrates which have potential to retain moisture and provide refuge to salamanders (Semlitsch et al. 2012). In the present study, the forest edge was at least 25 m from each salamander's release location in the timber harvest plot and an increase in movement rate, even for several minutes, would not have been sufficient to allow a salamander to reach the forest edge quickly. The majority of salamanders seem to have responded conservatively to this extended stretch of exposed habitat and decreased their movement rate, possibly to minimize their immediate desiccation risk. Salamanders released within the timber harvest plot also oriented their movement paths less strongly in the direction of their capture locations than salamanders released in the forest. It is possible that some individuals in the timber harvest plot instead oriented their movements towards scattered refuges or along favorable microclimatic gradients. In contrast to the general trend of shortened movement distances, a single individual released in the timber harvest area travelled a distance of 15.5 m during the tracking period and was found, still

moving, at the end of its powder trail. It is possible that this individual employed an alternative strategy of rapid movement in open-canopy habitat in order to minimize its time spent in unfavorable conditions. Although this individual had traversed over half the distance to the forest edge in 3 h of movement, it was not among the 69% of salamanders released in the timber harvest plot which were later detected in the vicinity of their home range.

The pattern of decreased movement rates and weaker orientation of individuals in the timber harvest plot is consistent with the hypothesis that salamanders exhibit context-dependent behavior by altering their movement behavior in response to the perceived risk of movement in different habitat types. Alternatively, differences in the physical structure of the two habitat types could have resulted in a reduced movement rate and in difficulty orienting for individuals in the timber harvest plot. Although it is possible that movement could have been impeded in a few areas of the timber harvest plot with high stem densities, we believe that the broad expanses of bare ground substrate and sparse leaf litter should have facilitated movement compared to the forest with its substrate of deep, uneven leaf litter. Furthermore, increased movement rates on bare ground would have been consistent with the findings of Semlitsch et al. (2012) in closely related *Plethodon*. Increased wind or the presence of unfamiliar olfactory cues could have also disrupted the ability of salamanders to effectively orient their movements towards their home ranges in the forest, leading to reduced movement rates as individuals spent more time attempting to detect olfactory cues and less time making directed movements. Whether reduced movement rates are due to difficulty orienting towards forested habitat or are the result of context-dependent behavioral strategies, the implication is that salamanders moving

through timber harvest plots will do so at a reduced rate compared to forested habitat, leading to prolonged occupation of areas with elevated desiccation risk. This supports the theoretical expectation that behavior in continuous habitat is likely to be a poor predictor of behavior in non-habitat (Fahrig 2007) and provides evidence for habitat-specific movement rates in plethodontid salamanders. Furthermore, the difference in movement behavior between the two habitat types in the present study could suggest that either perceived or experienced dispersal costs are habitat-specific.

Researchers are increasingly interested in parameterizing landscape connectivity models with empirical observations of movement in different habitat types (Zeller et al. 2012) and the present study contributes to a growing body of literature suggesting the importance of recognizing the context dependence of animal movement behavior. We found that movement rates of displaced salamanders were significantly reduced in open-canopy habitat, suggesting that dispersal rates in non-forest matrix are likely lower than in control forest. Although salamanders may partially mitigate the individual cost of movement in open-canopy habitat by seeking refuge and travelling only under highly favorable conditions, the resulting reduction in movement rate may function to reduce connectivity at the landscape scale. Our study also indicates the scale dependence of salamander movement behavior, as *Plethodon* have been shown to increase velocity to escape unfavorable conditions over short distances (<1 m; Semlitsch et al., 2012), while decreasing their movement rates to cover longer distances in non-habitat (>25 m; this study). We suggest that woodland salamanders likely cannot sustain such high movement rates over distances associated with large timber harvest plots or other land use of similar scale.

An important consideration is that habitat-specific movement rates may not be suitable to consistently predict behavioral preferences for habitat types (e.g., Stevens et al., 2006). Although a number of amphibians show behavioral avoidance of forest/grassland edges (Rittenhouse and Semlitsch 2006) or prefer closed-canopy forest (Chan-McLeod 2003, Vasconcelos 2004, Popescu and Hunter Jr 2011), other species readily enter clear-cuts (Graeter et al. 2008). In some cases, behavioral avoidance of habitat edges or landscape features may be a more important determinant of functional connectivity than the effect of the physical structure of habitat on animal movement (Rondinini and Doncaster 2002, Popescu and Hunter Jr 2011). Further mechanistic studies focusing on behavioral avoidance of landscape features as well as habitat-specific movement rates and survival costs will be valuable for effectively identifying and mitigating barriers to animal movement.

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Figure 1. Rose diagrams depicting the net bearings of salamanders displaced into forest (left) and open-canopy habitat (right). Net bearings are corrected such that zero degrees represents the direction to each salamander's home range.
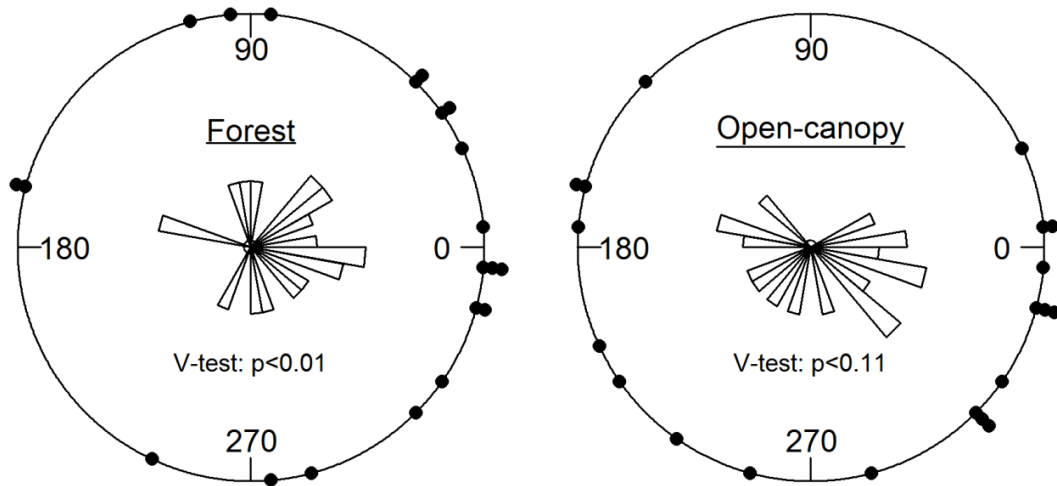
Figure 2. Mean distance travelled (±1 SD) during the initial 3 h of movement through forest and open-canopy habitat.
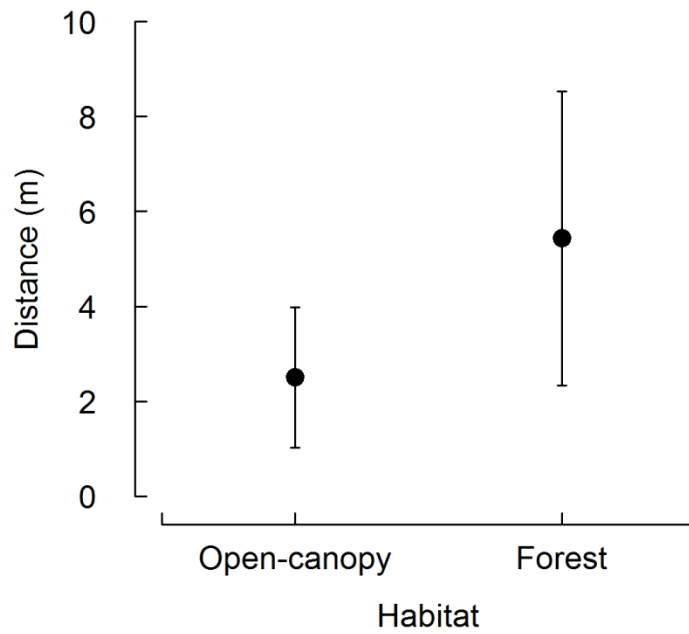
Figure 3. Number of salamanders known to have successfully returned to their home ranges by date. Identification of successful homing events was based on PIT telemetry surveys.
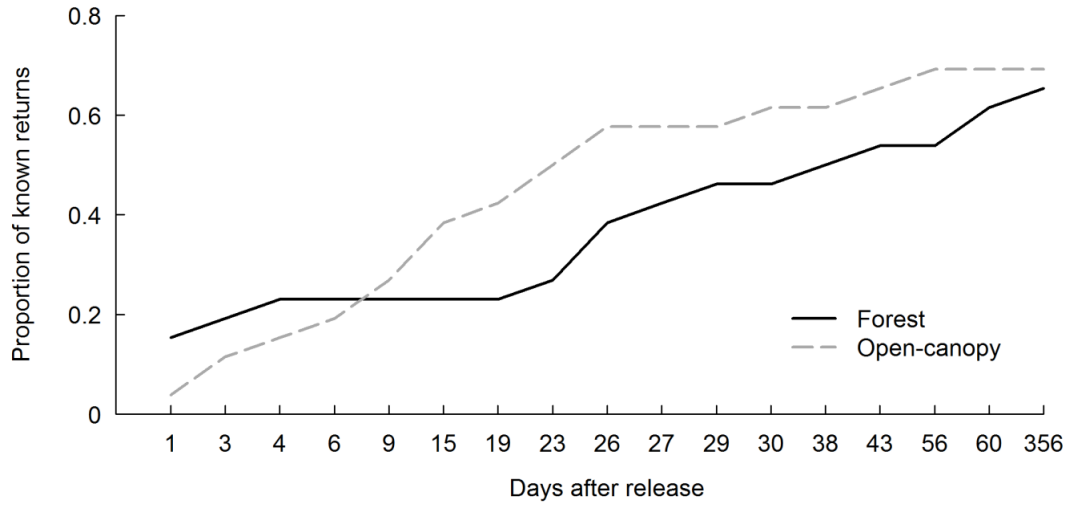
Chapter 4

USE OF AUXILIARY PIT-TAG TELEMETRY DATA TO ESTIMATE SURVIVAL

OF A TERRESTESTRIAL SALAMANDER FOLLOWING TIMBER HARVEST

Abstract

Individual survival probability is a critical component of individual fitness, population dynamics and the landscape ecology of organisms. Thus, survival estimation is often an objective of conservation or land management research. Survival in animal populations is frequently estimated from capture-mark-recapture studies, yet these estimates are biased low when the permanent emigration of individuals is interpreted as mortality. In this study, we estimated the effects of timber harvest on survival of the red-legged salamander, *Plethodon shermani*. We used a portable PIT-tag telemetry system to repeatedly locate salamanders in harvested- and un-harvested survey plots while concurrently recording whether individuals were active on the ground surface. We use a Bayesian state-space approach for survival estimation that incorporates auxiliary PIT-tag detection data to account for the probability of permanent emigration from our study area. We found that estimated survival probability was lower in harvested forest plots but that timber harvest did not cause a clear change in estimated emigration rates. Furthermore, salamander spatial position data from PIT-telemetry surveys indicated that movement levels did not differ between harvested and un-harvested areas. Whereas traditional

capture-recapture analysis tends to underestimate survival in the presence of permanent emigration, our analysis provided an upper estimate for salamander survival due to the fact that the limited detection range of our PIT-tag system would cause morality occurring deep below ground to be interpreted as permanent emigration. Taken together, survival estimates based on these two methods encompasses the value of true survival but, most importantly, allow us to identify increased mortality as a likely mechanism for the reduced counts of terrestrial salamanders commonly observed following timber harvest.

Introduction

Survival is a critical demographic process underlying the dynamics of animal populations (Semlitsch 1980). Survival can have a significant influence on population viability (Burt 1943, Millspaugh et al. 2006) and spatial or temporal variation in survival can contribute to the source-sink dynamics of populations (Gaona et al. 1998, Efford 2004). As a result, estimation of survival rates is frequently an objective of population ecology, wildlife management and conservation biology research. Many studies simply seek to estimate survival and its role in population growth trends, while others specifically examine possible relationships between factors such as climate, habitat characteristics or management practices and the survival of organisms (e.g., Gaillard et al. 1998, Sæther and Bakke 2000, DeCesare et al. 2012, Price et al. 2012).

Survival probabilities in animal populations are often estimated based on either radio-telemetry (Murray 2006) or capture-mark-recapture (CMR) study designs

(Lebreton et al. 1992, Williams et al. 2002). A commonality of these methods is that permanent emigration of individuals from the study area can lead to biased survival estimates. Permanent emigrants are often censored (i.e. removed) from telemetry datasets such that resulting survival estimates implicitly assume that censored individuals are a random sample from the population (Murray 2006). Survival is typically estimated from capture-recapture data using Cormack-Jolly-Seber (CJS) models (Cormack 1964, Jolly 1965, Seber 1965), which jointly estimate survival and recapture probabilities. Traditionally, these models underestimate survival rates in the presence of permanent emigration because mortality and emigration cannot be distinguished. As a result, estimated survival probabilities are often referred to as "apparent survival" and represent the joint probability that an individual survives and remains within the study area (Lebreton et al. 1992). When permanent emigration is common and not accounted for, there will be a large difference between true and apparent survival that could lead to poor inference about population dynamics. In two studies with birds, true annual survival has been estimated at 125% higher (Gilroy et al. 2012) and ~ 20% – 50% higher (Worton 1987) than apparent survival estimated from a traditional CJS analysis. A separate study with stream fish reported differences between true and apparent survival within seasons of 2 – 18% (Efford 2004).

A number of studies have incorporated auxiliary data to more accurately estimate true survival from CMR data. In many cases, the addition of movement data or information about the spatial locations of captures have allowed for inference about true survival rates (Mohr 1947, Worton 1987, Efford 2004, Gilroy et al. 2012). For this purpose, several spatial CMR models have incorporated explicit models for movement

data based on concurrent radio-telemetry studies (Mohr 1947, Worton 1987). Another study used passive PIT-tag arrays to integrate live recapture data with continuous monitoring of fish movements away from the study area to estimate true survival probability (Efford 2004). Although PIT-tag antennas typically have a limited read range (generally < 30 cm), this approach is promising for species that are too small to carry radio- or GPS-transmitters and which typically occupy a relatively restricted area.

Survival of lungless salamanders (Family Plethodontidae) may be particularly difficult to estimate because they are nocturnally active, highly fossorial and exhibit large variation in ground surface activity across locations and weather conditions (Bailey et al. 2004, Dodd and Dorazio 2004). These salamanders are extremely abundant in many forest and headwater stream ecosystems of eastern North America (Bailey 2004, Peterman et al. 2008). They may also be ecologically important as consumers of invertebrates (Wyman 1998, but see Homyack et al. 2010) and as a supply of energy and nutrients for higher trophic levels (Burton and Likens 1975). These salamanders breathe across their moist skin surface, making them sensitive to fluctuations in temperature and moisture conditions (Spotila 1972, Feder 1983). Thus, changes in habitat characteristics often have a considerable effect on populations of these salamanders. Numerous studies have reported a negative short-term response of plethodontid salamander abundance to timber harvest (reviewed by Tilghman et al. 2012), yet most do not attempt to establish the ultimate fate of individuals. Several studies have suggested that observed declines in salamander counts are at least partially explained by mortality (Petranka 1993, Homyack and Haas 2009), decreased activity and increased refuge use (Johnston and Frid 2002), or dispersal away from harvested areas (Ash and Bruce 1994, Reichenbach and Sattler 2007,

Peterman et al. 2011). These possible responses of amphibians to timber harvest have been summarized as: 1) mortality, 2) retreat and 3) evacuation (Semlitsch et al. 2008). These hypotheses are not mutually exclusive and clearly underscore the importance of accounting for behavior in studies of amphibian responses to land use. Specifically, emigration behavior can reduce relative counts and negatively bias CMR survival estimates while decreased surface activity would also result in reduced counts of salamanders in harvested areas.

In this study, we estimate the effects of a two-aged regeneration harvest method on survival of a terrestrial salamander, *Plethodon shermani*. We used a portable PIT-tag telemetry system to locate salamanders in harvested and un-harvested survey plots while recording whether individuals were active on the ground surface according to a CMR sampling design. Thus, live observations of individuals confirmed survival while PIT-tag detection confirmed that an individual, alive or dead, had not emigrated from our study area. We present a Bayesian state-space approach to survival estimation that incorporates auxiliary PIT-tag detection data to account for the probability of permanent emigration from the study area. Our study allows for a comparison among mortality, emigration and reduced activity as mechanisms for the reduced counts of salamanders commonly observed following timber harvest and provides an upper estimate for true survival in both harvested- and un-harvested areas.

Methods

Study Site and Species

Our study sites are located in the vicinity of Perry Gap (35.0887ºN, 83.6485ºW) on the Nantahala National Forest of southwestern North Carolina, U.S.A. This area primarily consists of mixed-hardwood forest along a ridgeline of approximately 1200 m in elevation and is currently the focus of a U.S. Forest Service management project that involves timber extraction, as well as a number of additional management activities. Timber is currently being harvested at eight separate stands (each 11-16 hectares) according to a two-aged regeneration harvest method. This approach was intended to create forest stands with interspersed trees of two distinct age classes by leaving approximately 20 square feet basal area of overstory trees during the current harvest operations.

The encompassing southern Appalachian region is a global hotspot for salamander diversity (Petranka 1998) and we have found 12 salamander species at our study sites. In spite of the high species diversity in the area, the red-legged salamander (*Plethodon shermani*) appears to be numerically dominant in terrestrial habitat away from streams (>86% of individuals observed, Connette & Semlitsch, *unpubl. data*). This species occurs in four geographically-isolated populations at high elevations and often hybridizes at its range limits with salamanders of the *P. glutinosus* complex (Weisrock et al. 2005). Many individuals at our study location exhibit morphological characteristics indicating hybridization with *P. teyahalee* (e.g., Walls 2009), yet we refer to them hereafter as *P. shermani*.

PIT-tag Telemetry

We used data from PIT-tag telemetry surveys to quantify movement and estimate pre- and post-harvest survival of *P. shermani* in four survey plots (25 x 25m). These plots were arranged as a transect that was bisected by the boundary of a timber stand (Fig. 1). Two plots were located within the harvest area (65m and 10m from adjacent forest) and two plots were located in nearby control forest (10m and ~400m from the harvest area). The point where the transect bisected the boundary of the harvest area was randomly determined and all survey plots were of similar elevation, slope, aspect and soil type.

Prior to timber harvest, we hand-collected salamanders at night and marked each individual's capture location with a numbered flag. We collected 74 and 61 *P. shermani* from our survey plots at the center and edge of the harvest area, respectively, as well as 50 individuals from each of the plots located in control forest. All salamanders collected were large juveniles or adults and ranged in size from 41 to 66 mm snout-vent length (mean ± 1 SD: 53.3 ± 5.0 mm). We then transported salamanders to the Highlands Biological Station in Highlands, NC (∼60 km away). The following day, we implanted each salamander with a 12.5-mm PIT tag (TX1411SST; Biomark, Boise, ID, USA) according to Connette & Semlitsch (2012). Each PIT tag has a unique code that allows salamanders to be individually identified from up to 30 cm away with a reader, including individuals belowground (Hamed et al. 2008, Lee et al. 2012). All salamanders were allowed a minimum recovery period of 32 hours and were released at their site of capture on the second night after capture. Flags at salamander capture locations were left in the field to serve as reference locations during subsequent surveys.

We conducted PIT-tag telemetry surveys (e.g., Gaona et al. 1998) on 24 nights from 1 June 2011 through 20 August 2011. On each survey night, we used the PIT-tag reader to systematically scan the entire ground surface within each 25 x 25m survey plot as well as an additional 10m band around the outside of each plot. We recorded the PIT-tag identification of each detected salamander and noted whether the individual was active on the ground surface. Generally, salamanders on the ground surface could be visually inspected to confirm the presence of a PIT tag along the side of the body. In a small number of cases, salamanders were captured by hand and inspected for the presence of a PIT tag. We summarized our PIT-tag detection and live observation data as separate capture histories for each individual. Thus, the live observation of an individual indicated survival through the current survey whereas detection with the PIT-tag reader provided the auxiliary information that an individual had not permanently emigrated from the study area, whether or not they were visually observed. For each detected salamander, we also recorded its spatial position in the survey area as a distance and bearing from the nearest reference location (capture flag). Timber was harvested in our two treatment plots between 20 June and 29 June 2011 (surveys 9 - 12). For the purpose of analysis, 17 June 2011 (survey 8) was treated as the last pre-harvest survey.

Data Analysis

Our analysis of individual survival is based on state-space representations of the Cormack-Jolly-Seber model (CJS; Schwarz and Arnason 1996, Lunn et al. 2009) but seeks to estimate individual survival probability while accounting for the possibility that individuals permanently emigrate from the survey area. At the population level, we can

define the number of previously-marked individuals that are alive and present in the study area, N_1, as the product of the previous number of individuals, N_0, the survival rate, s_1, and the rate of site fidelity, f_1.

$$N_1 = N_0 * s_1 * f_1$$

In this analysis, we used mark-resight and PIT-tag telemetry data to jointly estimate the values of two demographic parameters, survival and site fidelity, under a Bayesian framework. Mark-resight data allow for estimation of survival, while the PIT-tag telemetry data contribute to the estimation of site fidelity probability (through its complement, emigration probability).

We analyzed our PIT-tag telemetry data using a traditional CJS structure, where we model the presence of each individual in the study area as a function of an estimated emigration probability. The mark-resight data were analyzed using a modified CJS model, where the state of each individual ("alive and present" versus "dead or emigrated") is assumed to be a function of 1) its survival probability and 2) its emigration probability. This second parameter is shared between the models for each dataset. Both survival and emigration probability are allowed to differ between pre- and post-harvest time intervals. Because individuals observed alive on the ground surface are always detected with the PIT-tag reader, our two datasets provide non-independent information on emigration. Thus, we treat the estimation of emigration probability as a hidden Markov process to prevent our less complete dataset of live encounters from informing estimation of this parameter.

Both of the demographic process models described above are linked to the encounter history data via separate observation models that we used to account for

variation in individual detection probabilities across both our mark-resight and PIT-telemetry surveys. We allowed detection probability during mark-resight surveys to differ from pre- to post-harvest by using a logit-link function to introduce a site and survey specific covariate indicating whether timber harvest had previously occurred. In addition, we estimated the effect of days since rainfall on mark-resight detection probability, as well as a normally-distributed individual random effect to account for unexplained heterogeneity in individual encounter rates during both mark-resight and PIT-telemetry surveys. See Appendix A for complete details of the model specification.

We used OpenBUGS (Kie et al. 2010), to fit the model using Markov chain Monte Carlo (MCMC) simulation. All analysis was executed through program R (R Development Core Team 2012) using the R2OpenBUGS package (v. 3.2.2; Giuggioli et al. 2006). Posterior summaries from each of three parallel Markov chains were based on an arbitrarily large sample of 1,000,000 MCMC iterations thinned at a rate of 100 following an initial burn-in of 500,000 iterations. From these summaries, we calculated the mean and 95% credible interval (CRI) for all model parameters. We assessed model convergence using the Gelman-Rubin statistic ($\hat{R}$; Gelman et al. 2004) and found acceptable convergence ($\hat{R}<1.05$ for all parameters). Finally, we compared the overlap of our prior and posterior densities and found strong identifiability of all parameters except two parameters associated with the observation model for mark-resight data ($\tau > 0.35$; Borchers and Efford 2008). These were the intercept term and the coefficient for the effect of timber harvest on detection probability. Nonetheless, the posterior distribution for the effect of timber harvest on visual detection was clearly identified as non-negative (Fig. 2).

Results

We recorded a total of 3,228 PIT-tag detections of our 235 tagged salamanders and on 838 of these occasions the individual was observed alive on the ground surface. Thus, PIT-tag detections confirmed the presence of individuals within our study area in a large number of cases when those individuals were not observed on the ground surface (74% of PIT-tag detections). Just one individual was never detected within the survey area after release; 27 individuals were never visually observed on the ground surface. The mean (± 1 SD) percentage of individuals detected by PIT-tag telemetry during a given survey varied little among survey plots (Range: 55.5 ± 11.8% to 58.4 ± 12.8%). A majority of our marked population were known to survive the physical removal of timber, as we visually detected a combined 77% of individuals in our two harvested plots at least once following the end of all timber removal, compared to 71% over the same period in our control plots.

As a baseline for comparison, we used just our live (i.e., mark-resight) detection data to estimate the effects of timber harvest on apparent survival with a traditional CJS model (see Appendix B for details). Weekly survival preceding timber harvest and in un-harvested plots was estimated at 98.9% (95% CRI: 97.5 – 99.9%), versus 96.0% (95% CRI: 93.4 – 98.4%) following timber harvest. Conditional detection probability, or the probability of observing an individual given that they were alive and within the study area, was estimated at 17.6% (posterior mean) prior to harvest and in un-harvested plots, compared to 23.4% following timber harvest. Time since rainfall also had a large effect on salamander detection probability, with estimates for this parameter ranging from

17.6% to 3.8% (posterior means) across our observed range of rainfall (0-9 days since rain) in un-harvested plots.

Our joint analysis of PIT-tag and mark-resight data yielded weekly survival estimates of 99.4% pre-harvest and in un-harvested plots (95% CRI: 98.2 – 100%) and 97.6% post-harvest (95% CRI: 94.8 – 99.7%)(Fig 3). We observe that the 95% CRI for survival probability in un-harvested reference plots did not include the mean of the posterior distribution for survival probability in harvested plots. Furthermore, we estimated the difference in weekly survival between harvested and un-harvested plots at 1.8% (95% CRI: -0.01% – 4.8%). Predicted weekly emigration rates were 1.3% in un-harvested plots (95% CRI: 0.1 – 2.0%) versus 1.7% in harvested plots (95% CRI: 0.1 – 2.7%)(Fig. 3). The difference in emigration probability was not substantially different between harvested and un-harvested plots (95% CRI: -1.6 – 0.6%). Spatial relocation data from PIT-tag surveys provided no indication that the net displacement of individuals from their initial locations was influenced by timber harvest treatment, further indicating that emigration rates were likely similar (Fig. 4). Across our 3-month study period, we estimated that 73.3% of individuals survived and remained in the study area, 12.6% died within the study area, while the remaining 14.1% individuals were counted as permanent emigrants (Fig. 5). We also observed a clear positive relationship between timber harvest and our probability of visually encountering a salamander on the ground surface, conditional on their survival and presence in the study area (posterior mean: 17.4% pre- vs. 21.3% post-harvest; Figs. 2, 4). Visual detection was also negatively associated with days since rainfall (Fig. 2). Detection probability in un-harvested areas was estimated at 17.4% (posterior mean) on the day of a rainfall event and 3.6% on the 9th day after rain.

Discussion

When permanent emigration is not accounted for, survival probabilities estimated from capture-recapture data can be substantially lower than true survival (Worton 1987, Efford 2004, Gilroy et al. 2012). Furthermore, the degree to which survival is underestimated depends on the size of the study area relative to the scale of migratory movements (Brooks et al. 1999) or dispersal behavior (Van Horne 1983, Connette et al. 2014). Our study combined mark-resight and PIT-tag telemetry data for the purpose of estimating the initial effects of timber harvest on the survival of red-legged salamanders, *P. shermani*. Because these terrestrial salamanders spend much of their time below ground, the inclusion of supplementary PIT-tag detection data for below-ground individuals provides the additional information that these individuals have remained within the study area in many cases when they were not visually resighted. Thus, we were able to estimate a probability of mortality occurring within our search area that is not confounded with emigration and we found evidence that it was reduced after timber harvest. We were also able to use our PIT tag data to estimate the probability that individuals permanently left the study area and found that individuals in harvested- and un-harvested plots did not appear to differ in emigration probability. Conditional on their survival and presence in the study area, we also observed that detection probability was higher in harvested plots. Our modelling approach would be especially useful for future studies in which a subset of animals carry radio-transmitters or with stationary arrays of PIT-tag antennas enclosing a search area. In such cases, it is relatively certain whether an individual remains within the study area or has emigrated.

Because our portable PIT-tag system has a read range of around 30 cm through soil (Hamed et al. 2008, Lee et al. 2012), individuals would be treated as emigrants if

they either left the study area or permanently moved too deep below ground to be detected for the remainder of our study. In both cases, those individuals are assumed to have permanently left the monitored study area, as defined by the 3-dimensional space that is searchable with our PIT-tag system. Although we are unable to definitively quantify the relative contributions of vertical (below ground) and horizontal emigration to estimates of overall emigration probability, our spatial relocation data provide no indication that salamanders in harvested plots increased the scale of their ground surface movements relative to individuals in control forest. Furthermore, we conducted three exhaustive searches of a 50m radius around our survey plots as well as a single 10m-wide x 200m-long transect of forest habitat adjacent to the cut edge. On these occasions, we never detected a salamander that had left our survey areas. Thus, we believe that a majority of emigrating salamanders probably moved deep underground where they either died or simply remained beyond detection range.

Previous studies have provided evidence that ambystomatid (Semlitsch et al. 2008) and stream-breeding plethodontid salamanders (Peterman et al. 2011) emigrate, or evacuate, from harvested areas within 0-2 years of timber harvest. In addition, a study of the terrestrial plethodontid, *P. hubrichti*, indicated that 41% of individuals likely moved between 3 and 9m to nearby forest in the initial days to months after harvest (Reichenbach and Sattler 2007). It is possible that the greater distances to un-harvested forest in our study (10 - 90m) would be prohibitive for many terrestrial salamanders (*Plethodon spp.*), which show limited dispersal (Liebgold et al. 2011) and maintain very small home ranges (Madison and Shoop 1970, Kleeberger and Werner 1982, Nishikawa 1990, Marvin 1998). Although the ultimate fate of emigrating individuals in our study is

unknown, nearly all known males (96%; N=52 of 54) were detected at least once with the PIT tag reader during the post-harvest period while large juveniles, females and individuals of unknown sex were underrepresented (85% detected; N=154 of 181). It is possible that behavioral explanations, such as below-ground egg brooding by females (e.g., White and Burnham 1999), underlie the estimated level of permanent emigration during our study period. However, we found no evidence that emigration rates differed between our control and timber harvest treatments.

Although salamanders in our study made extremely small-scale ground surface movements relative to the size of the study area, we found that survival estimates based on a traditional CJS model were considerably lower than when emigration probability is explicitly accounted for in our analysis. In both models, however, survival probabilities for salamanders were lower after timber harvest than pre-harvest and in un-harvested control plots. Timber harvest has been shown to cause increased wind, light, air temperature and soil compaction while also altering leaf litter decomposition and reducing invertebrate abundance (e.g., Keenan and Kimmins 1993, Ash 1995, Heneghan et al. 2004, Brooks and Kyker-Snowman 2008, Siira-Pietikäinen and Haimi 2009). These changes to forest habitat could have either immediate or longer-term effects on forest-dependent species. In our study, we were able to confirm that at least 77% of *P. shermani* survived the process of timber extraction. This was a slightly higher portion of the population than were observed alive over the same post-harvest period in our control plots, a pattern which may also be reflected in the higher detection probabilities of salamanders after timber harvest. Thus, we suggest that the mechanism by which timber harvest affects salamander abundance is likely reduced survival due to a change in factors

such as habitat, microclimate or food availability rather than an immediate mortality event. Changes in temperature, soil moisture, or the quality and availability of suitable refuges are likely to have a considerable effect on the energy budgets of terrestrial salamanders (Homyack et al. 2011). This would require salamanders to spend greater amounts of time foraging on the ground surface, where they may be vulnerable to predation, desiccation and further energetic costs associated with extended activity.

Despite a general consensus in the literature concerning the immediate negative effects of timber harvest on the relative abundance of plethodontid salamanders (e.g., Petranka 1993, Ash 1997, Sattler and Reichenbach 1998, Knapp et al. 2003, Hocking et al. 2013), researchers have observed that few studies are able to establish the ultimate fates of most individuals (Ash and Bruce 1994, Homyack et al. 2011, Peterman et al. 2011, Hocking et al. 2013). Our study design allows for a comparison of emigration, mortality and ground surface activity as mechanisms for the observed counts of terrestrial salamanders immediately following timber harvest. We found that emigration probability did not differ significantly between harvested and un-harvested plots. Although we were unable to determine the fates of those individuals leaving the 3-dimensional area that was searchable with our PIT-tag system, we can conclude that this portion of individuals would not be responsible for differences in observed salamander counts from pre- to post-harvest. In contrast, our estimates of mortality rates, corrected for both emigration and detection probability, were higher after timber harvest. Finally, we found that salamanders which survived within our study area were actually more detectable than individuals in control areas during the initial period after timber harvest. As a result, nighttime counts of surface-active salamanders would have actually under-

represented the differences in abundance between harvested and un-harvested areas in our system. Interestingly, we found the opposite tendency during several non-systematic daytime searches of natural cover objects; although our study suggests that abundance should be only slightly reduced after timber harvest, salamanders were commonly encountered in control forest adjacent to our plots but were very infrequently encountered within the timber cut.

Management Implications

Forest management frequently involves balancing resource extraction with the habitat requirements of species. In many cases, managers may also be required to balance objectives of creating successional habitat for certain species while maintaining habitat quality and availability for species dependent on mature forest (Fink et al. 2006). To effectively evaluate these trade-offs, it is critical that studies identify the demographic or behavioral processes which are ultimately responsible for changes in wildlife populations due to forest management. Our research specifically identifies a negative effect of timber harvest on the survival of terrestrial salamanders but indicates that there is not pervasive mortality as a direct result of stand entry and the process of timber removal. Other studies which have monitored salamander abundance from pre-harvest to >5 years post-harvest have indicated that relative abundance declines rapidly but is not likely to reach a minimum for two or more years (Ash 1997, Morneault et al. 2004, Reichenbach and Sattler 2007, Homyack and Haas 2009). These studies also indicate that salamander abundance increases again shortly thereafter (i.e. year 3-9). Salamander abundance in recent timber cuts has also been shown to be influenced by the extent of

overstory, understory, and forest floor disturbance (Morneault et al. 2004). Collectively, these results suggest that salamander abundance is closely tied to habitat or microclimate conditions in early successional timber cuts and that encouraging rapid canopy closure and minimizing soil compaction and leaf litter disturbance may be more critical than minimizing initial impacts. It is therefore possible that selective harvesting, though generally less detrimental initially (Tilghman et al. 2012), may have large collective impacts when requiring multiple stand entries (Homyack et al. 2011).

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Figure 1. Schematic depicting positions of 25 x 25m survey plots relative to the edge of a timber cut.
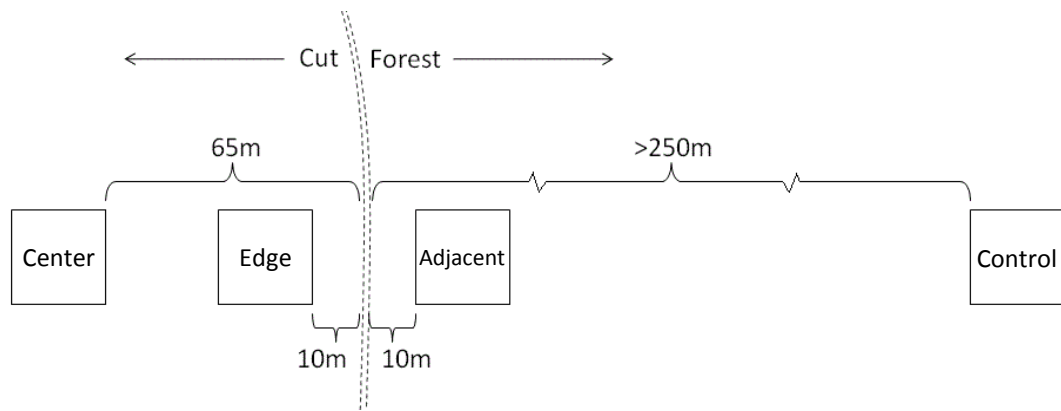
Figure 2. Posterior densities (solid lines) versus prior densities (dashed lines) for parameters related to the estimation of detection probability for the salamander *Plethodon shermani*. The parameters α_0 and $\alpha2_0$ represent the intercept terms for detection probabilities for visual mark-resight and PIT-tag surveys, respectively. α_1 represents the effect of rainfall on detection and α_2 represents the effect of timber harvest. All parameters are presented on the logit scale where positive values indicate higher detection probability. The extent of prior-posterior overlap is indicated by the value of τ, presented in either the upper right or left of each panel, where values > 0.35 indicate weak identifiability of the parameter (Gimenez et al. 2009).

Posterior Densities (p)
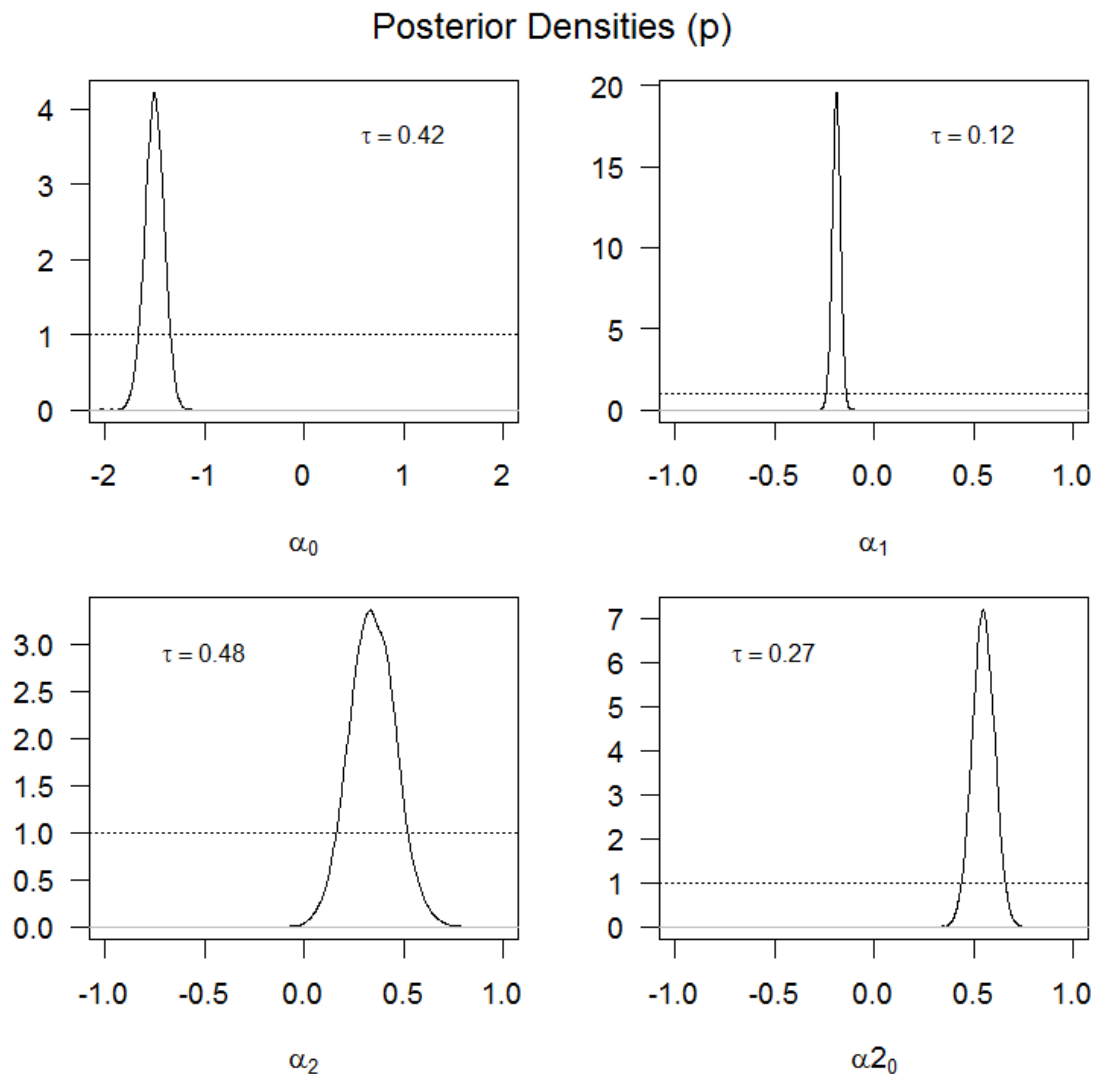
Figure 3. Posterior densities (solid lines) versus prior densities (dashed lines) for survival (ϕ) and emigration probabilities (γ) of *Plethodon shermani*. The vertical red lines in each panel indicate the posterior mean for the other treatment. The extent of prior-posterior overlap is indicated by the value of τ, presented in either the upper right or left of each panel, where values > 0.35 indicate weak identifiability of the parameter (Gimenez et al. 2009).

Posterior Densities (ϕ/γ)
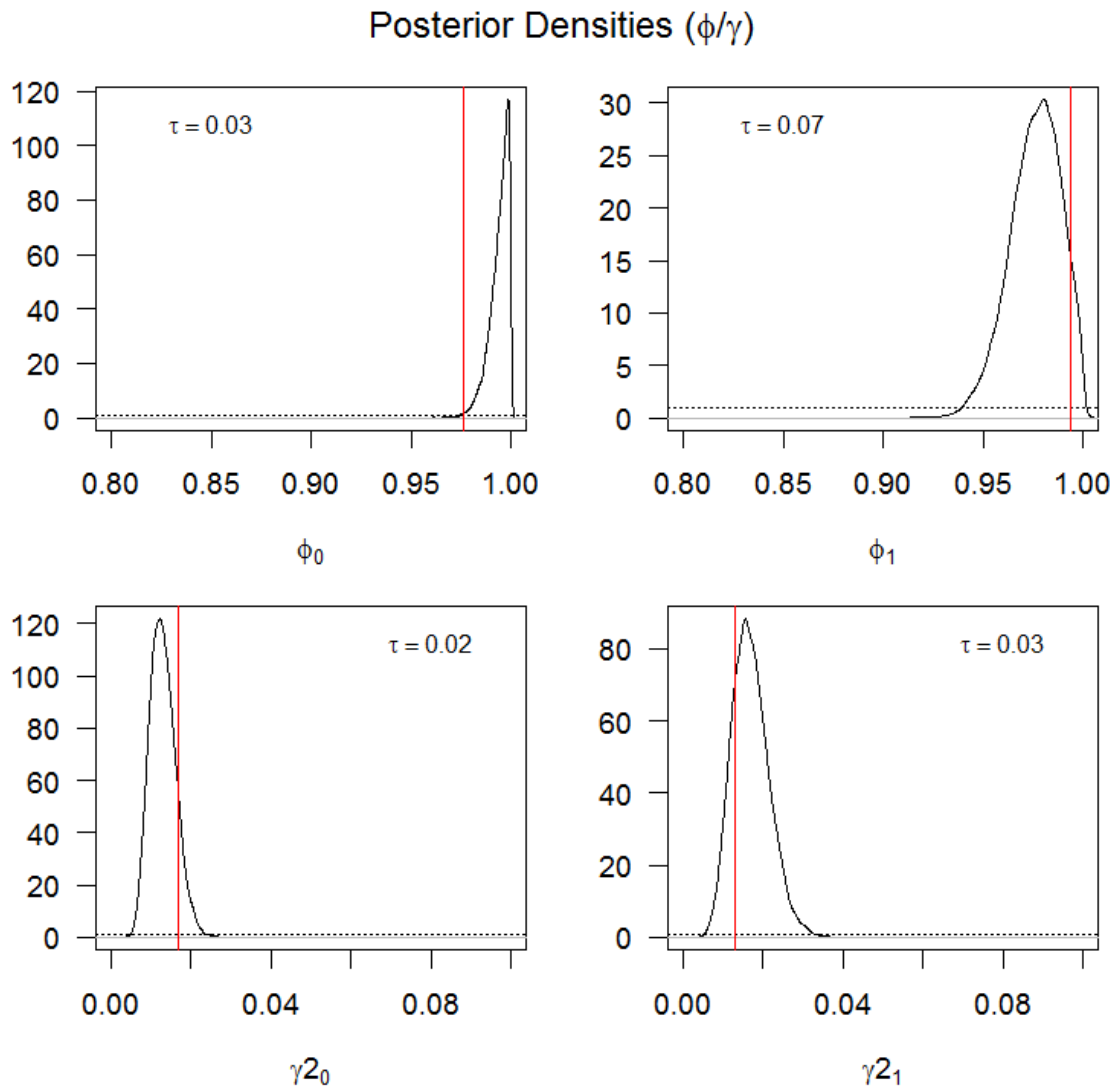
Figure 4. Posterior means (points) ± 95% CRI (solid vertical bars) for the cumulative number of emigrant (above left) and dead *Plethodon shermani* (above right) through time. The vertical dotted line in the top two panels indicates when timber harvest occurred. The boxplot (below) summarizes the posterior distribution for the mark-resight detection probability in post-harvest plots compared to pre-harvest and un-harvested plots.
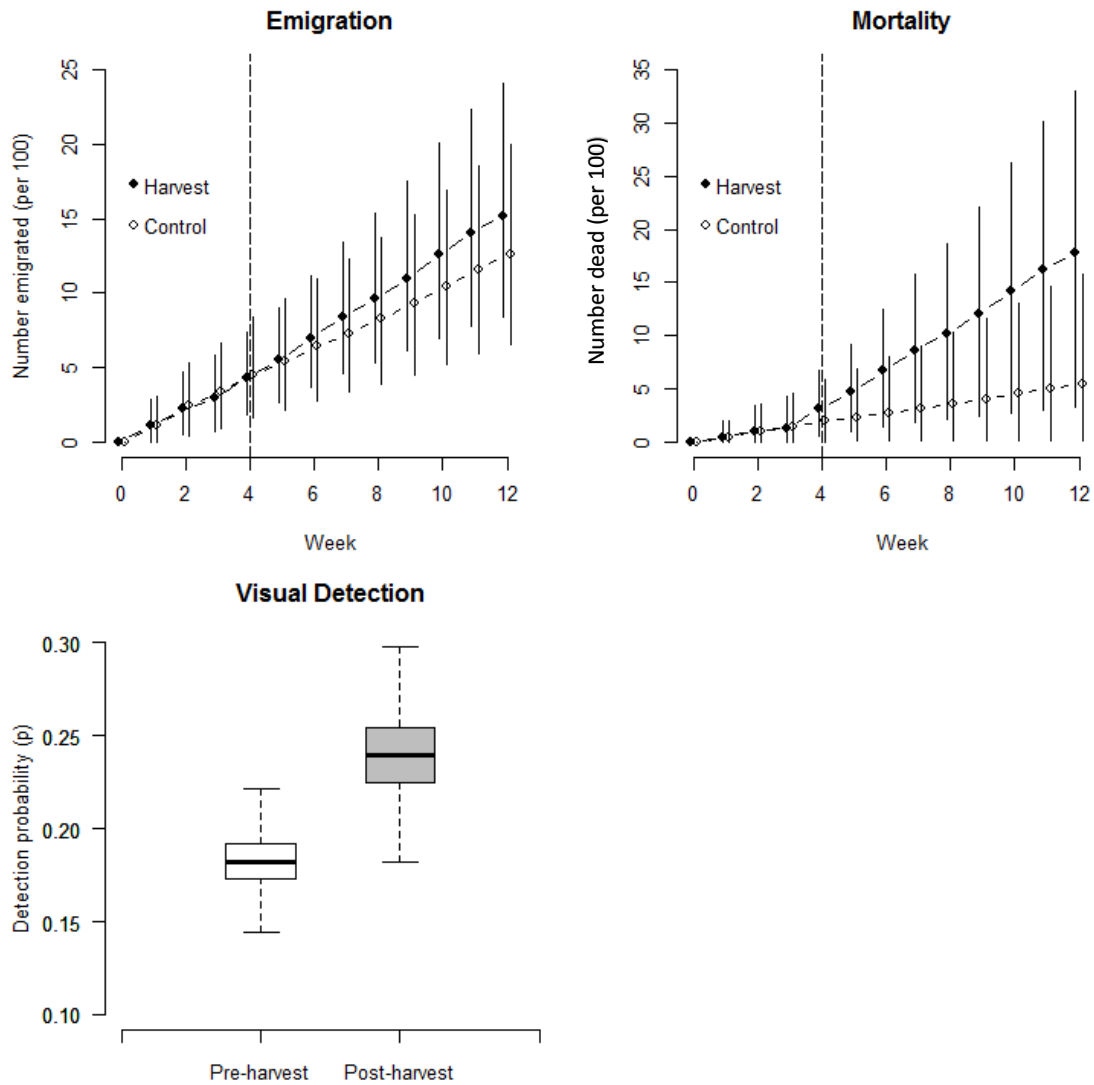
Figure 5. Mean net displacement of *Plethodon shermani* from their initial capture locations in relation to survey number.
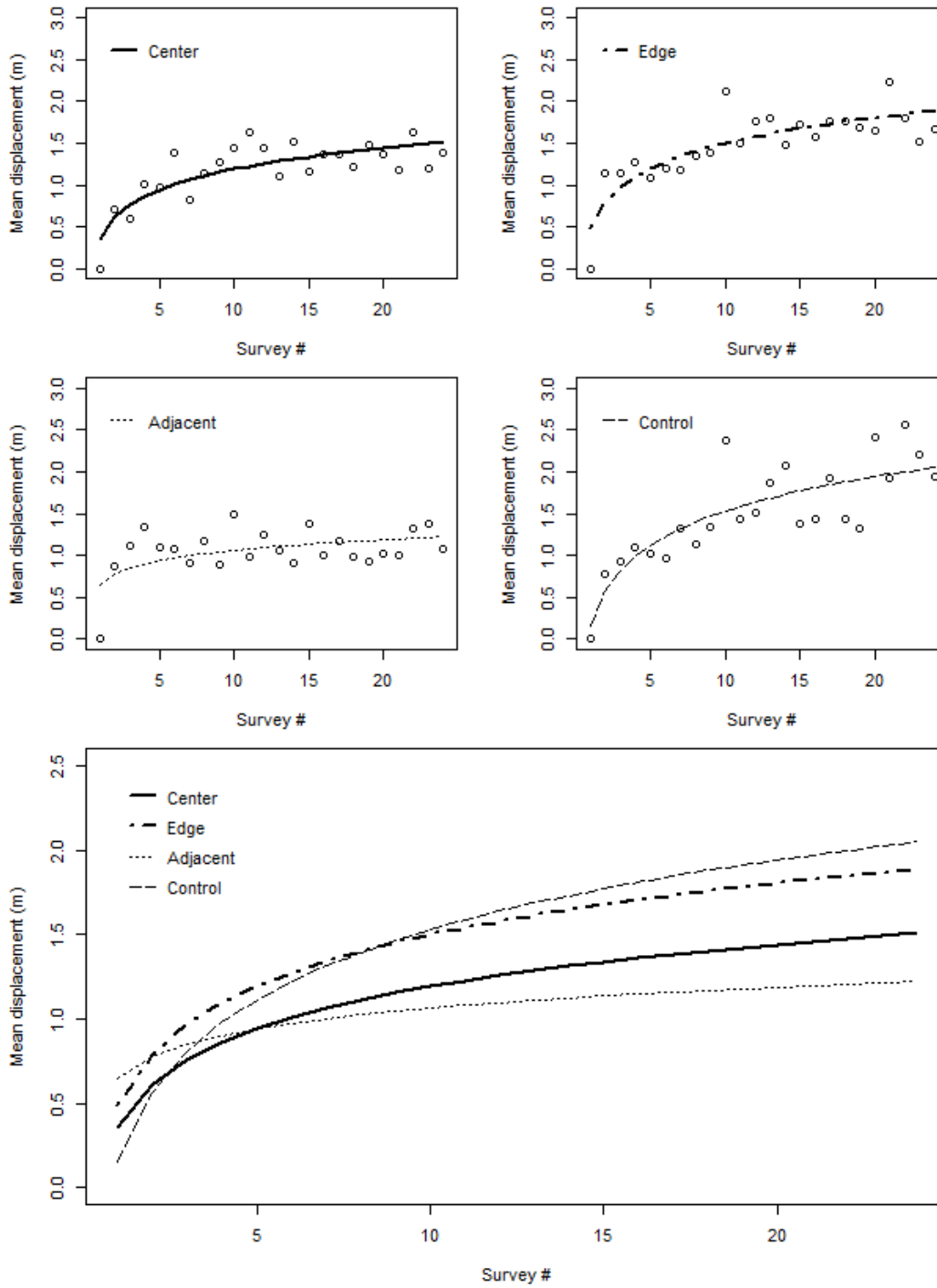
Chapter 5

LIFE HISTORY AS A PREDICTOR OF SALAMANDER RECOVERY RATE

FROM TIMBER HARVEST IN SOUTHERN APPALACHIAN FORESTS

Abstract

Forest management often represents a balance between social, economic, and ecological objectives. In the eastern United States, numerous studies have established that terrestrial salamander populations initially decline in abundance following timber harvest, yet the large-scale and long-term consequences are relatively unknown. We used count data from terrestrial survey points to examine the relation between salamander abundance and historic timber harvest while accounting for imperfect detection of individuals. Overall, stream- and terrestrial-breeding salamanders appeared to differ by magnitude of population decline, rate of population recovery, and extent of recolonization from surrounding forest. Specifically, estimated abundance of both species groups was positively associated with stand age and recovery rates were predicted to increase over time for red-legged salamanders (*Plethodon shermani*) and decrease in stream-breeding species. Abundance of stream-breeding salamanders was predicted to reach a peak by 100 years after timber harvest, and the population growth rate of red-legged salamanders was predicted to undergo a significant increase 100 years after harvest. Estimated abundance of stream-breeding salamanders was also negatively associated with the distance to adjacent forest in young timber stands, a result that suggests immigration has

a role in the recovery of these species. Our results indicate that salamander abundance in young forest stands may be only modestly lower than in more mature forest but that full recovery from timber harvest may take a substantial amount of time and that species life history may affect patterns of recovery.

Introduction

Due to high domestic demand for timber products (Shifley 2006) and growing interest in woody biomass as an alternative energy source (Berndes et al. 2003), forest-management objectives increasingly represent a balance between the socioeconomic demand for timber and ecological sustainability. Timber harvest may cause significant changes to forest ecosystems, such as soil compaction, reduced canopy cover, increased wind exposure, higher air temperatures, and changes in decomposition rates of leaf litter (e.g., Keenan & Kimmins 1993; Ash 1995; Brooks & Kyker-Snowman 2008). These changes can have varying effects on the abundance of organisms. For early-successional species, silviculture may be an important tool for creating habitat where land management has historically suppressed natural disturbances, such as fire or flooding (Brawn et al. 2001). In contrast, timber harvest may cause the loss or degradation of habitat for sensitive forest-dependent species (Thompson et al. 1992; deMaynadier & Hunter 1995; McLachlan & Bazely 2001).

Sustainable management of forest-dependent species depends on understanding how the timing, intensity, and spatial pattern of timber harvest affect ecological communities over the long term. In many cases, monitoring and management of species with high sensitivity to disturbance or habitat quality can be an effective tool for maintaining a broader community of species whose habitat requirements are encapsulated

by these focal species (Wiens et al. 2008). Recently, focal-species management has been integrated into existing land-management strategies by both the U.S. Fish and Wildlife Service (FWS & USGS 2006) and U.S. Forest Service (Federal Register 2012). In forested landscapes, the effectiveness of this management approach depends on determining rates of postharvest recovery and identifying factors limiting population growth for sensitive species.

Due to their high abundance, stable populations, and sensitivity to environmental stressors, plethodontid salamanders are considered useful as indicators of overall ecosystem health (e.g., Welsh & Droege 2001). These salamanders, like most amphibians, are highly sensitive to disturbance and typically experience reductions in abundance following timber harvest (deMaynadier & Hunter 1995; Tilghman et al. 2012). Relatively short-term monitoring of plethodontid salamander populations has established that significant population declines typically occur within 1-2 years of timber harvest (Ash 1997; Sattler & Reichenbach 1998; Knapp et al. 2003). Relative abundance in logged areas is likely to remain well below that of mature forest even through 10-15 years of forest regeneration (Ash 1997; Reichenbach & Sattler 2007; Homyack & Haas 2009). Projected recovery times have either been extrapolated from long-term monitoring or estimated from cross-sectional studies of various stand age classes, and results of these projections are highly disparate (20-100 years) (Petranka 1993; Ash 1997; Crawford & Semlitsch 2008; Welsh et al. 2008). Because of the uncertainty in these estimates and the high variability of terrestrial salamander counts among sites (Dodd & Dorazio 2004), studies in which the long-term recovery of salamander populations are assessed over

relatively large spatial scales are needed to understand the sustainability of current management practices.

Differentiating between biological signal and sampling variation is a critical element of ecological research. In cases where detection of organisms is imperfect and variable, inferences about management effects or habitat associations on the basis of relative counts may be biased or inaccurate (MacKenzie 2006). Hierarchical models of abundance (*N*-mixture models) allow for comparisons of species abundance at landscape scales while accounting for spatial and temporal variation in detection probability (Royle 2004). We used repeated-count data to examine the relation between plethodontid salamander abundance and past timber harvest. Salamander assemblages in terrestrial habitat may include both terrestrial-breeding species that lack an aquatic larval period and aquatic breeders with complex life cycles. Although empirical movement data is lacking for many species, terrestrial-breeding *Plethodon* are believed to have extremely limited dispersal (Liebgold et al. 2011) and maintain small home ranges (Nishikawa 1990), whereas aquatic breeders may occur in uplands over 100 m from streams (Crawford & Semlitsch 2007) and make periodic, larger-scale movements between terrestrial and stream habitat for reproduction (Table 1). We compared postharvest recovery rates and spatial distributions of species that differ in movement propensity. We hypothesized that abundance of relatively vagile species increases more rapidly in previously harvested stands and is related to proximity to forest edge due to higher levels of immigration.

Methods

Study Site

Our study sites were in the vicinity of Wayah Bald, Nantahala National Forest, Macon County, North Carolina (U.S.A.). (Fig. 1). The study area was approximately 4 x 5 km and had an elevational range of 1200-1600 m. Forest composition consisted primarily of upland oak-hickory, cove hardwood, and northern hardwood forest.

Salamander surveys

We conducted repeated-count surveys of salamanders at 68 timber stands to examine patterns of salamander abundance relative to historic timber harvest. Our surveys targeted 34 timber stands that had been harvested in the past 75 years (range 13-73 years) and 34 relatively late-successional stands (>82 years). Younger stands tended to be smaller (mean [SD] = 12.0 ha [17.5]) than older stands (26.0 ha [24.6]). Within each stand, we conducted counts at 2 independent survey points which were marked with a survey flag. One point was close to the center of the stand, and the second was between the center and the forest edge. Survey locations were accessed by foot, and the precise locations of survey points were determined in ArcGIS 9.3 (ESRI, Redlands, Calfornia) prior to visiting each site. Each survey point was 5 m in diameter and was surveyed on 5 separate dates between 25 June and 8 August 2012. During each survey, we performed a nighttime visual encounter survey during which a single observer exhaustively searched the survey area for salamanders active on the ground surface. Surveys were conducted between 21:20 and 05:59 eastern standard time and typically took 3-5 minutes. We recorded the time at which each survey was initiated and used an infrared thermometer to

measure ground surface temperature. Daily rainfall totals were obtained from a weather station in Rainbow Springs, North Carolina (<10 km from the study area). We also calculated the average leaf-litter depth for each survey point from 3 haphazard measurements taken within each survey area.

Landscape Covariates

To evaluate potential sources of variation in salamander abundance, we used ArcGIS to extract a number of land-use and topographic attributes for each survey point. Timber stand age was identified from an ArcGIS geodatabase provided by the U.S. Forest Service. We also calculated the shortest distance from each survey point to the edge of the encompassing timber stand. We derived aspect, topographic position index (TPI), topographic wetness index (TWI), and distance to stream from the 3-m resolution national elevation dataset (NED) (Gesch 2007). Aspect values were converted from degrees into 2 continuous components: northness and eastness (Deng et al. 2007). The TPI represented the slope position of each point relative to the surrounding 100 m (Jenness 2006). The TWI represented moisture that incorporates topography (water accumulation) and solar exposure (evapotranspiration), which we calculated using the solar position at 12:00 on 20 June (Theobald 2007). To identify stream locations, we derived a flow-accumulation surface from the national elevation dataset and identified drainage networks according to flow direction. By visually assessing the concurrence of this layer with known stream positions, we classified locations with a minimum drainage area of 0.75 ha as streams.

Data Analyses

We used the binomial mixture model of Royle (2004) to estimate salamander abundance from our spatially and temporally replicated count data. This model can be used to estimate site-level abundance (λ), individual detection probability (p), and the effects of site- and survey-specific covariates on these parameters. We independently analyzed our count data for terrestrial-breeding red-legged salamanders (*Plethodon shermani*) (Highton & Peabody, 2000). Count data for stream-breeding Ocoee salamanders (*Desmognathus ocoee*) and Blue Ridge two-lined salamanders (*Eurycea wilderae*) were pooled for analyses. These species groups differ in both their breeding habitat and their movement behavior (Table 1). Due to extra-Poisson variation in our count data, we modeled red-legged salamander abundance with a negative binomial distribution. Abundance of our stream-breeding group was modeled as a zero-inflated Poisson distribution due to large numbers of zero counts. We used a parametric bootstrapping approach to compare the fit of null (intercept-only) and global parameterizations (all parameters) of the binomial mixture models. We compared the observed Pearson's chi-squared fit statistic with its expected sampling distribution from 500 replicate data sets simulated from each fitted model. Only the global parameterization provided an acceptable fit for the red-legged salamander (*p-value*>0.15), whereas both the null and global parameterizations yielded acceptable models for our stream-breeding species (both *p-value* >0.41).

We used Akaike's information criterion (AIC) (Burnham & Anderson 2002) to identify the best supported model for each species groups from our a priori model set. We first identified the best supported model for detection probability with an intercept-only

model for abundance. We compared 5 a priori models that included subsets of 6 covariates: weekly rainfall, ground temperature, Julian date, time of day (minutes after 21:00), and quadratic effects of temperature and time of day. Models were ranked according to AIC, and covariates from the best supported model were used to represent the detection process in subsequent model fitting.

Our procedure for identifying the best supported model for the site-level abundance of salamanders involved a comparison of eight a priori models. In the abundance component of the model, we considered northness, eastness, distance to stream, elevation, TPI, TWI, leaf-litter depth, and a linear effect of stand age. Because we were interested in determining the effect of past timber-stand rotation on salamander abundance, stand age was represented as a covariate in each of the 8 models we considered. We used the best supported model for each species group as the null model for the final stage of our model selection process. We built on this base model by comparing linear, exponential, and logarithmic relations between timber stand age and salamander abundance to identify whether the rate of postharvest population growth changed over time. Additionally, some models included an interaction between stand age and distance to stand edge to test for a role of external immigration in the process of population recovery. To test the critical assumption that detection probability did not vary systematically with stand age, we also compared the best supported models for each species group with post hoc models that differed only by the addition of the stand-age covariate to the detection component of each model.

We explored potential threshold effects in the association between stand age and salamander abundance. Using a simple piecewise regression approach, we parameterized

the abundance component of *N*-mixture models as a piecewise function with a change of slope at a stand age of either 25, 50, 75, or 100 years (Toms & Lesperance 2003; Jones et al. 2011). The following represents our specification of a log-linear model of site-level abundance (λ_i):

$$\log(\lambda_i) = \beta_0 + \beta_1 x_i + \beta_2 \max[0, (x_i - t)] \,, \tag{1}$$

where x_i is site-specific stand age, t is the assumed threshold value, and β_2 is the estimated slope adjustment beyond the threshold value. These models incorporated stand age as a linear effect and included all detection and abundance covariates that were included in the best supported model for each species group. We compared these threshold models with a null model that had no threshold effect (i.e., a model with a single slope term for the entire range of stand ages). All models were fitted in the unmarked package (Fiske & Chandler 2011) in program R (R Development Core Team 2012).

Results

We observed 2284 salamanders during repeated visits to 136 survey locations. The majority of our detections were of red-legged salamanders (N=1689), followed by Ocoee salamanders (N=402), Blue Ridge two-lined salamanders (N=138), pygmy salamanders (*D. wright*) (N=49), eastern newt (*Notophthalmus viridescens* (N=3), spring salamanders (*Gyrinophilus porphyriticus*) (N=2), and seepage salamanders (*D. aeneus*) (N=1). The distributions of terrestrial-breeding red-legged salamanders and our most common stream-breeding species, Ocoee salamanders and Blue Ridge two-lined salamanders, differed in their relation to a number of natural landscape features and in

relation to patterns of past timber harvest. Detectability of both species groups increased

with date and rainfall during our study period and peaked at intermediate ground-surface

temperature and mid-night (Fig. 2). The addition of a stand-age covariate to the detection

component of our best supported models resulted in slightly less parsimonious models for

the red-legged salamander (ΔAIC=1.98, model likelihood=0.37) and for our stream-

breeding species group (ΔAIC=1.62, model likelihood=0.44).

Red-legged salamander abundance was positively related to age of forest stand in

all models (Fig. 3). The land-use model with the strongest support for this species

included the exponential of stand age, which represented the hypothesis that postharvest

population growth rates increase as forest succession proceeds (Table 2). According to

this model, red-legged salamander abundance in our youngest stands (13 years) was

22.3% lower, on average, than in our oldest stands (122 years). However, this best

supported model did not differ strongly from the next 2 competing models, which

included either a linear effect of stand age (ΔAIC=0.79) or the natural logarithm of stand

age (ΔAIC=1.11) as a covariate. A comparison of threshold models indicated strong

support for an acceleration in population growth 100 years after harvest (Table 2).

Models accounting for distance to forest edge were not well supported, indicating that

red-legged salamander abundance did not substantially differ with proximity to adjacent

forest stands (ΔAICs>3.42) (Fig. 4).

Topography also appeared to have a large effect on local abundance of the red-

legged salamander. The 2 best supported models for abundance of this species both

included elevation and aspect (Table 2). In both models, abundance declined as elevation

increased and these salamanders tended to occur in higher numbers on south-facing slopes (Fig. 3).

The combined abundance of our most commonly encountered stream-breeding species, the Ocoee salamander and the Blue Ridge two-lined salamander, also were positively associated with age of forest stand (Fig. 3). The best supported model for this species group included the natural logarithm of stand age as a covariate, indicating that the abundance of these species increased at a more rapid rate in younger forest stands (Table 2). The predicted abundance of these salamanders was 53.6% lower in our youngest stands (13 years) than in our oldest stands (122 years). The best supported threshold model indicated that abundance of these species reached a peak 100 years after harvest (Table 2). For these stream-breeding salamanders, models including an effect of distance to stand edge and an interaction between this distance and stand age were strongly supported. Abundance was negatively associated with distance to the stand edge in young timber stands, whereas these salamanders were more uniformly distributed in older timber stands (Fig. 4).

The combined abundance of these stream-breeding species was best predicted by the global model, which included covariates for leaf-litter depth, elevation, aspect, TPI, TWI, and distance to stream (Table 2). The parameter estimates for elevation, TPI, TWI, and distance to stream all had 95% CIs that overlapped zero. Abundance was strongly related to aspect; the highest predicted densities occurred on north- and east-facing slopes (Fig. 3). Predicted abundance also decreased as leaf-litter depth increased, and our survey locations with the highest raw counts tended to have intermediate to low leaf-litter depth.

Discussion

We identified a number of factors associated with salamander abundance or detection probability. Among these factors, we detected a positive relation between predicted abundance and timber stand age in the terrestrial-breeding red-legged salamander and in our 2 most common stream-breeding species, the Ocoee salamander and the Blue Ridge two-lined salamander. However, the overall magnitude of population decline, rate of population recovery, and spatial distribution of individuals within forest stands differed between these species groups. Additionally, the predicted abundance of these species varied relative to a number of natural landscape features, suggesting the importance of understanding and controlling for these factors in future land-use studies.

Detection Probability

Because of their extensive use of below-ground retreats and cover objects, salamanders active on the ground surface likely represent a relatively small proportion of the local population (Bailey et al. 2004). In our study, detectability was highest toward the middle of the night, at intermediate temperatures, and under moisture conditions that minimized evaporative water loss in these salamanders. Although weekly rainfall had a strong effect on predicted detectability, Julian date also was an important predictor and appeared to correspond with the broader trend of increasing rainfall from the start to the end of our study period. The addition of a stand-age covariate to the detection component of our best supported models for each species group resulted in slightly less parsimonious models, suggesting that detection probability did not have a strong and systematic relation with stand age.

Habitat Associations

In the context of land-use studies, it is important to recognize that past management activity is just one of many predictors of local salamander abundance. Results of several studies show that salamander abundance is related to elevation (Ford 2002; Dodd & Dorazio 2004). In our study area, predicted abundance of red-legged salamanders was lower at higher elevation sites, which tended to be on ridges. Ocoee salamanders and Blue Ridge two-lined salamanders were predicted to reach high abundance on north- and east-facing slopes and were often observed in large numbers in cove forest with dense layers of low herbaceous vegetation. Pygmy salamanders were excluded from analyses, but this species also showed a clear association with aspect; 48 of 49 observations of this species occurred on northeast-facing aspects. Red-legged salamanders were predicted to be most abundant on south-facing slopes. In general, sites that had the highest counts of one species group (red-legged salamander or Ocoee salamander and Blue Ridge two-lined salamander) tended to have low counts of our other species group. Thus, species with broadly overlapping distributions in terrestrial habitat may show spatial structuring in their most used habitats.

Land-Use Effects

Forest stands in our study ranged from 13 to 122 years in age, and red-legged salamander abundance in our most recently harvested stands was predicted to be 22% lower than in our oldest stands. On the basis of numerous studies of woodland salamanders (genus *Plethodon*), the generalized expectation is that the relative abundance of these species is typically reduced in the short term by >50% following timber harvest

(reviewed by Tilghman et al. 2012). No forest stands in our study landscape had been harvested in the previous 13 years, but presumably initial declines were either of limited severity or some population recovery occurred in the initial years after harvest. Shifts in activity patterns in response to logging (e.g., Johnston & Frid 2002) also could have led to reduced detectability of salamanders and a downward bias of relative count indices in studies conducted immediately after harvest. Over the range of stand ages we examined, however, including an effect of stand age on detection probability was not well-supported by our data.

Terrestrial abundance of our 2 stream-breeding species was predicted to be roughly 54% lower in our youngest stands relative to our oldest stands. This result is consistent with results of previous studies that show the abundance of these species in terrestrial habitat appears to decline following timber harvest (Crawford & Semlitsch 2008; Peterman et al. 2011). Although we did not assess the in-stream abundance of these species, stream-breeding salamander abundance in aquatic habitat is also likely to be positively related to stand age (Lowe & Bolger 2002; Moseley et al. 2008).

By comparing models representing linear, exponential, and logarithmic relations between forest stand age and salamander abundance, we were able to broadly characterize rates of postharvest population recovery through time. The best supported model for red-legged salamanders included the exponential of stand age as a covariate and indicates that postharvest populations showed an accelerating population growth rate as stand age increased. Furthermore, results of our comparison of threshold models revealed a similar pattern. They showed that abundance was not significantly related to stand age until 100 years post-harvest, at which point it was predicted to increase

relatively rapidly. In contrast, abundance of Ocoee salamanders and Blue Ridge two-lined salamanders was predicted to follow a logarithmic rate of increase relative to time since harvest; abundance increased relatively rapidly in younger timber stands. Although the predicted decline in the abundance of these species was greater than for the red-legged salamander overall (54 vs. 22%), these species were predicted to reach peak abundance around 100 years after harvest. Our long estimated recovery time for the red-legged salamander (>100 years) is consistent with results of other studies that show relative abundances of *Plethodon* in old-growth forest are greater than even mature second-growth forest (54-72 and 70-80 years) (Dupuis et al. 1995; Herbeck & Larsen 1999).

Patterns of salamander distribution within forest stands allow insight into potential mechanisms of population recovery. Many terrestrial-breeding species, such as the red-legged salamander, are believed to have extremely limited dispersal (Liebgold et al. 2011). This suggests that immigration from adjacent forest should make little contribution to postharvest population growth. Red-legged salamander abundance did not appear to correlate with distance to the stand edge, thus indicating no pattern of diffusion or recolonization from adjacent forest. Furthermore, long-term effects of timber harvest on *Plethodon* populations do not appear to vary with stand size (Tilghman et al. 2012), suggesting that overall proximity to potential sources of migrants does not significantly accelerate population recovery. In contrast, the interaction between stand age and distance to stand edge was an important predictor of Ocoee salamander and Blue Ridge two-lined salamander abundance. These species are often common in terrestrial habitat but make periodic movements to stream habitat for reproduction (Petranka 1998). It is

unknown whether these species show site fidelity in their terrestrial habitat selection, but presumably the increased frequency and scale of movements in these species plays an large role in their response to timber harvest. Immediately after logging, average distance from stream and relative abundance of these salamanders decreases in terrestrial habitat, and this corresponds to an initial increase in salamander densities in headwater streams (Peterman et al. 2011). We found that the combined abundance of these species was highest toward the stand edge in relatively young timber stands and became more uniform as stand age increased. We believe the relatively more severe declines, faster recovery rates, and pattern of increased abundance near stand edges in young forest indicate there is initial movement of these species away from cut sites and substantial immigration that contributes to the eventual reestablishment of these species in terrestrial habitat.

Management Implications

We found the relation between salamander abundance and historic timber harvest varied significantly between species groups with differing life histories. The more mobile species showed a pattern of diffusion into harvested stands from surrounding forest, but this was not the case in the dispersal-limited species. Some authors suggest that smaller harvest areas may promote faster recovery of populations (e.g., Knapp et al. 2003), yet species that do not seem to recolonize a cut area from surrounding forest may simply be too dispersal-limited to benefit from movement into harvested stands. Stands over 100 years old were well represented in our study and were predicted to have the highest abundances of salamanders. Furthermore, the red-legged salamander was predicted to

show little recovery from 13 to 100 years after harvest. This finding indicates that studies in which mature second-growth stands (i.e., 50-80 years) are used as reference areas may underestimate recovery times of plethodontid salamanders by assuming a low baseline for comparison with younger stand-age classes.

Since 1953, the rate of forest growth has exceeded the rate of timber harvest in the United States and has resulted in a 50% increase in overall timber biomass (Smith et al. 2009). However, 64% of forest land in the eastern United States has been harvested within 60 years, and 86% of forest land is <80 years old (Smith et al. 2009). Thus, optimal habitat may still be limited for species that reach their highest densities in late-successional or old-growth forest (i.e., >80 years). Population recovery may be limited by the rate at which areas become suitable after timber harvest, the extent of recolonization from surrounding forest, and the rate of population growth in harvested stands. Species dependent on highly mature forest, such as large senescing trees or coarse woody debris at various decay stages, may require a century or more to reach peak densities in previously-harvested stands (Fisher & Wilkinson 2005; Josefsson et al. 2010). Although dispersal limitation and long generation times may limit postharvest population growth in plethodontid salamanders, it also is possible that abundance of these salamanders reaches a peak in response to structural characteristics of mature forest, such as coarse woody debris availability (McKenny et al. 2006).

Plethodontid salamanders likely play an important role in many forest ecosystems as abundant consumers of invertebrates (Wyman 1998) and as a significant source of energy and nutrients for species at higher trophic levels (Burton & Likens 1975). Current timber stand rotation does not appear to threaten the regional persistence of the common

salamander species we studied, and relatively robust populations still exist in late-successional forest. However, maximizing the percentage of forest managed as old growth will likely support the highest salamander densities and best preserve their role in forest ecosystems.

Acknowledgements

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Table 1. Life-history information relevant to the movement patterns of *Plethodon shermani*, *Desmognathus ocoee,* and *Eurycea wilderae*

Species	Breeding location	Movement range (m)	Justification[a]
P. shermani	terrestrial	~ 10	recaptures of all *P. shermani* age classes typically <7 m from initial capture locations (G.M.C., unpubl. data)
			mean dispersal distance of *P. cinereus* likely 2-4 m; movements of >10 m infrequent (Liebgold et al. 2007)
			small home range; all observed movement distances <8 m for *P. jordani* (Nishikawa 1990)
D. ocoee	stream	> 30	*D. ocoee* encountered up to 30 m from streams (Crawford & Semlitsch 2007)
			at high elevations, 29% of *D. carolinensis* found >60 m from streams (Hairston 1949)[b]
E. wilderae	stream	> 100	*E. wilderae* commonly encountered 50-100 m from streams (Crawford & Semlitsch 2007)
			E. bislineata routinely migrated >100 m from a steam (MacCulloch & Bider 1975)

[a] Empirical movement data are lacking for most plethodontid species and estimated movement ranges are in part based on data from congeneric species believed to be similar in the extent to which they use terrestrial habitat.

[b] High-elevation sites were >1370 m.

Table 2. Best supported models for the abundance (λ) and detectability (p) of salamanders in terrestrial habitat*

Model Name	Model covariates	K	ΔAIC	Model likelihood	ω_i
Detection models					
Plethodon shermani					
global^2	$\lambda(\bullet)p($date+time+time^2+rain+temp+temp$^2)$	9	0.00	1.00	1.00
D. ocoee/E. wilderae					
global^2	$\lambda(\bullet)p($date+time+time^2+rain+temp+temp$^2)$	9	0.00	1.00	1.00
Abundance models					
Plethodon shermani					
simple topo	$\lambda($aspect+elev+age$)p($global$^2)$	13	0.00	1.00	0.68
complex topo	$\lambda($TPI+aspect+elev+age$)p($global$^2)$	14	2.40	0.30	0.20
global	$\lambda($leaf+stream+TWI+TPI+aspect+elev+age$)$ $p($global$^2)$	17	3.59	0.17	0.11
D. ocoee/E. wilderae					
global	$\lambda($leaf+stream+TWI+TPI+aspect+elev+age$)$ $p($global$^2)$	17	0.00	1.00	0.68
local factors	$\lambda($leaf+stream+TPI+aspect+age$)p($global$^2)$	15	1.70	0.43	0.29
Land-use models					
Plethodon shermani					
exponential	$\lambda($aspect+elev+exp(age)$)p($global$^2)$	13	0.00	1.00	0.37
linear	$\lambda($aspect+elev+age$)p($global$^2)$	13	0.79	0.67	0.25
logarithmic	$\lambda($aspect+elev+log(age)$)p($global$^2)$	13	1.11	0.57	0.21
D. ocoee/E. wilderae					
log distance	$\lambda($leaf+stream+TWI+TPI+aspect+elev+ log(age)+dist+dist*log(age)$)p($global$^2)$	19	0.00	1.00	0.50
linear distance	$\lambda($leaf+stream+TWI+TPI+aspect+elev+age +dist+dist*age$)p($global$^2)$	19	1.82	0.40	0.20
logarithmic	$\lambda($leaf+stream+TWI+TPI+aspect+elev +log(age)$)p($global$^2)$	17	2.47	0.29	0.15
Threshold Models					
Plethodon shermani					
100 year	$\lambda($aspect+elev+age+max(0, age-100)$)$ $p($global$^2)$	14	0.00	1.00	0.88
75 year	$\lambda($aspect+elev+age+max(0, age-75)$)$ $p($global$^2)$	14	5.20	0.07	0.07
D. ocoee/E. wilderae					
100 year	$\lambda($leaf+stream+TWI+TPI+aspect+elev+age +max(0, age-100)$)p($global$^2)$	20	0.00	1.00	0.99

* Table includes only models with $\omega_i > 0.10$. The $\bullet$ symbol indicates no covariates were fitted to abundance. K gives the number of parameters in a model. ΔAICc , indicates the difference in AICc value between each model and the best model in the set. Model likelihood was calculated as e$^{-\Delta AIC/2}$. ω_i gives the Akaike weight for each model.

Abbreviations: age, years since harvest; aspect, northness and eastness included in model; dist; distance to stand edge (m); elev, elevation (m); leaf, leaf litter depth (cm); stream, distance to nearest stream (m); TPI, topographic position index; TWI, topographic wetness index; global^2, all detection parameters included in model.

Figure 1. Locations of salamander survey points in the Nantahala National Forest, North Carolina (U.S.A.).
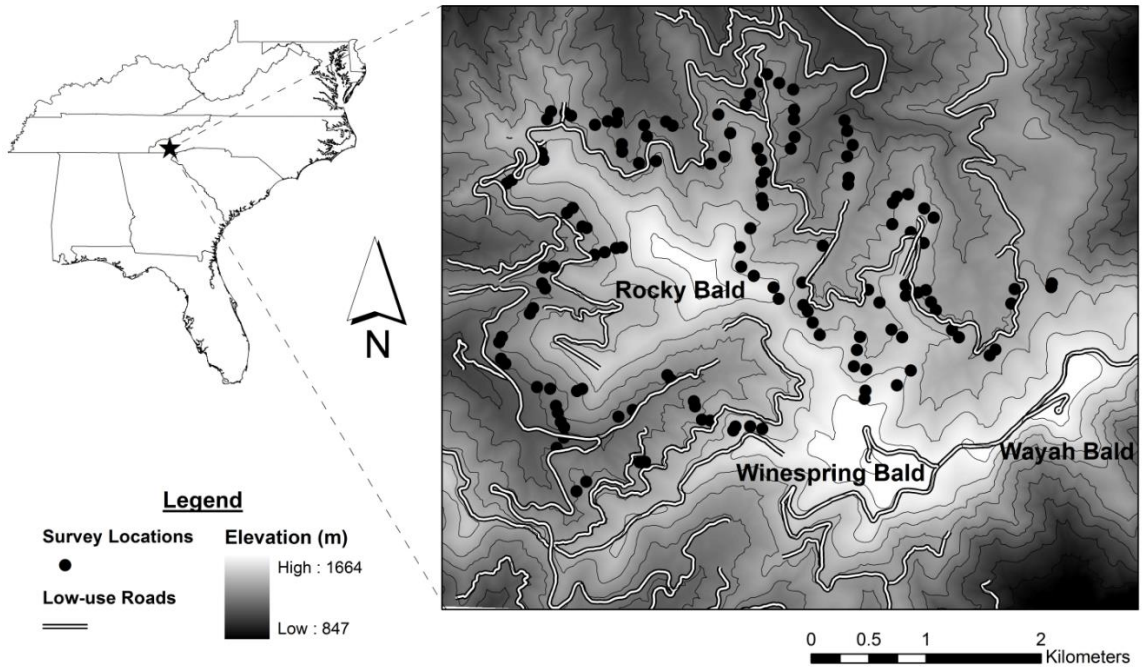
Figure 2. Predicted relations between survey-specific covariates and individual detection
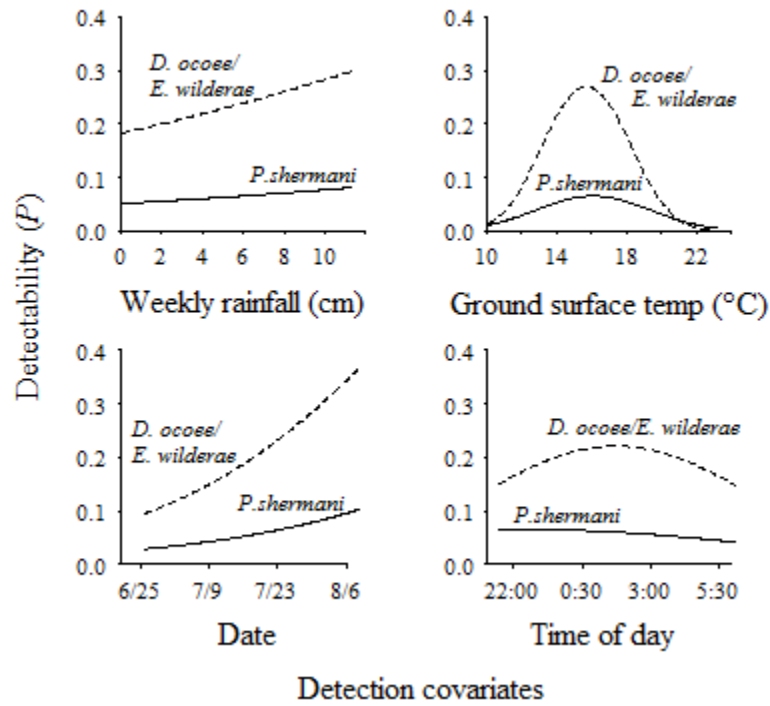probabilities in the best supported land-use model for each species group (see Table 2).

Figure 3. Predicted relations between salamander abundance and site-specific covariates in the best supported land-use model for each salamander species group (Table 2). Only significant covariates are shown (95% CI excludes zero).
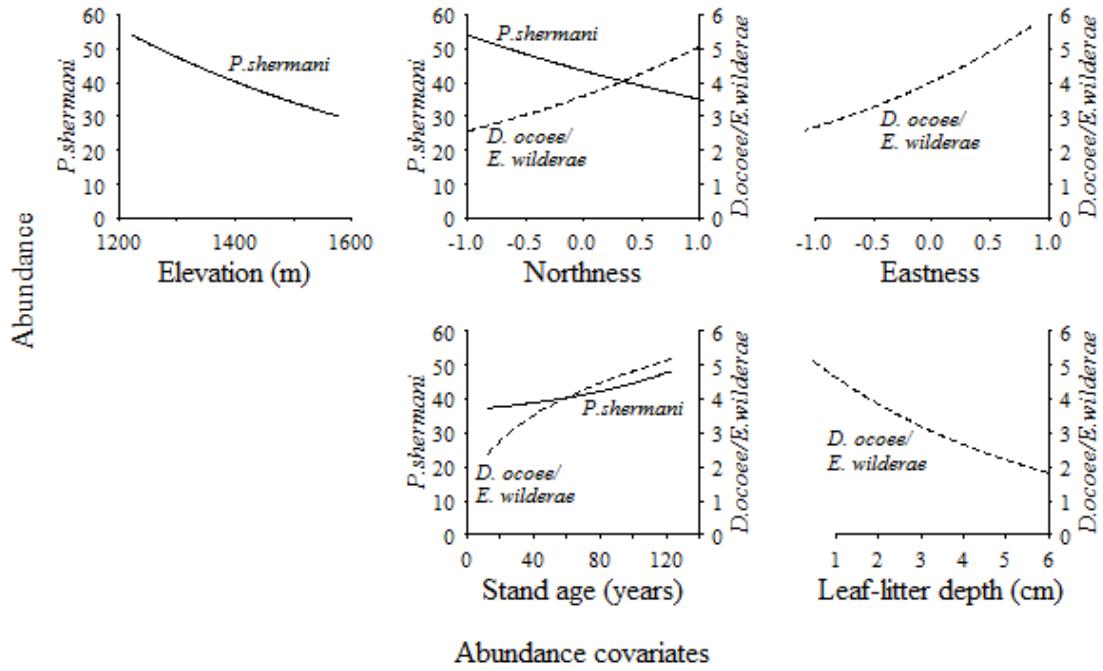
Figure 4. Predicted salamander abundance per survey point (approximately 19.6 m^2) in relation to forest stand age and distance to stand edge. Plots represent predicted abundance according to the exponential distance model (*Plethodon shermani*) and the logarithmic distance model (*Desmognathus ocoee* and *Eurycea wilderae*). Distance to edge and distance*stand age interactions were significant only for *D.ocoee* and *E. wilderae*. Models without these factors were more strongly supported for *P. shermani*.
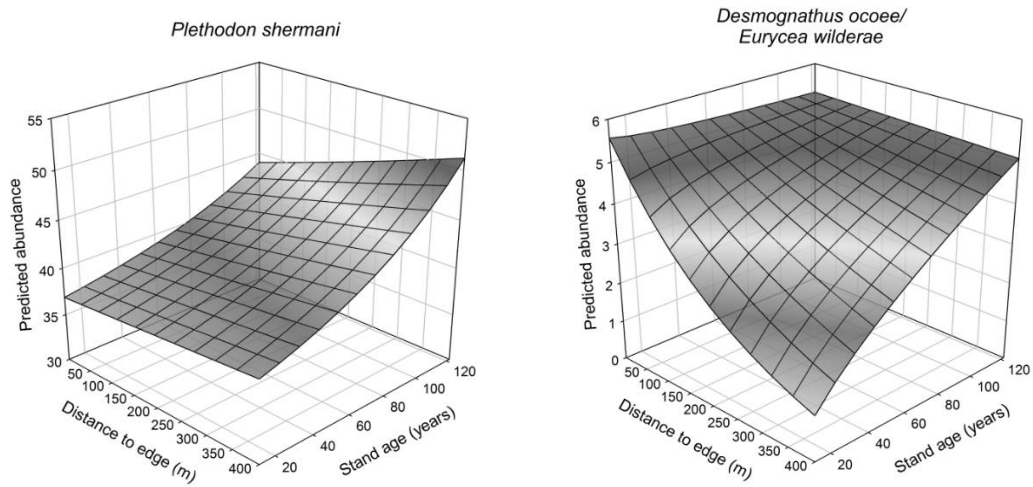
Chapter 6

SUMMARY

Changes in population size are of critical interest in the fields of ecology, wildlife management and conservation biology. In particular, there is a pressing need to understand the responses of species to habitat loss and fragmentation. However, variable activity patterns, uneven distributions and context-dependent behavior of animals often provide a complex background from which to isolate important land use effects. Furthermore, identifying the demographic processes responsible for changes in populations (i.e., survival, recruitment, migration) can be especially important for developing effective conservation and management strategies. This dissertation provides a broad overview of the individual-, population- and landscape-level responses of terrestrial salamanders to timber harvest. The following sections provide a summary of the key findings and conclusions of each dissertation chapter.

Chapter 2 – Local populations of a woodland salamander (*Plethodon shermani*) show considerable variation in population size, apparent survival and recruitment

- Local salamander populations showed considerable spatial and temporal variation in abundance, survival and recruitment

- Initial differences in abundance between harvested and un-harvested sites appeared to be a result of higher recruitment and over-winter survival in un-harvested plots

Chapter 3 – Context-dependent movement behavior of woodland salamanders (*Plethodon*) in two habitat types

- Salamanders homing through forest oriented more strongly towards their territories and moved significantly farther on their release night than those in a timber cut
- Return rates of salamanders did not differ between forest and open-canopy habitat

Chapter 4 – Use of auxiliary PIT-tag telemetry data to estimate survival of a terrestrial salamander following timber harvest

- Weekly survival of salamanders was higher in control forest than in a two-aged regeneration harvest
- Estimated emigration rates were similar between harvested and un-harvested plots
- Detection probability, conditional on survival and presence in the survey area, was higher in harvested areas than in control forest

Chapter 5 – Life history as a predictor of salamander recovery rate from timber harvest in southern Appalachian forests

- Abundance of stream- and terrestrial-breeding salamanders was positively associated with forest stand age

- Abundance of stream-breeding species was predicted to reach a peak by 100 years after harvest while population growth of our terrestrial species was predicted to undergo a significant increase 100 years after harvest

- Estimated abundance of stream-breeding salamanders in young forest stands was negatively associated with distance to adjacent forest, a result that suggests immigration has a role in the recovery of these species with migratory life histories.

Appendix A

FULL SURVIVAL/EMIGRATION MODEL DESCRIPTION

Data from capture-recapture studies are often summarized as a matrix of binary observations, $y_{i,j}$, where $y_{i,j} = 1$ indicates that individual i was captured at time j and $y_{i,j} = 0$ indicates that the individual was not captured. In this latter case, the individual was either dead or, if it was alive, it was present and not detected or had emigrated from the study area. In this study, our analysis of individual survival is based on a state-space representation of the Cormack-Jolly-Seber model (Royle 2008, Kery and Schaub 2012) but seeks to estimate individual survival probability while accounting for the possibility that individuals permanently emigrate from the survey area. In our study, we estimate the values of two demographic rates, survival and emigration probability, on a weekly basis and in most cases have multiple secondary samples within our assumed primary periods (i.e. the "robust design" survey procedure; Williams et al. 2002). Thus, our individual observations are indexed as $y_{i,j,k}$, representing whether an individual i was detected at time j and survey k with demographic closure assumed among surveys that occur within the same week. See Appendix B for complete R/WinBUGS code specifying this model.

Overall State Process Model

Our overall state process is denoted by a binary state variable $z_{i,j}$, which designates whether individual i is alive and within the survey area at time t ($z_{i,j} = 1$) or has either died or emigrated ($z_{i,j} = 0$). The following model specifies the true state of

individual i at time j as the outcome of a Bernoulli trial with a success probability defined by the product $z_{i,j-1}\,\phi_{i,j}(1-\gamma_{i,j})$, where $z_{i,j-1}$ represents the previous state of individual i, $\phi_{i,j}$ represents the probability of survival and $(1 - \gamma_{i,j})$ represents the reciprocal of the emigration probability $(\gamma_{i,j})$ over the interval $[j-1, j]$.

$$z_{i,j}|z_{i,j-1} \sim \text{Bernoulli}(z_{i,j-1}\phi_{i,j}(1-\gamma_{i,j}))$$

Thus, if an individual was alive and present at time $j - 1$, its probability of being alive and present within the survey area at time j is simply the product of its survival probability $\phi_{i,j}$ and its probability of remaining within the survey area $(1-\gamma_{i,j})$. Emigration probability is estimated in a model for auxiliary PIT-tag telemetry data (see below). If an individual was not alive and present at $j - 1$, then $z_{i,j}$ is a Bernoulli random variable with success probability 0. We introduced a fixed treatment effect to independently estimate survival rates for both harvested and unharvested plots.

$$\phi_{i,j} = \beta_{HARVEST_{i,j}}$$

Here the parameter index $HARVEST_{i,j}$ denotes whether individual i is located in a harvested or unharvested area at time j.

Overall Observation Model

Conditional on individual i being alive and within the study area at time j, it may be observed on the ground surface at each survey k with probability $p_{i,j,k}$. Thus, the live observations of individuals present in the area, $y_{i,j,k}$, are also modelled as realizations of independent Bernoulli trials with success probability $p_{i,j,k}$.

$$y_{i,j,k}|z_{i,j} \sim \text{Bernoulli}(z_{i,j}p_{i,j,k})$$

Intuitively, if an individual is dead or emigrated ($z_{i,j} = 0$), then it cannot be observed alive and $y_{i,j,k} = 0$. Otherwise, $y_{i,j,k}$ is the outcome of a Bernoulli trial with success probability $p_{i,j,k}$. Due to the sensitivity of terrestrial salamander activity to moisture conditions and to account for the possibility that individuals change their activity patterns following timber harvest, we used a logit-link function to represent variation in detection probability:

$$\text{logit}(p_{i,j,k}) = \alpha_0 + \alpha_1 RAIN_k + \alpha_2 HARVEST_{i,j} + \varepsilon_i$$

$$\text{where } \varepsilon_i \sim \text{Normal}(0, \tau)$$

where α_0 represents the intercept, α_1 represents the slope, $RAIN_k$ is a survey-specific covariate indicating days since the last rainfall of greater than 0.25 cm and $HARVEST_{i,j}$ indicates whether or not timber harvest had occurred at an individual's location. We included an individual random effect due to the obvious discrepancy among individuals in their respective encounter frequencies.

Auxiliary Emigration Model

The primary data set, consisting of live detection histories for each individual, provides limited information for estimation of the parameter γ, emigration probability, because mortality and emigration are completely confounded. PIT-tag telemetry data provides additional information that individuals have remained within the study area and includes observations of live individuals on the ground surface and of individuals which are below-ground or are not visually observed at a given survey (either alive or dead). We use our auxiliary PIT-tag detection histories, which independently provide no information on survival, to estimate γ. Because individuals observed alive on the ground

surface are always detected with the PIT-tag reader, our two datasets provide non-independent information on emigration. Thus, we use the "cut" function in WinBUGS to treat the estimation of γ as a hidden Markov process and prevent our less complete dataset of live encounters from informing estimation of this parameter. Here our state variable, $z2_{i,j}$, designates whether individual i is within the survey area at time j (alive or dead). We model the true state of individual i at time j as the outcome of a Bernoulli trial with success probability defined by $z2_{i,j-1}(1 - \gamma_{i,j})$.

$$z2_{i,j}|z2_{i,j-1} \sim \text{Bernoulli}(z2_{i,j-1}(1 - \gamma_{i,j}))$$

If an individual was present in the area at time $j - 1$, its probability of being present at time t is the complement of its emigration probability $(1 - \gamma_{i,j})$. We introduced a fixed treatment effect to independently estimate emigration rates for both harvested and unharvested plots.

$$\gamma_{i,j} = \beta2_{HARVEST_{i,j}}$$

Here the parameter index $HARVEST_{i,j}$ denotes whether individual i is located in a harvested or unharvested area at time j.

Auxiliary Observation Model

Overall, detection rates of PIT-tagged individuals were quite high relative to the probability of visually observing an individual on the ground surface. However, given the relatively large areas searched and the limited detection range of our PIT-tag reader, we also assume that there was imperfect detection associated with PIT-tag searches. Thus, our series of PIT-tag detections $y2_{i,j,k}$ are modelled as independent Bernoulli trials

with success probability, $p2_i$, conditional on each individual i being present in the study area.

$$y2_{i,j,k}|z2_{i,j} \sim \text{Bernoulli}(z2_{i,j}p2_i)$$

If random temporary emigration from the study area were to occur, then its probability of occurrence would be confounded with $p2_i$ but would not be expected to bias survival or emigration probabilities.

To represent the detection process associated with PIT tag telemetry searches, we again use a logit-link function in order to introduce an individual random effect to account for the discrepancy among individuals in relative encounter rates, where $\alpha2_0$ represents the mean probability of detection on the logit scale.

$$\text{logit}(p2_i) = \alpha2_0 + \varepsilon2_i$$

$$\text{where } \varepsilon2_i \sim \text{Normal}(0, \tau2)$$

Analysis of the Full Model

We used OpenBUGS (Lunn et al. 2009), to fit the model using Markov chain Monte Carlo (MCMC) simulation. All analysis was executed through program R (R Development Core Team 2012) using the R2OpenBUGS package (v. 3.2.2; Sturtz et al. 2005). We assigned uninformative uniform priors [0, 1] to all survival and emigration parameters ($\beta_{Control}$, $\beta_{Harvest}$, $\beta2_{Control}$, $\beta2_{Harvest}$). We assigned uniform priors [-5, 5] to the intercept terms α_0 and $\alpha2_0$, [-10, 10] to the regression coefficients α_1 and α_2, and [0, 5] to the standard deviations for individual random effects $1/\sqrt{\tau}$ and $1/\sqrt{\tau2}$. Posterior summaries from each of three parallel Markov chains were based on an arbitrarily large sample of 1,000,000 MCMC iterations thinned at a rate of 100 following

an initial burn-in of 500,000 iterations. From these summaries, we calculated the mean

and 95% credible interval (CRI) for all model parameters. We assessed model

convergence using the Gelman-Rubin statistic (R̂; Gelman et al. 2004) and found

acceptable convergence ($\hat{R}$<1.05 for all parameters). Finally, we compared the overlap of

our prior and posterior densities and found strong identifiability of all parameters except

two parameters associated with the observation model for mark-resight data ($\tau > 0.35$;

Gimenez et al. 2009). These were the intercept term and the coefficient for the effect of

timber harvest on detection probability. Nonetheless, the posterior distribution for the

effect of timber harvest on visual detection was clearly identified as non-negative (Fig.

2).

We evaluated the fit of our model by comparing our empirical capture history

with 1,000 replicate data sets generated from the posterior summaries of our Markov

chains. Each simulated dataset was generated by recovering the parameters $p_{i,t}, \phi_{i,t},$

and $\gamma_{i,t}$ from a randomly-selected MCMC iteration and sampling $z_{i,t}$ from a Bernoulli

distribution with success probability given by the product $\phi_{i,t}(1 - \gamma_{i,t})z_{i,t-1}$.

Conditional on $z_{i,t} = 1$, we then sampled $y_{i,t}$ from a Bernoulli distribution which success

probability $p_{i,t}$. Finally, we calculated the mean number of observations per individual

for each simulated dataset and found that our empirical data placed in the 80th percentile

of simulated datasets.

Appendix B

SURVIVAL ANALYSIS RESULTS FROM A CORMACK-JOLLY-SEBER MODEL

The figure below conveys the results of an analysis of salamander mark-recapture based on a traditional Cormack-Jolly-Seber model (Royle 2008; Kery & Schaub 2012). Analysis was executed through program R (R Development Core Team 2012) using the R2OpenBUGS package (v. 3.2.2; Sturtz, Ligges & Gelman 2005). Posterior summaries from each of three parallel Markov chains were based on a sample of 100,000 MCMC iterations thinned at a rate of 20 following an initial burn-in of 50,000 iterations.
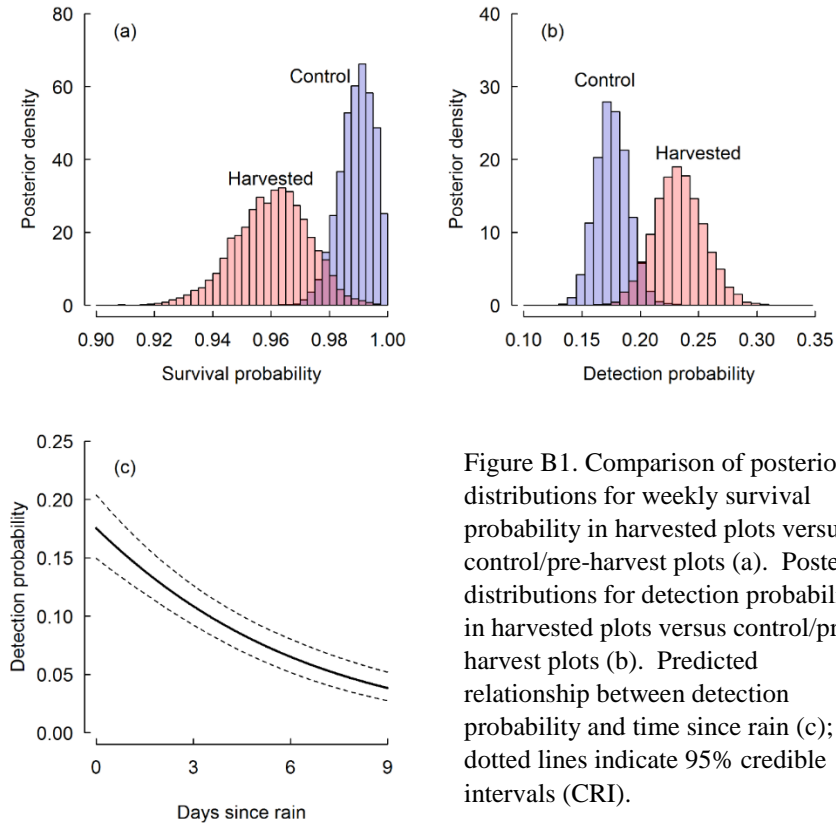

Figure B1. Comparison of posterior distributions for weekly survival probability in harvested plots versus control/pre-harvest plots (a). Posterior distributions for detection probability in harvested plots versus control/pre-harvest plots (b). Predicted relationship between detection probability and time since rain (c); dotted lines indicate 95% credible intervals (CRI).

Vita

   Grant McClintock Connette was born on 9 March 1986 in San Jose, Costa Rica.

He grew up in Virginia and graduated from Western Albemarle High School in 2004 and

went on to earn a B.S. in Biology at Davidson College in 2008. Grant began his Ph.D. at

the University of Missouri in June 2009 with an emphasis in Ecology and Evolution and

in September 2012, Grant was married to Katherine J. LaJeunesse. His dissertation

research was based out of the Highlands Biological Station and investigated the effects of

timber harvest on terrestrial salamander populations in the southern Appalachian

Mountains. Grant will begin a post-doctoral appointment at the University of Missouri in

September 2014 where he will study the population dynamics of golden-cheeked

warblers.