ESTIMATING POPULATION PARAMETERS OF HYBRID SALAMANDERS IN RESPONSE TO FOREST MANAGEMENT

by

KIRSTINE M. GRAB

(Under the Direction of John C. Maerz)

ABSTRACT

A fundamental question in conservation is how animal populations dynamics, both patterns and process, respond to land management practices. The U.S. Forest Service at Coweeta Hydrologic Laboratory began a paired watershed experiment where one watershed was treated with midstory shrub removal and repeated application of prescribed fire and was compared with another nearby watershed as a reference. I estimated changes in abundance, population structure, and juvenile growth and survival of hybrid salamanders (*Plethodon* spp.) between the two watersheds using a hierarchical and integrated modelling approach. Consistent with my hypothesis, hatchling and juvenile salamanders experienced stronger negative effects of management actions on abundance than subadults or adults. I found weak evidence for a small, negative effect of treatment on growth but a small, positive effect on survival; however, these results are unreliable due to bias. This thesis provides a starting point for future research and understanding of this salamander population.

INDEX WORDS: *Plethodon*, forest management, southern Appalachia, hierarchical modeling, integrated modeling, abundance, age structure, growth, survival

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B.S., University of Minnesota, 2018

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2024

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The University of Georgia
December 2024

DEDICATION

To Warner Nature Center

ACKNOWLEDGEMENTS

This thesis would not have been possible without the help and support of many people. I would like to thank John Maerz, my advisor, for taking me on as a grad student, his guidance, and all the learning opportunities. I'd like to thank my committee, Dr. Michel Kohl and Dr. A. Chris Oishi, for their thoughtful input and feedback. I am so grateful for the graduate students who helped me along the way. I'd especially like to express profound gratitude to Shelby Bauer for her comradery and data wrangling, Danielle Bradke for her coding genius, and Cyndi Carter for her knowledge on Coweeta and the hybrid zone.

A huge thank you to Vanessa C. Terrell Kinney for doing much of the organizing for the field trips and logistics such as permits, supplies, etc. Thank you from the bottom of my heart to all the volunteers that helped in the field: John, Cyndi, Shelby, Justin, Cory, Seamus, Ally, Noah, Catie, Keeta, Karin, Tyler, Tara, Paul, Zachary, Reed, Eva, Jade, Wilson, Erin, Roxanna, Sam, and Natane. And a big thank you to Catie Elder for her help on the growth analysis. Thank you to all the folks that collected data for the long-term CMR project and the hemlock project.

Thank you to the folks in the Branch of Permits who supported me and made it possible for me to go to graduate school while working part time. I would especially like to thank Jorge for being so incredibly flexible and supportive of this pursuit. I genuinely don't think that this would have been possible without it. I am so incredibly grateful to Emma for encouraging me to go to graduate school and doing it with me. Thank you to Michelle for her mentorship, encouragement, and friendship. To Su Jewell, Brooke

Stansberry, Dr. Lisa Ferguson, Dr. Marlene Zuk, and Dr. Susan Balenger: thank you so much for your support and mentorship.

Thank you to U.S. Forest Service for letting me futz around the mountains at ungodly hours looking at salamanders. Thank you to River Basin Center for adopting me this summer, specifically I would like to thank Dr. Wenger, Philip Bumpers, and Eric for their help with analysis and coding. I would also like to thank Dr. Richard Chandler and Heather Gaya for their help with statistical analysis.

So many hugs and gushy thanks to my friends and family. I couldn’t have gotten through this endeavor without you. Thank you to Mom and Dad for their unwavering support and guidance. Thank you to Sarah, Elle, and Emma for listening to several presentations, being sources of good, wholesome energy, and being the sisters I have always needed. Thank you to the sprawling gang, Noah, Elsie, and Connor; fire finches, Vanessa and Clara, for engaging in the praxis of good fire; and the ever-delightful Kristen and Birdie. Thank you to Dash for reminding me to take naps, soak up the sun, and express my boundaries. You are a trooper.

This research was made possible through funding by a Faculty Seed Grant awarded to John C. Maerz from the University of Georgia Research Foundation, Inc. The main study was performed in compliance with Institutional Animal Care and Use Committee Animal Use protocols A2018 07-007-Y3-A0, A2020 06-028-Y3-A6, and A2023 08-025-Y1-A0. The animal use collection permits for this research were permitted under North Carolina Wildlife Resources Commission Wildlife Collection Licenses 18-SC00896, 19-SC00896, 20-SC00896, 21-SC00896, 22-SC00896, and 23-SC00896. This study was supported in part by resources and technical expertise from the Georgia Advanced Computing Resource

Center, a partnership between the University of Georgia’s Office of the Vice President for Research and Office of the Vice President for Information Technology.

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CHAPTER 1

Introduction

A fundamental question in conservation is how animal populations respond to land management practices (Darracq et al., 2016; Harper et al., 2016). We know that land management practices shape landscapes, which in turn may impact species that occupy those landscapes. However, to optimize management objectives to maintain regional biodiversity, it is important to understand how species, even those that are not the target of management actions, are impacted by different management practices.

Many studies that investigate the effects of forest management activities on wildlife focus on species presence, abundance, or richness (Cosset et al., 2019; Harper et al., 2016). Fewer studies estimate the effects of management on population vital rates that govern those patterns or the behavioral, physiological, or evolutionary responses to management actions and how they affect the demography of species on managed landscapes (Harper et al., 2016; Pabijan et al., 2020; Walls and Gabor, 2019). Incorporating demographic processes, like survival, that drive the larger population patterns, such as abundance, can help us understand how management activities impact species and lead to improved management actions (Otto et al., 2014).

Southern Appalachia

The southern Appalachian Mountains have been managed by people for millennia (Delcourt and Delcourt, 1997, 1998; Yarnell, 1998). Frequent, low-intensity fires lit by Native Americans and natural phenomena, such as lightning, led to forests dominated by oak (*Quercus* spp.), American chestnut (*Castanea dentata*), hickory (*Carya* spp.), and pine (Pinus spp.) prior to European colonization in southern Appalachia (Brose et al., 2001; Cooley, 2004; Delcourt and Delcourt, 1997, 1998). High intensity, stand-replacing fires followed by fire suppression policies of the early 20th century coupled with the chestnut blight (*Cryphonectria parasitica*) caused southern Appalachian forests to shift away from more xeric tree species to more mesophytic ones, such as maple (*Acer* spp.), tulip poplar (*Liriodendron tulipifera*), and birch (*Betula* spp.) with dense understories of rhododendron (*Rhododendron* spp.) and mountain laurel (*Kalmia latifolia*) (Brose et al., 2001; Harrod et al., 1998; Nowacki and Abrams, 2008). In recent decades, prescribed fire is increasingly being applied to the landscape to aid oak regeneration and more generally, to restore or improve habitat for species that had previously occupied the region, such as red-cockaded woodpeckers (*Leuconotopicus borealis*) (Brose et al., 2001; Fouts et al., 2017; Harper et al., 2016). With this recent push to enhance oak recruitment on the southern Appalachian landscape, researchers have been investigating how wildlife respond to prescribed fire, mechanical shrub, and shelterwood removal (e.g., Campbell et al., 2007; Greenberg et al., 2018a; Harper et al., 2016). These forest management practices can create forests that are warmer and drier compared to their fire-suppressed counterparts (Brose et al., 2001; Fouts et al., 2017), which impact the broader community of fauna and flora. Therefore, to determine the impacts of land management on wildlife populations, especially populations that are not always the focus of management actions, land managers need information on how and to what extent these management actions have on wildlife species and their populations.

Plethodontid Salamanders

Among vertebrates, the Southern Appalachian Mountains are a global hotspot for salamanders (Vieites et al., 2007; Wake, 2017). Approximately 70% of amphibian species in Appalachia are salamanders, and the highest global densities of salamander species occur in the region (Kozak and Wiens, 2010; Mitchell et al., 1999). Most of this diversity resides within the family Plethodontidae, which are lungless salamanders that depend on passive cutaneous gas exchange (Feder, 1983). Cutaneous gas exchange makes them reliant on cool, moist microclimates and most aspects of their ecology including their abundance, survival rates, and surface activities are highly weather dependent (Feder, 1983; Peterman and Semlitsch, 2013). Natural or anthropogenic disturbances that cause temperatures and associated vapor pressure deficits to increase, rainfall or soil moisture to decrease or reduces the availability or access to cool, moist refugia such as leaf litter, downed woody debris, or subterranean habitat can lead to reduced plethodontid fitness and abundance (Feder, 1983; Gade et al., 2020; Peterman and Semlitsch, 2013; Spotila, 1972). Though plethodontid salamanders have some behavioral and physiological adaptations for dealing with variation in moisture and temperature (McEntire, 2016; McEntire and Maerz, 2019; Riddell et al., 2018), range expansions and contractions over the millions of years that plethodontid lineages have occupied Appalachia suggest that these salamanders are conservative in their climatic niche and their range usually follows their preferred climate rather than individuals adapting to the changing climate at a given location (Gifford and Kozak, 2012; Kozak and Wiens, 2006). Because of their potentially high abundance and biomass, plethodontid salamanders are both predators and prey which can be influential in ecosystem processes (Best and Welsh, Jr., 2014; Davic and Welsh, 2004; Semlitsch et al., 2014). It is unclear how plethodontid populations may respond to contemporary forest management practices. On the one hand, what we know about their ecological sensitivity to warmer, drier conditions and their niche conservatism over long time scales of environmental change suggest actions such as midstory removal and prescribed fire would negatively impact plethodontid abundance. On the other hand, physiological and behavioral adaptations might be sufficient to compensate for forest management effects, leading to little or no influence on abundance or vital rates. Given their importance in regional biodiversity and influence on ecosystems, plethodontid salamanders are a compelling taxon for studying wildlife responses to landscape management.

Salamanders and Forest Management

Salamanders have been a relatively common focal taxa of researchers studying the impacts of forest management activities (Tilghman et al., 2012). However, despite their common use in forest management studies, the effects of prescribed fire or midstory shrub removal on salamander populations appear equivocal and there remain significant gaps in our understanding effects on population dynamics. Some studies report no effect of mechanical treatment, prescribed fire, or both on salamanders (Ford et al., 1999; Greenberg et al., 2018a, 2018b, 2016; Greenberg and Waldrop, 2008; Ochs et al., 2024) while other studies report a negative effect of those actions on salamanders (Chelgren et al., 2011; Head, 2020; Hocking et al., 2013a; Homyack and Haas, 2009; Hromada et al., 2018; Jacobsen et al., 2020; Matthews et al., 2010; Ochs et al., 2022; Petranka et al., 1994; Schurbon and Fauth, 2003; Sutton et al., 2013). Alternatively, one study reported an increased numbers of salamanders associated with forest management actions (Ford et al., 2010), but the use of cover boards in that study may have attracted salamanders which could bias the results and confound inferences (Tilghman et al., 2012). This variety in responses is likely a result of the wide variety of management practices that fall under the umbrella of forest management. The methods covered include clearcutting (e.g., Ash et al., 2003), thinning (e.g., Grialou et al., 2000), prescribed fire (e.g., Jacobsen et al., 2020), herbicide (e.g., O’Donnell et al., 2015), and a combination of the aforementioned treatments (e.g., Sutton et al., 2013).

In addition, the types of metrics used to measure responses by salamanders and the methods used to quantify those responses vary considerably and confound general inferences. Response metrics have included a range of techniques such as naive capture rates (Greenberg et al., 2018b), occupancy (Chelgren et al., 2011), and abundance

(Hromada et al., 2018; Jacobsen et al., 2020; Mossman et al., 2019; O'Donnell et al., 2015). Few studies have directly estimated the effects of forest management actions on vital rates that drive those patterns of abundance or occupancy even though understanding the underlying demographic mechanisms could lead to more effective management decisions (Otto et al., 2014). Limited reporting of vital rates is common for plethodontid salamanders even though they are frequent study species (Howard and Maerz, 2021). Some studies do report how different age classes respond to forest management treatments, and many of those studies report a reduction in the proportion of juveniles associated with forest management (Ash, 1997; Ash et al., 2003; Ford et al., 2010; Grialou et al., 2000; Halloran et al., 2021; Head, 2020; Hocking et al., 2013b; Homyack and Haas, 2009; Mazerolle et al., 2021; Otto et al., 2014). This reduction in the proportion of juveniles could be indicative of a variety of different mechanisms including reduced reproductive rates of adult females or reduced growth and survival rates of juveniles. These vital rates are not well studied in the context of forest management effects on salamanders. One study found that the number of eggs per females was lower in plots following timber harvest (Homyack and Haas, 2009). Other studies have found that survival rates are lower in harvested forest plots compared to control or reference plots (Connette and Semlitsch, 2015; Ochs et al., 2024; Otto et al., 2014). One study found no difference in apparent survival in response to timber harvest (Halloran et al., 2021). Vital rates for juvenile plethodontid salamanders are even more limited (Howard and Maerz, 2021), including in the literature on salamander responses to forest management. These smaller life stages are more sensitive to climatic and microhabitat changes than adults (Howard, 2018; McEntire and Maerz, 2019; Peterman and Semlitsch, 2013). Increased sensitivity of smaller juveniles to changes in the hydroclimate of forests may make them more susceptible to forest management activities compared to larger age classes. I found one study that reported increased growth rates of juvenile stream salamanders in response to timber harvest (Guzy et al., 2021).

A small number of studies have addressed behavioral or other responses of salamanders to forest management (Ford et al., 2010; Halloran et al., 2021; Head, 2020; Ochs et al., 2024; O'Donnell et al., 2016). Increased movement of salamanders was reported in two studies after timber harvest and prescribed fire, and both suggested that the increased movement may have been a response by animals seeking refugia or other resources that had become less available (Halloran et al., 2021; O'Donnell et al., 2016). Consistent with the knowledge or belief that forests actively managed with vegetation removal or prescribed fire are warmer and drier, several researchers report decreased surface activity of salamanders in areas where prescribed fire or vegetation removal was implemented (Head, 2020; O'Donnell et al., 2016).

Most studies of forest management impacts on salamanders focus on short or near-term responses. However, some studies show that forest management activities can have long-term impacts resulting from small-scale responses that might be difficult to detect with short-term studies but accumulate to larger effects over time (Homyack and Haas, 2009; Ochs et al., 2022; Schurbon and Fauth, 2003). For example, one study found that over a ten-year period, a measurable reduction in salamander captures was not observed until at least three years following timber harvest (Ochs et al., 2022).

Thesis Goals & Objectives

The goal of this thesis was to use a paired watershed experiment to estimate changes in *Plethodon* population abundance, structure, and juvenile vital rates in response to forest management activities. This study took place at Coweeta Hydrologic Laboratory (herein Coweeta) in Macon County, North Carolina, which is part of the U.S. Forest Service's Nantahala National Forest. The U.S. Forest Service implemented a project, called the "Future Forest Experiment", in 2018 with midstory removal in 2018 and prescribed fire beginning in February 2019. The broader goal of this project is to create more resilient forests in the future that use less water (A. Chris Oishi, *personal communication*). This project also investigates how forest biota and key ecosystem processes (e.g., water fluxes) respond to midstory removal and prescribed fire in the near term and the subsequent longer-term changes in tree community composition and forest characteristics, including hydroclimate. The treatment, applied to watershed 31 (WS31), involved the manual removal of understory *Rhododendron* spp. and application of herbicide to the *Rhododendron* stumps application followed by prescribed fire with a 2-year burn interval in February/March of 2019, 2021, and 2023 (Miniat et al., 2021). Watershed 32 (WS32) was designated as the reference watershed. Sampling of both watersheds began in 2018 prior to the implementation of forest management actions, and sampling has continued since. The results reported in this thesis are from April 2018 through October 2023.

The objectives of this thesis were to (1) estimate changes in abundance and population structure of *Plethodon* in response to management actions and (2) estimate differences in juvenile growth and survival in response to forest management actions. In addition to modeling data directly measured within the focal study watersheds of the FFE, I used integrated modelling approaches to leverage other larger different datasets to improve estimates of abundance and juvenile growth, thereby improving my ability to estimate potential management effects. This thesis is separated into four chapters, this introduction, chapters two and three that are written as independent manuscripts to be submitted to journals for publication, and chapter four that summarizes the results and findings of chapters two and three and provides concluding remarks and reflections. Chapter two uses an integrated abundance model incorporating a broader regional dataset to estimate changes in abundance and population structure of a Plethodon population in response to forest management activities. Chapter three estimates juvenile growth and survival rates using a capture-mark-recapture study over the course of one active season and an integrated growth model that used data from a nearby long-term capture-mark-recapture study to jointly estimate the effects of precipitation on growth and a hierarchical Cormack-Jolly-Seber model to estimate survival rates.

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CHAPTER 2

CHANGES IN POPULATION STRUCTURE AND BEHAVIOR OF PLETHODONTID SALAMANDERS IN RESPONSE TO MIDSTORY REMOVAL AND PRESCRIBED FIRE[1]

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[1] Grab, K. M., D. R. Bradke, and J. C. Maerz. To be submitted to Forest Ecology and Management.

Abstract

A key component of conservation and management is understanding how wildlife populations respond to environmental change and landscape disturbances, such as those attributed to forest management practices. As a result of decades of fire suppression, the current composition of southern Appalachian forests is dominated by mesophytic species and dense understories of *Rhododendron* spp. Mechanical removal of midstory shrubs and prescribed fire are being used as management actions to increase recruitment of xeric tree species, especially oak (*Quercus* spp.), and to create habitat for species once more common in the region. To guide decisions regarding future forest management, information on the potential non-target effects of management actions on other priority taxa is needed. The objectives of this study was to use six years of data from a paired watershed manipulation integrated with a longer-term data set to estimate the effects of midstory removal and repeated prescribed fire on the abundance and structure of *Plethodon* populations, and to estimate whether there were changes in *Plethodon* behavior consistent with any estimated management effects. Midstory removal and prescribed fire was associated with a decline in *Plethodon* abundance, particularly among smaller, younger age classes of juveniles. There were consistently lower proportions of hatchlings and juveniles compared to subadults and adults in the treated watershed after management began. These results indicated that, over the initial six-year period of this study, *Plethodon* abundance has been negatively affected by the loss of midstory and, most likely, through the introduction of regular prescribed fire. It is not known whether *Plethodon* populations will continue to

decline or simply persist at a lower abundance over the longer term in response to ongoing forest management.

Introduction

A fundamental component of wildlife management and conservation is reducing uncertainty in our understanding of how target and non-target species respond to land management practices. Understanding how species respond is important for our success in maintaining biodiversity (Darracq et al., 2016). However, not fully understanding the impact of management actions on non-target species may be problematic for sensitive non-target species (Zarri et al., 2024). Therefore, it is critical to balance the impacts of target and non-target species and understanding how non-target species respond is a key step.

The southern Appalachian Mountains is a hotspot of biodiversity in the United States that has been managed and altered by people for millennia (Jenkins et al., 2015; Yarnell, 1998). This biodiversity and history make the southern Appalachian Mountains an interesting place to study the impacts of land management on wildlife. Historically, prior to European colonization, frequent, low-intensity fires lit by Native Americans and natural phenomena, such as lightning, led to forests dominated by oak (*Quercus* spp.), chestnut (*Castanea dentata*), and pine (*Pinus* spp.) in southern Appalachia (Brose et al., 2001; Delcourt and Delcourt, 1997, 1998). Though generally a region of high rainfall, the southern Appalachian Mountains also included relatively xerophytic forests that supported a range of wildlife otherwise associated with southeastern pine savannas (e.g., Red-cockaded woodpecker *Leuconotopicus borealis*). Following European settlement, high intensity, stand-replacing fires followed by fire suppression policies of the early 20th century caused southern Appalachian forests to shift away from more xeric tree vegetation to more mesophytic vegetation, such as maple (*Acer* spp.) and birch (*Betula* spp.) species (Brose et al., 2001; Harrod et al., 1998; Nowacki and Abrams, 2008). In recent decades, primarily in an effort to increase oak recruitment but also to increase habitat for some declining wildlife species, prescribed fire is being applied to forests (Brose et al., 2001; Fouts et al., 2017; Harper et al., 2016). Following the widescale loss of Eastern hemlock (*Tsuga canadensis*) and Carolina hemlock (*Tsuga caroliniana*) from the wooly adelgid (*Adelges tsugae*) invasion, the mesophication of forests has also included an increase in midstory *Rhododendron* spp. cover (Ford et al., 2012; Vose et al., 2013). Therefore, management agencies such as the U.S. Forest Service have also been experimenting with the mechanical removal of *Rhododendron* midstories alongside the use of prescribed fire to alter forest communities. As part of the experimental management efforts, researchers have been investigating how wildlife respond to prescribed or natural fire and mechanical shrub and shelterwood removal (e.g., Campbell et al., 2007; Fouts et al., 2017; Greenberg et al., 2018; Harper et al., 2016; Wilk and Peterman, 2024). For example, prescribed fire and mechanical shrub removal increased both abundance and species richness of insect pollinators in Southern Appalachia, likely due to an increase in nesting and feeding areas (Campbell et al., 2007). Another study found that capture rates of squamates increased with similar management practices (Greenberg et al., 2018). Another study found higher levels of abundance and activity of northern fence lizards (*Sceloporus undulatus hyacinthinus*) in naturally burned forests (Fouts et al., 2017). Thus, understanding how forest management actions impact wildlife is important for making management decisions about such actions and achieving management goals.

Among vertebrates, the Southern Appalachian Mountains are a global hotspot for salamanders (Vieites et al., 2007; Wake, 2017). Most of this diversity resides within the family Plethodontidae, which are lungless salamanders that depend on cutaneous gas exchange. That cutaneous gas exchange makes them reliant on cool, moist microclimates and sensitive to environmental change that increases the temperature or vapor pressure deficit, reduces precipitation or ground moisture, or limits access to cool, moist refugia such as leaf litter, downed woody debris, or subterranean habitat (Feder, 1983; Peterman and Semlitsch, 2013). Because of their exceptional abundance and biomass, plethodontid salamanders can be influential predators and prey in forest ecosystems (Best and Welsh, Jr., 2014; Davic and Welsh, 2004; Semlitsch et al., 2014). Because of their known sensitivity to dehydrating conditions, it is generally expected that plethodontids will respond negatively to conditions associated with prescribed fire, and indeed studies of natural fires show a negative effect on plethodontid abundance (Gade et al., 2019; Wilk and Peterman, 2024). However, some studies suggest plethodontids may be resilient to low-intensity prescribed fire (Jacobsen et al., 2020; Ochs et al., 2024), and plethodontid salamanders have behavioral and physiological adaptations to warmer, drier conditions

(McEntire and Maerz, 2019; Riddell and Sears, 2015) that might make them resilient to the environmental changes associated with some forms of forest management. However, forest management activities, such as timber harvest and prescribed fire, open up the canopy and reduce understory vegetation that reduces overall moisture and increases temperature (Hossack et al., 2009; Jacobsen et al., 2020). These changes are energetically costly for plethodontid salamanders and the sensitivity to these changes likely increases with decreasing body size (Feder, 1983; Homyack et al., 2011; Peterman and Semlitsch, 2013). While many studies report larger scale population parameters in response to forest management activities, such as density, capture rate, and abundance (e.g., Greenberg et al., 2018; Greenberg and Waldrop, 2008; Jacobsen et al., 2020; Mossman et al., 2019; Schurbon and Fauth, 2003), much fewer reported changes in population structure that could indicate variable effects across age or size classes (Grialou et al., 2000; Hocking et al., 2013; Homyack et al., 2011; Mazerolle et al., 2021).

The goal of this study was to use a paired watershed experiment and an integrated model with a larger data set to estimate changes in abundance and population structure of terrestrial salamanders in response to midstory *Rhododendron* removal and recurrent prescribed fire. We hypothesized that the management-driven changes in forest conditions in the short-term, such as increased soil temperature and accelerated soil drying from the loss of leaf litter and some downed woody debris, and increased air temperature and vapor pressure deficit from the loss of midstory and ground cover will lead to changes in abundance and population structure between the two populations. Specifically, we predicted reduced abundance of *Plethodon* in the treated watershed with the largest reduction in abundance among the smallest juvenile size classes that are most sensitive to drying conditions.

Methods

Study Site

The study took place at the U.S. Forest Service's Coweeta Hydrologic Laboratory (hereafter "Coweeta") within the Nantahala National Forest in Macon County, North Carolina. The forests at Coweeta are characterized by mixed deciduous forests, dominated by maples (*Acer* spp.) and oaks (*Quercus* spp.), with an understory of predominately *Rhododendron maximum* and mountain laurel (*Kalmia latifolia*) (Elliott et al., 1999; Elliott and Swank, 2008; Miniat et al., 2021). In 2018, the USFS initiated the "Future Forest Experiment" (FFE). The experiment uses two adjacent watersheds, Watershed 31 (WS31) and Watershed 32 (WS32), with similar climate, slope, aspect, and history. The watersheds range in elevation from 869 m to 1146 m in WS31 and 920m to 1236m in WS32 (Miniat et al., 2021). Watershed 31 was designated as the "treated" watershed and in 2018 underwent manual removal of the *Rhododendron* spp. understory with herbicide application to the *Rhododendron* stumps followed by prescribed burns of the entire watershed in February of 2019, 2021, and 2023 (Miniat et al., 2021). Watershed 32 (WS32) was designated as the reference watershed. Monitoring of salamanders in both watersheds began in 2018 within 9 plots in each watershed. The elevation of the original plots ranged from 952 m to 1004 m in WS31 and from 997 m to 1026 m in WS32. Given the initial number of study plots, the relatively consistent and narrow range of elevation for the initial plots was a decision to minimize other factors that might affect salamander abundance. In 2021, six plots were added to WS32 as part of a broader regional study. In 2023, we replaced three of the 2021 WS32 study plots with new plots in different locations to expand the elevational range of the plots. In WS31, one plot was added as a part of a basin-wide salamander abundance model project in 2022, and we added an additional five plots in 2023 so that both watersheds ultimately contained 15 plots. The elevation ranges of the final 15 plots were 883m to 1004 m in WS31 and 962 m to 1026 m in WS32. The salamander populations at this elevation within our study site are of an ancestral hybrid lineage (introgression) between *Plethodon shermani* and *P. teyahalee* (see Carter 2023 for a summary). It has been shown that patterns of genetic and phenotypic variation among the hybrid salamanders correspond strongly to hydroclimatic variation across Coweeta (Carter 2023). Though not germane to the present study, the adaptive introgression apparent among the large *Plethodon* spp. at Coweeta (and elsewhere across the Nantahala National Forest) create the potential for evolutionary response to forest management.

Sampling Design

Beginning in 2018, one year prior to the first prescribed burn, we sampled nine 25m^2 plots in each watershed three times a year (primary period) in the Spring, Summer, and Fall, on three consecutive nights (secondary periods) during the salamander active season. We conducted visual encounter surveys beginning after dark and individuals surveyed the plots for a minimum of four complete passes over the plot for a minimum of 15 person minutes (Bradke, 2023; Head, 2020; Howard, 2018). For every salamander, we noted whether the salamander was on the surface, climbing vegetation, or in a burrow. After capture, we recorded the size or age class (hatchling (<30 mm), juvenile (31 to 45 mm), sub-adult (46 to 60 mm), and adult (> 61 mm) (Howard, 2018)) of each salamander and determined the sex of adult sized salamanders using secondary sexual characteristics including the presence of a mental gland, enlarged nasal cirri, or an enlarged cloaca for males and the visible presence of eggs for females. Salamanders large enough to be classified as an adult that lacked any secondary sexual characters or visible eggs were presumed to be adult females. For all females, we measured snout-to-vent length (SVL), total length (TotL), and wet mass. Because all of the *Plethodon* at our study location are of hybrid ancestry, we gave each salamander a hybrid score following a modified version of the Hairston (1973) scoring system (Carter, 2023).

After 2020 we determined that the original sampling design was inadequate for estimating availability and detection separately, likely because of high, weather-driven variability in salamander surface activity (availability for capture) during secondary periods when populations are assumed to be closed (Bradke, 2023). The original sampling design resulted in low-biased estimates of abundance (Bradke, 2023). Therefore, in 2021, we implemented a new sampling design in which we sampled plots once during the same three seasons using a depletion sampling design. In 2023, plots were sampled seven times during the salamander active season (April to October). With the depletion sampling design, we searched the plot for at least 15-person minutes, with one person completing a minimum of one full pass for a minimum of 3.75 minutes (a minimum of four total passes over a minimum of 15 minutes). Thus, the total time and area search effort was the same as our prior sampling methodology, but by removing salamanders from the plot during each pass, we could estimate detection using a depletion model and by repeating surveys multiple times throughout the year under different weather conditions, we could separately estimate surface availability as a function of weather. In addition, for all salamanders captured, we measured body size (SVL, TotL, and wet mass), estimated age-class, recorded the presence of secondary sexual characteristics, and assigned the salamander a hybrid score. During analysis, the age classes of all salamanders was re-assigned using SVL measurement, if it was measured at the time of capture, to correspond with the SVL categories used in Howard (2018): hatchling (<30 mm), juvenile (31 to 45 mm), sub-adult (46 to 60 mm), and adult (> 61 mm). If there was not a SVL measurement for an individual, the age class originally noted in the data was used. This re-assignment of age classes was done to make age classes categorization as consistent as possible across the earlier and later datasets.

Measurement or Interpolation of Covariates

During the original sampling methodology and the revised methodology, we measured temperature, wind speed, and relative humidity using a Kestrel™ 3000 Weather Meter (KestrelMeters.com) during or immediately at the conclusion of sampling a plot. Vapor pressure deficit (VPD) impacts the probability that salamanders are surface-active and available for us to capture (Gade et al., 2020; Riddell and Sears, 2015). We used the measured relative humidity and temperature to calculate VPD at the time of each sample. Additionally, beginning in 2021, we recorded the observers visual estimate of the percentage of the plot covered by intact leaf litter, a ground moisture category, the percentage of the plot covered by vegetation below eye level, and the observers perceived ability to search the plot due to vegetation or other obstructions below eye level. The surveyor estimated ground moisture by determining how wet or dry the leaf litter and bare soil right below the leaf litter were (Table 2.1). The surveyor estimated leaf litter by estimating the total percent cover of leaf litter and woody debris on the ground versus bare soil and then estimated an approximate leaf litter cover category (Table 2.1). The surveyor estimated the percentage of vegetation cover below eye level and their perceived ground visibility by determining as a percent category of the ground visually obstructed by vegetation below eye level (Table 2.1). Herbaceous vegetation cover was estimated using a similar percentage-based cover of herbaceous vegetation (Table 2.1). Plot characteristics were used to evaluate changes in plot conditions between watersheds and as covariates in our subsequent detection model for estimating abundance. Vegetation cover and ground visibility were expected to be inversely correlated, so only ground visibility was used in our detection model.

Hydroclimate is also a strong predictor of spatial variation in *Plethodon* abundance and mean daily VPD during the salamander active season (April 1 – October 31) is highly predictive of mean *Plethodon* abundance among sites across our study region (Maerz, unpublished data). Therefore, we calculated mean daily VPD between 2011-2020 data using modeled relative humidity and temperature from Daymet (Thorton et al., 2022). We then used the mean daily VPD as a climate covariate in the abundance portion of our model. We also used measured and interpolated rainfall values as covariates in our availability model. For modeling the Coweeta FFE dataset, we used rainfall from precipitation data from rain gauge 12 at Coweeta as our measure of the amount of rainfall in the preceding one (rain1) and five days (rain5). We used data from the National Oceanic and Atmospheric Administration (NOAA) for estimates of the one- and five-day rainfall totals among sites in a second data set that we leveraged in an integrated model to improve our estimates of abundance and increase our sensitivity to detect management effects between our two study watersheds.

Data Analysis

To estimate the effect of forest management on abundance and population structure of hybrid salamanders, we adapted the integrated model from Bradke (2023) that used data from both sampling designs for the FFE study watersheds and a broader regional dataset (Figure 2.1). Integrating data from a broader regional study allows us to incorporate what we know about relationships between salamander abundance and the environment, which increases our ability to detect an effect of management on salamander abundance. We adapted the model to separately estimate abundances of each size class. The broader regional dataset (here in “regional dataset”) was collected in 2021 and 2022 across 24 sites in eastern Tennessee, western North Carolina, and northern Georgia using the same depletion sampling design as the later portion (2021-2023) of the FFE project and includes spatial overlap of the Coweeta study sites (J.C. Maerz, unpublished data).

We used hierarchical N-mixture models for each dataset in an integrated model to estimate abundance, detection, and availability (Table 2.2). The three-level hierarchical structure of N-mixture models uses unmarked count data to simultaneously estimate abundance, availability, and detection (Chandler et al., 2011; Royle, 2004). The N-mixture model used for the robust design, while it does allow us to estimate detection, does not allow us to separate detection from availability, which can be an important driver in detecting salamanders because of temporary emigration (O'Donnell and Semlitsch, 2015). Additionally, neglecting to model detection heterogeneity in N-mixture models make them prone to negative bias (Kéry and Royle, 2016), which was found for the robust design model in Bradke (2023). Because the robust model was not able to separately estimate detection and availability, the implementation of the depletion sampling design allowed us to estimate these two mechanisms separately (Bradke, 2023). Furthermore, using the hemlock project dataset to help inform detection and availability estimates helped determine if there is an effect of treatment on salamander abundance (Bradke, 2023; Fonnesbeck et al., 2009). Therefore, an integrated model provides an opportunity to use different datasets and sampling designs to improve parameter estimates (Hostetter et al., 2019; Zipkin and Saunders, 2018).

For the state process model, we estimated lambda for age class *a* at site *i* during visit *j* as a log link function of treatment, VPD calculated from DayMet data, and elevation

(Table 2.2). The estimated population of salamanders, $N_{i,j,a}$, was a Poisson distribution of lambda. Because of the broad regional scale of the hemlock project and because there were replicates at all sites, a random effect of site on abundance was included in the model. Mean abundance of each class was estimated each year for the FFE dataset (2018-2023). The effects of management and mean daily VPD on abundance were estimated separately for each age class while the effect of mean daily VPD was jointly estimated across both datasets.

For the observation process model, we used a logit link function to estimate salamander availability for each age class *a* at site *i* during visit *j* as a function of temperature, rainfall in the preceding 24 hours, rainfall in the preceding 5-days, and VPD (Table 2.2). Vapor pressure deficit for this level of the model was calculated using the relative humidity and temperature values measured in the field during the sampling event. All effect sizes for the covariates were jointly estimated across both datasets and the effect of VPD on availability was estimated separately for each age class. Availability was modeled as a binomial distribution of the probability a salamander was surface active given the total estimated population (Table 2.2).

We used a logit link function to estimate detection for each age class *a* at site *i* during visit *j* as a function of ground visibility and a random effect of site and visit (i.e., each time we visited a plot; Table 2.2). The effect of ground visibility on detection was jointly estimated across both datasets. The counts observed using the robust sampling design were modeled using a binomial distribution of the individuals available given the salamanders available. The counts observed using the depletion sampling design were modeled using a multinomial distribution of the total population size (*N*) given the probabilities of detecting salamanders in each pass.

During 2018 and 2019, vegetation values in each watershed were collected by estimating Daubenmire Cover Classes for each plot (Head, 2020). However, this methodology of evaluating visual obstruction was not continued after 2019 or collected in a comparable method to how ground visibility is currently estimated. Therefore, these vegetation values were not used in the final analysis for this project. The values of ground visibility for the plots in WS32 that were sampled between 2018 and 2020 were assigned values based on the mean ground visibility values of those same plots collected between 2021 and 2023. For the plots that did not have ground visibility values in WS31 prior to 2020, we had the model estimate the ground visibility values for these plots by providing it with prior values including the potential range (0 to 5) and an estimated variance. Then, using a normal distribution with the estimated variance, the model included this estimated value in the ground visibility parameter of the detection sub-model of the robust design. The proportion of each age class was calculated by taking the estimated total population size for the size class divided by total population (N) for the watershed for that year.

We used a linear regression with a random effect of plot to determine if VPD and percent litter cover differed between watersheds using the lme4 and lmerTEST packages in R (Bates et al., 2015; Kuznetsova et al., 2017). We used an ordinal regression model to determine if leaf litter, ground visibility, vegetation, and ground moisture differed between plots using the ordinal package in R (Christensen, 2023). we included a random effect of each ordinal regression analysis except for ground moisture because ground moisture was likely the same for all plots in a watershed for a given night. For this analysis, we only used data from 2021-2023 because we had minimal data from before the management treatment began in WS31 and the midstory removal would have been fully complete and prescribed fire would have already been applied once.

All the priors used for this model were vague (Table A1). We determined that the model was not sensitive to the priors by conducting a prior predictive check. To evaluate the predictive power of the model, we ran the model without data from the plots at lower elevations in both watersheds. Using a blocking method to determine which data to remove for evaluating a model can allow for a better understanding of the predictive power of the model especially when those blocks are spatially or temporally related (Roberts et al., 2017). We visually inspected and compared what the model estimated for observed counts on these plots to the observed counts.

Using a chi-squared discrepancy analysis, we calculated Bayesian p-values and c-hat values, a measure of overdispersion, to estimate goodness-of-fit (Kéry and Royle, 2016). The Bayesian p-value for the robust model indicated adequate fit and the c-hat value did not indicate overdispersion (Table 2.3). Visual inspection of fit statistic plot for the robust sampling design corroborated our determination of model fit (Figure 2.3). We evaluated model convergence by visually inspecting the posterior trace plots and the Gelman-Rubin statistic, $\widehat{\mathrm{R}} < 1.1$ (Gelman and Rubin, 1992).

We ran the models in R using JAGS with the jagsUI package (Kellner, 2021; Plummer, 2003; R Core Team, 2024). For the Bayesian analysis, we ran the model using 3 chains for 800,000 iterations with 500,000 burn-in, a thin rate of 25, and 1000 in the adaptive phase. We used the r packages lubdridate, dplyr, stringr, ggdist, ggpubr, reshape2 and tidyr to format my data (Grolemund and Wickham, 2011; Kassambara, 2023; Kay, 2024; Wickham, 2022, 2016, 2007; Wickham et al., 2023a, 2023b). We used MCMCvis, ggplot2, ggdist, and gridExtra to create figures (Baptiste, 2017; Kay, 2024; Wickham, 2016; Youngflesh, 2018). The code for the model can be found in Appendix A and output for the hemlock portion of the model are located in Table A2.

Results

Between 2018 and 2023, we captured 1,588 *Plethodon* among all plots across 22 primary sampling events. Of those captured, 241 salamanders were hatchlings, 561 were juveniles, 382 were subadults, and 404 were adults. The model output indicated convergence with adequate mixing of the trace plots and $\widehat{R} < 1.05$ for model parameters. Neither of the Bayesian p-values for the state and observation processes indicated adequate fit and suggests that the model is more likely to underestimate than overestimate compared to the observed data (Table 2.3), which is consistent with the model evaluation process. However, visual inspection of fit statistic plots for the depletion sampling design indicates better fit for the depletion sampling than the Bayesian p-values would suggest (Figure 2.2). There was no indication of overdispersion for all parts of the model because the c-hat values for all portions of the depletion and robust models were close to one (Table 2.3). For the model evaluation, the model estimated the same number of counts as was observed during sampling more than half the time and there were similar numbers of estimated counts that were overestimated and underestimated.

Following forest management treatments, estimated abundances of hatchling (mean = 4.108; 95% Bayesian Credible Interval (BCI): 2.330 – 6.989), juveniles (mean = 6.533; 95% BCI: 4.073 – 10.632), and subadult (mean = 3.439; 95% BCI: 2.268 – 5.266; Figure 2.3). *Plethodon* were 24% - 54% lower after forest management treatment compared to mean estimated abundances for hatchlings (mean = 8.947; 95% BCI: 5.520 – 14.406), juveniles (mean = 11.170; 95% BCI: 7.124 – 17.910), and subadults (mean = 4.528; 95% BCI: 3.120 – 6.741) in WS32 or WS31 prior to treatment. The negative effect of management on abundance was largest for hatchlings, followed by juveniles and then subadults (Table 2.4; Figure 2.4). We estimated a higher mean abundance of adult salamanders in WS31 after treatment (mean = 6.042; 95% BCI: 4.002 – 9.100) compared to WS32 and WS31 before treatment (mean = 4.800; 95% BCI: 3.236 – 7.107; Figure 2.3). Population age structured varied across time and between watersheds (Figure 2.5). Juveniles and hatchlings were more consistently a lower proportion of the population among plots within WS31 after treatment compared to plots within reference WS32 (Figure 2.5). As expected, vapor pressure deficit (VPD) calculated from the DayMet data was negatively correlated with the abundance of juveniles and weakly negatively correlated with abundance of subadults, though we did not detect a strong, independent effect of VPD on the abundance in hatchlings or adults (Table 3.1; Figure 2.4).

Salamander availability varied across age class with hatchlings (mean = 0.105; 95% BCI: 0.059 – 0.166) and adults (mean = 0.117; 95% BCI: 0.072 – 0.172) having lower availability than juveniles (mean = 0.130; 95% BCI: 0.072 – 0.199) and subadults (mean = 0.169; 95% BCI: 0.108 – 0.230; Table 2.4; Figures 2.6 and 2.7). Availability was positively influenced by temperature and rain in the preceding five days (Table 2.4; Figures 2.4 and 2.6), while rainfall in the preceding 24-hours had little to no estimated effect on availability (Table 2.4; Figure 2.4). As expected, increasing vapor pressure deficit measures taken at the plots during the surveys were negatively correlated with availability across all age classes (Table 2.4; Figures 2.4 and 2.7). Consistent with differences in body size, mean estimated detection probability was lowest for hatchlings (mean = 0.040; 95% BCI: 0.026 - 0.059), intermediate for juveniles (mean = 0.067; 95% BCI: 0.048 - 0.091) and subadults (mean = 0.091; 95% BCI: 0.066 - 0.121), and highest for adults (mean = 0.138; 95% BCI: 0.100 - 0.183). As expected, reported increased ground visibility was positively correlated with detection probability (Table 2.4; Figure 2.7).

Mean estimated ground visibility for 2018-2020 was 2.906 (range = 1.308 – 4.923) for the reference watershed and 2.956 (range = 0.000-5.000) and 2.907 (range = 0.000 – 5.000) for the treated watershed before and after prescribed fire was introduced, respectively. For the environmental covariates from 2021-2023, ground visibility was higher in the treated watershed (mean = 3.9; range = 0 - 5) compared to the reference watershed (mean = 3.52; range = 0 – 5; β = -1.47, z = -2.5, p = 0.011; Figure 2.8). Vapor pressure deficit was lower in treated watershed (mean = 0.33, range = 0.00 – 1.39) compared to the reference watershed (mean = 0.37, range = 0.00 – 1.23; β = -0.043, $F_{1,349}$ = 2.80, p = 0.259; Figure 2.8). Temperature was 7% warmer in the treated watershed (mean = 16.7°C, range = 6.3 – 25.3) compared to the reference (mean = 15.6°C, range = 5.8 – 23.4; β = -1.059, $F_{1,349}$ = 6.46, p = 0.011; Figure 2.8). Reported leaf litter cover was less in the treated watershed (mean = 1.84, range = 0 - 4) compared to the reference (mean = 3.83, range = 2 – 4; β = 5.02, z = 8.79, $p < 2 \times 10^{-16}$; Figure 2.8), which was consistent with reported leaf litter percentage which was also lower in the treated watershed (mean = 46.77, range = 0 - 100) compared to the reference (mean = 93.81, range = 50 – 100; β = 45.48, $F_{1,29}$ = 101.05, $p = 1.95 \times 10^{-7}$; Figure 2.8). Ground moisture categorization was lower in WS31 (mean = 1.49, range = 0 - 5) compared to WS32 (mean = 1.73, range = 0 – 5; β = 0.338, z = 1.744, p = 0.081; Figure 2.8). Categorization of vegetation obstructing visibility below eye level was lower in WS31 (mean = 1.00, range = 0 - 4) compared to WS32 (mean = 2.00, range = 0 – 5; β = 2.22, z = 2.55, p = 0.001; Figure 2.8).

Discussion

As predicted, we found a negative effect of treatment (midstory removal and prescribed fire) on *Plethodon* salamander abundance in the near-term, and the effects were strongest for smaller size classes. Other studies that have reported similar changes or differences in salamander population size/age-structure in response to clearcuts, thinning, burning, or herbicide treatments (Hocking et al., 2013; Homyack and Haas, 2009); though some studies have also reported no change in size class structure (Grialou et al., 2000; Mazerolle et al., 2021). The stronger effect of midstory removal and burning seen among smaller salamander size classes might be because of reduced leaf litter, marginally reduced ground moisture, and higher temperatures, all of which would be expected to reduced juvenile fitness because of their high sensitivity to conditions that increase evaporative water loss (Feder, 1983; Homyack et al., 2011; Peterman and Semlitsch, 2014). It is also possible that the lower abundance of smaller size classes reflects reduced fecundity of adult salamanders within the treated watershed (WS31). It is possible that drier conditions or the reduction in leaf litter among treated plots lead to reduced foraging activity or prey availability, which could cause a reduction in female fecundity. In a previous study on the FFE project, Head (2020) found that salamander use of burrows increased and the probability of being observed active on the forest floor decreased among the plots in the treated watershed following prescribed fires. This behavioral observation is corroborated by O'Donnell et al. (2016), who found a decrease in *Plethodon albagula* surface activity on plots treated with prescribed fire. Further studies of age or size-dependent behavioral adaptations are required to fully understand the relative contributions of the specific mechanisms driving the differences in salamander abundance in response to forest management.

Age structure fluctuated for both watersheds in all years (Figure 2.5). However, in WS31, after the midstory thinning and start of the prescribed burning, there were consistently higher proportions of subadults and adults compared to pre-treatment WS31 and WS32 proportions across all years (Figure 2.5). These changes in age structure could be associated with altered reproduction and recruitment (Grialou et al., 2000; Homyack and Haas, 2009). Reproduction and recruitment may play critical roles in the population persistence and recovery of plethodontid salamanders in during and after management activities (Connette and Semlitsch, 2015; Tilghman et al., 2012). Therefore, further research on the impacts of reproduction and recruitment is warranted to better understand the mechanisms driving the abundance and age structure patterns in these watersheds. Juvenile growth and survival, one aspect of recruitment, will be investigated in the next chapter.

Interestingly, we found evidence of a small positive effect of the forest management treatments on adult abundance (Figure 2.3). Adult salamanders may be able to withstand the environmental changes associated with management, such as increased temperatures and reduced relative humidity, better than juveniles because of their larger body size (Homyack et al., 2011; Peterman and Semlitsch, 2014). Although, this idea would not fully explain why there is an increase in adult abundance in WS31. Because salamanders continue growing after they reach maturity, albeit at a much slower rate than before, they may be allocating resources to increasing their body size to better be able to withstand the harsher conditions (Feder, 1983; Hairston, 1983; Halliday and Verrell, 1988). Connette and Semlitsch (2015) found that, despite initially lower survival after timber harvest, salamanders experienced a relatively high survival rate in areas of forest that were harvested. The increased use of burrows following prescribed fire and midstory thinning from Head (2020) suggests an adaptive behavioral response to the conditions created by management actions. It is likely that increasing burrow use reduces evaporative water loss and potentially buffers larger salamanders against increased mortality from dehydration or – indirectly - predation [though potentially still decreasing fitness through effects on fecundity as discussed previously]. *Plethodon* are territorial and larger individuals tend to monopolize access to burrows (Nishikawa, 1990). Therefore, holding of burrows and increased use may buffer against declines in abundance among adult salamanders in the near term following prescribed burning or midstory thinning. However, if the reduction in surface activity does reduce foraging success and fecundity, we would expect to see declines in adult abundance over the longer term.

Following the last burn in 2023, the managers at Coweeta are planning on moving to a burn interval of five years (A. C. Oishi, personal communication), which may allow for more recovery of leaf litter and improved conditions for salamanders between treatments. The previous three cycles of a two-year burn interval may have had a significant, immediate impact on the abundance and structure of the *Plethodon* population in WS31 because of the consistent removal of the leaf litter for half of the prior six years. Mazerolle et al. (2021) found that abundances of large and small *P. albagula* were similar more than 5 years after shelterwood treatment. Because forest management can have long-term impacts on salamanders (Cosentino and Brubaker, 2018; Homyack and Haas, 2009; Wilk, 2022), a shorter burn interval, like the one for this study, could explain the negative effect of management on abundance. Recovery time for salamander populations have been postulated to be on the scale of decades and time since management action, or forest age, is positively correlated with salamander abundance (Connette and Semlitsch, 2013; Homyack and Haas, 2009; Tilghman et al., 2012). Environmental characteristics of managed forests do become less harsh over time, but the initial forest characteristics post-management that are energetically costly to salamanders may be exacerbated by a changing climate, which could increase the negative impact (Homyack et al., 2011; Tilghman et al., 2012). Thus, future monitoring can help determine how populations recover from frequent management interventions, especially in a changing climate.

A limitation of this study is that we could not address variation in fire intensity. We know that some areas in WS31 burned with a higher intensity than others (A. C. Oishi, *personal communication*); however, we do not know how fire intensity varied among our study plots, though we do know that all our plots ended up in areas of relatively low intensity fire. If our results represent responses to relatively low intensity of prescribed fire, it is possible that effects could be larger when including areas of moderate or severe burn intensity. For example, Wilk and Peterman (2024) showed that abundance of plethodontid salamanders declined with increasing burn severity and Gade et al. (2019) found that not only did populations decline, but juveniles totally disappeared in uplands after a wildfire. A mosaic of fire intensity can create different abundances of refugia such as downed woody debris that may be important for predicting population persistence (Harper et al., 2016; Meddens et al., 2018). Including additional spatial aspects across a variety of scales to this study, such as burn severity at watershed level and refugia characteristics at plot level, could allow for a greater understanding of the impact of management on demography and distribution of salamanders.

Surface activity, or temporary emigration, must be accounted for in abundance estimation, particularly when evaluating environmental changes or management actions that might affect salamander surface behavior or observer detection (Bailey et al., 2004; O'Donnell et al., 2016; O'Donnell and Semlitsch, 2015). We estimated low rates of surface availability across all age classes with lower availability of adults and hatchlings than subadults and juveniles (Figure 2.6). This pattern was inconsistent with other research that found smaller salamanders were more likely to be surface active (Bailey et al., 2004; Howard, 2018). This inconsistency may be attributable to altered burrow usage because salamanders in areas with forest management activities, such as prescribed fire, do increase burrow usage and reduce surface activity (Head, 2020; O'Donnell et al., 2016). Adults (the largest age class) may be monopolizing burrows which likely causes the subadults and potentially juveniles to spend more time on the surface (Nishikawa, 1990). Although smaller age classes are likely more sensitive to changes in moisture (Howard, 2018; McEntire and Maerz, 2019; Peterman and Semlitsch, 2013; Spotila, 1972), hatchling availability was less affected by VPD than the larger age classes (Figure 2.4), suggesting that there may be other moisture-related factors influencing hatchling availability. Cumulative rainfall in the preceding five days had a larger effect on salamander availability than rain in the preceding 24 hours (Figure 2.4), maybe because rainfall over those preceding five days could be a better indicator of overall environmental moisture level during a sampling event than rainfall only during the preceding day.

Smaller salamanders had a lower detection than larger salamanders, with detection increasing with age class (Figure 2.7). This trend is likely because larger salamanders are generally easier to see even if they are less likely to be available for capture than other age classes. Across all age classes, detection increased with increasing ground visibility (Figure 2.7). Intuitively, when visible obstruction is lower, we would expect higher detection of salamanders. However, when ground visibility is highest there was little to no herbaceous or shrub cover, which may also have indirect effects on salamander behavior especially if the forest is warmer and drier as a result of the absence of midstory or ground cover (Homyack et al., 2011; Hossack et al., 2009). Additionally, plethodontid salamanders are known to climb understory vegetation (McEntire, 2016), and other studies have shown that increased ground vegetation can enhance detection of species or smaller size classes that have a greater propensity to climb (Bauer, 2024).

A strength of this study over some prior studies was the use of an integrated model to leverage additional large data sets to improve estimates and increase sensitivity to detect management effects (Bradke, 2023). Integrated models can prove useful when there is a need to change sampling methodologies, as was the case in this study, and when leveraging other datasets to compensate for limited or deficient data sets to improve estimates of population dynamics and conservation outcomes (Bradke et al., 2023; Fletcher et al., 2019; Zipkin and Saunders, 2018). For example, in this study, but using a larger regional data set, we could obtain more precise, unbiased estimates of weather effects on *Plethodon* availability and climate effects on abundance. The ability to use other data to improve estimates of these parameters made our analysis more sensitive to detecting management actions across a relatively smaller set of study plots. Had our study depended strictly on modeling the data from the FFE study, our sensitivity to detect management effects would have been lower and the uncertainty around our estimates of management effects would have been greater (Bradke 2023). Bias or more uncertainty in estimates of management effects can lead to poor or misguided management decisions.

The results from this study provide information on how a non-target species responds to midstory thinning and frequent prescribed fire in the near term. The near-term negative effects of midstory thinning and frequent prescribed fire on the abundance of smaller salamander age classes may be concerning; however, we caution that it remains unclear if this *Plethodon* population will continue to decline, persist at lower abundances, or rebound over the long-term as planned future forest management becomes less intense. The initial management activity was relatively intense over a short period of time to push forest conditions quickly. In particular, the goal was to reduce the abundance of midstory *Rhododendron* and young mesophytic trees such as red maple (*Acer rubrum*) and tulip poplar (*Liriodendron tulipifera*). Though low in intensity, the two-year interval for the first three prescribed burns nearly eliminated leaf litter on the forest floor for half of the prior six-year period (Figure 2.8). This reduction in leaf litter likely impacted salamander fitness, particularly for smaller age classes. However, the U.S.F.S. plans to reduce fire frequency to a five year burn interval moving forward (A. C. Oishi, *personal communication*), allowing time for leaf litter levels to recover on the forest floor for 3-4 years between each burn. This longer burn interval may reduce the negative impacts on salamander abundance going forward. In addition, if forest management goals are successful, a shift to a xerophytic forest dominated by species such as oaks may have longer-term benefits to salamander populations. For example, oak-dominated forests may have different soil moisture and leaf litter composition than a maple-dominated forest (Alexander et al., 2021; Alexander and Arthur, 2014). Oak litter is more recalcitrant and slower to decompose, and oak tree species use less water and allow for more precipitation through the canopy than mesophytic tree species (Alexander and Arthur, 2014, 2010; Von Allmen et al., 2015), potentially leading to increased soil moisture (Alexander et al., 2021). Soil moisture drives salamander rehydration rates, which has a significant effect on salamander activity levels (Feder, 1983; McEntire and Maerz, 2019). Moreover, moderate frequency, low intensity prescribed burns may reduce the risk of catastrophic fire effects on salamander populations. Regional forecasts for the Southern Appalachian mountains include more frequent and intense droughts, increasing the risk of period forest fires (Mitchell et al., 2014). Recent non-prescribed fires in the region during periods of drought resulted in high intensity burns of forest, which severely reduced salamander populations with longer-term legacy effects on salamander abundance (e.g., Gade et al., 2019; Wilk and Peterman, 2024). Forest management actions including regular, low intensity prescribed burns can reduce burn severity of wildfires (Davis et al., 2024; Petrakis et al., 2018), potentially reducing the risk of catastrophic fires to salamander populations with shifting climates. Because of the uncertainty there is a need to understand the longer-term impacts of forest management on salamander populations; therefore, we recommend continued long-term monitoring of the FFE and other sites. If coordinated across management agencies and units over a broader region, the use of an adaptive management framework could lead to improved management decisions for forest management across the region.

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TABLES

Table 2.1: Table of categorical variables and how they were scored. The surveyor estimated ground moisture by determining dryness of the leaf litter and bare soil right below the leaf litter. The surveyor estimated leaf litter by estimating the total percent cover of leaf litter and woody debris on the ground versus bare soil. The ground visibility category and herbaceous vegetation cover were estimated by the surveyor as a percent category of the ground visually obstructed by vegetation below eye level.

	Score					
Environ-mental Variables	**0**	**1**	**2**	**3**	**4**	**5**
Ground moisture	litter and soil are dry	litter is dry and soil surface are moist to dry	litter surface is dry but within litter and soil surface are moist	litter and soil are moist	litter surface is moist and within litter and soil surface are wet	litter and soil are wet
Leaf litter	little to no leaf litter on ground	patchy leaf litter covering ~25% of ground	patchy leaf litter covering ~50% of ground	mostly continuous leaf litter covering ~75% of ground	nearly contiguous leaf litter covering ~100% of ground	NA
Ground visibility	100% obstructed	90 – 75% obstructed	75 – 50% obstructed	25 – 50% obstructed	10 – 25% obstructed	0% obstructed
Herbaceous vegetation cover	little to no herbaceous /low shrub cover	~20% herbaceous /low shrub cover	~40% herbaceous /low shrub cover	~60% herbaceous /low shrub cover	~80% herbaceous /low shrub cover	~100% herbaceous /low shrub cover

Table 2.2: Equations for each of the three levels in the hierarchical model used for each dataset for the integrated population model. The subscripts indicate that *i* is for each plot, *y* for each year, *j* for each visit, and *a* for each age class. Letters in brackets indicate that parameter was allowed to vary by age class [a], year [y], or both [y,a].

Model Name	**Equations**
Abundance	$\log\left(\lambda_{i,y,a}\right) \sim \beta_{0[y,a]} + \beta_{1[a]} * VPD.Day_{i,j} + \beta_{2[a]} * mgmt_i + \beta_3 * elev_i$ $N_{i,y,a} \sim pois\ (\lambda_{i,y,a})$
Availability	$logit\left(\Omega_{i,j,a}\right) \sim \Omega_{0[a]} + \Omega_1 * temp_{i,j} + \Omega_{2[a]} * VPD_{i,j} + \Omega_3 * rain1_{i,j} + \Omega_4 * rain5_{i,j}$ $Availability\ _{i,j,a} \sim binomial\ (\Omega_{i,j,a}, N_{i.y,a})$
Detection	$logit\left(p_{i,j,a}\right) \sim \alpha_{0[a]} + \ \alpha_1 * vis_{i,j} + \epsilon_{i,j}$ $\left\{y_{i,j,a,1}, y_{i,j,a,2}, y_{i,j,a,3}, y_{i,j,a,4}\right\} \sim Multinomial(N_{i,y,a}, \pi\left(p_{i,j,a,1}, p_{i,j,a,2}, p_{i,j,a,3}, p_{i,j,a,4}\right))$ -or- $y_{i,j,a} \sim binomial(1 - ((1 - {p_{i,j,a}}^4), Availability\ _{i,j,a})$

Table 2.3: Mean estimated Bayesian p-values (BPV) and c-hat values, a measure of overdispersion, with standard deviation, lower and upper Bayesian credible intervals, and effective sample size (n.eff). This table reports goodness-of-fit metrics for the Future Forest Experiment portion of the integrated abundance model for *Plethodon* salamanders for both robust (2018-2020) and depletion (2021-2023) sampling designs.

Fit Metric	**Sampling Design**	**Model Level**	**Mean**	**SD**	**2.5%**	**97.5%**	**n.eff**
C-hat	Robust	NA	1.065	0.110	0.865	1.299	19,073
BPV	Robust	NA	0.285	0.452	0	1	12,215
C-hat	Depletion	Abundance	1.016	0.010	0.997	1.037	17,131
BPV	Depletion	Abundance	0.052	0.222	0	1	36,000
C-hat	Depletion	Detection	0.918	0.052	0.824	1.024	36,000
BPV	Depletion	Detection	0.946	0.226	0	1	36,000

Table 2.4: Parameters and posterior estimates of abundance, availability, and detection and estimated covariate effects for each age class of *Plethodon* hybrids for the Future Forest Experiment project at Coweeta Hydrologic Laboratory in Macon County, North Carolina. Abundance values are taking the mean across all years of the study, 2018-2023, for each age class.

Parameter	**Hatchling**					**Juvenile**				
Covariate	**Mean**	**SD**	**2.5%**	**97.5%**	**N.eff**	**Mean**	**SD**	**2.5%**	**97.5%**	**N.eff**
Abundance	8.685	1.722	-	-	-	10.862	1.605	-	-	-
Management	-0.788	0.197	-1.176	-0.403	12,672	-0.539	0.156	-0.841	-0.231	16,117
Mean daily VPD (kPa)	-0.121	0.202	-0.484	0.298	23,851	-0.663	0.198	-1.022	-0.251	10,064
Availability	0.105	0.027	0.059	0.166	421	0.130	0.032	0.072	0.199	48
Temperature (°C)	0.047	0.011	0.025	0.070	642	0.047	0.011	0.025	0.070	642
VPD (kPa)	-0.371	0.076	-0.522	-0.226	709	-0.470	0.063	-0.596	-0.350	161
Rain prior 24 h (mm)	-0.085	0.041	-0.165	-0.002	7,102	-0.085	0.041	-0.165	-0.002	7,102
Rain prior 5 d(mm)	0.297	0.056	0.193	0.410	2,054	0.297	0.056	0.193	0.410	2,054
Detection	0.040	0.009	0.026	0.059	10,422	0.067	0.011	0.048	0.091	894
Ground visibility	0.225	0.040	0.146	0.302	14,905	0.225	0.040	0.146	0.302	14,905
Site (random effect)	1.124	0.051	1.027	1.228	36,000	1.124	0.051	1.027	1.228	36,000
Parameter	**Subadult**					**Adult**				
Covariate	**Mean**	**SD**	**2.5%**	**97.5%**	**N.eff**	**Mean**	**SD**	**2.5%**	**97.5%**	**N.eff**
Abundance	4.439	1.707	-	-	-	4.703	1.643	-	-	-
Management	-0.279	0.175	-0.620	0.064	36,000	0.228	0.158	-0.077	0.543	8,152
Mean daily VPD (kPa)	-0.340	0.199	-0.695	0.075	36,000	-0.080	0.202	-0.442	0.344	36,000
Availability	0.169	0.032	0.108	0.230	2,532	0.117	0.025	0.072	0.172	8,201
Temperature (°C)	0.047	0.011	0.025	0.070	642	0.047	0.011	0.025	0.070	642
VPD (kPa)	-0.682	0.071	-0.825	-0.545	10,575	-0.558	0.074	-0.706	-0.415	7,975
Rain prior 24 h (mm)	-0.085	0.041	-0.165	-0.002	7,102	-0.085	0.041	-0.165	-0.002	7,102

Rain prior 5 d(mm)	0.297	0.056	0.193	0.410	2,054	0.297	0.056	0.193	0.410	2,054
Detection	0.091	0.014	0.066	0.121	4,496	0.138	0.021	0.100	0.183	8,646
Ground visibility	0.225	0.040	0.146	0.302	14,905	0.225	0.040	0.146	0.302	14,905
Site (random effect)	1.124	0.051	1.027	1.228	36,000	1.124	0.051	1.027	1.228	36,000

FIGURES

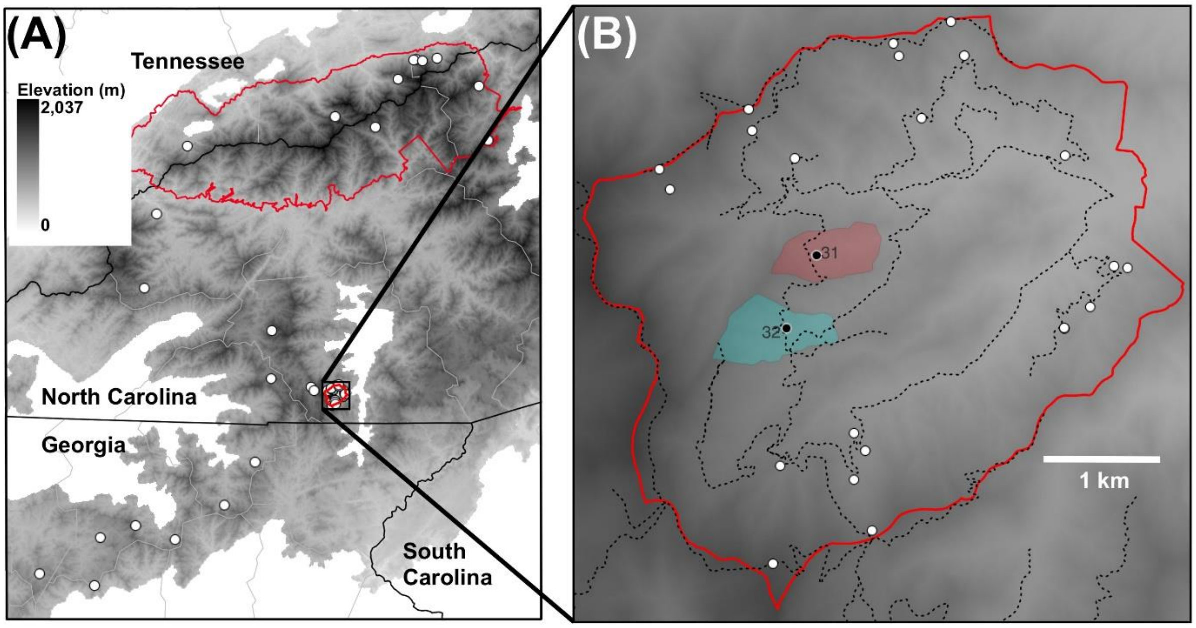

Figure 2.1: Map of study site locations across A) the broader region project and in B) Coweeta across an elevational gradient. The study sites for the broader regional dataset are represented as white dots. The study sites for the Future Forest Experiment are located in the shaded watersheds with WS31 (treated watershed) in red and WS32 (reference watershed) in blue.

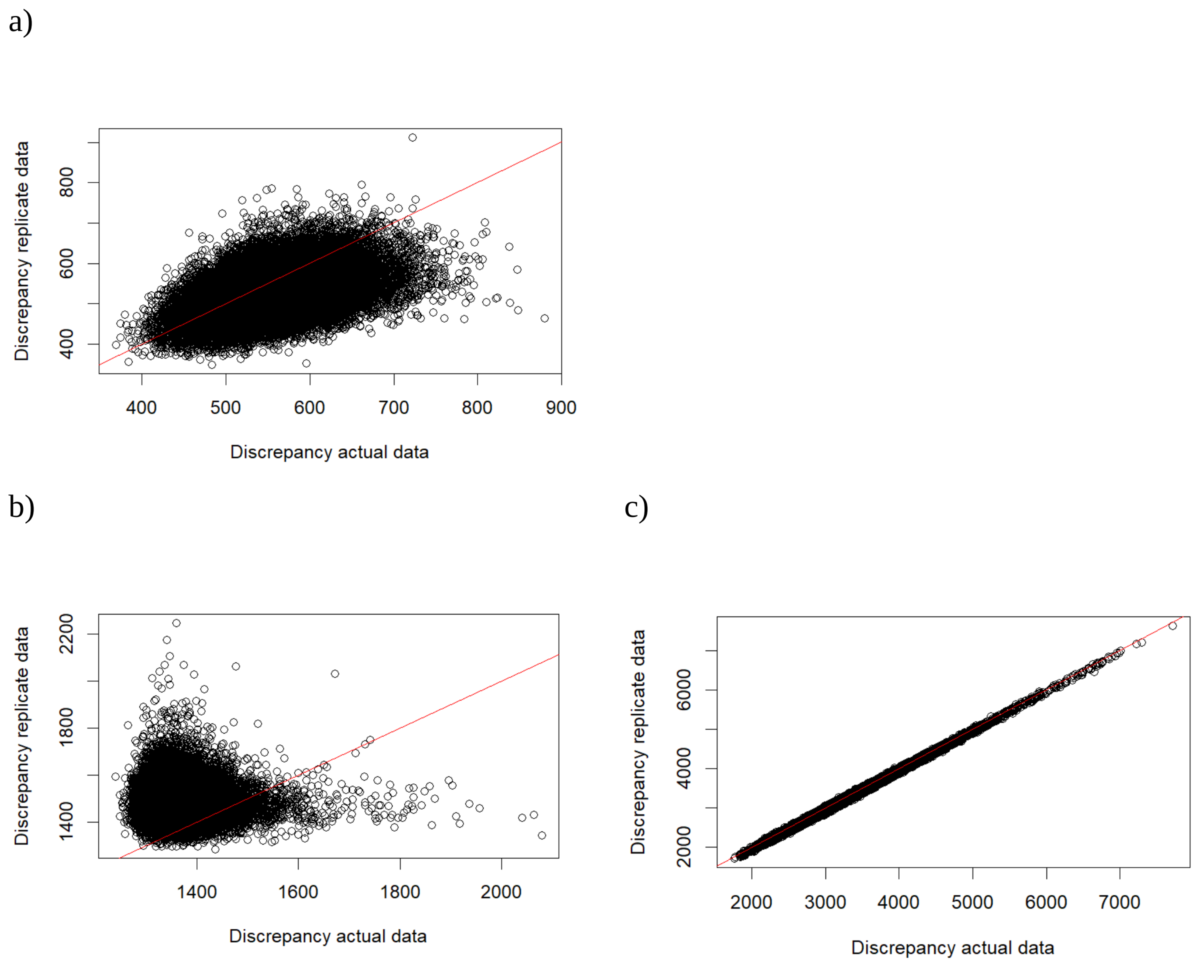

Figure 2.2: Scatter plot of the goodness-of-fit Chi-squared discrepancy values for the Future Forest Experiment portion of the integrated abundance model with the 1:1 line in red for the a) robust sampling design and for the b) observation process and c) state process of the depletion sampling design.

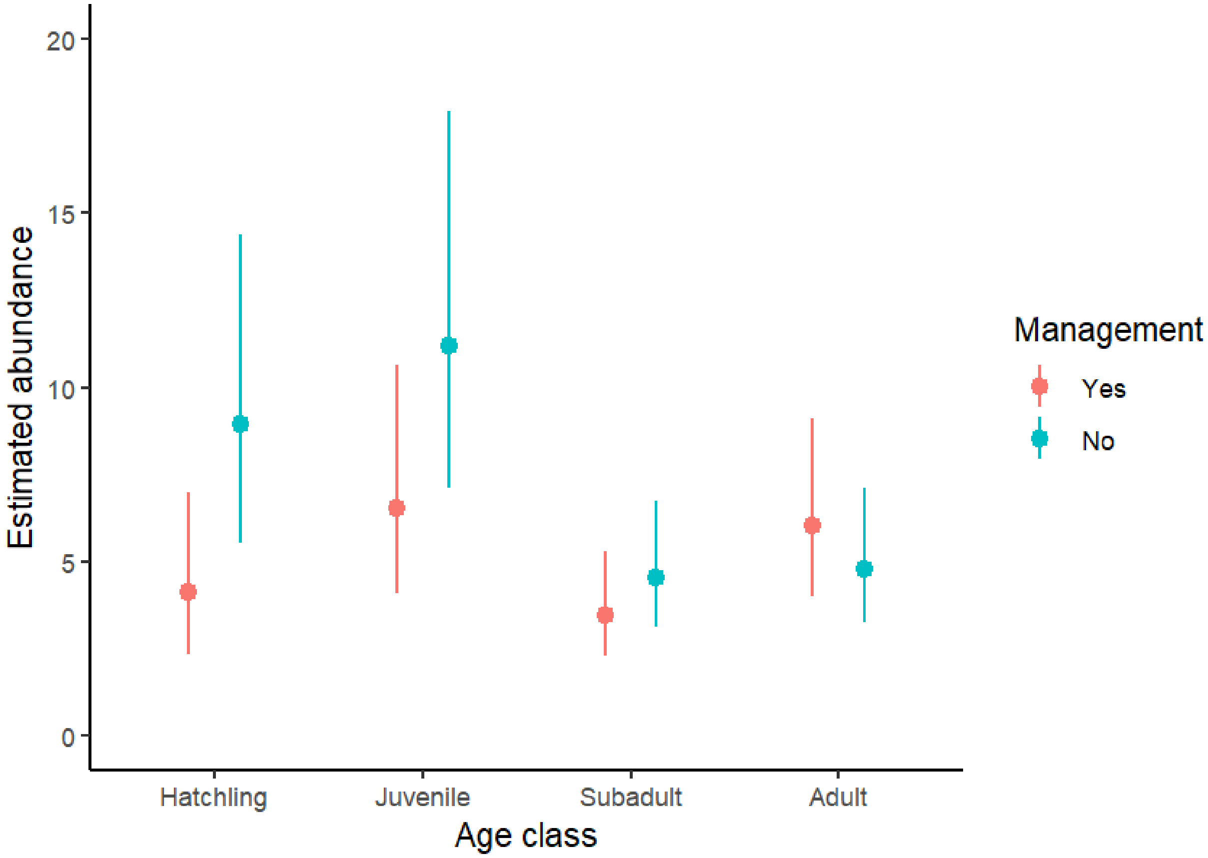

Figure 2.3: Mean abundance estimates with 95% Bayesian credible intervals for each age class and treatment. Blue is estimated abundance where there has not been midstory thinning and repeated prescribed burning. Red is estimated abundance where these management activities have occurred.

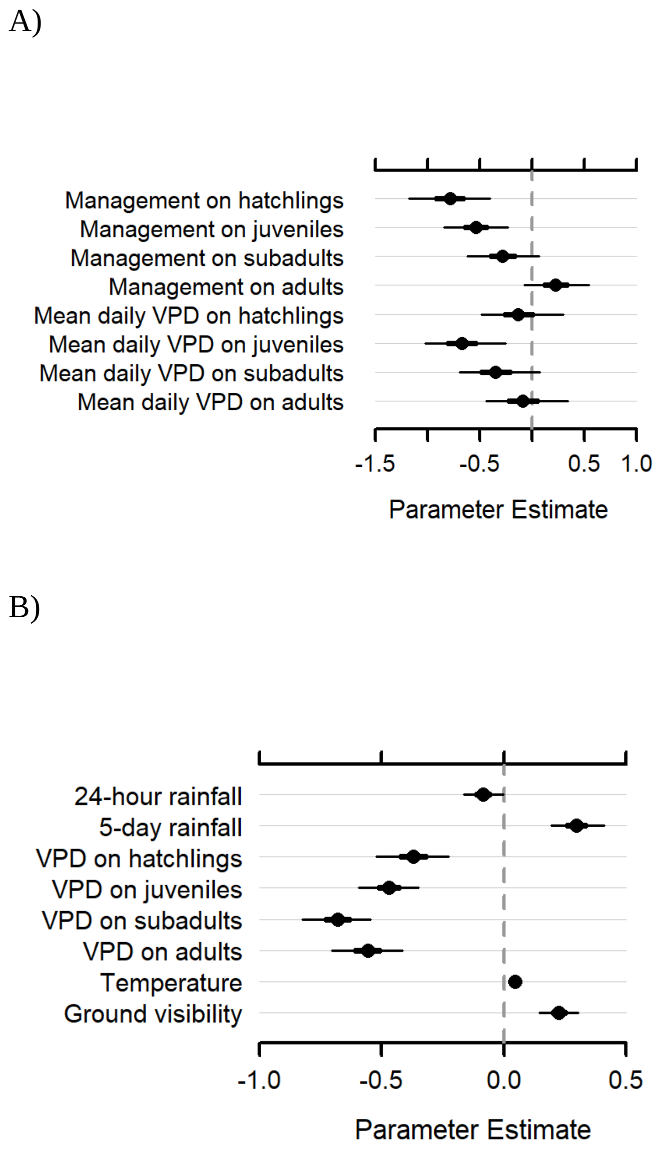

Figure 2.4: Caterpillar plots for each parameter for A) the abundance portion and B) the capture probability component, which includes availability and detection, of the integrated abundance model, with 50% and 95% Bayesian credible intervals. Vapor pressure deficit is calculated using DayMet weather data for the abundance portion of the model and measurements using a Kestrel during the sampling time for the capture probability of the model.

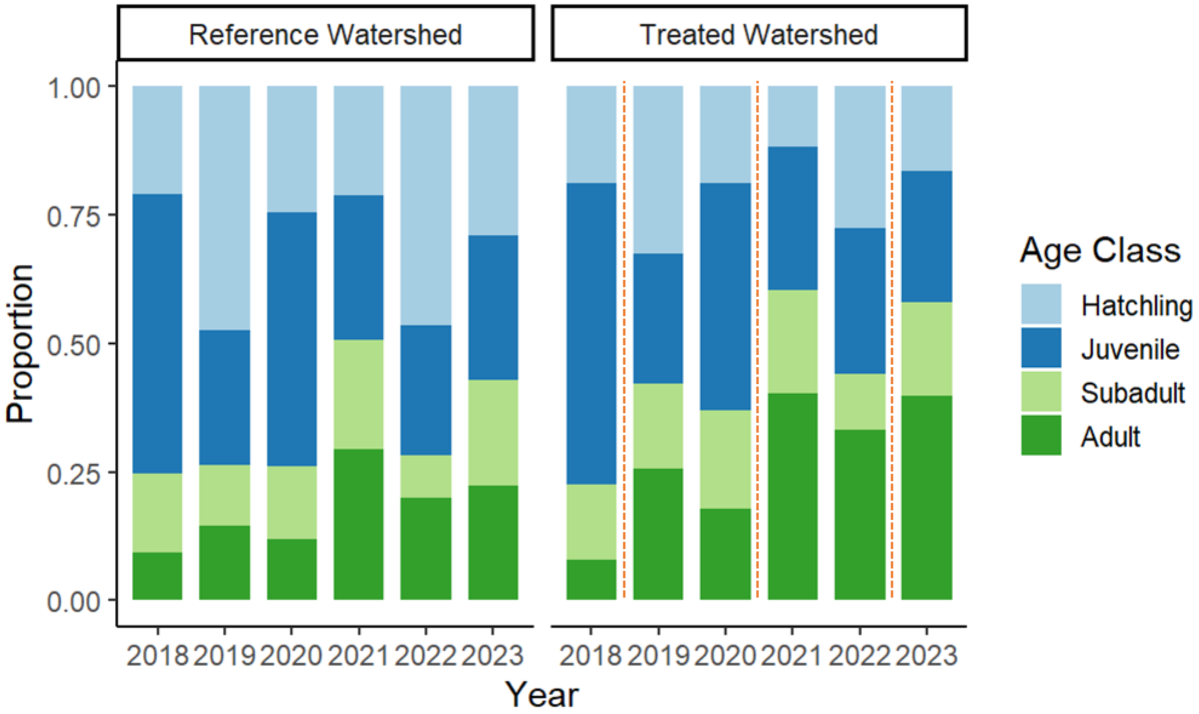

Figure 2.5: Mean proportion of each age class of *Plethodon* hybrids for each watershed at Coweeta across all years of the study (2018-2023). The dotted, orange lines in the treated watershed section of the graph indicate when prescribed fire in 2019, 2021, and 2023.

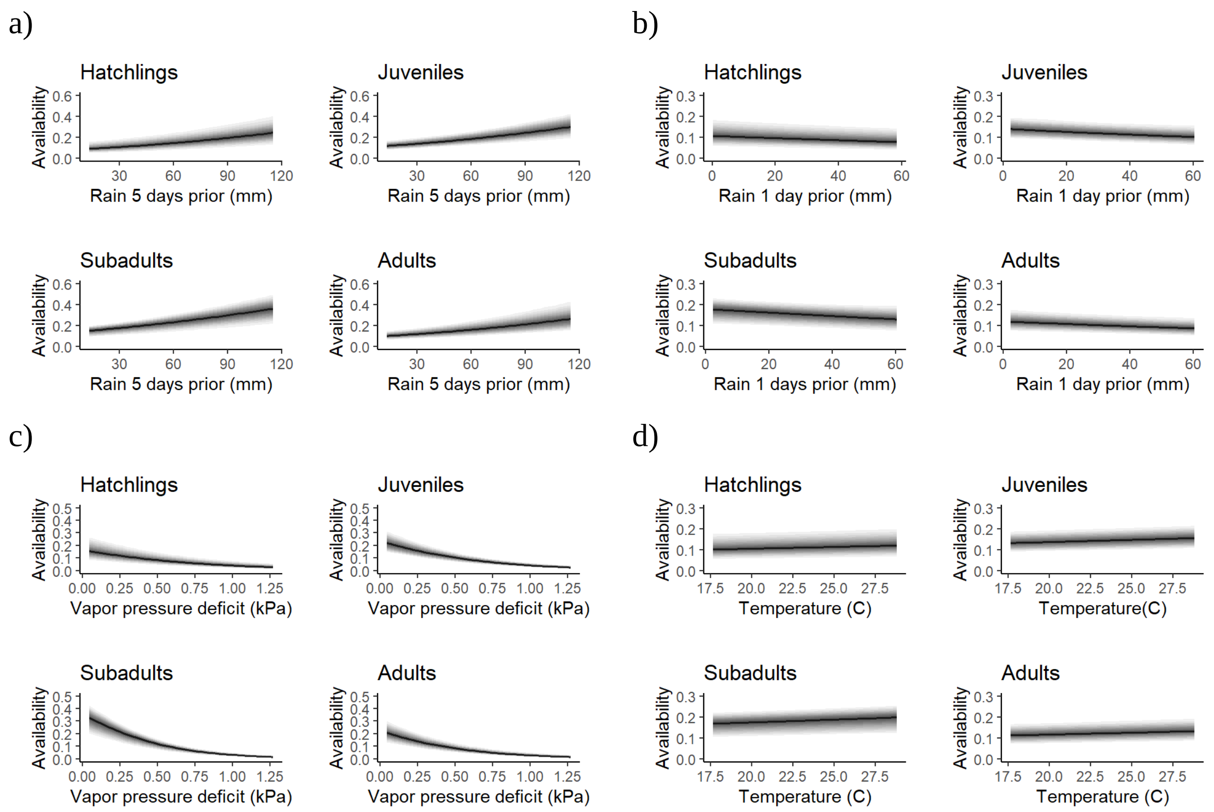

Figure 2.6: Availability of each *Plethodon* hybrid age class as a function of a) rain in the preceding five days of a sampling event, b) rain in the preceding 1 day, c) vapor pressure deficit (VPD), and d) temperature. The black line is at the mean with the multilayered ribbon surrounding the lines shows the Bayesian credible interval increasing by 5% up to the 95% credible interval.

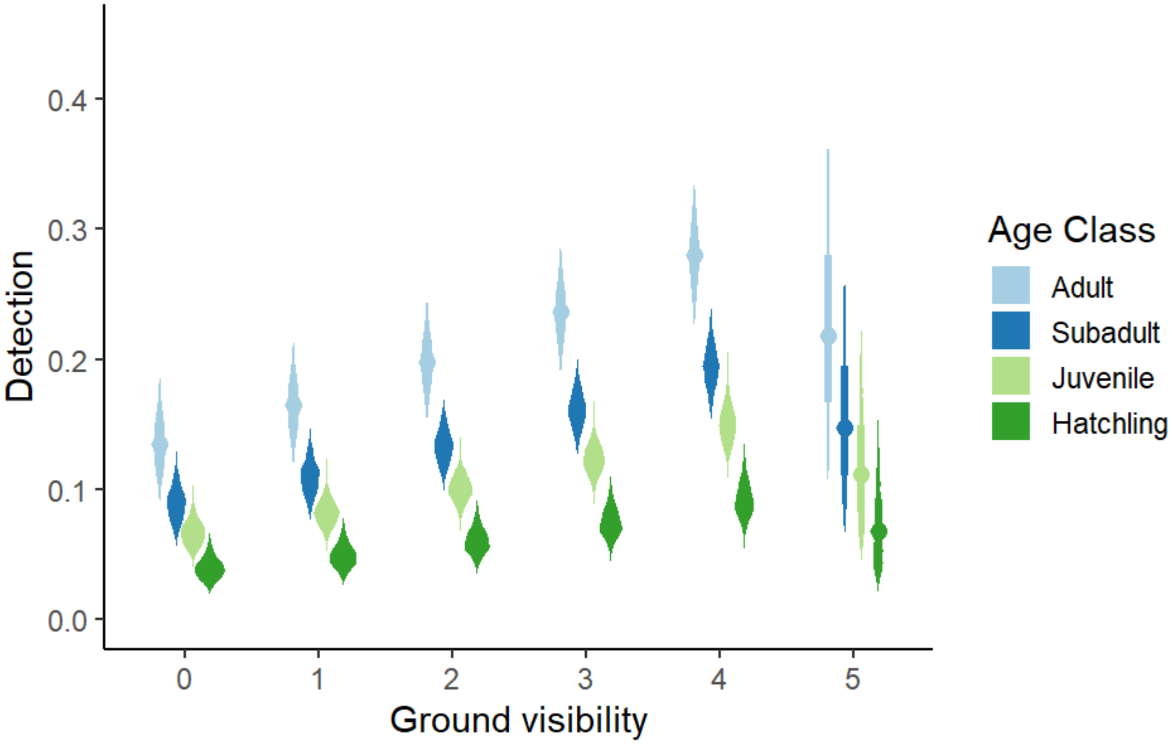

Figure 2.7: Detection as a function of observer-reported ground visibility for each age class of *Plethodon* salamanders. The tails are at the 50% and 95% Bayesian credible interval.

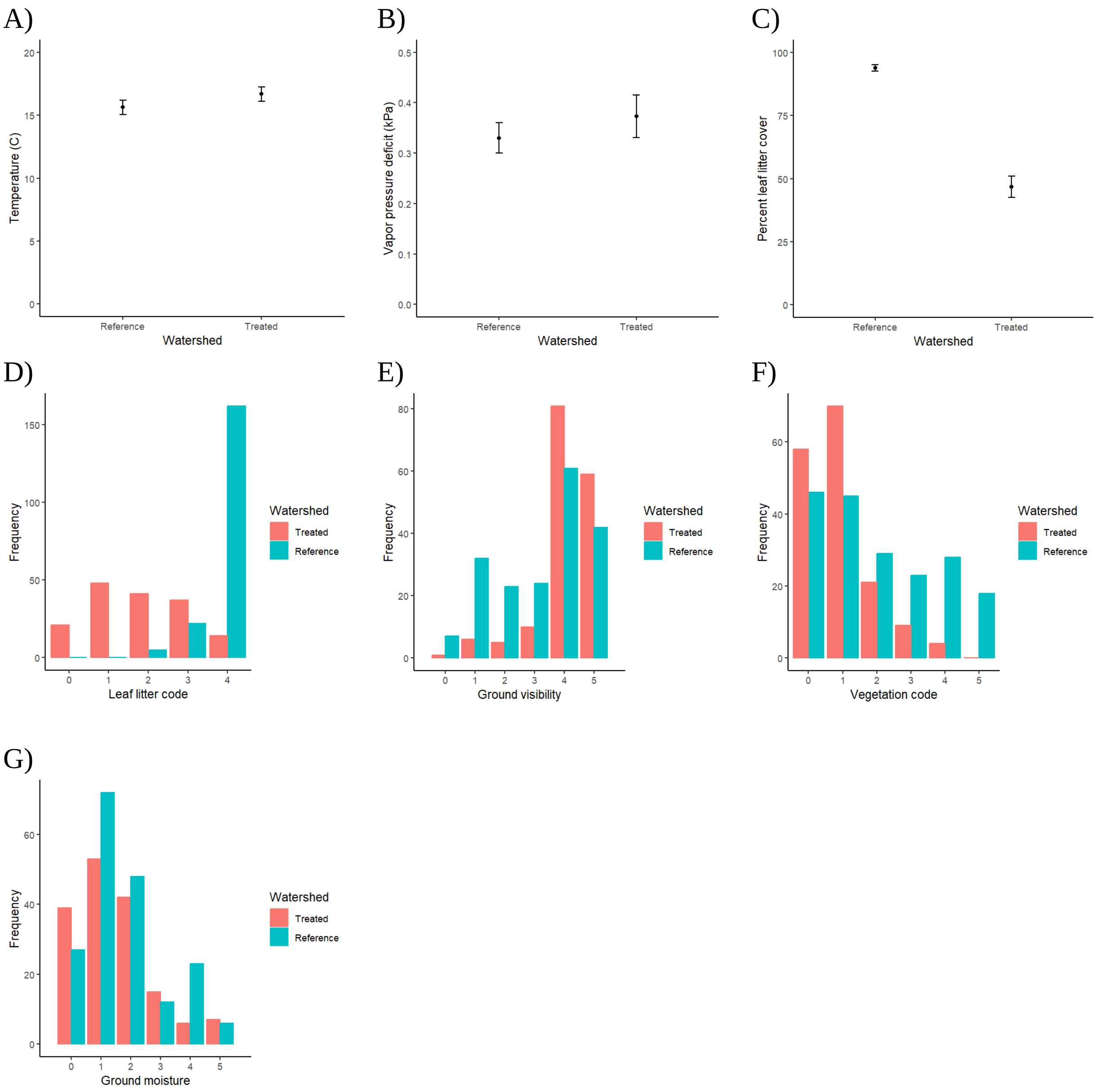

Figure 2.8: Mean values and error bars at 95% confidence intervals for the environmental covariates of A) temperature, B) vapor pressure deficit (kPa) and C) percent leaf litter; and frequency histograms of the environmental covariates for D) litter code, E) ground visibility, F) vegetation code, and G) ground moisture with red representing the treated watershed (WS31), and blue representing the reference watershed (32).

CHAPTER 3

QUANTIFYING JUVENILE SALAMANDER GROWTH AND SURVIVAL IN RESPONSE TO FOREST MANAGEMENT[2]

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[2] Grab, K. M., and J. C. Maerz. To be submitted to a peer-reviewed journal.

Abstract

A common objective of land management is to maximize the effect of the main objective, while minimizing impacts on non-target species. The Southern Appalachian Mountains are a global hotspot for plethodontid salamanders, and understanding how forest management activities impact salamander demographics is important for informing management actions. We used a 7-month capture-mark-recapture study within a paired watershed study integrated with a longer-term capture-mark-recapture data set to estimate the effects of forest management (midstory removal and repeated prescribed fire) on juvenile terrestrial salamander growth and survival. Though several factors likely limited our ability to detect effects, we found weak evidence that juvenile growth rates were lower in the treated watershed, but additional weak evidence that apparent survival rates were marginally higher in the treated watershed. We found no evidence of a measurable effect of precipitation on juvenile growth or survival, countering what is widely known and previously demonstrated for these taxa. We hypothesized that our attempts to estimate effects of forest management and precipitation were compromised by survival bias affecting our ability to measure growth rates of juveniles. An early dry period relative to the duration of the study limited our ability to estimate management effects on survival. Thus, we feel that inferences made from our results should be made with caution until future studies can better resolve weather and management effects on juvenile growth or survival.

Introduction

Understanding how animal population dynamics are affected by management actions is important for informing land management decisions. A common objective of land and wildlife management is to maximize the effectiveness of management objectives while minimizing negative impacts of actions on non-target ecosystem services and species. Optimizing target and non-target impacts can be key to maintaining regional biodiversity. In order to fully understand the nature of these impacts, investigating both population patterns, like abundance, and processes, like survival, is key (Otto et al., 2014). Most studies that investigate the effects of forest management activities on wildlife focus on species presence, abundance, or richness, while fewer studies estimate management effects on population vital rates that govern those patterns (as reviewed by Harper et al. 2016). Patterns of occupancy or abundance may sometimes be insufficient for understanding the impact of management activities on populations and, in some cases, incorporating vital rates may improve our understanding of land management impacts and lead to more effective actions and better decisions (Cosset et al., 2019; O'Donnell et al., 2015; Otto et al., 2014; Tian and Hua, 2023).

Unfortunately, vital rates are often under-reported despite their critical role in our understanding of population dynamics especially in the context of conservation and management (Heppell et al., 2000; Howard and Maerz, 2021). Although vital rates at each stage impact population dynamics, vital rates in juveniles, which are even less frequent in the literature, may be particularly important for population dynamics (Halliday and Verrell, 1988; Howard, 2018). In amphibians, much of the growth occurs in the early life stages, prior to maturation (Hairston, 1983; Halliday and Verrell, 1988). Growth at this life stage may impact the age or size an animal reaches maturity and survival and reproduction as adults (Halliday and Verrell, 1988).

The southern Appalachian Mountains are a global hotspot of salamander diversity and, therefore, a priority region for the conservation of salamander species. Concurrent forest management activities in the southern Appalachian Mountains are being used to increase the recruitment of some tree species such as oaks (*Quercus* spp.) and restore habitat for priority species that were historically more abundant in the region (e.g., Red-cockaded woodpecker, *Leuconotopicus borealis*) (Brose et al., 2001; Fouts et al., 2017; Harper et al., 2016). However, the recently documented negative effects of unmanaged and severe fires on salamanders in the region (Gade et al., 2019; Wilk and Peterman, 2024) have motivated research into the effects of prescribed fire and other forest management actions on salamander populations (Fouts, 2014). Actions including harvest, thinning, and prescribed burning can create forests that are warmer and drier, which can be more physiologically challenging for plethodontid salamanders (Homyack et al., 2011; Hossack et al., 2009; Jacobsen et al., 2020; Schurbon and Fauth, 2003). This physiological challenge may be especially true for smaller species and individuals such as juveniles because their small body makes them more sensitive to reduced moisture and increased evaporative water loss (Feder, 1983; Howard, 2018; Peterman and Semlitsch, 2013). Other studies of plethodontid salamander responses to shelterwood treatments, timber harvest, or prescribed fire generally found reduced abundances of smaller age classes (Grab 2024, Chapter 2; Ash, 1997; Grialou et al., 2000; Halloran et al., 2021; Head, 2020; Homyack et al., 2011; Mazerolle et al., 2021; Otto et al., 2014). For example, in the previous chapter of this thesis (Grab 2024, Chapter 2), I documented reduced abundance of *Plethodon* salamanders corresponding with manual midstory shrub removal and repeated prescribed burning over a six-year period. Reductions in *Plethodon* abundance were greatest for the two smallest age/size classes, hatchlings, and small juveniles, respectively. I predicted that this reduction in juvenile abundance could be the result of reduced juvenile growth and survival or female fecundity.

The objectives of this study were to use a paired watershed manipulation to estimate the predicted reduction in juvenile *Plethodon* salamander growth or survival in response to midstory shrub removal and repeated, high frequency, low intensity prescribed burning. In addition to data collected among plots within the paired watershed, we used an integrated model to leverage a 15 year capture-mark-recapture data set from sites near the paired watershed to estimate the effects of weather on juvenile growth rates, potentially increasing our sensitivity to detect forest management effects on growth during this shorter-term study (Hostetter et al., 2019; Zipkin and Saunders, 2018). Consistent with well documented and accepted effects of reduced moisture on juvenile plethodontid ecology, including foraging activity, we predicted that juvenile salamander growth would be positively correlated with daily rainfall rates during intervals within the active season.

Methods

Study Species and Site

Our focal study took place at Coweeta Hydrologic Laboratory (herein Coweeta) in Macon County, North Carolina, which is part of the U.S. Forest Service's Nantahala National Forest. The U.S. Forest Service implemented a projected, beginning in 2019, called the "Future Forest Experiment" (FFE). The experiment uses two adjacent watersheds, Watershed 31 (WS31) and Watershed 32 (WS32), with similar climate, slope, aspect, and history. The watersheds range in elevation from 869 m to 1146 m in WS31 and 920m to 1236m in WS32 (Miniat et al., 2021). The goal of this project is to increase oak recruitment on a watershed at Coweeta. Watershed 31 was designated as the “treatment” watershed and in 2018 underwent manual removal of the *Rhododendron* spp. understory with herbicide application to the *Rhododendron* stumps followed by prescribed burns of the entire watershed in February of 2019, 2021, and 2023 (Miniat et al., 2021). Watershed 32 (WS32) was designated as the reference watershed. In 2018, we began monitoring plots in each watershed. For this study, we monitored fifteen 5 x 5 m plots in each watershed during the salamander active season, and they ranged in elevation from 883 m to 1004 m in WS31 and from 962 m to 1026 m in WS32.

Since 2010, the Maerz lab has also been conducting a long-term capture-mark-recapture (CMR) study among six plots at three sites along Ball Creek Road in Coweeta between 838 m and 973 m elevation. These study plots are ~1.0 km from the study plots in WS32 and 1.3 km from the study plots in WS31 (Figure 3.1). At the time of conducting our analysis, this long-term CMR data set included 8,215 captures of 3,278 individuals including 799 individuals who were captured at least twice as juveniles. The time span and large number of marked individuals in this study creates a rich data set for estimating weather effects on juvenile growth rates.

The salamander populations at this elevation within our study site are of an ancestral hybrid lineage (introgression) between *Plethodon shermani* and *P. teyahalee* (see Carter 2023 for a summary). It has been shown that patterns of genetic and phenotypic variation among the hybrid salamanders correspond strongly to hydroclimatic variation across Coweeta (Carter, 2023). Though not germane to the present study, the adaptive introgression apparent among the large *Plethodon* spp. at Coweeta (and elsewhere across the Nantahala National Forest) creates the potential for evolutionary response to forest management.

Sampling Design

We conducted nocturnal visual encounter sampling that began after sunset starting in April 2023 with approximately monthly visits through October 2023 for a total of seven sampling occasions. We surveyed each plot using a depletion sampling design with four passes for a total of at least 15 minutes of sampling time per 5 m by 5 m plot. Salamanders that were captured and removed from the plot during sampling were not released until the surveying of the plot was completed. We identified captured salamanders to species, measured their body condition, gave them a hybrid score, and sexed them, if possible. All *Plethodons* at these plots are hybrids (Carter, 2023). We marked juveniles (snout-vent-length < 50 mm) using a unique visual implant elastomer code for identification (Northwest Marine Technology, Inc., Anacortes, WA). We collected weather and plot level data to account for environmental characteristics that influence detection, availability, growth, and survival. Air temperature, relative humidity, and wind speed were collected during or after each sampling event using a Kestrel™ 3000 Weather Meter (KestrelMeters.com) and soil temperature was taken using a Luster Leaf digital soil thermometer. Ground moisture, leaf litter, and vegetation cover were estimated during each sampling event by the surveyor, details of which can be found in the previous chapter (Grab 2024, Chapter 2). Precipitation data for both projects was collected at nearby weather stations in Coweeta.

The sampling procedure for the CMR project followed a robust sampling design in which primary periods contain multiple secondary sampling periods where the population is assumed to be closed between secondary periods and open between primary periods (Pollock, 1982). When sampling for the CMR project first began in 2010 through 2014, the primary periods were approximately monthly from March through November with three secondary periods, where plots were sampled on three consecutive nights (Howard, 2018). In 2015 through 2022, each year contained three primary periods from April through October with three secondary periods (Howard, 2018). Beginning in 2023, there number of primary periods remained the same, but the number of secondary periods was reduced to two consecutive nights. For our analysis, we only used individuals from the long-term CMR project that were initially captured as young juveniles likely less than 2 years of age (SVL < 46 mm; Howard, 2018). Of these individuals, we filtered out all growth intervals that were less than three days apart to avoid recaptures in the same primary period or those that were more than two years apart to make sure that we were capturing growth rates in hatchlings and juveniles. After filtering, there were 1,537 growth intervals across 639 individuals from the long-term CMR project that we used for this analysis.

Because these salamanders are generally not surface active in the winter and appear to grow little during this season, we excluded the period from November 15 to March 15 for those growth intervals that carried over to the next year and subtracted 120 days for each year passed from the total number of days in an interval to create a category called "active days". Cumulative precipitation during the non-active period was also not included in the analysis.

Data Analysis

We estimated the differences in growth rates between juvenile salamanders in WS31 and WS32 using Fabens (1965) von Bertalanffy growth model in which we integrated growth increment data from the long-term CMR study using a Bayesian framework. Additionally, because the CMR study is not limited to juvenile salamanders, using a von Bertalanffy growth model allowed for asymptotic growth, because growth in amphibians tends to slow once maturity is reached (Hairston, 1983; Halliday and Verrell, 1988).

For the focal study, we filtered out individuals with incomplete growth interval data so that only individuals with complete growth intervals remained. After filtering out these individuals, there were 24 individuals that were recaptured with measurements and there were 31 growth intervals. We did not remove records where there was a negative change in SVL to account for measurement error.

This model estimates growth by using growth increments and size at the start of the interval instead of age because age is not always known (Fabens, 1965; Wang, 1998). We used a modified Fabens model that allowed for the parameterization of the growth increment and a sub model for the growth parameter, k (Guzy et al., 2021; Wang, 1998).We modified the model used in Guzy et al. (2021) so that the growth interval is estimated as

$$Z_i = (SVL_\infty - \beta * (SVL1_i - E(x)) - SVL1_i) * (1 - e^{(-k_i * days_i)}) + \varepsilon$$

Where Z, the change in SVL in a growth interval, is a function of the estimated asymptotic size (SVL_∞), the sample mean [E(x)] of the starting SVL, a measure of variance (β), the SVL at the start of the interval (SVL1), the growth coefficient (k_i), the time of the growth interval (days), and an error term. Because there were multiple recaptures for several individuals in both studies, we included a random effect of the individual to account for the lack of independence among growth intervals from the same individual. The growth parameter can be modeled using the methods found in Wang (1998) and Guzy et al. (2021). The submodel for k is:

$$k_i = \alpha_0 + \alpha_1 * mgmt_i[i] + \alpha_2 * precip_i[i]$$

Where k of growth interval *i* is a log-link function of management treatment and precipitation per day during the active period. Higher precipitation is associated with higher growth rates, likely because of increased foraging opportunities (Caruso and Rissler, 2018). The submodel of k for the long-term CMR project does not include an effect of management but does include an effect of daily precipitation. The model estimated SVL_∞, β, and k separately for the two datasets. The models for each dataset were integrated by allowing the joint estimation of the effect of precipitation on k.

The estimates of k and asymptotic size from the growth model were used to estimate SVL for each visit after the first capture for marked individuals if SVL was not recorded for a given visit (Henderson et al., 2021; Rose et al., 2022). These estimated SVLs were used in the survival model to estimate detection in the survival analysis to account for size-based detection.

To estimate mean juvenile survival for each watershed, we used a hierarchical Cormack-Jolly-Seber (CJS) model using a Bayesian framework (Connette and Semlitsch, 2015; Cormack, 1964; Howard, 2018; Jolly, 1965; Seber, 1965). This hierarchical structure separates capture probability into two parts, detection and availability, to account for weather driven surface activity of salamanders and imperfect detection of available salamanders by observers (Howard, 2018; O’Donnell and Semlitsch, 2015). Unlike the growth model, this survival model was not integrated with the long-term CMR dataset because that specific analysis was beyond the scope of this thesis.

For the survival model, z, which is the state of the individual at the first capture is 1, state of the individual is dependent upon the previous state, either alive (1) or dead (0) (Kéry and Royle, 2021). The state ($z_{i,t}$) of an individual at a visit given their state in the previous visit is a Bernoulli distribution of the state of the individual at the previous time interval multiplied by the survival probability ($\phi_{i,t-1}$) of that individual in that previous visit:

$$z_{i,t}|z_{i,t-1} \sim Bernoulli(z_{i,t-1} \times \phi_{i,t})$$

The survival probability ($\phi_{i,t}$) of an individual at a given visit is a logit-link function of the treatment effect, mean daily precipitation between visits, and observed or estimated SVL for individual *i* at visit *t* such that:

$$logit(\phi_{i,t}) = \beta_0 + \beta_1 * WS_i + \beta_2 * precip_{i,t} + \beta_3 * SVL_{i,t}$$

To account for other variation in survival outside of the effect of the management treatment, we included mean daily precipitation between each visit (Caruso and Rissler, 2018; Gade et al., 2022; Howard, 2018). Integration of this survival analysis with the long-term CMR data is critical to improving estimates for this model, but this work was beyond the scope of this thesis and is forthcoming. Additionally, size is often attributed to survival, where larger bodies are likely to have increased survival (Howard, 2018; Sauer and Slade, 1987).

The observation process of this model includes two parts: availability and detection. These salamanders spend a majority of their time underground and are only surface active under certain environmental conditions, which means they are not always available to be detected (Gade et al., 2020; Heatwole, 1962; O'Donnell and Semlitsch, 2015; Taub, 1961).

This limited surface activity, or availability, is critical to account for when modeling the observation process as omitting availability can bias our estimates particularly when availability is low, like it is for salamanders (Bailey et al., 2004; DiRenzo et al., 2022; O'Donnell and Semlitsch, 2015). Therefore, availability of an animal ($a_{i,t}$) is a Bernoulli distribution of their surface activity ($g_{i,t}$)

$$a_{i,t} \sim Bernoulli(g_{i,t})$$

If a salamander is surface active, then it is available for capture. Salamander surface activity is dependent upon moisture levels and vapor pressure deficit (VPD), which is the difference between the water vapor in the air and the saturation point, is a good indicator of surface activity (Gade et al., 2020; Riddell et al., 2018; Riddell and Sears, 2015). Therefore, availability can be modeled using a logit link function such that:

$$logit\left(g_{i,t}\right) = \Omega_0 + \Omega_1 * VPD_{i,t}$$

The second part of the observation process is what we observe. The salamanders observed at a plot during a visit ($y_{i,j,t}$) can be modeled as a Bernoulli distribution of the animal's state ($z_{i,t}$) at that plot and visit multiplied by the probability we detect ($p_{i,t}$) that individual on that plot during that visit multiplied by whether or not the animal is available ($a_{i,t}$) for capture (Howard, 2018):

$$y_{i,j,t} \sim Bernoulli(z_{i,t} \times p_{i,t} \times a_{i,t})$$

The detection probability of individual *i* at visit *t* is a logit-link function of ground visibility, which is a measure of the visual obstruction of a plot at a given visit. Therefore,

$$logit\left(p_{i,t}\right) = \alpha_0 0 + \alpha_1 * vis_{i,t}$$

Our ability to observe an individual ($y_{i,j,t}$) at a given plot during a given visit is a Bernoulli distribution of their state ($z_{i,t}$) multiplied by the probability we detect ($p_{i,t}$) that individual on that plot during that visit multiplied by whether or not the animal is available ($a_{i,t}$) for capture (Howard, 2018). For capture probability, it is critical that we account for imperfect detection of salamanders. Therefore, the capture probability portion of the model contains two parts. In the submodel for detection, we included ground visibility which was an estimate of how much visual obstruction there is on a plot. Herbaceous vegetation cover is on a scale from 0 to 5 with 0 representing little to no herbaceous vegetation cover and 5 being near complete herbaceous vegetation cover.

We used a sum-squared test statistic to assess goodness-of-fit for both models to calculate Bayesian p-values (Kéry and Royle, 2016). Convergence of both models was evaluated through visual inspection of the posterior trace plots and the Gelman-Rubin statistic, $\widehat{R}$, (Gelman and Rubin, 1992). We used uninformative priors, and, through a prior predictive check, we determined that both models were not sensitive to the priors we chose (Table 3.1).

We conducted the statistical analysis in R using JAGS with the jagsUI packages (Kellner, 2021; Plummer, 2003; R Core Team, 2024). For the growth model, we ran the model with 3 chains with 15,000 iterations and 5,000 burn-in and 1,000 iterations in the adaptive phase with a thinning rate of 2. For the survival model, we ran the model with 3 chains, 35000 iterations, with 25,000 burn-in and 1000 iterations in the adaptive phase with a thinning rate of 2. We used the r packages lubridate, dplyr, maggritr, and tidyr to format the data (Bache and Wickham, 2022; Grolemund and Wickham, 2011; Wickham et al., 2023a, 2023b). Graphics were made using base R and the ggplot2, ggdist, and MCMCvis packages (Kay, 2024; Wickham, 2016; Youngflesh, 2018).

Results

Across the two watersheds, 80 and 51 individuals were marked in WS32 and WS31, respectively (n = 131 total). There were 31 recapture records among 24 individuals. In WS31 there were 11 growth intervals across 9 individuals and in WS32 and 20 growth intervals across 15 individuals in WS31.

For the growth model, Bayesian p-values and plots of the fit statistics indicated adequate fit for both data sets (FFE: Bayesian p-value = 0.65; CMR: Bayesian p-value = 0.43; Figure 3.2). The CJS survival model Bayesian p-value (Bayesian p-value = 0.59) and fit statistic plots also indicated adequate fit (Figure 3.2). The parameters for both models had an $\widehat{\mathrm{R}} < 1.05$ and visual inspection of the trace plots indicated that these parameters converged.

The mean estimated juvenile growth parameter (k) in WS31 (mean = 0.0029; 95% Bayesian Credible Interval (BCI) = 0.0010– 0.0085) was only marginally lower than the estimated mean k for the reference watershed (mean = 0.0040; 95% BCI = 0.0016 – 0.0115; Figure 3.3). Mean estimated k in the treated watershed was lower than k in the reference watershed in 90.2% of the posterior samples. For the long-term CMR data set, mean k was 0.0019 (95% BCI: 0.0018 – 0.0021; Table 3.1), which was similar to the estimate k for in the treated watershed. The mean estimated asymptotic SVL among juvenile salamanders on the FFE plots was 69.71 mm (95% BCI: 42.37 – 98.26; Table 3.1) and beta, a measure of covariance, was -0.472 (95% BCI = -1.452 – 0.851; Table 3.1). The mean estimated asymptotic size for the CMR project was 68.50 mm (95% BCI: 67.27 – 69.80; Table 3.1) and beta was 0.028 (95% BCI = -0.026 – 0.086; Table 3.1).

There was little evidence of forest treatment or precipitation on juvenile growth (Figure 3.4). The mean estimated effect of forest management treatment on juvenile salamander growth was negative but relatively small and the 95% posterior BCI overlapped zero (mean = -0.343; 95% BCI = -0.963 – 0.150; Table 3.1; Figure 3.4). However, there was a 90.2% probability that the posterior samples showed a negative effect of treatment on growth. The mean estimated effect of precipitation on juvenile growth was positive but small. There was only a 31.8% chance that there was a positive relationship between precipitation and juvenile growth rate in this model. The 95% posterior BCI for the effect of growth overlapped zero (mean = 0.008; 95% BCI = -0.026 – 0.042; Table 3.1; Figure 3.4).

The mean estimate for apparent juvenile survival in the treated watershed was 0.924 (95% BCI: 0.703 – 0.997) and in the reference watershed was 0.815 (95% BCI: 0.584 – 0.972). Again, there was weak support for an effect of management treatment on apparent survival and in this case the effect was opposite the direction we predicted (mean = 1.44; 95% BCI = - 0.44 – 3.60; Table 3.2; Figure 3.4). This positive relationship occurred in 93.2% of the posterior samples. There was also weak support for the effect of precipitation on juvenile survival. The mean estimated effect of precipitation on juvenile survival was positive but the 95% posterior BCI overlapped zero (mean = 1.22; 95% BCI = -0.91– 2.72; Table 3.2; Figures 3.4 & 3.6). The positive relationship between survival and mean daily precipitation occurred in 92.3% of the posterior samples. There was also weak evidence for a negative effect of body size on survival (mean = -0.83; 95% BCI = -2.00 – 0.12; Table 3.2; Figures 3.4 & 3.6), which contradicts our hypothesis and a separate analysis of juvenile survival using the longer-term CMR data set from Coweeta (e.g., Howard 2018). There was a 95.4% chance that the relationship between survival and salamander body size was negative for the data we collected on the FFE plots in 2023.

The mean estimate availability of juvenile salamanders was 0.39 (95% BCI = 0.13 – 0.87). There was weak evidence of a negative effect of VPD on availability because the 95% BCI overlaps 0 (mean = -0.41; 95% BCI = -1.30 – 0.29; Table 3.2; Figures 3.4 & 3.7). The negative effect occurred in 89.5% of the posterior samples. The mean estimated detection probability was 0.47 (95% BCI: 0.14 – 0.93). There was weak evidence of a negative effect of ground visibility on detection (mean = -0.31; 95% BCI = -1.29 – 0.34; Table 3.2; Figures 3.4 & 3.7). This negative effect occurred in 82.3% of the posterior samples.

Discussion

We found weak evidence for a small negative effect of forest management treatments on juvenile salamander growth. The mean effect of forest management on growth was consistent with our prediction, as was the small apparent effect of precipitation on juvenile growth (Figure 3.4). We found little evidence of an effect of management treatment on apparent juvenile survival, which was inconsistent with other studies (Connette and Semlitsch, 2015; Ochs et al., 2024; Otto et al., 2013). Apparent juvenile survival decreased with increasing SVL (Figure 3.6), which also contradicts the finding of other studies (Lee et al., 2012; Messerman et al., 2020; Sauer and Slade, 1987), including analysis of long-term data from the CMR study conducted nearby within Coweeta (Howard, 2018). Although the effect was small, there was a positive relationship between mean daily precipitation and apparent juvenile survival (Figure 3.6), which was consistent with expectations (Caruso and Rissler, 2018; Howard, 2018). We caution that the mean estimated effects for the growth and survival models were generally very small and had high uncertainty, and therefore, should be interpreted and any inferences used with caution.

The inconsistency between our results and those of other studies could be attributed to sample size and other sources of bias that could have led to spurious or misleading results. One form of bias that was likely occurring in this study is survivorship bias. Because the salamanders need to be recaptured to obtain a growth interval, the growth estimates are only from salamanders that have survived sufficiently long enough to be recaptured. If, as other studies indicate (Feder, 1983; Howard, 2018), juvenile survival increases with body size, then we would expect those juveniles that have survived to be recaptured to be a non-random set of individuals who did not experience growth retardation from management activities or low rainfall. Because plethodontids retreat into refugia inaccessible to observers during dry periods (Feder, 1983; Gade et al., 2020; Jaeger, 1980), we assume that individuals who do not grow sufficiently either perish in refugia or are depredated at a faster rate when active on the surface. Salamanders that are dead or not surface active because of harsh surface conditions are not available for us to capture and not part of this study. Therefore, it is likely that we are not capturing salamanders that are growing slower at the same level than those that are surface active, which leads to bias in these estimates. Such a sampling bias would affect our ability to detect a management or precipitation effect on growth.

Another type of bias in these analyses was terminal bias. This type of bias can occurs at the end of capture-recapture studies when there is uncertainty about an animal's fate (Langtimm, 2009; Peñaloza et al., 2014). Often, researchers will truncate the results towards the end of the study to reduce bias in their survival estimates (Bradke et al., 2023; Langtimm, 2009). Our study was short-term (only seven months) and, because of a very dry spring in 2023 and smaller age classes are more active later in the active season (Hairston, 1983), most of the initial captures of salamanders in the focal study occurred during the latter half of the seven-month study period (Figure 3.8), which makes our analyses and associated results vulnerable to terminal bias. A longer-term CMR study on the FFE plots could alleviate the terminal bias. In addition, using models to integrate datasets and jointly estimate parameters may help to reduce the types of bias that might have affected our results (Peñaloza et al., 2014). Given the rich amount of data, both in capture histories and precipitation, from the long-term CMR study, future work should integrate these two datasets to estimate management and precipitation effects on survival. As we did with our growth analysis, integrating the FFE data with the long-term CMR data could allow for better estimates of management effects. Creating an integrated survival model was discussed as part of our larger project but was beyond the scope of this thesis. The survival model for the long-term CMR data is more complex and its development has been underway and is nearly complete. Once that model is complete, its integration with the FFE juvenile survival model should be a priority to produce more robust estimates of management effects on juvenile survival.

Detection decreased with increasing ground visibility, which is initially counter intuitive and contradicts the results previously reported when we modeled management effects on abundance (Grab 2024, Chapter 2) (Figure 3.7). However, other analyses of stream-breeding plethodontids in our region have shown that detection of small species and juvenile salamanders increases with herbaceous or shrub cover (Bauer, 2024). Herb and shrub ground cover may increase detection because plethodontid salamanders are known to climb plants and smaller species and individuals have a higher propensity to climb (McEntire, 2016; McEntire and Maerz, 2019). Given that vegetation is the major factor affecting ground visibility and that we were focused on small juvenile salamanders, our finding that ground visibility was negatively correlated with detection is consistent with prior research. As expected, salamander surface availability decreased with increasing VPD (Figure 3.7). This result is corroborated by previous studies that have found that increasing vapor pressure deficit reduces salamander surface activity (Carter, 2023; Gade et al., 2020; Riddell et al., 2018). It is likely that VPD and ground visibility are not the only factors influencing availability and detection, respectively. We found that temperature and cumulative rainfall in the preceding five days affected availability and body size positively influenced detection (Grab 2024, Chapter 2). Therefore, future iterations of this analysis may want to include these additional sources that could influence detection and availability (Grab 2024, Chapter 2).

Changes to juvenile vital rates can have carryover effects on population dynamics. Growth rates of juvenile amphibians can impact time to and size at maturity, which can influence adult mortality and fecundity (Halliday and Verrell, 1988). In Chapter 2 of this thesis, we found that hatchlings and juveniles experienced the strongest negative effect of management treatment. The reduced proportion of these age classes in the population could be due to reduced growth and survival as investigated in this chapter. Alternatively, the reduced proportion of smaller age classes may be a result of reduced female fecundity. Forests where timber harvest and prescribed fire occur are warmer and drier, which can be physiologically challenging and energetically costly for plethodontid salamanders

(Homyack et al., 2011; Hossack et al., 2009; Jacobsen et al., 2020; Schurbon and Fauth, 2003). These unfavorable climatic conditions reduce foraging opportunities and salamanders are less likely to be surface active (Feder, 1983; Feder and Londos, 1984; Head, 2020; O'Donnell et al., 2016). However, because of their low metabolic rate, salamanders are able to withstand periods where they are unable to forage, but usually at the cost of growth and reproduction (Feder, 1983). Future research should investigate management effects on fecundity to determine if reproduction is negatively impacted by management treatment and leading to reduced recruitment of juveniles.

Previous research has shown that the impact of forest management may be short-term, delayed, or have legacy impacts on salamander populations (Cosentino and Brubaker, 2018; Schurbon and Fauth, 2003). A prescribed fire at Coweeta took place in 2023 just prior to our capture-mark-recapture study of juvenile growth and survival (A. C. Oishi, *personal communication*). In addition to this recent burn, there were prescribed burns in 2019 and 2021, which means the salamander population has had little time to recover between burns. The high frequency of fire and relatively recent but extended period without leaf litter on the forest floor within WS31 may have had a significant near-term impact on juvenile salamanders. Longer-term, forest management with the FFE is expected to move to a five-year burn rotation. The less frequent burn regime may provide sufficient time between burns to limit any negative effects of prescribed fire on salamander population dynamics. Additionally, a forest that is more oak-dominated than maple-dominated may have wetter soil and more leaf litter (Alexander et al., 2021; Alexander and Arthur, 2014), which is beneficial to salamanders, especially smaller ones. For this reason, it will be important to continue to monitor the salamander populations within the FFE and to consider more intensive study components such as the inclusion of long-term capture-recapture studies within the FFE.

The results from this study are weak and spurious so we caution their use in evaluating the effect of forest management practices on juvenile vital rates of *Plethodon* salamanders. It is also critical to look at these results within the larger context of forest management objectives and subsequent practices. For example, these prescribed burns occurred during the dormant season, which means that the impact of fire on salamanders is limited because they are underground during the dormant season, where a low intensity fire would have little effect compared to a fire in the fall when these life stages are more active (Hairston, 1983). Furthermore, the midstory thinning and prescribed fire regime of the FFE was a relatively intense management regime that significantly reduced the leaf litter in the treated watershed (Grab 2024, Chapter 2), which likely impacted salamander fitness, especially at smaller life stages. Furthermore, with the goal of increasing oak regeneration understanding the impacts of the tools used to shift stable states is important, but it may be more beneficial to understand the effects of the new state compared to the old one. While the management actions required to move a mesic forest to a xeric forest may have detrimental effects in the near-term, the end result of a xeric forest may be more beneficial for salamanders due to the potential increase in soil moisture and leaf litter accumulation (Alexander et al., 2021; Alexander and Arthur, 2014, 2010; Feder, 1983; McEntire and Maerz, 2019; Von Allmen et al., 2015). Moreover, prescribed fire reduces the severity of wildfires (Davis et al., 2024; Petrakis et al., 2018). A reduction in wildfire severity can reduce the negative effects of high intensity burns on salamander populations and subsequent legacy impacts (Gade et al., 2019; Wilk and Peterman, 2024), especially in a world where wildfires are likely to become more frequent and intense in Southern Appalachia (Mitchell et al., 2014). Thus, continued monitoring is required to help alleviate the issues with the small sample size. Additionally, using an integrated modelling approach that uses the long-term CMR dataset for the survival model will help understand the impact of forest management for oak regeneration on salamander vital rates for more informed forest management decisions across the region.

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TABLES

Table 3.1: Priors and posterior estimates, including mean, standard deviation (SD), lower and upper 95% credible intervals, and effective sample size (n.eff) for the integrated growth model for juvenile and hatchling *Plethodon* salamanders of both the Future Forest Experiment (FFE) dataset (2023) and the long-term capture-mark-recapture (CMR) dataset (2010-2023) in Coweeta Hydrologic Laboratory.

Parameter			**Posterior**				
Covariate	**Dataset**	**Prior**	**Mean**	**SD**	**Lower**	**Upper**	**n.eff**
Growth parameter	FFE	dnorm(0,0.25)	-5.685	0.542	-6.449	-4.467	485
Growth parameter	CMR	dnorm(0,0.25)	-6.238	0.035	-6.307	-6.170	1,116
Management	FFE	dnorm(0,0.25)	-0.343	0.284	-0.963	0.150	7,615
Mean daily rain	Both	dnorm(0,0.25)	0.008	0.017	-0.026	0.042	15,000
Individual (random effect)	FFE	dunif(0,3)	0.715	0.538	0.021	2.027	194
Individual (random effect)	CMR	dunif(0,3)	1.597	0.138	1.334	1.871	914
Asymptotic length	CMR	dunif(15,100)	68.501	0.643	67.279	69.805	1,047
Asymptotic length	FFE	dunif(15,100)	69.707	16.517	42.367	98.262	533

Table 3.2: Priors and posterior estimates, including mean, standard deviation (SD), lower and upper 95% credible intervals, and effective sample size (n.eff) for the hierarchical Cormack Jolly Seber survival model for juvenile and hatchling *Plethodon* salamanders in Coweeta Hydrologic Laboratory during the 2023 active season.

Parameter		**Posterior**				
Covariate	**Prior**	**Mean**	**SD**	**Lower**	**Upper**	**n.eff**
Survival	dnorm(0,0.5)	1.669	0.820	0.338	3.561	152
Treatment	dnorm(0,0.5)	1.441	1.032	-0.441	3.600	247
Precipitation	dnorm(0,0.5)	1.221	0.844	-0.915	2.716	75
SVL	dnorm(0,0.5)	-0.828	0.536	-2.000	0.121	187
Availability	dnorm(0,0.5)	-0.453	1.004	-1.876	1.879	160
VPD	dnorm(0,0.5)	-0.415	0.394	-1.296	0.290	1,840
Detection	dnorm(0,0.5)	-0.107	1.196	-1.802	2.653	792
Ground visibility	dnorm(0,0.5)	-0.308	0.397	-1.288	0.339	2,653

FIGURES

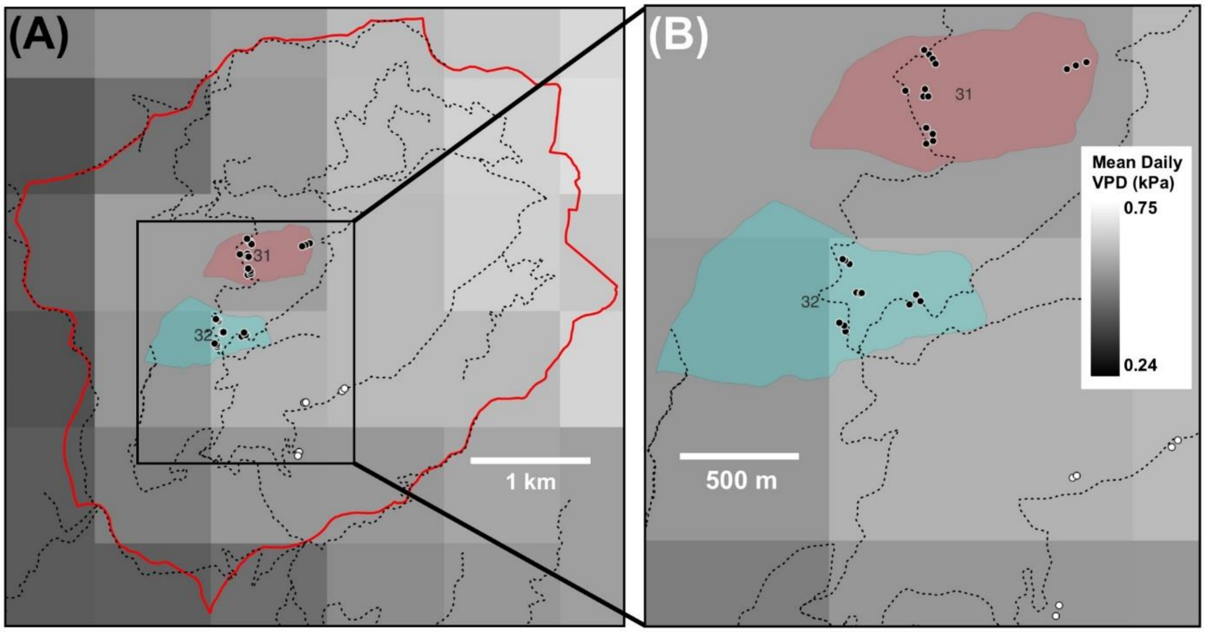


Figure 3.1: Maps of the plot locations for the Future Forest Experiment project and the long-term CMR project over a gradient of vapor pressure deficit (VPD) across A) the Coweeta basin and B) a zoomed in map of the plot locations for both projects. The blue shape is the reference watershed (WS32), and the red shape is the treated watershed (WS31).

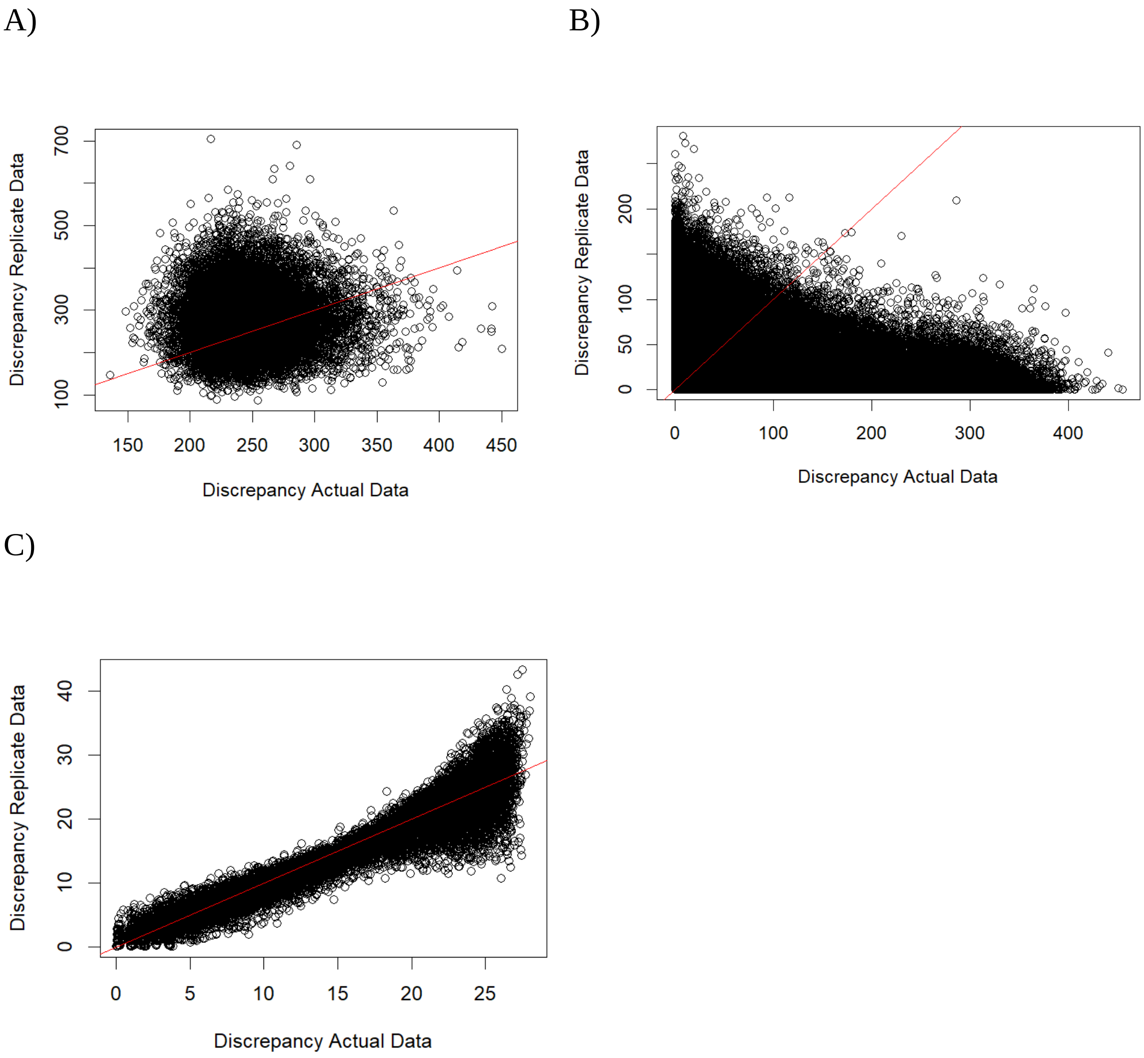


Figure 3.2: Scatter plot of the sum-of-squared discrepancy values for the goodness-of-fit test for A) the Future Forest Experiment dataset and B) the long-term CMR project for the integrated growth model and C) the hierarchical Cormack-Jolly-Seber survival model. The red line is the 1:1 line for the discrepancy values.

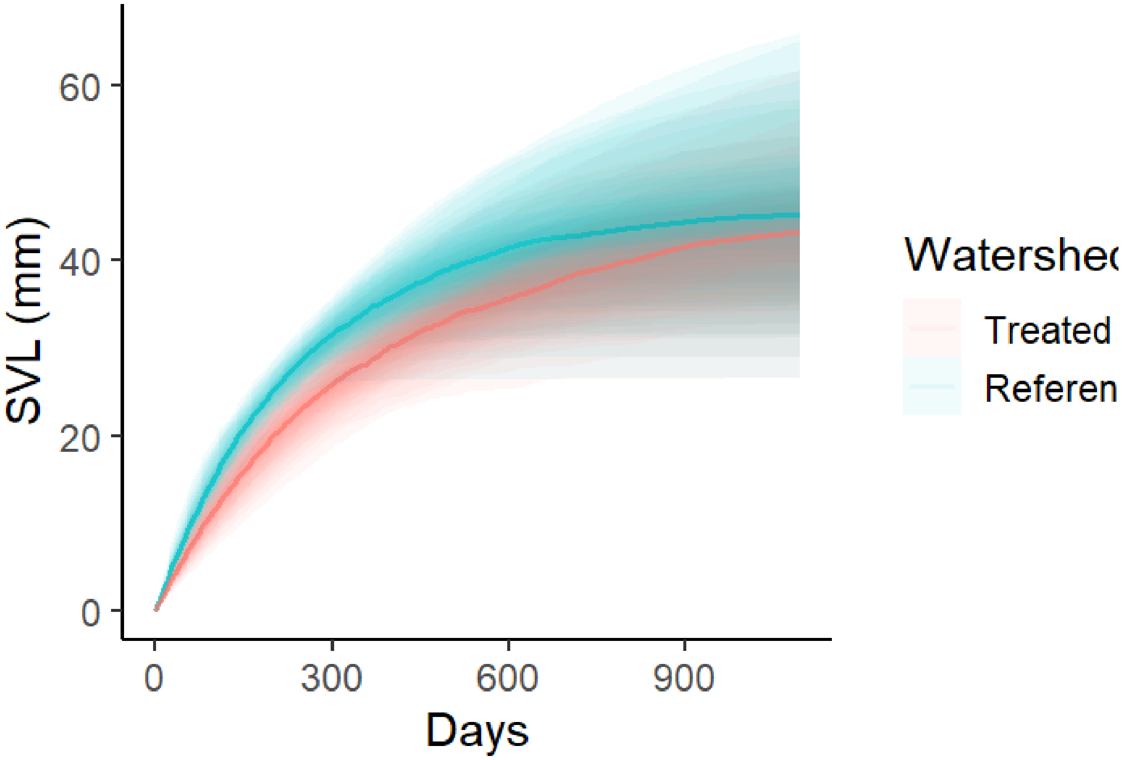
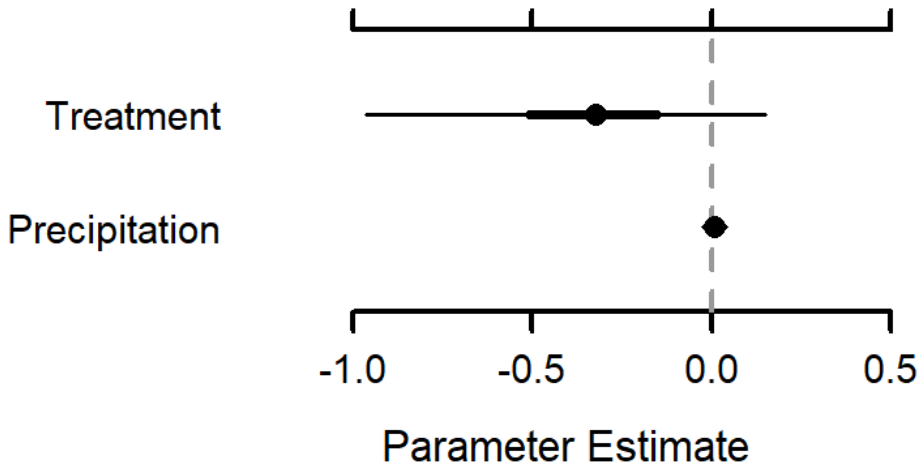


Figure 3.3: von Bertalanffy growth curve for the watershed 32 (blue) and watershed 31 (red) predicted for three years with snout-vent-length (SVL) on the y-axis. The equation used an initial SVL of 15mm, a common SVL length at hatching for *P. jordani* (Hairston, 1983). The bold lines depict the mean projected growth for the treated watershed (red) and reference watershed (blue) with the multilayered ribbon surrounding the lines shows the Bayesian credible interval increasing by 5% up to the 95% credible interval in the corresponding colors.

A)



B)

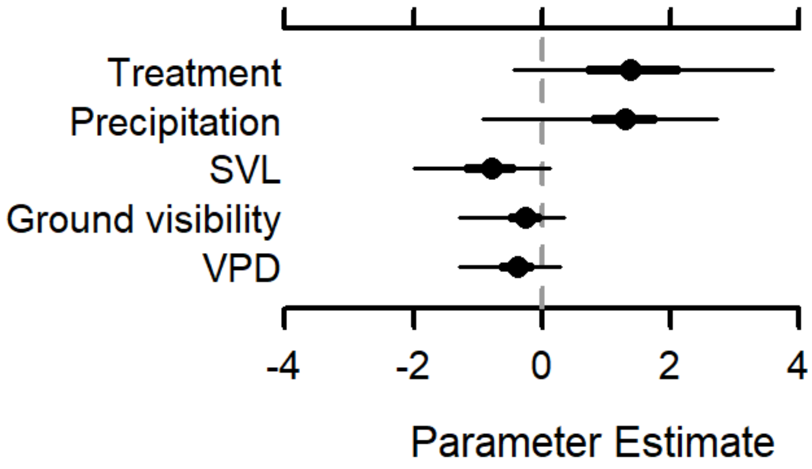


Figure 3.4: Posterior distribution of the (A) integrated growth model parameters and (B) hierarchical Cormack-Jolly-Seber model covariates with tails at 95% and 50% credible intervals. In B), SVL is snout-vent-length and VPD is vapor pressure deficit.

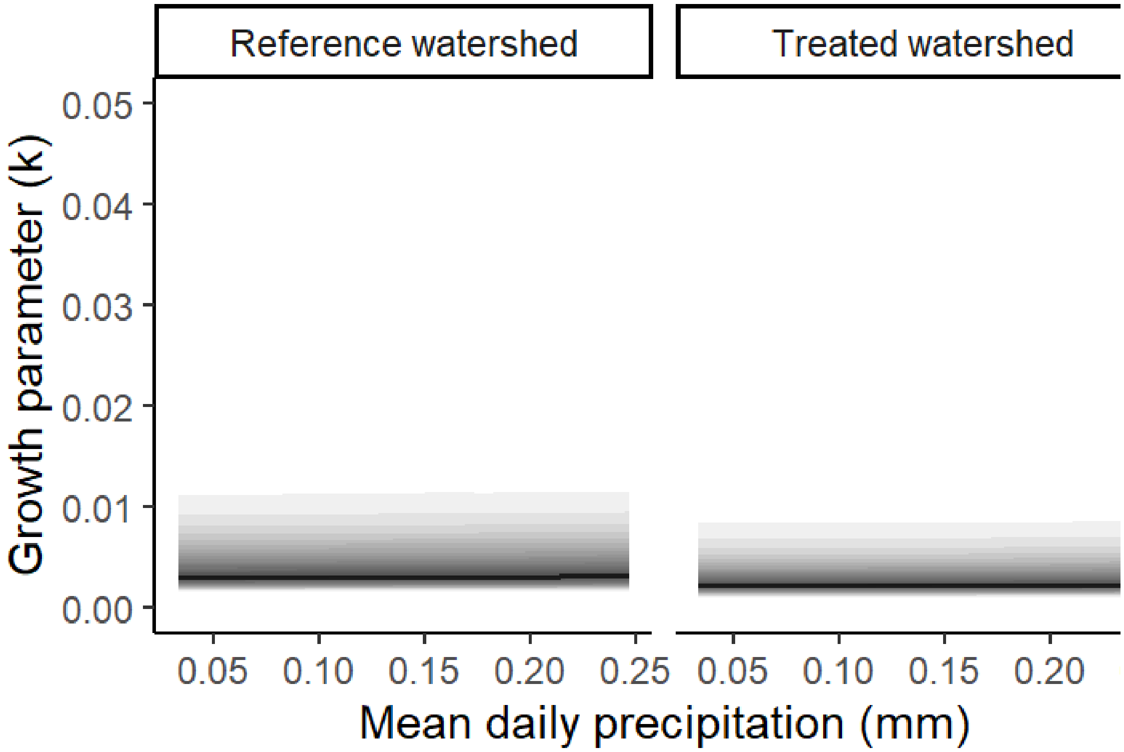


Figure 3.5: Growth parameter (k) as a function of mean daily precipitation of hatchling and juvenile *Plethodon* salamanders for the Future Forest Experiment during the 2023 active season (April - October). The bold lines depict mean availability with the multilayered ribbon surrounding the lines shows the Bayesian credible interval increasing by 5% up to the 95% credible interval.

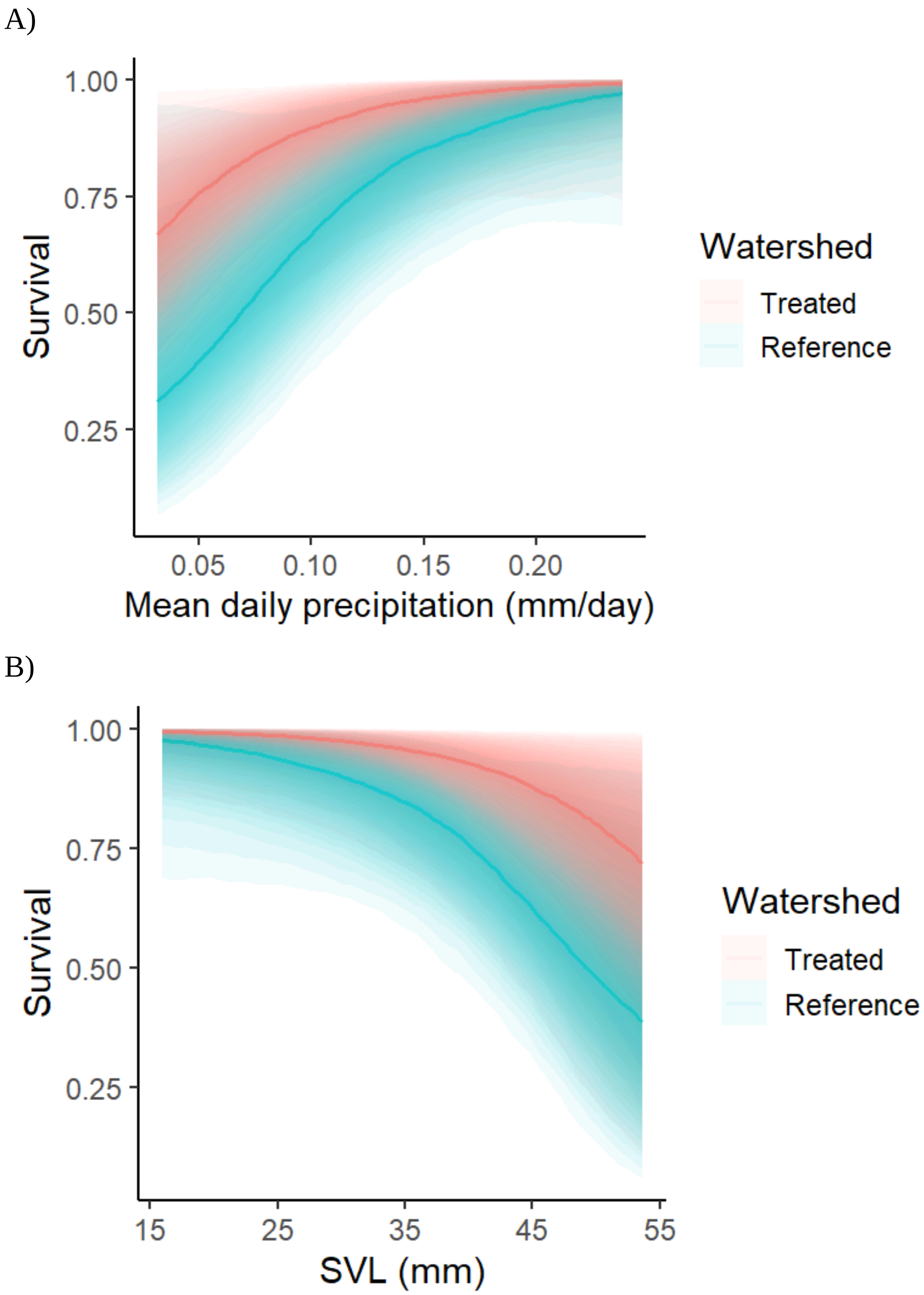


Figure 3.6: Predicted survival as a function of (A) mean daily precipitation and (B) SVL of juvenile and hatchling *Plethodon* salamanders during the 2023 active season (April - October). The bold lines depict the mean projected growth for the treated watershed (red) and reference watershed (blue) with the multilayered ribbon surrounding the lines shows the Bayesian credible interval increasing by 5% up to the 95% credible interval in the corresponding colors.

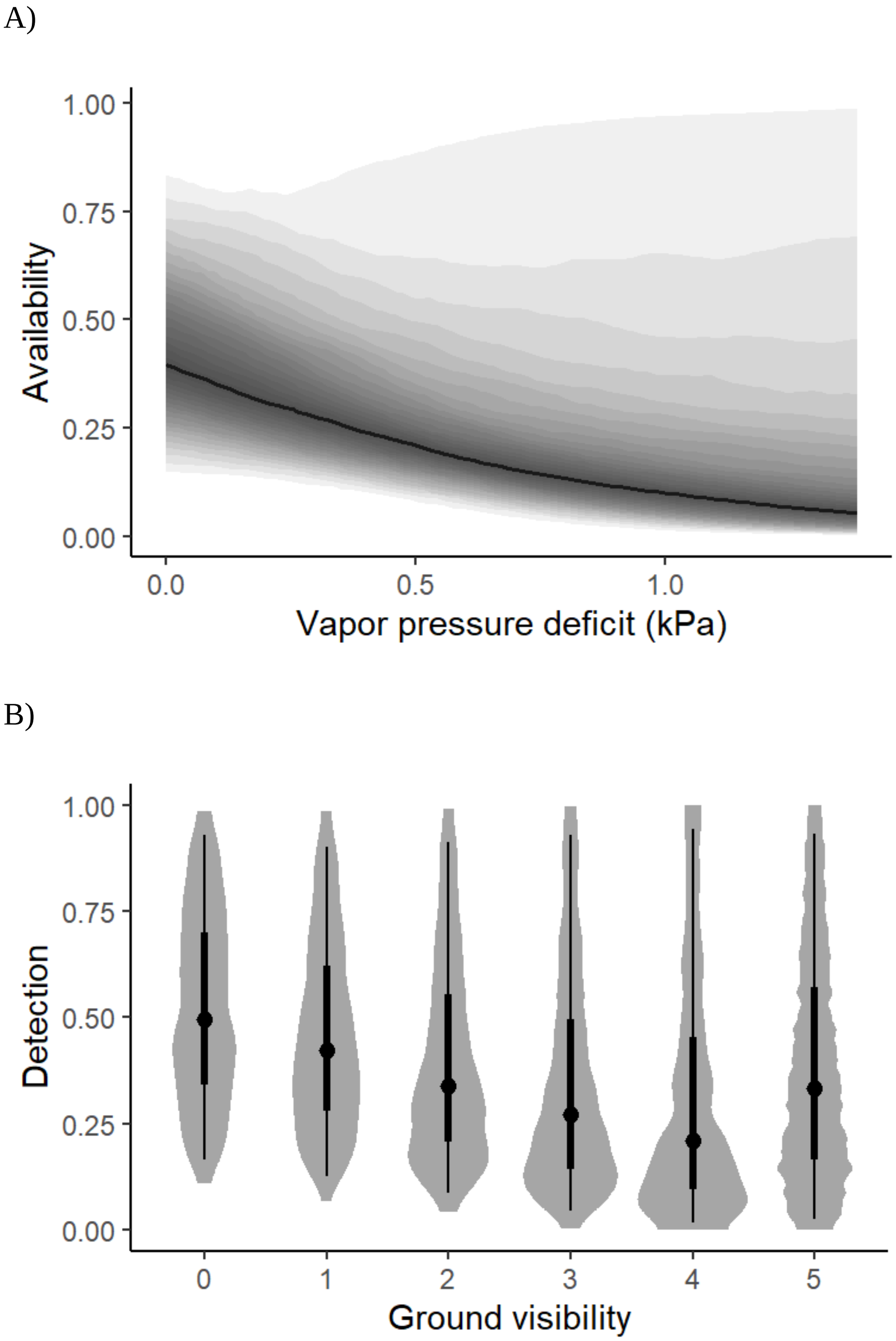


Figure 3.7: Predicted mean A) availability as a function of vapor pressure deficit and B) detection as a function of ground visibility. In A), the bold line depicts mean availability with the multilayered ribbon surrounding the lines shows the Bayesian credible interval (BCI) increasing by 5% up to the 95% BCI. In B), the circle represents mean detection at a ground visibility level with tails at 50% and 95% BCI and gray area showing the value density.

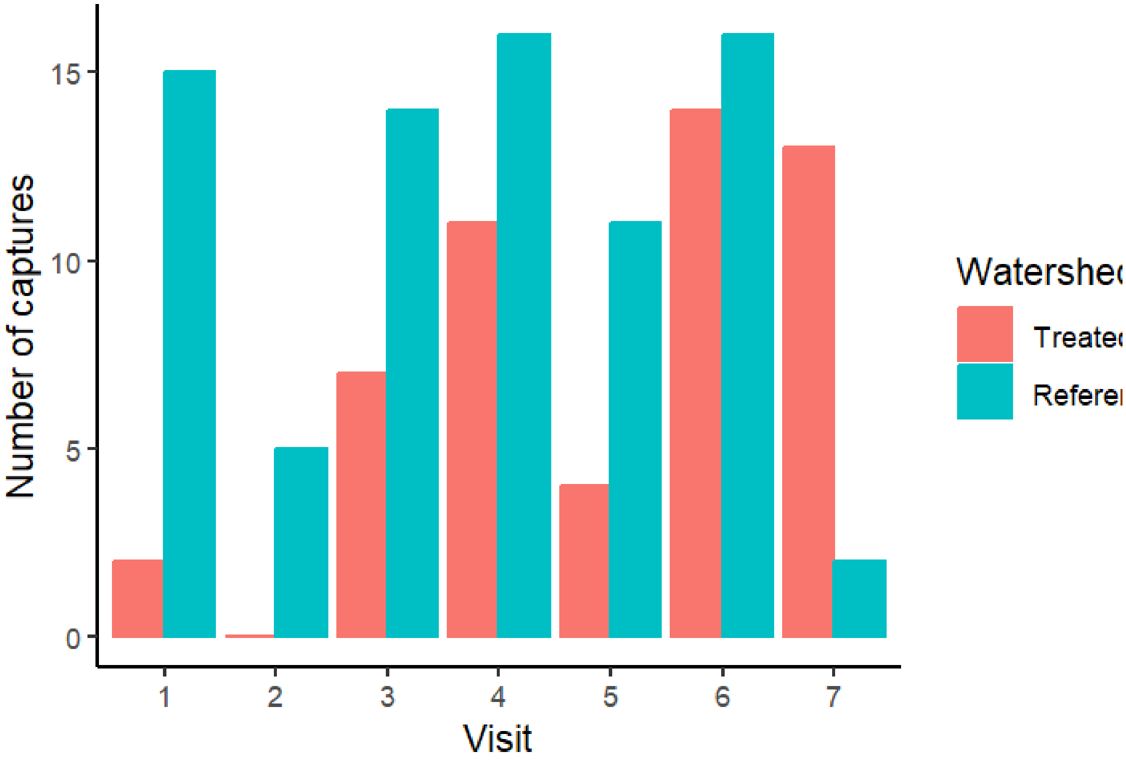


Figure 3.8: Number of initial captures of hatchling and juvenile *Plethodon* salamanders for each visit with red noting captures in the treated watershed (WS31) and blue noting captures in the reference watershed (WS32) during the 2023 active season (April - October).

CHAPTER 4

CONCLUSIONS

Summary of findings

The goal of this thesis was to use a paired watershed experiment and leverage other data sets through integrated models to estimate changes in population dynamics of *Plethodon* salamanders in response to forest management activities. I estimated changes in abundance, population structure, and juvenile growth and survival between a treated watershed and a reference watershed using a hierarchical and integrated modelling approach. This thesis is one of the first studies to investigate the effects of midstory thinning and repeated application of prescribed fire on woodland salamanders (*Plethodon* spp.).

As hypothesized, I found a negative effect of midstory thinning and repeated prescribed fire application on *Plethodon* salamander abundance, particularly among smaller size/age classes of salamanders compared to the larger age classes (Grab 2024, Chapter 2). I found weak evidence of a slight positive effect of forest management on adult abundance. Age structure fluctuated across all years for both watersheds, but there were consistently lower proportions of the smaller age classes in WS31 after the management treatment began. The population responses may be indicative of near-term responses to management actions, particularly because of the high frequency of initial prescribed burns. The initial short 2-year burn interval may have created persistently low leaf litter and down woody debris that are important for salamanders (Harper et al., 2016; Schurbon and Fauth, 2003) that will lessen over the longer term with a planned shift to from two year to five year burn intervals. However, the desired shifts in forest composition and structure might also create longer term changes in forest conditions that could lead to persistently lower salamander abundance or continued population declines. Continued research on salamander demographics will be needed to determine the longer-term impacts of management (Driscoll, 1999; Hoy et al., 2020; Middleton and Green, 2015). A slightly longer burn interval, especially one that maintains key structural components, may continue to meet the objective of oak regeneration while reducing the negative impact on salamanders.

Contrary to my hypothesis and inconsistent with our broader understanding of plethodontid salamander ecology (Feder, 1983), I found no evidence that mean daily precipitation affected mean juvenile *Plethodon* growth rate (Grab 2024, Chapter 3), and I found only weak evidence for a negative impact of midstory thinning and repeated application of prescribed fire on mean juvenile *Plethodon* growth. Also contrary to my hypothesis, I found weak evidence for a small positive effect of midstory thinning and repeated application of prescribed fire on juvenile survival and a negative effect of body size on juvenile survival. As expected, I found weak evidence of a positive effect of mean daily precipitation on juvenile survival. If the estimates of small management effects on growth are true, they may be the result of reduced surface activity of juvenile salamanders in response to the loss of leaf litter, which would likely limit foraging time and prey availability (Caruso and Rissler, 2018; Feder, 1983).

Alternatively, the weak evidence for most of these results could be artifacts of data limitations and survivorship and terminal bias. To obtain a growth interval measurement for a salamander, the animal to be captured, survive, and be re-captured during a future primary period. We know from prior studies that larger salamanders have higher survival and are more likely to surface active for longer periods of time (Feder, 1983; Howard, 2018), which should predispose us to resampling larger salamanders who have been better able to grow under more challenging conditions. Salamanders that have experienced limited growth may be less likely to be active on the surface, active for shorter durations, and more likely to die either while in refugia or when surface active. The result would be a bias against recapturing smaller individuals who experienced slower growth. Currently, I do not know of a method for addressing potential survivorship bias in studying juvenile salamander growth. However, the use of passive integrated transponder (PIT tag) tracking could create a means to estimate the mortality rates of animals of different sizes or with different growth histories. This technology has been used to successfully study surface and subsurface behavior of *Plethodon* spp., but because of the tag size, which to date, has been restricted to use on larger, predominantly adult individuals (Carter, 2023; Connette and Semlitsch, 2015, 2012). Terminal bias refers to the bias and highly uncertain estimates of survival for the terminal sampling periods due to uncertainty in animal fates (Langtimm, 2009). It is a common problem in capture-mark-recapture survival analyses, particularly for shorter term studies. Because of a dry spring, most of the juvenile captures in my study occurred during the later sampling periods, creating limited opportunity for future recaptures and increasing the potential for spurious results from terminal bias. Longer-term capture-recapture studies integrated with other data sets for joint estimation of parameters may help reduce sources of bias in future efforts (Peñaloza et al., 2014).

By investigating both population patterns and demographic processes, we can begin to understand how demographic process influence the larger population patterns we observe (Otto et al., 2014). It is clear the smaller age classes experienced a stronger negative effect of the midstory removal and, most likely, the repeated, short interval prescribed burning. I was unsuccessful in determining whether the change in *Plethodon* abundance and population structure in response to management actions was the result of increased juvenile mortality. I also did not have the opportunity to consider other demographic rates such as female fecundity that might be affected by management actions. I do know that *Plethodon* in the treated watershed reduced their surface activity and are more likely to confine their activity to burrow entrances, particularly when conditions are drier and in the years immediately following a prescribed burn (Head, 2020). We found some evidence this change in behavior might increase adult survival slightly, but we would expect this restriction in activity to reduce female foraging rates and, subsequently, female fecundity. I contend that it is important that we understand the specific mechanisms that lead to population changes to make robust predictions about short and long-term responses of salamander populations to ongoing forest management. For example, studies of other forest management actions suggest that warmer, drier conditions that result from forest management may lead to energetic constraints whereby adults increase resource allocation to survival and the expense of reproduction (Homyack and Haas, 2009).

Future Directions

Better Life History Estimates and Leveraging of Multiple Data Sets Through the Use of Integrated Population Models

A recent review highlights the need for more and unbiased estimates of vital rates for plethodontid salamanders to produce credible population models (Howard and Maerz, 2021). In addition, there is an urgent need to understand how plethodontid vital rates vary in space and time in response to environmental gradients including human management actions. Such information is critical to developing models that can be used to generate robust predictions of short- and longer-term responses to environmental change that will guide management decisions. In addition to supporting long-term studies, including those that use landscape manipulations or adaptive management frameworks, there is the opportunity for collaboration and leveraging of different data sets to improve models and experimental analyses. Integrated modelling approaches, like the ones I used in this study, can help improve estimates of population dynamics and observation processes (Hostetter et al., 2019; Schaub et al., 2007). While my analyses incorporated similar data for the joint estimation of shared parameters for the abundance and growth models, integrated population models (IPM) combine different sources of data, such as capture-recapture and unmarked count data, of different population processes to estimate broader population parameters and dynamics (Schaub and Abadi, 2011; Zipkin and Saunders, 2018). Integrated population models have gained popularity in recent years as a way to model population dynamics and to inform and evaluate conservation and management efforts (Gade et al., 2022; Plard et al., 2019; Saunders et al., 2018; Zipkin and Saunders, 2018). For example, Gade et al. (2022) used an integrated population model to estimate demographics across spatial scales. In their analysis, they found that hybridization of *P. shermani* with *P. teyahalee* impacted survival at lower elevations and found that growth, movement, and survival varied across small and large spatial scales. The chapters in this thesis provide the building blocks for an integrated population model that could be built for the FFE project and incorporate the data from the long-term CMR study, the larger regional study, and other basin-wide population monitoring studies. Additionally, integrated population models may be able to provide historical context to the analyses. Studies that have investigated salamander response to forest management indicate that there may be long-term effects of those activities and other land-use legacies on salamander distribution and abundance (Homyack and Haas 2009, Cosentino and Brubaker 2018, Wilk 2022). Given that the Southern Appalachian forests are different now than they have been historically (Brose et al. 2001, Cooley 2004), it is important to understand how a landscape's disturbance history has altered species ecology and evolution. Therefore, incorporating management and fire history into an integrated population model may be better able to situate the results within the context of our current socio-ecological time.

Hybrid Zone Dynamics and Evolutionary Responses to Forest Management

Plethodontid salamanders one of several groups of animals where adaptive introgression appears to have be very influential in how lineages persist and adapt to environmental change (Patton et al., 2020). Hybrid zones are a controversial topic in the world of conservation and wildlife management because they have the potential to increase diversification or imperil either of the parent lineages (Muhlfeld et al., 2014;

Patton et al., 2020). Especially in conservation and management, hybridization brings up questions about species ranges (McQuillan and Rice, 2015; Pfennig et al., 2016) and how we mange populations threatened with extinction (Muhlfeld et al., 2014) among other ecological and evolutionary questions. In particular, hybrid zones are often used to understand how a changing climate will impact species (Taylor et al., 2015). Researchers suggest that hybridization is likely to become increasingly common in a changing climate (Chunco, 2014), and natural hybrid zones may be important for evolutionary responses to environmental changes including human landscape alterations and climate change (Taylor et al., 2015).

Across the southern Appalachian Mountains there are numerous expansive zones of introgression between salamander species. The genetic and phenotypic patterns of introgression suggest that these hybrid systems are under strong selection in relation to climate (Carter, 2023; Hairston Sr., 1973; Hairston et al., 1992; Weaver, 2022). For example, across much of the Nantahala Mountains, there is a broad zone of mid elevation forests where are the *Plethodon* are individuals of hybrid ancestry and intermediate phenotypes between *P. shermani* and *P. teyahalee* (Carter, 2023). Most of these extensive hybrid zones are situated within National Forests, but there has been little attention to how forest management practices might affect salamander hybrid zone dynamics. I was only able to find one example that reported survival of hybrid salamanders in response to timber harvest (Connette and Semlitsch, 2015). In their findings, they acknowledged that their study species, *Plethodon shermani*, exhibited morphological traits of hybridization with *P. teyahalee*, but referred to them as only one parent species throughout the paper and did not extrapolate on the implications of the study to hybrid zone dynamics

(Connette and Semlitsch, 2015). Forest management activities within the salamander hybrid zones likely have a higher capacity to drive evolutionary responses among hybrid salamander populations. These evolutionary responses may affect longer-term population responses to forest management. For example, there may be an increase in traits from more xerophylic species such as *P. teyahalee* if forest management results warmer, drier forest climates. These adaptive responses could include changes in morphology, behavior, or life history (Carter, 2023), which in turn would affect population dynamics and persistence. These hybrid zones may also be evolutionarily important in predicting long-term persistence of salamanders to climate change. Decisions regarding forest management actions that affect population sizes or persistence within hybrid zones should consider potential effects on the evolutionary resilience of salamander populations.

The Future Forest Experiment provides a highly unique opportunity to simultaneously study the ecological and evolutionary responses of salamander populations in response to forest management activities and climate change. Because all the salamanders with the FFE watersheds are hybrid descendants of intermediate genetic composition, there appears to be maximal potential for genetic and phenotypic change. Research on this hybrid zone suggests it is old and stable, yet there is active selection occurring on traits (Carter, 2023; Lowe, 2016). Previous research on this hybrid zone indicates that alleles and phenotypic traits of the lower elevation generalist, *P. teyahalee*, are moving up in elevation while some alleles and traits of higher elevation *P. shermani* traits are migrating down in elevation in response to climate (Carter, 2023; Hairston et al., 1992; Walls, 2009). Hairston et al. (1992) speculated that the hybrid zone formed during a period of intense logging towards the beginning of the 1900's and the movement observed is likely tied to that disturbance, though Carter (2023) provides compelling evidence that the hybrid zone is older and its distribution of hybrid genotypes and phenotypes is more closely linked to hydroclimate variation. Nonetheless, the idea that forest management activities and climate have and can continue to alter the dynamics of this hybrid zone is interesting and merits future study. One would hypothesize that long-term study of salamanders within the FFE will show an increase in *P. teyahalee* alleles and traits in response to changes in forest conditions resulting from long-term management. With the southern Appalachian region predicted to become warmer with more frequent and intense droughts (Mitchell et al., 2014), analogous to the warmer, drier conditions associated with active forest management, this study site could provide insights into the eco-evolutionary trajectories of this hybrid salamander.

Management Implications

The key role of research in the context of wildlife conservation and management is to reduce uncertainty that affects management decisions. Sources of uncertainty include understanding how systems work and what effects – intended and unintended – management actions have on components of those systems. The goal of the Future Forest Experiment is to test hypotheses about how forest management actions can increase the resilience of forests to a changing climate (A. C. Oishi, U.S.F.S., *personal communication*). With the southeastern U.S. predicted to become warmer with more frequent and intense droughts (Mitchell et al., 2014), creating forests that are resilient to these changes are critical for maintaining biodiversity and ecosystem services. Some xeric tree species such as oak species (*Quercus* spp.) are important to that biodiversity and influence ecosystem services (Bargali et al., 2015; Stavi et al., 2022). Xeric forest species are also important habitat and resources for wildlife through their effects on resources such as acorn masts and structures that serve as refugia (Bargali et al., 2015). Xeric tree species tend to be more drought tolerant than mesic tree species, potentially increasing forest resilience to climate change (Caspersen and Kobe, 2001; Klos et al., 2009). Independent of the effects on biodiversity and ecosystem services, forest management actions are also used to reduce risks to disturbances such as wildfire. Increased frequency and intensity of drought is expected to increase wildfire risk (Mitchell et al., 2014), so forest management activities such thinning and prescribed fire are useful tools to reduce the potential severity of wildfire (Davis et al., 2024; Petrakis et al., 2018). It is within the context of forest management objectives that we ask how the results of our research inform Southern Appalachian forest management decisions regarding conservation objectives related to salamanders?

At first glance, our results indicate that midstory thinning and high frequency prescribed fire will have a negative impact on terrestrial salamander abundance and population structure in the near-term. The potential for near term impacts on terrestrial salamander populations from high intensity management activities, particularly the initial use of high frequency fire, may require caution in areas of low population abundance, particularly for high conservation priority species. However, our research cannot yet address the longer-term effects of forest management actions or decisions not to implement actions such as prescribed fire on salamander populations. The initial management activity was relatively intense over a short period of time to push forest conditions quickly. This push likely impacted salamander fitness, particularly for smaller age classes. However, plans to reduce fire frequency to a five year burn interval moving forward may reduce the negative impacts on salamander abundance going forward. In addition, shifting the forest to a xerophytic forest dominated by species such as oaks may have longer-term benefits to salamander populations. For example, oak-dominated forest may have different soil moisture and leaf litter composition than a maple-dominated forest (Alexander et al., 2021; Alexander and Arthur, 2014). In particular, oak tree species use less water than mesophtyic tree species (Von Allmen et al., 2015), potentially leading to increased soil moisture (Alexander et al., 2021), which could have a positive effect on salamander activity levels (Feder, 1983; McEntire and Maerz, 2019). Because high intensity forest fires can severely, negatively impact salamander populations (e.g., Gade et al., 2019; Wilk and Peterman, 2024), moderate frequency, low intensity prescribed burns may reduce the risk of catastrophic fire under future climate change. Because we do not yet know the longer-term effects of forest management actions on salamander populations; there is a clear need to continue long-term monitoring of salamanders within the FFE and other sites. If coordinated across management agencies and units over a broader region, the use of an adaptive management framework could lead to improved management decisions for forest management across the region.

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APPENDIX A

SUPPLEMENTAL INFORMATION FOR CHAPTER 2

Table A1: Priors for the parameters for all parts of the integrated abundance model. Beta0, beta0.d, p0, and avail0 varied across age class and were used to calculate the intercepts for their respective portions of the model. Beta0 additionally varied across year for the duration of the study 2018 to 2023. Beta.mgmt, beta.vpd.day, and omega.vpd were varied across age class. Mu.vis and sd.vis were used to estimate ground visibility codes in WS31 from 2018 to 2020. Sd.p and sd.site were used to calculated tau.p and tau.site which were used to create random site-visit effects for detection probability, eps.p and esp.lam, respectively.

Parameter	**Prior**
beta0	dnorm(0,0.25)
beta0.d	dnorm(0,0.25)
beta.mgmt	dnorm(0,0.25)
beta.vpd.day	dnorm(0,0.25)
p0	dunif(0,1)
alpha.vis	dnorm(0,0.25)
avail0	dunif(0,1)
omega.temp	dnorm(0,0.25)
omega.vpd	dnorm(0,0.25)
omega.rain1	dnorm(0,0.25)
omega.rain5	dnorm(0,0.25)
mu.vis	dunif(0,5)
sd.vis	dunif(0,3)
sd.p	dunif(0,2)
sd.site	dunif(0,3)

Table A2: Estimates and outputs for the broader regional dataset portion of the integrated abundance model showing mean, lower and upper 95% Bayesian Credible Interval, Rhat, and effective sample size (n.eff). The numbers in the brackets for beta0.d indicate age class (1 = hatchling; 2 = juvenile; 3 = subadult; 4 = adult). 3,057 *Plethodon* salamanders were captured during the broader regional project (2021-2022). The two fit metrics are Bayesian p-values (BPV) and c-hat, a measure of overdispersion. C.hat1 and bpv1 are fit metrics for the detection portion of the model for the broader regional dataset and c.hat2 and bpv2 are fit metrics for the abundance portion.

Parameter	Mean	Lower	Upper	Rhat	n.eff
beta0.d[1]	2.287	1.618	2.944	1.003	754
beta0.d[2]	2.041	1.395	2.707	1.021	100
beta0.d[3]	1.882	1.285	2.462	1.001	2,817
beta0.d[4]	1.475	0.841	2.091	1.000	18,101
sd.site	1.089	0.662	1.739	1.001	2,828
c.hat1.hem	1.108	1.037	1.194	1.000	36,000
bpv1.hem	0.003	0	0	1.002	36,000
c.hat2.hem	1.004	0.993	1.017	1.000	1,325
bpv2.hem	0.224	0	1	1.000	8,492

Code for integrated model

```
model{
  ## Prior Distributions
  #fixed effect of year and age class- different mean for each
year
  for(y in 1:nYear.r){
    for(a in 1:nClass){
      beta0[y,a] ~ dnorm(0, 0.25)
    } # loops through age class
  }    # loops through year

  for(y in (nYear.r+1):(nYear.r + nYear.d.ws)){
    for(a in 1:nClass){
      beta0[y,a] ~ dnorm(0, 0.25)
    } # loops through age class
  }  # loops through year

  for(a in 1:nClass){
    beta0.d[a] ~ dnorm(0, 0.25)
  }

  for(a in 1:nClass) {
    beta.mgmt[a] ~ dnorm(0, 0.25)   #management effect on N
    beta.vpd.day[a] ~ dnorm(0, 0.25)  #VPD effect on N
  }

  omega.temp ~ dnorm(0, 0.25)  #Temp effect on avail
  omega.rain1 ~ dnorm(0, 0.25) #1 day precip effect on avail
  omega.rain5 ~ dnorm(0, 0.25) #5 day precip effect on avail

  for(a in 1:nClass){
    p0[a] ~ dunif(0,1)            #detection probability -
intercept
    alpha0[a] <- logit(p0[a])     #detection probability -
intercept on logit scale
    avail0[a] ~ dunif(0,1)        #availability probability -
intercept
    omega0[a] <- logit(avail0[a]) #availability probability -
intercept on logit scale
    omega.vpd[a] ~ dnorm(0, 0.25)   #VPD effect on avail
  }
  alpha.vis ~ dnorm(0, 0.25) #visibility effect on p

  ### FOR ESTIMATING MISSING VIS COVARIATE VALUES
```

```
  # priors for the mean and sd/precision of vis.r covariate
  mu.vis ~ dunif(0,5)
  sd.vis ~ dunif(0,3)
  tau.vis <- 1 / (sd.vis*sd.vis)
  ############################
  sd.p ~ dunif(0, 2)         #expected abundance SD (site
specific)
  tau.p <- 1 / (sd.p*sd.p)   # expected abundance precision
(hyperparameter 2)

  ### The following loops are accounting for the different
dimensions for each dataset
  for (i in 1:nPlots.r){
    for (j in 1:nVisits.r){
      eps.p[i,j] ~ dnorm(0, tau.p) #detection probability random
site-visit effect
    } # loops through visits
  }  # loops through plots for FFE robust design

  for (i in (nPlots.r+1):(nPlots.r+nPlots.d.ws)){
    for (j in 1:(nVisits.d.ws[i-nPlots.r])){ # added i for
indexing each plot
      eps.p[i,j] ~ dnorm(0, tau.p) #detection probability random
site-visit effect
    } # loops through visits
  }  # loops through plots for FFE depletion design

  for (i in
(nPlots.r+nPlots.d.ws+1):(nPlots.d.hem+nPlots.r+nPlots.d.ws)){
    for (j in 1:nVisits.d.hem[i-nPlots.r-nPlots.d.ws]){ # this
used to read nPlots.d.hem updated to nVisits.d.hem[i]
      eps.p[i,j] ~ dnorm(0, tau.p) #detection probability random
site-visit effect
    } # loops through visits
  }  # loops through plots for hemlock project

  sd.site ~ dunif(0, 3)             #Expected abundance SD (site
specific)
  tau.site <- 1 / (sd.site*sd.site) #Expected abundance precision
(hyperparameter 2)

  for (j in 1:nSites.hem){
    eps.lam[j] ~ dnorm(0, tau.site) #  Random site effect - site
specific effect on abundance
  }
```

```
  ######## MODEL BEGINS
  ## Likelihood - ROBUST + DEPLETION
  ## Ecological Model of True Abundance (N) - ROBUST + DEPLETION

  # Model for the robust data
  for(i in 1:nPlots.r) {
    for(y in 1:nYear.r) {
      for(a in 1:nClass) {
        log(lambda.r[i,y,a]) <- beta0[y,a] +
beta.vpd.day[a]*vpd.day.r[i] + beta.mgmt[a]*mgmt.r[i,y]
        N.r[i,y,a] ~ dpois(lambda.r[i,y,a])
      } # loops through age classes
    }   # loops through year

    ## Logit-linear - ROBUST
    ## Model of Availability and Imperfect Detection (y) - ROBUST
    for(j in 1:nVisits.r) {
      vis.r[i,j] ~ dnorm(mu.vis, tau.vis) T(0,5) ### ADDED FOR
ESTIMATING MISSING VIS

      for(a in 1:nClass){
        logit(omega.r[i,j,a]) <- omega0[a] +
omega.temp*temp.r[i,j] + omega.vpd[a]*vpd.r[i,j] +
omega.rain1*rain1.r[i,j] + omega.rain5*rain5.r[i,j]
        omega.eff.r[i,j,a] ~ dbin(omega.r[i,j,a],
N.r[i,Year.r[j],a])  #removed index [j] for Year.r

        logit(p.r[i,j,a]) <- alpha0[a] + alpha.vis*vis.r[i,j] +
eps.p[i,j] #
        p.eff.r[i,j,a] <- 1-((1-p.r[i,j,a])^4)

        y.r[i,j,a] ~ dbin(p.eff.r[i,j,a], omega.eff.r[i,j,a])
      } # loops through age class
    }   # loops through visits
  }     # loop through i plots

  #goodness of fit for robust portion of model
  for(i in 1:nPlots.r) {
    for(j in 1:nVisits.r) {
      for(a in 1:nClass){
        y.pred.r[i,j,a] ~ dbin(p.eff.r[i,j,a],
omega.eff.r[i,j,a]) # Create new data set under model
        e.count.r[i,j,a] <- omega.eff.r[i,j,a] * p.eff.r[i,j,a] #
Expected datum
```

```
        # Chi-square discrepancy for the actual data
        chi2.actual.r[i,j,a] <- pow((y.r[i,j,a]-
e.count.r[i,j,a]),2) / (e.count.r[i,j,a]+e)
        # Chi-square discrepancy for the simulated ('perfect')
data
        chi2.sim.r[i,j,a] <- pow((y.pred.r[i,j,a]-
e.count.r[i,j,a]),2) / (e.count.r[i,j,a]+e)
        # Add small value e to denominator to avoid division by
zero
      }
    }
  }

  fit.actual.r <-
sum(chi2.actual.r[1:nPlots.r,1:nVisits.r,1:nClass]) # Fit
statistic for actual data set
  fit.sim.r <- sum(chi2.sim.r[1:nPlots.r,1:nVisits.r,1:nClass]) #
Fit statistic for a fitting model
  c.hat.r <- fit.actual.r / fit.sim.r # c-hat estimate - measures
overdispersion
  bpv.r <- step(fit.sim.r-fit.actual.r) # Bayesian p-value

  ############################################################
  ### Sub model 2 - New data set - depletion sampling design ###
  ## Abundance
  for(i in 1:nPlots.d.ws) {
    for(y in (Year.min.d.ws[i]):(Year.max.d.ws[i])) { # created
variable for first and last year for each plot
      for(a in 1:nClass){
        log(lambda.d.ws[i,y,a]) <- beta0[(y+nYear.r),a] +
beta.vpd.day[a]*vpd.day.d.ws[i] + beta.mgmt[a]*mgmt.d.ws[i]
        N.d.ws[i,y,a] ~ dpois(lambda.d.ws[i,y,a])
      } # loops through age class
    } # loops through year

    ## Availability
    for(j in 1:nVisits.d.ws[i]) {
      for(a in 1:nClass) {
        logit(omega.d.ws[i,j,a]) <- omega0[a] +
omega.temp*temp.d.ws[i,j] + omega.vpd[a]*vpd.d.ws[i,j] +
omega.rain1*rain1.d.ws[i,j] + omega.rain5*rain5.d.ws[i,j]
        omega.eff.d.ws[i,j,a] ~ dbin(omega.d.ws[i,j,a], N.d.ws[i,
Year.d.ws[i,j],a])

        ##  Detection
```

```
        logit(p.d.ws[i,j,a]) <- alpha0[a] +
alpha.vis*vis.d.ws[i,j] + eps.p[(i+nPlots.r),j]

        pi.ws[i,1,j,a] <- p.d.ws[i,j,a]
## Pr(first captured in first pass)
        pi.ws[i,2,j,a] <- p.d.ws[i,j,a]*(1-p.d.ws[i,j,a])
## Pr(first captured in second pass)
        pi.ws[i,3,j,a] <- p.d.ws[i,j,a]*((1-p.d.ws[i,j,a])^2)
## Pr(first captured in third pass)
        pi.ws[i,4,j,a] <- p.d.ws[i,j,a]*((1-p.d.ws[i,j,a])^3)
## Pr(first captured in fourth pass)
        pi0.ws[i,j,a] <- (1-p.d.ws[i,j,a])^4
## Pr(not captured)
        pcap.ws[i,j,a] <- 1 - pi0.ws[i,j,a]

        for(p in 1:4){
          pic.ws[i,p,j,a] <- pi.ws[i,p,j,a] / pcap.ws[i,j,a]
        } # loops through passes

        n.ws[i,j,a] ~ dbin(1-pi0.ws[i,j,a],
omega.eff.d.ws[i,j,a])    ## nCaptured at plot i on visit j
        y.d.ws[i,1:4,j,a] ~ dmulti(pic.ws[i,1:4,j,a],
n.ws[i,j,a])

        #goodness of fit - 2 is for abundance, 1 is for detection
        #for observation model
        y.pred.d.ws[i,1:4,j,a] ~ dmulti(pic.ws[i,1:4,j,a],
n.ws[i,j,a])
        e1.d[i,1:4,j,a] <- pic.ws[i,1:4,j,a] * n.ws[i,j,a]
        chi2.actual1.d[i,1:4,j,a] <- pow((y.d.ws[i,1:4,j,a]-
e1.d[i,1:4,j,a]),2) / (e1.d[i,1:4,j,a]+e)
        chi2.sim1.d[i,1:4,j,a] <- pow((y.pred.d.ws[i,1:4,j,a]-
e1.d[i,1:4,j,a]),2)/(e1.d[i,1:4,j,a]+e)

        #for the abundance model
        n.pred.d[i,j,a] ~ dbin(1-pi0.ws[i,j,a],
omega.eff.d.ws[i,j,a])
        e2.d[i,j,a] <- (1-pi0.ws[i,j,a]) *
lambda.d.ws[i,Year.d.ws[i,j],a]
        resid2.d[i,j,a] <- pow(pow(n.ws[i,j,a], 0.5) -
pow(e2.d[i,j,a], 0.5), 2)
        chi2.actual2.d[i,j,a] <- pow((n.ws[i,j,a]-e2.d[i,j,a]),2)
/ (e2.d[i,j,a]+e)
        resid2.pred.d[i,j,a] <- pow(pow(n.pred.d[i,j,a], 0.5) -
pow(e2.d[i,j,a], 0.5), 2)
```

```
        chi2.sim2.d[i,j,a] <- pow((n.pred.d[i,j,a]-
e2.d[i,j,a]),2) / (e2.d[i,j,a]+e)

      } # loop through a age class
    }  # loop through j visits
  }     # loop through i plots

  for(i in 1:nPlots.d.ws){
    temp.fit.actual1.d[i] <-
sum(chi2.actual1.d[i,1:4,1:nVisits.d.ws[i],1:nClass])
    temp.fit.sim1.d[i] <-
sum(chi2.sim1.d[i,1:4,1:nVisits.d.ws[i],1:nClass])
    temp.fit.actual2.d[i] <-
sum(chi2.actual2.d[i,1:nVisits.d.ws[i],1:nClass])
    temp.fit.sim2.d[i] <-
sum(chi2.sim2.d[i,1:nVisits.d.ws[i],1:nClass])
  }

  #goodness of fit - 2 is for abundance, 1 is for detection
  fit.actual1.d <- sum(temp.fit.actual1.d[1:nPlots.d.ws]) # Fit
statistic for actual data set
  fit.sim1.d <- sum(temp.fit.sim1.d[1:nPlots.d.ws]) # Fit
statistic for a fitting model
  fit.actual2.d <- sum(temp.fit.actual2.d[1:nPlots.d.ws]) # Fit
statistic for actual data set
  fit.sim2.d <- sum(temp.fit.sim2.d[1:nPlots.d.ws]) # Fit
statistic for a fitting model

  #Bayesian p-values and c-hat values for depletion portion of
model
  c.hat1.d <- fit.actual1.d / fit.sim1.d # c-hat estimate
  bpv1.d <- step(fit.sim1.d-fit.actual1.d) # Bayesian p-value
  c.hat2.d <- fit.actual2.d / fit.sim2.d # c-hat estimate
  bpv2.d <- step(fit.sim2.d-fit.actual2.d) # Bayesian p-value

  ##### begin hemlock portion of the model
  # Loop over plots
  for(i in 1:nPlots.d.hem){
    for(a in 1:nClass){
      # log-linear model for abundance:
      log(lambda.hem[i,a]) <- beta0.d[a] +
beta.vpd.day[a]*vpd.day.d.hem[i] + eps.lam[Site.hem[i]]
      N.hem[i,a] ~ dpois(lambda.hem[i,a])
    }  # loops through age class
```

```
    for (j in 1:nVisits.d.hem[i]){
      for(a in 1:nClass) {
        # logit-linear model for availability:
        logit(omega.hem[i,j,a]) <- omega0[a] +
omega.temp*temp.d.hem[i,j] + omega.vpd[a]*vpd.d.hem[i,j] +
omega.rain1*rain1.d.hem[i,j] + omega.rain5*rain5.d.hem[i,j]
        omega.eff.hem[i,j,a] ~ dbin(omega.hem[i,j,a], N.hem[i,a])

        # logit-linear model for detection:
        logit(p.hem[i,j,a]) <- alpha0[a] +
alpha.vis*vis.d.hem[i,j] + eps.p[(nPlots.r+nPlots.d.ws+i),j]

        # Conditional multinomial cell probabilities
        pi[i,1,j,a] <- p.hem[i,j,a]
        pi[i,2,j,a] <- p.hem[i,j,a]*(1-p.hem[i,j,a])
        pi[i,3,j,a] <- p.hem[i,j,a]*((1-p.hem[i,j,a])^2)
        pi[i,4,j,a] <- p.hem[i,j,a]*((1-p.hem[i,j,a])^3)
        pi0[i,j,a] <- (1-p.hem[i,j,a])^4              ### prob of
not detecting
        pcap[i,j,a] <- 1 - pi0[i,j,a]

        for(p in 1:4){
          pic[i,p,j,a] <- pi[i,p,j,a] / pcap[i,j,a]
        }# loops through passes

        n.hem[i,j,a] ~ dbin(pcap[i,j,a], omega.eff.hem[i,j,a])
# model for the observed sample size
        y.d.h[i,1:4,j,a] ~ dmulti(pic[i,1:4,j,a], n.hem[i,j,a])
# uses the conditional cell probabilities

        #goodness of fit - 1 is for abundance, 2 is for detection
        n.pred.hem[i,j,a] ~ dbin(pcap[i,j,a],
omega.eff.hem[i,j,a])
        y.pred.hem[i, 1:4,j,a] ~ dmulti(pic[i,1:4,j,a],
n.hem[i,j,a])

        e1.hem[i,1:4,j,a] <- pic[i,1:4,j,a] * n.hem[i,j,a]
        chi2.actual1.hem[i,1:4,j,a] <- pow((y.d.h[i,1:4,j,a]-
e1.hem[i,1:4,j,a]),2) / (e1.hem[i,1:4,j,a]+e)
        chi2.sim1.hem[i,1:4,j,a] <- pow((y.pred.hem[i,1:4,j,a]-
e1.hem[i,1:4,j,a]),2) / (e1.hem[i,1:4,j,a]+e)

        e2.hem[i,j,a] <- pcap[i,j,a] * lambda.hem[i,a]
        resid2.hem[i,j,a] <- pow(pow(n.hem[i,j,a], 0.5) -
pow(e2.hem[i,j,a], 0.5), 2)
```

```
        chi2.actual2.hem[i,j,a] <- pow((n.hem[i,j,a]-
e2.hem[i,j,a]),2) / (e2.hem[i,j,a]+e)
        resid2.pred.hem[i,j,a] <- pow(pow(n.pred.hem[i,j,a], 0.5)
- pow(e2.hem[i,j,a], 0.5), 2)
        chi2.sim2.hem[i,j,a] <- pow((n.pred.hem[i,j,a]-
e2.hem[i,j,a]),2) / (e2.hem[i,j,a]+e)

      } # loops through age class
    }
  }

  for(i in 1:nPlots.d.hem){
    temp.fit.actual1.hem[i] <-
sum(chi2.actual1.hem[i,1:4,1:nVisits.d.hem[i],1:nClass])
    temp.fit.sim1.hem[i] <-
sum(chi2.sim1.hem[i,1:4,1:nVisits.d.hem[i],1:nClass])
    temp.fit.actual2.hem[i] <-
sum(chi2.actual2.hem[i,1:nVisits.d.hem[i],1:nClass])
    temp.fit.sim2.hem[i] <-
sum(chi2.sim2.hem[i,1:nVisits.d.hem[i],1:nClass])
  }

  fit.actual1.hem <- sum(temp.fit.actual1.hem[1:nPlots.d.hem]) #
Fit statistic for actual data set
  fit.sim1.hem <- sum(temp.fit.sim1.hem[1:nPlots.d.hem]) # Fit
statistic for a fitting model
  fit.actual2.hem <- sum(temp.fit.actual2.hem[1:nPlots.d.hem]) #
Fit statistic for actual data set
  fit.sim2.hem <- sum(temp.fit.sim2.hem[1:nPlots.d.hem]) # Fit
statistic for a fitting model

  ## C-hat and Bayesian p-values for hemlock data
  c.hat1.hem <- fit.actual1.hem / fit.sim1.hem # c-hat estimate
  bpv1.hem <- step(fit.sim1.hem-fit.actual1.hem) # Bayesian p-
value
  c.hat2.hem <- fit.actual2.hem / fit.sim2.hem # c-hat estimate
  bpv2.hem <- step(fit.sim2.hem-fit.actual2.hem) # Bayesian p-
value

  #Getting total abundance estimates for sites and age classes
each year for FFE project
  for (y in 1:nYear.r){
    for(a in 1:nClass){
      Ntotal.age.32[y,a] <- sum(N.r[10:18,y,a])
```

```
      Ntotal.age.31[y,a] <- sum(N.r[1:9,y,a]) # year 1 is pre-
management
    } # loops through age class
  }  # loops through year

  # Getting total abundance for each year and age class
  for (y in (1+nYear.r):(nYear.r + nYear.d.ws)) {
    for(a in 1:nClass){
      Ntotal.age.32[y,a] <- ifelse(y == 4,
sum(N.d.ws[16:30,1,a]), ifelse(y == 5, sum(N.d.ws[16:30,2,a]),
sum(N.d.ws[c(16:27,31:33),3,a])))
      Ntotal.age.31[y,a] <- ifelse(y == 4, sum(N.d.ws[1:9,1,a]),
ifelse(y == 5, sum(N.d.ws[1:10,2,a]), sum(N.d.ws[1:15,3,a])))
    } # loops through age class
  }  # loops through year

  # Age structure metrics
for (y in 1:(nYear.r + nYear.d.ws)) {
 for(a in 1:nClass){
   AgeStr.31[y,a] <- Ntotal.age.31[y,a]/sum(Ntotal.age.31[y,1:4])
   AgeStr.32[y,a] <- Ntotal.age.32[y,a]/sum(Ntotal.age.32[y,1:4])
    } # loops through age class
}  # loops through year

  for(a in 1:nClass){ ## getting average annual lambda across all
six years
    log(lam.pred.0[a]) <- mean(beta0[1:6,a]+ beta.mgmt[a]*0)
    log(lam.pred.1[a]) <- mean(beta0[1:6,a]+ beta.mgmt[a]*1)
  } # loops through age class
  Ntotal <- sum(N.hem[1:nPlots.d.hem,1:4])
}
```

APPENDIX B

SUPPLEMENTAL INFORMATION FOR CHAPTER 3

Integrated Growth Model Code

```
model{
  ## priors for FFE
  SVLinf ~ dunif(15,100)
  beta ~ dnorm(0,0.25)
  alpha0 ~ dnorm(0,0.25)
  alpha.mgmt ~ dnorm(0,0.25)      #effect of management
  alpha.precip ~ dnorm(0,0.25)    #effect of precipitation
  #variation for goodness of fit
  sd ~ dunif(0,3)
  tau <- 1 / (sd*sd)
#random effect for individuals
  sd.i ~ dunif(0,3)
  tau.i <- 1/(sd.i*sd.i)
    for(j in 1:n.vie){
  id.e[j] ~ dnorm(0, tau.i)
  }

  ## priors for CMR
  SVLinf.cmr ~ dunif(15,100)
  beta.cmr ~ dnorm(0,0.25)
  alpha0.cmr ~ dnorm(0,0.25)
  #alpha1.cmr ~ dnorm(0,0.25)
  #random effect for individuals
  sd.c ~ dunif(0,3)
  tau.c <- 1/(sd.c*sd.c)
    for(j in 1:cmr.id){
  id.c[j] ~ dnorm(0, tau.c)
  }
  ######################
  #model for FFE dataset
  ######################
  for(i in 1:n.int){
  k[i] <- exp(alpha0 + alpha.mgmt*mgmt[i] +
alpha.precip*precip[i])
```

```
  Z[i] <- (SVLinf - beta*(SVL1[i]-E_x) - SVL1[i])*(1-exp(-
k[i]*days[i])) + id.e[vie.index[i]]
  dSVL[i] ~ dnorm(Z[i], tau)       #Data
  #Goodness of fit
  resid[i] <- dSVL[i] - Z[i]            #residual
  Z.sim[i] ~ dnorm(Z[i], tau)           #simulated data
  chi2[i] <- pow(resid[i],2)#/(sqrt(Z[i])+e)
  chi2.sim[i] <- pow((Z.sim[i] - Z[i]),2)#/(sqrt(Z[i])+e)
  }
  #Goodness of fit
  fit.FFE <- sum(chi2[])
  fit.sim.FFE <- sum(chi2.sim[])
  #c.hat.FFE <- fit.FFE/fit.sim.FFE # c-hat estimate - measures
overdispersion
  bpv.FFE <- step(fit.sim.FFE-fit.FFE) # Bayesian p-value
  #estimating average k for each watershed
  log(k.pred0) <- alpha0 #+ mean(id.e[])
  log(k.pred1) <- alpha0 + alpha.mgmt #+ mean(id.e[])
  ######################
  #model for CMR dataset
  ######################
    for(c in 1:n.cmr) {
  k.cmr[c] <- exp(alpha0.cmr + alpha.precip*precip.cmr[c])
  Z.c[c] <- (SVLinf.cmr - beta.cmr*(SVL1.c[c]-E_cmr) -
SVL1.c[c])*(1-exp(-k.cmr[c]*days.c[c])) + id.c[cmr.index[c]]
  dSVL.c[c] ~ dnorm(Z.c[c], tau)
  #Goodness of fit
  resid.c[c] <- dSVL.c[c] - Z.c[c]      #residual
  sq.c[c] <- pow(resid.c[c],2)
  Z.c.sim[c] ~ dnorm(Z.c[c], tau)       #Simulated dataset
  #Z.c.pred[c] <- Z.c[c]                 #Predicted dataset
  sq.c.sim[c] <- pow((Z.c.sim[c] - Z.c[c]),2)
  }
  #Goodness of fit
  fit.CMR <- sq.c[]
  fit.sim.CMR <- sq.c.sim[]
  #c.hat.CMR <- fit.CMR/fit.sim.CMR # c-hat estimate - measures
overdispersion
  bpv.CMR <- step(fit.sim.CMR-fit.CMR) # Bayesian p-value
  }
```

Hierarchical Cormack-Jolly-Seber Survival Model Code

```
model {
    ## Priors
    beta0 ~ dnorm(0,0.5)
    beta1 ~ dnorm(0,0.5)
    beta2 ~ dnorm(0,0.5)
    beta3 ~ dnorm(0,0.5)
    alpha0 ~ dnorm(0,0.5)
    alpha1 ~ dnorm(0,0.5)
    omega0 ~ dnorm(0,0.5)
    omega1 ~ dnorm(0,0.5)

   for(i in 1:n) {
    z[i,first[i]] <- 1 ## Known alive at time of release
    for(t in (first[i]+1):K) {
     logit(phi[i,t]) <- beta0 + beta1*WS[i] + beta2*prcp[i,t]+
beta3*SVL[i,t]
     logit(p[i,t]) <- alpha0 + alpha1*vis[i,t]
     logit(g[i,t]) <- omega0 + omega1*VPD[i,t]
     a[i,t] ~ dbern(g[i,t])                  ## Availability
     z[i,t] ~ dbern(z[i,t-1]*phi[i,t])       ## Survives with
probability phi
     y[i,t] ~ dbern(z[i,t]*p[i,t]*a[i,t])    ## Detected with
probability p

    #Goodness of fit stuff
    y.sim[i,t]  ~ dbern(z[i,t]*p[i,t]*a[i,t])#Simulated dataset
    y.e[i,t] <- z[i,t]*p[i,t]*a[i,t]         #Predicted datum
    sq.s[i,t] <- pow((y[i,t] - y.e[i,t]),2) #actual - predicted
    sq.s.sim[i,t] <- pow((y.sim[i,t] - y.e[i,t]),2) #simulated -
predicted
      } #loops through visits

    }  #loops through individuals
    #Predicted survival between watersheds
    logit(phi.pred0) <- beta0 + beta1*0
    logit(phi.pred1) <- beta0 + beta1*1
    }
```