# MODELING THE EFFECTS OF PRECIPITATION ON SALAMANDER DEMOGRAPHY FOR CONSERVATION PLANNING

by

### JILLIAN SLOPER HOWARD

(Under the Direction of John C. Maerz)

#### ABSTRACT

Conservation of natural resources is complex because most human and natural systems are coupled. Integrative conservation planning requires tools that transcend disciplines to understand ecological and human aspects of systems. Southern Appalachia contains exceptional biodiversity which provides ecosystem services across the southeastern United States. The region is rapidly exurbanizing and expected to experience significant climate change. Residential development on mountain slopes is impacting economies, public safety, and ecosystem integrity. To manage natural systems, we need rigorous models identifying areas of current and future suitability for sensitive taxa and understanding of stakeholder perspectives that may affect conservation priorities. Here, I address these needs in the context of salamander ecology and conservation.

I reviewed the literature to assess current knowledge of demographic rates for directdeveloping North American Plethodontid salamanders. Some rates are well-documented and transferrable across species, but there are few published estimates of survival, and half, though estimated from field data, may not be realistic. I developed a Bayesian model for an eight-year *Plethodon* dataset to estimate survival rates and their sensitivity to precipitation. I developed a novel algorithm estimating final clutch size from ovarian follicle counts. I used N-mixture models of repeated counts across a spatial precipitation gradient to estimate precipitationdependent abundance and reproductive rates. I used the survival and reproductive rates to project salamander population growth across the landscape under multiple climate scenarios. Model projections suggest only a small proportion of the region supports consistent positive population growth. Many areas occupied by salamanders likely have limited abundance and depend on source habitats to support local populations.

In identifying concerns of stakeholders regarding forest land use, archival and interview sources suggest locals are concerned about economic impacts and regulation of steep slope development, while scientists working in the region are concerned with impacts to biodiversity and natural resources. Nonetheless, participants in a mapping study consistently placed conservation uses at higher elevations than development, suggesting some intrinsic connection between steep slopes and conservation. A map of stakeholder land use priorities and projected population growth rates identified consistencies between areas people prioritized for conservation and areas likely to sustain salamander populations.

INDEX WORDS:biodiversity conservation, coupled human and natural systems,Plethodontidae, salamander, southern Appalachian Mountains, stakeholdervalues, wildlife population dynamics

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### JILLIAN SLOPER HOWARD

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# MODELING THE EFFECTS OF PRECIPITATION ON SALAMANDER DEMOGRAPHY

### FOR CONSERVATION PLANNING

by

### JILLIAN SLOPER HOWARD

Major Professor: Committee: John C. Maerz Nik Heynen Richard Chandler Jeff Hepinstall-Cymerman Marshall Shepherd

Electronic Version Approved:

Suzanne Barbour Dean of the Graduate School The University of Georgia May 2018

### DEDICATION

for Stephanie

your love, support, and dedication to our future is what made obtaining this degree possible, thank you for always being your strong and courageous self

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#### CHAPTER 1

#### INTRODUCTION

Integrative conservation research is conducted primarily by crossing the boundaries between academic disciplines, and between academia and other epistemologies. It requires the use of multiple methods to examine complex socio-environmental problems from different perspectives and thereby gain a more comprehensive and varied picture of those problems. One key component is the idea that knowledge created through research should not be produced in a one-sided manner by academics, but instead that it should be the outcome of iterative dialogues between researchers and stakeholders, the people and organizations who will make use of the research findings or be affected by the policies and practices that stem from those findings. Complexity is inherent in conservation problems, due to both the interconnectedness of human and natural systems, and the plurality of perspectives, goals, and ways of knowing possessed by the individuals and institutions linked by these problems and by efforts to resolve them. Additionally, conservation efforts inevitably require trade-offs and are rarely win-win, so transparent and thorough examination of both the negative and positive impacts of these efforts is essential.

The Integrative Conservation (ICON) Program at the University of Georgia was developed with the goal of training agile conservation scientists who can bridge the boundaries between disciplines and appreciate, understand, and engage with multiple epistemologies both within and distinct from academia. The initial generation of this dissertation was profoundly shaped by the philosophy and values of the integrative conservation movement in that I made a conscious effort to study a complex system through ecological and sociological research methodologies, and in the way that the final outcomes of the project were shaped by the challenges and discoveries that occurred during the research process.

Few places in the world, if any, can be considered outside the context of human activities. Most systems are best described as coupled human and natural systems, in which events in one part of the system have a reciprocal effect on the other (Alberti et al., 2011). Conservation efforts in coupled systems must balance the importance of maintaining ecosystem integrity to avoid loss of biodiversity and ecosystem services, with the economic and cultural interests of people living within these systems. Meeting both these goals requires conservation practitioners and researchers to examine coupled systems through multiple disciplinary and non-disciplinary lenses to incorporate the complex and multiple ways of knowing that exist within these systems (Hirsch and Brosius, 2013), and to assess the trade-offs inherent in conservation decisions in a transparent manner (McShane et al., 2011).

Often, examination of the relationships between human and natural systems is limited to the effects of natural resource use and anthropogenic disturbance on natural resources, and sometimes the reciprocal effect of degraded natural resources on the ecosystem services upon which people rely. These relationships represent a relatively limited view of the complex reciprocal interactions between human and natural systems, which each include many components with their own intrinsic complexity (Figure 1.1).

In the southern Appalachian Mountains, landscapes are rapidly changing due to the process of exurbanization, the movement of people from metropolitan to rural areas in search of a variety of natural, and sometimes cultural amenities (Egan and Luloff, 2000). This process can produce an array of impacts on rural places (as described in Vercoe et al., 2014). One outcome

has been the increased frequency of residential development on steep mountain slopes for access to scenic views, an activity with a complex suite of associated impacts on both human and natural systems (Figure 1.2) (for example: Wear and Bolstad, 1998; Price and Leigh, 2006; Chamblee et al., 2009; Band et al., 2012; Evans, 2013; Gragson et al., 2013; Kirsch and Peterson, 2014; Cecala et al., 2018). This development is enabled by a weak regulatory environment (Gustafson, 2015), and driven primarily by consumer demand through the real estate market. Steep slope development produces three primary impacts on natural systems, including reduction of forest cover, altered disturbance regimes, and non-native species and disease introductions. These impacts result in terrestrial and aquatic habitat degradation through a number of pathways including modification of forest microclimates (Band et al., 2012), erosion, sedimentation of waterways, increased landslides due to slope destabilization and forest removal associated with road and home site construction (Band et al., 2012; Wooten et al., 2017), altered disturbance regimes including fire suppression that can paradoxically lead to infrequent high intensity fires (Rankin and Herbert, 2014), and the introduction of invasive species and diseases (for example McAvoy et al., 2017). All of these alterations can affect the availability and quality of wildlife habitat including endemic and range-margin species that depend on high elevation forest environments (Kirsch and Peterson, 2014; Abernathy, 2017; Ferguson et al., 2017; Cecala et al., 2018). Feedback loops from these processes to the human system are numerous including altered yields and quality of drinking water that supplies many populations across the southeastern U.S. (Webster et al., 2012), increased incidence of landslides that cause loss of human life and property that may, in turn, lead to changes in the regulatory environment (Wooten, 2017), and the loss of natural amenities such as birds or sport fish that are important recreation opportunities. Degradation of the natural services that have fueled exurbanization in Southern

Appalachia may eventually produce negative impacts on the real estate market if the area becomes less desirable to exurbanites (Wear and Bolstad, 1998; Gragson and Bolstad, 2006a).

Effective conservation in coupled human and natural systems requires the understanding of ecological processes and stakeholder values and dynamics to produce a more holistic and actionable understanding of the system. In this dissertation I developed rigorous ecological models to predict the location of areas capable of supporting positive salamander population growth under current and future precipitation regimes. At the same time, I endeavored to understand how stakeholder priorities link and compare to ecological research in the region, and to identify spatially explicit stakeholder values. I then integrated this new knowledge of both components of the complex system in southern Appalachia by layering the spatially explicit projections of salamander population growth rates and self-reported stakeholder values about land use in one unified map of Macon County, North Carolina to visualize the intersections between two seemingly disparate ways of identifying land conservation priorities.

*Rigorous ecological models* – Land managers, conservation organizations, state natural resource agencies, and other practitioners engaged in biodiversity conservation can better predict wildlife population responses to changing environmental conditions if they have access to rigorous working models of the natural components of the system. Too often, the foundational information needed for such models is lacking. This knowledge gap is particularly concerning when sensitive species are found in regions undergoing rapid anthropogenic change, as the ability to plan proactively for species conservation is significantly limited by a lack of understanding of population dynamics and the effect of environmental variation on vital rates.

The southern Appalachian region is recognized to be a global hotspot of Plethodontid salamander diversity. Temperate Plethodontids are among the most abundant vertebrates in forest ecosystems (Burton and Likens, 1975; Hairston, 1987; Ovaska and Gregory, 1989; Welsh Jr. and Lind, 1992), where they are important prey for other taxa and can influence key ecosystem processes including the abundance of soil invertebrates, leaf litter decomposition, and nutrient dynamics (Davic and Welsh, 2004; Best and Welsh, 2014). However, a variety of anthropogenic factors can impact the current and future distribution and abundance of salamanders, including habitat loss and degradation (Stuart et al., 2004; Wake and Vredenburg, 2008; Meredith et al., 2016; Cecala et al., 2018), species invasions (Maerz et al., 2009), emerging disease (Martel et al., 2013), and climate change (Milanovich et al., 2010).

The process of exurbanization and associated residential development on steep mountain slopes is likely to produce negative impacts on salamander populations (Connette and Semlitsch, 2013; Cecala et al., 2018), particularly in combination with potential future climate regimes which may prove to be both drier and hotter than in the past (Milanovich et al., 2010). Clearing the forest for home sites reduces canopy cover and alters leaf litter composition, both of which can increase temperature and reduce moisture levels of both the litter and the upper layers of soil (Figure 1.2). Plethodontid salamanders rely on cool moist conditions to facilitate gas exchange across their skin, as they are lungless (Feder, 1983; Feder and Londos, 1984), and the drier and warmer conditions in their primary microhabitats created by forest clearing has been shown to reduce abundance and skew populations toward adults, presumably, by reducing survival of young animals (Ash et al., 2003). Other studies also indicate that reductions in salamander abundance associated with increased drying is the result of reductions in fecundity or juvenile survival (Peterman and Semlitsch 2014). In addition, the infrastructure and increased human

activity increases the potential for the spread of invasive species and diseases that may be harmful to salamander populations. In addition to the risk of salamander declines in a region of global importance to salamander diversity, the loss of salamanders can feedback on stream and terrestrial processes including decomposition, carbon storage, and nutrient cycling in deciduous forest ecosystems (Wyman, 1998; Davic and Welsh, 2004; Keitzer and Goforth, 2013; 2013b; Best and Welsh, 2014; Milanovich et al., 2015).

The ability to identify areas of high habitat suitability for salamanders under current and potential future climates requires rigorous working models for priority salamander species. However, as I present in this dissertation, rigorous estimates of even the most fundamental demographic rates needed for such models are currently lacking, as is information about how those vital rates vary spatially or temporally in response to environmental parameters (Chapter 2). I reviewed and synthesized available vital rate estimates for direct-developing North American Plethodontinae and modeled the plausibility of those rates in a Leslie matrix population model. I then modeled intensive, long-term capture-recapture data and spatially-extensive repeated counts of *Plethodon* located within the Coweeta Basin, Macon County, North Carolina, to estimate size-specific vital rates and abundance and how those estimates vary in response to precipitation. I used a matrix population model to project salamander population dynamics over the extent of Macon County, thereby creating a spatially explicit view of potential high-quality habitat for these sensitive forest amphibians (Chapter 3).

*Understanding spatially explicit stakeholder values* – In addition to rigorous ecological models of species responses to natural or anthropogenic environmental change, working knowledge of human perspectives on environmental issues that underpin current and future land

use and conservation priorities is needed. Because most systems are best described as coupled human and natural systems, in which events in one part of the system have a reciprocal effect on the other (Alberti et al., 2011), conservation efforts which fail to balance ecosystem protection goals with the economic and cultural interests of people living within these systems can result in conflicts with local stakeholders, and even increased rates of natural resource losses (for example Raik, 2009). Examination of human dimensions of conservation problems enables transparent assessment of the trade-offs inherent in conservation decisions (McShane et al., 2011).

Because of the weak regulatory environment in southern Appalachia, much of the responsibility for land conservation and preservation falls to local grassroots organizations such as land trusts and watershed protection groups. These institutions rely on the maintenance of good relationships with the public, local, state, and federal government agencies, Native American tribes, and other regional stakeholders to accomplish conservation goals. Therefore, a clear understanding of stakeholder perspectives regarding key conservation issues is an important part of effective natural resources protection and management in the region.

As described previously, residential development on steep mountain slopes is a significant issue for people and natural resources resulting from the process of exurbanization. Scientists working in the region have reported a wide range of negative ecological and human health and safety impacts resulting from this kind of development, and I sought to understand how the perspectives of local stakeholders align with the concerns reported by the scientific community, and how stakeholders value specific places when given the opportunity to apply their views and beliefs about land use in a spatially explicit way through participatory mapping.

Steep slope development in southern Appalachia is enabled by the same weak regulatory system at the local and state level regarding land subdivision and development (Figure 1.2) that

makes land trusts such essential local conservation institutions. At the local level, this weakness is largely due to a profound cultural resistance to regulation. Economics may be a primary modern driver of this resistance as regulations are often described in archival resources as having negative impacts on residential construction, one of the few industries remaining in the region.

Economics in the form of the real estate market drive steep slope development (Figure 2.1) through demand created by exurbanites moving to the region in search of natural amenities. Because steep slope development can degrade natural resources through processes such as erosion and stream sedimentation, altered disturbance regimes, and decreased habitat quality and biodiversity, the very features of the region that drive exurbanites to build homes on steep slopes, feedbacks to the human system may include dampening of the real estate market if reduced water quality, reduced recreation opportunities, and increased risk of loss of life and property to landslides (Figure 1.2) make moving to the southern Appalachians less appealing for exurbanites.

In Chapter 4, I report on the perspectives of local people living in Macon County, North Carolina, regarding land use generally and steep slope development specifically, through the use of artifacts (news articles, opinion editorials, and letters to the editor), semi-structured interviews, and participatory mapping of land use priorities intended to elucidate how people view their regional land use priorities in explicitly defined space.

In combination, the information I collected and analyzed about human perspectives on land use, and current and potential future habitat suitability for salamanders increases understanding of the stakeholders who stand to have the most influence over future land use decisions and enables mechanistic understanding of the way changing climate may affect salamander biodiversity. Integrating these two kinds of information may serve to inform regional conservation priorities and planning efforts.

### **Figures**



**Figure 1.1.** Diagram of the limited relationships between human and natural systems that are commonly examined in conservation research. Examination typically begins with the impacts of human use or misuse of natural resources or anthropogenic disturbances on various components of the natural system. In some cases, feedbacks are examined, though these typically focus on the ways that impairment of the natural system impacts ecosystem services upon which humans depend. A deeper understanding of these relationships requires the examination to extend to such factors as the driving social, cultural, or economic processes behind the use of natural resources or disturbances caused by humans.



**Figure 1.2.** Diagram of one layer of the complex relationships between human and natural systems present in the rapidly exurbanizing southern Appalachian region. Black lines and text indicate the topics that have been studied by scientists working in the region, while grey lines indicate those topics and connections that have not been studied. Dashed grey lines indicate feedbacks that are likely but speculative.

### CHAPTER 2

# LITERATURE REVIEW AND SYNTHESIS OF ESTIMATED VITAL RATES FOR TERRESTRIAL SALAMANDERS IN THE FAMILY PLETHODONTIDAE <sup>1</sup>

<sup>&</sup>lt;sup>1</sup> Howard, J.S. and J.C. Maerz. To be submitted to *Copeia* 

#### <u>Abstract</u>

Population models are fundamental to understanding animal ecology, diagnosing anthropogenic causes of decline, and to developing effective management strategies. Rigorous population models depend on rigorous estimates of vital rates, yet for many taxa, such estimates and how they vary in response to spatial or temporal environmental gradients are lacking. In this review, we synthesized our current knowledge of survival rates, age and size at maturity, clutch frequency, and clutch size for temperate, direct-developing Plethodontid salamanders (subfamily Plethodontinae). We examined patterns and relationships among vital rates and other factors such as body size and latitude, and found that some vital rates, including clutch size, clutch frequency, and age and size at maturity are reasonably transferrable among direct-developing genera in the subfamily Plethodontinae. However, few reliable estimates of hatch rate exist, and we were unable to find any predictive relationships for survival rates, suggesting low transferability, or reflecting the logistic and methodological challenges of survival estimation for these animals. We used matrix models to judge the reasonableness of published estimates and found that for a range of hatch rate and clutch frequency values, only a small number of survival estimates appear to be plausible. Finally, we outlined the key knowledge gaps that limit basic demographic modeling of these remarkably common, influential, and otherwise well-studied salamanders, and made recommendations for future research efforts.

### Introduction

Population models are fundamental for understanding animal ecology, diagnosing anthropogenic causes of decline, and for developing effective management strategies. Rigorous population models depend on rigorous estimates of vital rates, yet for many taxa, such estimates and how

they vary in response to spatial or temporal environmental gradients are lacking. For amphibians, missing vital rates is a chronic problem which likely stems from their largely latent lives (Bailey et al., 2004a; 2004b; Wells, 2007). We lack essential vital rates that can populate demographic models for even the most well-studied and abundant amphibian species. This fundamental knowledge gap can hinder our ability forecast how populations may fluctuate in space and time in response to global change.

Salamanders in the family Plethodontidae are among the most widely studied amphibians in temperate North America. A Web of Science (Clarivate Analytics, 2018) search using the keyword 'Plethodontidae' returns 5,572 published studies between 1864 and 2018; however, among all 468 species combined, there are only a small number of estimates for the most basic vital rates, and few attempts to model population dynamics have been made for any species. Temperate Plethodontids are often the most abundant vertebrates in forest ecosystems (Burton and Likens, 1975; Hairston, 1987; Ovaska and Gregory, 1989; Welsh Jr. and Lind, 1992), where they are important prey for other taxa and can influence key ecosystem processes including the abundance of soil invertebrates, leaf litter decomposition, and nutrient dynamics (Davic and Welsh, 2004; Best and Welsh, 2014). Our lack of understanding of population dynamics for this important group of organisms is a serious conservation problem considering potential threats to their persistence resulting from climate change and habitat loss (Milanovich et al., 2010; Barrett and Price, 2014; Mallakpour and Villarini, 2016; Cecala et al., 2018), species invasions (Maerz et al., 2009), and emerging diseases (Martel et al., 2013; Fish and Wildlife Service, 2015).

In this review, we summarized and synthesized published vital rate estimates for temperate, direct-developing species within the family Plethodontidae, subfamily Plethodontinae (Wake, 2012). Specific vital rates included: stage- or age-specific survival from egg to adult, size and age at first reproduction, clutch frequency, and clutch size. We examined whether vital rate estimates varied based on methodology, study duration, body size, other life history traits, or geography. Then we used a Leslie matrix model and sensitivity analysis to evaluate published vital rate estimates and putative estimates for survival of highly latent life stages (e.g., egg survival). Ultimately, the goal of this paper was to scrutinize the limited numbers of vital rates available for these species, thereby illustrating a need that will motivate more efforts to estimate vital rates over temporal and spatial gradients, and to suggest elements of study designs to yield more rigorous estimates in the future.

#### Materials and Methods

*Literature review* – We reviewed published estimates of direct-developing North American members of the family Plethodontidae, subfamily Plethodontinae, including the genera *Plethodon, Aneides, Ensatina,* and the Desmognathinii species *Desmognathus aeneus, D. wrighti,* and *Phaeognathus hubrichti,* in addition to the direct-developing Asian genus *Karsenia,* also a member of the Plethodontinae (Wiens et al., 2006; Wake, 2012). We did not include any estimates for the genus *Batrachoseps,* which do occur in North America and have direct development but are within the subfamily Bolitoglossinae. We used several approaches to identify primary sources for estimates of vital rates. References were collected from the extensive species accounts found in Lannoo (2005). In addition, between January 1, 2015 and October 31, 2017, we conducted literature searches in the Google Scholar (Google Inc., 2018) and Web of Science databases (Clarivate Analytics, 2018) spanning the years 1900 to 2017 using the terms Plethodontidae, *Plethodon, Aneides, Ensatina, Karsenia, Desmognathus aeneus, D. wrighti,* or *Phaeognathus* paired with the words 'life history', 'demography', 'natural history', 'survival', 'survival rate', 'fecundity', 'reproduction', 'reproductive rates', 'maturation', 'sexual maturity', 'hatch rate', 'eggs', or 'clutch size'. We identified additional sources from references within papers collected through the prior two methods. We excluded sources, or some data contained within a source, when they were clearly inaccurate. For example, one source stated a nest of *Plethodon elongatus* contained 100 eggs (Wood, 1934), a claim which was questioned by several later sources and which seems unlikely when compared to other reported clutch size for the genus. Similarly, some studies reported hatching success of eggs in a laboratory setting without an attending female, and some allowed only part of a clutch to hatch (Cochran, 1911; Dumas, 1956; Highton, 1956; Brode and Gunter, 1958; Wells and Gordon, 1958).

*Modeling vital rate relationships* – We selected relationships between published vital rate estimates and other commonly available factors based on theorized and observed plethodontid life history patterns. A pillar of life-history theory is the idea that relationships exist among some life-history traits such as age at maturity and adult survival, and body size and fecundity (Gadgil and Bossert, 1970; Stearns, 1989; Winemiller and Rose, 1992). Generally, plethodontid life histories are characterized by delayed maturity to maximize adult body size, intermediate frequency of reproduction among females, high adult survival; and relatively larger eggs and smaller clutch size (Sayler, 1966; Salthe, 1969); however, there are potential exceptions to this general pattern.

We used regression analysis to model the following relationships among vital rates: (1) clutch size and snout-vent-length at maturity; (2) annual clutch frequency and latitude of studied population; and (3) age at maturity, snout-vent-length at maturity, and latitude of studied population. For some vital rates where there was insufficient data to model, we used visual

examination to determine whether potential relationships might exist. We did this to compare (1) adult survival and snout-vent-length at maturity; and (2) adult survival and age at maturity. Population latitude used in all regressions and plots was taken from GPS data published with the rate, or, if this data was not provided, we used Google Earth Pro (Google Inc., 2017) to determine the latitude of the approximate center of the study area described in the publication reporting the rate.

*Sensitivity analysis* – We used a females-only, Leslie matrix model (Figure 2.1) to conduct a sensitivity and elasticity analysis of mean reported vital rates using the R package 'popbio' (Stubben and Milligan, 2007), and to construct isoclines examining the relationship between pairs of the most sensitive vital rates when a third vital rate was held constant. We superimposed published estimates of vital rates on isocline plots to assess whether estimates could plausibly result in a stable population. The use of stable lambda isoclines to evaluate the plausibility of published vital rates is premised upon the assumption that rates were estimated from data collected on stable salamander populations, that stability is achieved through intrinsic rates of survival and recruitment [not through immigration], and that vital rates are not density dependent. These assumptions are discussed later.

### Results

*Adult survival.* – We found fourteen studies with published estimates of survival or apparent survival [does not distinguish between permanent emigration and mortality] for direct-developing Plethodontinae. Twelve studies estimated juvenile or adult apparent survival rates for a single species of *Aneides* (1 study), *Desmognathus* (2 studies), or *Plethodon* (9 studies). The

thirteenth study estimated a single, composite apparent survival rate for two Plethodon and one Ensatina species (Olson and Kluber, 2012). No study reported survival rates for *Phaeognathus* hubrichti. Study duration averaged 2.6 years and ranged from 0.25 to 5.0 years. Four of the fourteen studies did not use capture-mark-recapture (Organ, 1961a; Hairston, 1983; Welsh et al., 2008; Bruce, 2013). Hairston (1983) and Organ (1961a) created life tables from counts of sizeestimated age distributions. Bruce (2013) calculated instantaneous mortality rates applied to all age classes of two separate populations under the assumption that the populations were stable, and that mortality rates were constant in each from year to year. Welsh et al. (2008) estimated adult apparent survival using the ratio juveniles to adults counted (Ricklefs, 1997). Ten of the fourteen studies used individual capture-mark-recapture (CMR) to generate survival estimates (Welsh Jr. and Lind, 1992; Marvin, 1996; Kniowski and Reichenbach, 2009; Lee et al., 2012; Olson and Kluber, 2012; Otto et al., 2014; Connette and Semlitsch, 2015; Taylor et al., 2015; Peele et al., 2017; Caruso and Rissler, in review); however, only three studies (Lee et al., 2012; Otto et al., 2014; Peele et al., 2017) used a robust design (Pollock, 1982), which reduces bias in survival estimates (Bailey et al., 2004a; 2004b). Peele et al. (2017) used the "Robust Design" parameterization in Program MARK and assumed constant survival over the four year study, while Otto et al. (2014) used the "Huggins" parameterization of the robust design model in MARK (Cooch and White, 2016). The remaining CMR studies used Jolly-Seber models (Welsh Jr. and Lind, 1992; Taylor et al., 2015), a Cormack-Jolly-Seber model (Olson and Kluber, 2012), a multi-state model in a Bayesian framework (Connette and Semlitsch, 2015), or an unspecified model type (Kniowski and Reichenbach, 2009).

Only three studies generated separate apparent survival estimates for juvenile and adult life stages. Lee et al. (2012) used the "Multistrata" open population robust design multistate model in MARK, with survival dependent on snout-vent-length, then used snout-vent-length as an index of age to yield age-specific annual survival estimates for years one through five, and a single sixth survival estimate for all ages over six. Only two other capture-mark-recapture studies estimated survival for multiple life stages. Marvin (1996) used a Jolly-Seber model to estimate adult apparent survival for *P. kentucki*, but he relied on recapture rates within years to estimate apparent survival of two- and three-year-old juveniles, and he did not provide estimates of variation or uncertainty for the juvenile rates. Caruso and Rissler (in review) created a Bayesian Cormack-Jolly-Seber model that incorporated capture probabilities and predicted survival based on SVL and several environmental covariates. We calculated a mean survival value across sites for each of the five size classes they designated from their SVL- and precipitation-dependent survival estimates, and assumed each class corresponds roughly to the ages from one year to five years and older. Of all thirteen studies, Lee et al. (2012) was the only study to evaluate the plausibility of their survival estimates within a matrix model. Based on their survival estimates and other assumed vital rates, they estimated the growth rate ( $\Lambda$ ) for an A. *lugubris* population was between 0.928 and 1.093.

Among all studies, the estimates of apparent annual survival ranged from 0.190 to 0.998, and when provided, standard errors of ranged from 0.030 to 2.38 (Table 2.1, Figure 2.2). We did not find any discernable pattern between apparent survival estimates and the method used to estimate the parameter, whether the study was conducted in disturbed or undisturbed habitat, age at maturity, or adult size as measured by body length at maturity (Figures 2.2 and 2.3).

*Egg survival (hatch rate).* – Because Plethdontinae lay eggs in locations difficult to access without disturbing the nest site such as underground burrows, beneath rocks and logs, or in

natural caves and abandoned mines (Wells, 2007), making repeated observations of nests *in situ* is challenging. We found only twelve published reports of egg hatch rates and use one unpublished data set from coauthor Maerz for *P. cinereus* (Table 2.2). We excluded five of the *Plethodon* studies and the *Ensatina* report because they contained hatch rate data that is not reliable, either because eggs were raised in a laboratory setting without a female present, or the observations were based on a single clutch where only a subset of eggs was allowed to hatch (Cochran, 1911; Dumas, 1956; Highton, 1956; Brode and Gunter, 1958; Wells and Gordon, 1958; Sundell and Norman, 2002). Of the remaining studies, two hormonally-induced gravid females to lay eggs in the lab (Highton and Savage, 1961; Wareing, 1998), five collected clutches and attending females from the field and housed them in the lab (Organ, 1961b; Valentine, 1963; Harrison, 1967; Marvin, 1996) or in outdoor enclosures (Yurewics and Wilbur, 2004), and three published studies and the one unpublished data set observed clutches repeatedly *in situ* (Gordon, 1952; Blessing et al., 1999; Briggler and Puckette, 2003; Maerz, unpublished data). The range of mean reported hatch rates was 0.216 to 0.819 (Table 2.2).

Age and Size at Maturity. – Combined age and SVL at maturity, and population latitude data was available for Aneides lugubris, Ensatina eschscholtzii, Desmognathus aeneus, and nineteen *Plethodon* species. Some species had data on all three life history values reported by multiple studies, so we treated each study as an independent data point in our analyses (Table 2.3). Mean age at maturity was positively correlated with both length at maturity and the population latitude. The regression equation is age = 3.176 + 0.556 \* SVL + 0.527 \* latitude. The standard errors of the coefficients for SVL and latitude are both 0.185, and the adjusted R<sup>2</sup> value is 0.339 (Figure 2.4).

*Clutch frequency.* – Across most, if not all, Plethodontid species, males are assumed to have an annual reproduction probability of 1.0, while the probability of reproduction among females is expected to be less than one and variable among environments (examples in Highton, 1956; Fraser, 1974; Salthe and Mecham, 1974; Bull and Shine, 1979; Semlitsch and West, 1983; Lynch, 1984; Herrington, 1985; Ovaska, 1987; Takahashi and Pauley, 2010).

We found thirty-nine publications representing 31 studies with estimates of clutch frequency for twenty-two species. Of these, nineteen studies estimated clutch frequency by the ratio of gravid to non-gravid females observed in the study area (see Table 2.4), five more studies and one of the previous nineteen assumed clutch frequency of 0.5 based on the presence of two groups of gravid females with two different egg sizes (Highton, 1962; Sayler, 1966; Angle, 1969; Peacock and Nussbaum, 1973; Canterbury and Pauley, 1994; Herbeck and Semlitsch, 2000), and the remaining seven studies stated clutch frequency without a specific description of estimation method (Reagan, 1972; Williams, 1972; 1976; Nagel, 1977; Nagel, 1979; Jaeger, 1981; Lynch, 1984) (Table 2.4). Among all published studies, clutch frequency declined with increasing population latitude (Figure 2.5). The logarithmic regression equation was

$$clutch frequency = 4.682 - 1.126 * \ln(latitude).$$

The standard error of the coefficient for latitude is 0.280, and the adjusted  $R^2$  value is 0.291.

*Clutch size.* – We collected 141 mean clutch size estimates from 103 sources. Only 40 of these estimates also had estimates of mean SVL at maturity (Table 2.5); therefore, we used those 40

studies in our analysis. Clutch size increased with SVL (Figure 2.6). *Phaeognathus hubrichti* was a clear outlier among all studies, having among the largest SVLs at maturity, but among the smallest clutch sizes of all species in our review. With *Phaeognathus* included in the analysis, the regression equation was

 $clutch \, size = 2.741 + 0.176 * SVL$ 

The standard error of the coefficient for SVL is 0.0603, and the adjusted  $R^2$  value is 0.161. However, with *Phaeognathus* excluded, the regression equation was

$$clutch\ size = -1.430 + 0.237 * SVL$$

the standard error of the coefficient for SVL is 0.0668, and the adjusted  $R^2$  value is 0.293, indicating that both the slope and the fit of the regression line increased (Figure 2.6).

*Sensitivity analysis* – Sensitivity analysis showed that population growth should be most sensitive to changes in adult (year 6+) survival, followed by juvenile (year 2) survival, annual clutch frequency, and hatch rate. The most elastic rate was adult survival (Table 2.6).

Three of 14 published survival rates appeared improbably low, and two of 14 appeared improbably high across all combinations of adult and juvenile survival, egg hatch rate, and frequency of reproduction (Figure 2.7). If egg hatching rates were 0.3 or lower, nine published survival estimates seemed improbably low and two are improbably high (Figure 2.7). At an intermediate (0.5) and high (0.75) egg hatch rates, nine or ten published survival estimates
seemed plausible provided the probability of female reproduction is at or above 0.5 or 0.33, respectively (Figure 2.7). Assuming an egg hatch rate of 0.568, and frequency of reproduction of 0.560, 9 of 14 published survival rates seemed plausible for clutch sizes ranging between 7 and 16 eggs (Figure 2.8).

### Discussion

The information summarized in this review represents the current, relatively limited knowledge of vital rates of temperate, direct developing Plethodontinae – arguably among the most widely studied amphibian clade. One way to address limitations on species-specific data is to evaluate the transferability of vital rate estimates across species and populations (e.g., Heppel 1998). Aside from survival and hatch rate, we found evidence for moderate predictive relationships among vital rates and geography that suggest there is reasonable transferability among species. In the absence of direct measures of population vital rates, the ability to estimate proxy rates from available published data is reasonable.

The challenge of estimating egg hatch rates is understandable given the highly latent nature of this life stage. Natural clutches of salamander eggs have not been observed for many species, and for those that have been observed, observations require high frequency intrusion on nesting females *in situ* or the use of *ex situ* environments that may alter rates. Our models suggest that a wide range of egg hatching rates are plausible across a reasonable range of adult and juvenile survival and clutch frequencies. Given the latent nature of this life stage for most species, alternative ways to estimate reproductive rates of Plethodontinae such as using pre- or post-birth estimates of adult and hatchling ratios may be needed. Such estimates would require rigorous estimates of age- or size-class-specific abundances that account for age- or size-class-

specific differences in capture probabilities and should not rely on strictly on ratios of direct counts.

Perhaps more surprising, given the extensive study of temperate terrestrial salamanders, is the limited number of studies that have estimated survival rates. Only 14 published or inreview studies have estimated survival, and of those 14 studies, five had survival rates that – assuming they were estimated from stable populations – appear implausible given a reasonable range of egg hatching rates, frequency of reproduction, and clutch sizes. If published estimates were derived from data on declining or growing populations, particularly if vital rates are density dependent and populations are above or below their carrying capacity, then survival rates identified by our evaluation as implausible might be accurate. Additionally, lower survival rates could be possible for a stable population provided the immigration rate is sufficiently high. Very little is known about dispersal or immigration rates among Plethodontinae (e.g., Marsh et al., 2004), which is a key gap for understanding local population dynamics and larger scale sourcesink or metapopulation dynamics. Information on the context around vital rate estimates including whether populations appear stable and an assessment of the plausibility of vital rate estimates through PVAs or other approaches would add clarity to the sources of variation among estimates and should be routine among future studies.

Prior to this paper, only a single study with estimated survival rates had examined whether those estimates were plausible (Lee et al., 2012). Our evaluation suggests that, at a minimum, 5 of 14 survival estimates for terrestrial plethodontids are untenable. We believe this analysis reveals an even more depauperate knowledge than is apparent from the few published estimates of terrestrial salamander survival, and illustrates the caution needed when 'borrowing' published rates for population models when the plausibility of those rates has not been evaluated critically through the use of PVAs or other means. This is likely a problem that transcends the terrestrial salamander literature and is likely a more pervasive problem for a large number of wildlife species.

Only four studies provided stage or age-specific survival rates, and given the dramatic differences in size between hatchling, juvenile and adult salamanders and the relatively long time to maturity, this assumption is unrealistic. Because of their small size and higher surface-to-volume ratio, we would expect survival of young animals to be more sensitive to weather, particularly recent precipitation. We would also expect predation risk to be size dependent and, therefore, higher among juveniles. Certainly, estimating survival rates for different ages, life stages, or body sizes may be more challenging, particularly in light of the low capture probabilities of individual terrestrial salamanders; however, a few studies referenced in this review have shown it is both possible and important. We believe that future studies should be designed to estimate age, stage, or size-specific vital rates in relation to weather and other habitat covariates.

Also problematic is the short duration of most studies since direct-developing terrestrial salamanders require three to four years, or more, to reach sexual maturity. Most studies are less than four years long and only one in-review study has exceeded the four year mark (5 years, Caruso and Rissler, in review). Further, given the extended time to maturity, generation time is likely about 10 years, and no study estimating survival has yet come close to that threshold. Duration is also critical in understanding population response to interannual variation in environmental factors. If studies are short, then a year of extreme drought or unusually abundant rainfall can create a bigger effect on vital rate estimates than it would if the study extended across more years. Recent reviews and syntheses have emphasized a need for more studies of

hierarchical landscape-scale patterns of demography to better understand natural and anthropogenic effects on population dynamics, but acknowledge the logistical and funding resource challenges of such efforts (Gurevitch et al., 2016). Nonetheless, it should be alarming that even among an extensively studied group of animals, we lack a most basic understanding of demography for nearly all species.

We expected that the duration of study and methodology would explain some of the wide variation in published survival rates; however, this was generally not the case among the limited number of studies available. The lowest and least plausible published survival rate estimates were for *Desmognathus aeneus* and *D. wrighti*. The low estimates for these species are likely a result of the approach. Notably, the *Desmognathus* estimates came from two studies that probably used count data (the kind of data is unclear in Bruce, 2013), and relied on older methods of analyzing population dynamics via life tables (Organ, 1961a) and instantaneous mortality rate estimation (Bruce, 2013). These approaches assume capture probabilities are constant among individuals and through time (Conroy and Carroll, 2009), and furthermore, they do not include the two sub-components of capture probability, detection probability and temporary emigration probability, without which, abundance and survival estimates for terrestrial salamander populations are likely to be biased low (Bailey et al., 2004a; Bailey et al., 2004b; O'Donnell et al., 2015). Both probability of detection and of temporary emigration in terrestrial salamanders have been shown to be highly variable spatially and temporally (Bailey et al., 2004b), almost certainly as a result of variation in ambient moisture levels and certain characteristics of habitat type (O'Donnell et al., 2015). A model that does not account for these important factors will assume the observer has perfect or near-perfect detection, and that animals only emigrate permanently, and thus counts will be interpreted as directly proportional to the

number of animals present at the sampling location. When detection is low and temporary emigration occurs frequently (and at a rate unequal to the rate of return to the sampling area from the temporarily emigrated state), as in studies of terrestrial salamander populations, estimates of survival and abundance from this kind of model will inevitably be lower than reality.

Among the remainder of wide-ranging survival estimates, we did not observe any clear relationship between study duration or methodology. We note that count data can be analyzed more robustly using N-mixture models (Royle, 2004; Zipkin et al., 2014), especially if counts are repeated and employ a robust design (Pollock, 1982). Additionally, O'Donnell et al. (2015) developed a N-mixture model specifically with terrestrial salamander populations in mind, which expands on those versions previously cited by adding estimation of temporary emigration probabilities in addition to detection probabilities in the estimation of abundance.

Understanding the sensitivity and elasticity of vital rates can guide management efforts toward greater effectiveness by directing focus to the most sensitive or elastic rates. The sensitivity analysis we conducted showed that adult survival has the highest elasticity. This is generally consistent with expectations for species with delayed maturity and low fecundity, like terrestrial plethodontids. However, we caution that this should not be interpreted as the vital rate most responsible for natural variation in population growth. Elasticity is a measure of the instantaneous change in population growth rate given a proportionate change in a vital rate, and we do not know how variable adult survival is for terrestrial plethodontids. Some published survival estimates show adult survival can be reduced by as much as 20% - 62% in disturbed habitats [usually logging or forest clearing] (Table 2.1). However, other studies indicate that, compared to juveniles, adult salamanders appear proportionately more resilient to habitat disturbance (Ash et al., 2003) and drying (Peterman and Semlitsch, 2014; Caruso and Rissler, in

review). The variability of vital rates – not simply the estimated elasticity – is often recognized as an important determinant of population growth (Biek et al., 2002) and critical for identifying conservation management opportunities (De Kroon et al., 2000)

Our elasticity and sensitivity analyses also revealed the strong potential influence of the frequency with which females reproduce on population growth. Terrestrial salamanders are capital breeders, meaning that during the year, at least in temperate regions (Salthe and Mecham, 1974), there is only one time at which a female will lay eggs if she is going to do so, and a female will lay eggs at that time of year whenever she has the bodily resources, or capital, to do so. The production of eggs is energetically costly, and female plethodontids further commit themselves to approximately two months of brooding time, during which they appear to fast (Ng and Wilbur, 1995; Yurewics and Wilbur, 2004). If most females in a population can acquire enough resources during the active season to reproduce every year, then population growth should be significantly higher than in a population where females require on average two, or even three active seasons to be able to produce a clutch. We described the apparently strong relationship between clutch frequency and population latitude through a regression analysis, which suggests substantial spatial variation in clutch frequency at a broad scale. Variation may also occur at a finer spatial scale, particularly in highly variable landscapes, such as mountainous regions with complex topography and many unique microclimate zones. For example, populations on dry ridges may produce clutches less frequently than populations in wetter sites at the base of slopes. Additionally, temporal variation in clutch frequency may also be relatively common as, for example, several 'good' years in which active season is extended through a latearriving first winter frost or an extended rainy season could allow females to acquire enough resources to reproduce more often. Changing climate and land use patterns could produce more

frequent 'bad' years, in which conditions are drier for more of the year, either because of reduced frequency or intensity of precipitation or because timber harvest or land conversion for development or agriculture has reduced the prevalence or quality of moisture-retaining ground covers. Thus,(White and Burnham, 1997) future environmental conditions could result in population declines not necessarily through reduced survival, but through reduction in recruitment rates if clutch frequencies drop below some fundamental threshold level.

In this review, we have shown that most existing survival estimates seem implausible when hatch rate and clutch frequency are set to reasonable levels, which is a troubling indication of the lack of knowledge of Plethodontid population dynamics. While some transferability of vital rates such as age and size at maturity, and clutch size and frequency appears to exist between species, we still know very little about the transferability of survival rates among Plethodontid species, as there is so much variation in estimates and no apparent pattern relating to study characteristics. Given the multiple pressures facing amphibians, from habitat degradation and loss to emerging diseases and changing climate, gaining a better understanding of demographic rates and population dynamics, and how these rates and processes are affected by environmental variation is essential for effective conservation efforts.

## Figures and Tables

**Table 2.1.** Published survival estimates for temperate, terrestrial salamanders in the subfamily Plethodontinae. The comments column contains distinguishing information for multiple rates produced by the same study. The annual survival rates for *Desmognathus wrighti* produced by Organ (1961a) are odd among estimates for these animals in that Organ estimated a decline in survival after the fifth year of age. Additionally, Organ determined that females brooding a clutch of eggs (he assumed they produced a clutch every other year) had survival reduced to 0.19, and then experienced a higher rate again the next year. Hairston (1983) did estimate the highest survival for the youngest age class of *Plethodon metcalfi* but did not identify a decrease in survival from early adult years to later life.

		Aı	nnual su	rvival ra	ates		Comments	Sources
Species		luvenile	s		Adults			
ľ	year 1	year 2	year 3	year 4	year 5	year 6+		
Aneides lugubris	0.363	0.45	0.552	0.625	0.668	0.783		Lee et al. 2012
Desmognathus			0.2	214			from annual mortality rate	Bruce 2013
aeneus			0.2	215			from annual mortality rate	Bruce 2013
			0.2	276		-	from annual mortality rate	Bruce 2013
Desmognatnus wrighti	0.91	0.91	0.91	0.19	0.91	0.24	females	Organ 1961a
	0.91	0.91	0.91	0.91	0.91	0.29	males	Organ 1961a
Ensatina eschscholtzii, Plethodon dunni, Plethodon vehiculum			0.	64				Olson and Kluber 2012
Plethodon			0.	71			surface population	Taylor et al 2015
albagula			0.	67			cave population	Taylor et al 2015
			0.	64			40 to 60 years post timber harvest	Otto et al 2014
			0.	62			1 to 5 years post timber harvest	Otto et al 2014
Diethodon			0.2	774			unharvested forest	Peele et al 2017
cinereus			0.8	800			harvested forest, woody debris retained	Peele et al 2017
			0.0	530			harvested forest, no woody debris	Peele et al 2017
			0.8	825			clearcut	Peele et al 2017

			0.9	998			Kniowski and Reichenbach 2009
				0.47		old growth forest	Welsh et al 2008
Plethodon elongatus					0.25	young forest	Welsh et al 2008
cionguius			0.	44			Welsh and Lind 1992
Plethodon hubrichti			0.9	993			Kniowski and Reichenbach 2009
Plethodon		0.48	0.68	0.72		females	Marvin 1996
kentucki		0.48	0.68		0.85	males	Marvin 1996
Plethodon metcalfi	0.837	0.364	0.484		0.81		Hairston 1983
Plethodon montanus	0.525	0.728	0.831	0.933	0.963		Caruso and Rissler, in review
Plethodon					0.66	unharvested forest, from monthly survival	Connette and Semlitsch 2015
shermani					0.25	harvested forest, from monthly survival	Connette and Semlitsch 2015

**Table 2.2.** Published hatch rates for temperate, terrestrial salamanders in the family Plethodontinae. Observations of hatch rate *in situ* were typically made by repeatedly uncovering a known nest sight over the brooding period. *Ex situ* observations were usually made in a laboratory either of females collected with nests or of females hormonally induced to oviposit. We did not include any studies in which partial clutches were allowed to hatch, or in which clutches were maintained without a parent.

Species	Mean hatch rate by study size Study-specific mean clutch size Number of Clutches location		Source		
Aneides aeneus	0.689		7	in situ	Gordon 1952
Desmognathus aeneus	1.000	13.0	4	ex situ	Harrison 1967
Desmognathus aeneus	0.400		6	ex situ	Valentine 1963
Desmognathus wrighti	0.819	6.5	4	ex situ	Organ 1961a, 1961b
Plethodon angusticlavius	0.617	4.4	11	in situ	Briggler and Puckette 2003
Plethodon cinereus	0.216	8.9	14	in situ	Maerz, unpublished data 1998 - 2000
Plethodon cinereus	0.357	8.3	7	ex situ	Wareing 1998
Plethodon cinereus	0.378	5.7	6	ex situ	Highton and Savage 1961
Plethodon cinereus	0.632		18	ex situ	Yurewicz and Wilbur 2004
Plethodon kentucki	0.481	10.0	3	ex situ	Marvin 1996, Marvin pers. comm.
Plethodon vandykei	0.600	10.0	1	in situ	Blessing et al 1999

**Table 2.3.** Published ages and snout-vent-lengths at maturity for temperate, direct-developing Plethodontinae. Many other estimates of age and size at maturity exist, but here we have included only those studies for which both age and size at maturity were estimated and for which the study location was included.

Species	Mean snout- vent-length at maturity	Mean age at maturity	Latitude of studied population	Sources
Aneides lugubris	46.0	3.00	37.700000°	Lee et al. 2012
Desmognathus aeneus	18.5	2.00	35.052591°	Harrison 1967
Ensatina eschscholtzii	54.3	3.50	36.734088°	Stebbins 1954
Plethodon albagula	51.6	1.50	31.194099°	Taylor et al. 2015
Plethodon angusticlavius	35.0	3.00	36.102547°	Meshaka and Trauth 1995
Plethodon cinereus	33.0	2.00	39.649808°	Bausmann and Whitaker 1987
Plethodon cinereus	38.2	5.00	46.666667°	Leclair et al 2008
Plethodon cinereus	34.5	2.00	39.600973°	Sayler 1966
Plethodon dunni	40.0	2.00	44.559554°	Dumas 1956
Plethodon electromorphus	39.0	2.00	40.171536°	Pfingsten 1989
Plethodon glutinosus	65.0	5.00	39.671867°	Highton 1962
Plethodon glutinosus	53.5	3.00	37.323438°	Pope and Pope 1949
Plethodon grobmani	41.0	2.00	29.689153°	Highton 1956, 1962
Plethodon hoffmani	42.0	2.75	40.282030°	Angle 1969
Plethodon idahoensis	45.0	4.00	47.120739°	Lynch 1984
Plethodon kentucki	50.0	4.00	36.916670°	Marvin 1996
Plethodon larselli	41.7	3.50	45.693370°	Herrington 1985, Herrington and Larsen 1987
Plethodon metcalfi	45.0	4.00	35.258169°	Hairston 1983
Plethodon mississippi	48.0	3.00	30.940204°	Highton 1956, 1962
Plethodon ouachitae	49.3	3.00	34.529417°	Pope and Pope 1951
Plethodon petraeus	62.5	3.50	34.641270°	Jensen et al 2002
Plethodon stormi	51.6	5.50	41.997209°	Nussbaum et al. 1983
Plethodon vehiculum	40.0	2.00	44.559554°	Dumas 1956
Plethodon vehiculum	42.0	5.50	48.466670°	Ovaska 1987
Plethodon vehiculum	44.0	2.50	44.578705°	Peacock and Nussbaum 1973

Plethodon wehrlei	59.7	4.33	40.203893°	Hall and Stafford 1972
Plethodon welleri	32.5	2.67	36.201427°	Thurow 1963
Plethodon yohnalossee	60.7	3.00	37.374564°	Pope 1950

**Table 2.4.** Published estimates of clutch frequency for temperate, direct-developing Plethodontinae. Each row represents a single estimate produced by a single study.

Species	Clutch frequency	Latitude of studied population(s)	Source
Aneides aeneus	0.50	38.664928°	Canterbury and Pauley 1994
Desmognathus aeneus	1.00	35.052591°	Harrison 1967
Desmognathus wrighti	0.50	36.637215°	Organ 1961a
Plethodon angusticlavius	0.96	36.102547°	Meshaka and Trauth 1995
Plethodon caddoensis	0.40	34.418913°	Taylor et al 1990
Plethodon cinereus	0.75	41.788490°	Lotter 1978
Plethodon cinereus	1.00	36.253746°	Nagel 1977
Plethodon cinereus	0.50	39.600973°	Sayler 1966
Plethodon cinereus	1.00	39.150000°	Takahashi and Pauley 2010
Plethodon cinereus	0.63	38.250000°	Takahashi and Pauley 2010
Plethodon cinereus	0.92	42.379759°	Werner 1971
Plethodon dorsalis	0.78	35.932271°	Wilkinson et al 1993
Plethodon dunni	0.20	44.488479°	Freiburg 1954
Plethodon dunni	0.27	45.539779°	Herrington 1985
Plethodon elongatus	0.22	41.021798°	Welsh and Lind 1992
Plethodon fourchensis	0.60	34.678807°	Taylor et al 1990
Plethodon glutinosus	0.50	39.674891°	Highton 1962
Plethodon glutinosus	0.48	37.323438°	Pope and Pope 1949
Plethodon glutinosus	0.38	39.692857°	Semlitsch 1980
Plethodon grobmani	1.00	29.480590°	Highton 1956
Plethodon grobmani	1.00	30.314844°	Highton 1962
Plethodon hoffmani	0.50	40.282030°	Angle 1969
Plethodon idahoensis	0.50	47.120739°	Lynch 1984
Plethodon kentucki	0.50	36.916670°	Marvin 1996
Plethodon larselli	0.29	45.693370°	Herrington 1985
Plethodon larselli	0.37	45.693370°	Herrington and Larsen 1987
Plethodon neomexicanus	0.50	35.833271°	Reagan 1972

Plethodon neomexicanus	0.50	35.818320°	Williams 1972
Plethodon neomexicanus	0.50	35.818320°	Williams 1976
Plethodon neomexicanus	0.39	35.818320°	Williams 1978
Plethodon ouachitae	0.45	34.691209	Taylor et al 1990
Plethodon richmondi	0.50	36.253746°	Nagel 1979
Plethodon serratus	0.50	37.833266°	Herbeck and Semlitsch 2000
Plethodon serratus	0.82	34.418913°	Taylor et al 1990
Plethodon shenandoah	0.50		Jaeger 1981
Plethodon vehiculum	0.42	44.488479°	Freiburg 1954
Plethodon vehiculum	0.23	45.664897°	Herrington 1985
Plethodon vehiculum	0.38	48.466670°	Ovaska 1987
Plethodon vehiculum	0.50	44.578705°	Peacock and Nussbaum 1973

**Table 2.5.** Published reports of mean clutch size, range, and snout-vent-length at maturity for temperate, direct-developing Plethodontinae. Each row represents a single study, and method of clutch size determination (either by counting follicles in live or dead specimens, or by observing nests) is also noted.

Species	Cluch size from follicle count or nest?	Mean clutch size	Clutch size range	SVL at maturity (from same study)	Source
Desmognathus aeneus	follicles	11.7	6 to 17	18.5	Harrison 1967
Desmognathus aeneus	nests	10.7	6 to 18	18.5	Harrison 1967
Plethodon websteri	follicles	5.8	3 to 8	28.3	Semlitsch and West 1983
Plethodon serratus	follicles	5.9		33	Taylor et al. 1990
Plethodon angusticlavius	follicles	5.3	3 to 9	35.0	Meshaka and Trauth 1995
Plethodon richmondi	follicles	8.3		35.0	Wallace 1969
Plethodon cinereus	follicles	7.4	3 to 12	35.3	Lotter 1978
Plethodon cinereus	follicles	9.0	5 to 13	36.5	Blanchard 1928
Plethodon serratus	nests	5.0		38.9	Camp 1988
Plethodon serratus	follicles	5.5		38.9	Camp 1988
Plethodon serratus	follicles	5.6		38.9	Camp 1988
Ensatina eschscholtzii	nests	8.3	3 to 11	40.0	Olson et al. 2006
Plethodon caddoensis	follicles	11.3		40.0	Taylor et al. 1990
Plethodon dunni	nests	9.0		40.0	Dumas 1956
Plethodon grobmani	nests	9.0	7 to 11	41	Highton 1956
Plethodon grobmani	nests	5.0		41	Highton 1962
Plethodon grobmani	follicles	15.6	10 to 22	41	Highton 1962
Plethodon larselli	follicles	7.3	2 to 12	41.7	Herrington 1985, Herrington and Larsen 1987
Plethodon hoffmani	follicles	4.7	3 to 8	42.0	Angle 1969
Plethodon vehiculum	follicles	10.4		44.0	Peacock and Nussbaum 1973
Plethodon idahoensis	follicles	6.0	1 to 13	45	Lynch 1984
Plethodon ouachitae	follicles	16.7	13 to 23	49.25	Pope and Pope 1951
Plethodon dunni	follicles	9.4	4 to 15	50.0	Nussbaum et al 1983
Plethodon kentucki	nests	10.0	9 to 12	50.0	Marvin 1996

Plethodon ouachitae	follicles	15.4		50	Taylor et al. 1990
Plethodon elongatus	follicles	7.9	3 to 11	51.5	Nussbaum et al. 1983
Plethodon stormi	follicles	9.2	2 to 18	51.6	Nussbaum 1974, Nussbaum et al. 1983
Plethodon glutinosus	follicles	23.4	17 to 33	53.5	Pope and Pope 1949
Plethodon neomexicanus	follicles	7.7	5 to 12	54.0	Reagan 1972
Ensatina eschscholtzii	follicles	12.8	7 to 17	54.3	Stebbins 1954 (in Petranka 1998)
Plethodon chlorobryonis	nests	7.0		56.8	Wood and Rageot 1955
Plethodon chlorobryonis	follicles	17.5	16 to 19	56.8	Wood and Rageot 1955
Ensatina eschscholtzii	follicles	10.5	5 to 16	57.0	Nussbaum et al. 1983
Plethodon fourchensis	follicles	14.1		57	Taylor et al. 1990
Plethodon glutinosus	follicles	16.7	13 to 25	59.0	Highton 1962
Plethodon glutinosus	follicles	26.1	16 to 34	59.0	Highton 1962
Plethodon wehrlei	follicles	16.4		59.7	Hall and Stafford 1972
Plethodon yonahlossee	follicles	20.0	19 to 27	60.7	Pope 1950
Plethodon petraeus	follicles	19.3	15 to 30	62.5	Jensen, Camp, and Marshall 2002
Phaeognathus hubrichti	follicles	8.5	8 to 9	90.0	Brandon 1965

Vital Rate	Sensitivity	Elasticity
year 6+ survival	0.372	0.261
year 2 survival	0.271	0.157
annual clutch frequency	0.267	0.157
hatch rate	0.259	0.157
year 3 survival	0.238	0.157
year 1 survival	0.238	0.157
year 4 survival	0.231	0.157
year 5 survival	0.154	0.111
clutch size	0.0142	0.157

**Table 2.6.** Sensitivity and elasticity analysis results for the matrix model assessing plausibility of published vital rates for temperate, direct-developing Plethodontinae.

**Table 2.7.** Rates used in the Leslie matrix model for sensitivity analyses and construction of isoclines. The bottom two rows of the table show the mean and standard deviation of each rate, these are the exact values used in the matrix model.

Species	Species specific hatch rate			Annual	surviva	<u>1</u>		Species specific mean age at maturity	Species specific regression predicted clutch size	Species specific annual clutch frequency
		year 1	year 2	year 3	year 4	year 5	year 6+			
Aneides lugubris		0.363	0.45	0.552	0.625	0.668	0.783	3.0	11.4	
Desmognathus aeneus	0.700			0.2	215			3.0	4.3	1.00
Desmognathus wrighti	0.819	0.593	0.593	0.593	0.233	0.593	0.252			0.50
Ensatina eschscholtzii, Plethodon dunni, Plethodon vehiculum			0.640					3.0	12.0	0.31
Plethodon albagula				0.0	690			1.5	12.6	
Plethodon cinereus	0.312			0.3	804			3.3	8.6	0.80
Plethodon elongatus						0.470			12.8	0.22
Plethodon hubrichti				0.9	993					
Plethodon kentucki	0.481		0.480	0.680		0.720		4.0	11.5	0.50
Plethodon metcalfi		0.837	0.364	0.484		0.810		4.0		
Plethodon montanus		0.525	0.728	0.831	0.933	0.9	963			
Plethodon shermani						0.660				
mean	0.578	0.629	0.552	0.648	0.649	0.685	0.667	3.1	10.5	0.56
standard deviation	0.196	0.227	0.179	0.202	0.233	0.200	0.236	0.7	2.8	0.27

			Juveniles	5	Adults			
		year 1	year 2	year 3	year 4	year 5	years 6+	
	year 1	0	0	0	$f \ast \phi_4$	$f * \phi_5$	$f\ast\phi_6$	
Juveniles	year 2	φ1	0	0	0	0	0	
	year 3	0	φ <sub>2</sub>	0	0	0	0	
	year 4	0	0	φ <sub>3</sub>	0	0	0	
Adults	year 5	0	0	0	φ4	0	0	
	years 6+	0	0	0	0	φ5	$\phi_{6+}$	

**Figure 2.1.** Structure of the Leslie matrix model used to test the plausibility and sensitivity of mean reported vital rates for temperate, direct-developing salamanders in the subfamily Plethodontinae. In the body of the table, f stands for fecundity, which we did not allow to vary by age as we did not find any age-specific information. The f term is equal to the product of clutch size, clutch frequency, hatch rate, and offspring sex ratio, while the  $\phi_x$  are age specific survival estimates (see Table 2.7 for values).



**Figure 2.2.** Relationship between estimated annual survival and study duration for temperate, direct-developing salamanders in the subfamily Plethodontinae. Symbols represent estimates for different genera: *Aneides* = triangle, *Desmognathus* = squares, *Plethodon* = circles, and the one combined estimate for *Plethodon* and *Ensatina* = diamond. Open symbols denote estimates from studies in 'undisturbed' habitats, and black symbols denote estimates from studies in 'disturbed' habitats.



**Figure 2.3.** Relationship between published estimates of adult or non-age specific survival and age at maturity or snout-vent-length for temperate, direct-developing salamanders in the subfamily Plethodontinae. Symbols denote study design (CMR = white; counts = gray, other = black), genus (*Aneides* = square, *Desmognathus* = circle, *Plethodon* = triangle, and the one combined estimate for *Plethodon* and *Ensatina* = diamond). Error bars represent the standard errors reported by the study. If no error bar is present, the study did not report a measure of error.



**Figure 2.4.** Relationships between age at maturity and body length and population latitude for temperate, direct-developing salamanders in the subfamily Plethodontinae. Grey lines represent 95% confidence intervals. Data sources are summarized in Table 2.3.



**Figure 2.5.** Relationship between frequency of reproductive females, which is interpreted as the probability of female reproduction, and population latitude for temperate, direct-developing salamanders in the subfamily Plethodontinae. Grey lines represent 95% confidence intervals.



**Figure 2.6.** Relationships between clutch size and body length for temperate, direct-developing salamanders in the subfamily Plethodontinae. The left plot includes a single estimate for *Phaeognathus hubrichti*, marked in red, which is the longest species but has one of the smallest reported clutch sizes. The right plot excludes *Phaeognathus hubrichti*. Between the left and right figures, the slope increased from 0.176 to 0.273, and the adjusted  $R^2$  increased from 0.160 to 0.293.



**Figure 2.7.** Stable population growth isoclines for a generic, temperate, direct-developing salamander in the subfamily Plethodontinae. Each isocline represents different combinations of adult survival, juvenile survival, frequency of female reproduction, and three levels of egg hatch rate that result in stable population growth ( $\lambda = 1$ ). Hollow points show published estimates (see Table 2.1), and the red point corresponds to the mean estimates used in the Leslie matrix model (see Table 2.7 and Figure 2.1) relative to isoclines. Points to the left of an isocline would represent a declining population ( $\lambda < 1$ ), and points to the right of an isocline would represent a growing population ( $\lambda > 1$ ).



**Figure 2.8.** Stable population growth isoclines for a generic, temperate, direct-developing salamander in the subfamily Plethodontinae. Each isocline represents different combinations of adult survival, juvenile survival, and clutch size that should result in stable population growth ( $\lambda = 1$ ). Frequency of female reproduction was assumed to be 0.56, and hatch rate was assumed to be 0.578. Hollow points show published survival estimates (see Table 2.1), and the red point corresponds to the mean survival estimates used in the Leslie matrix model (see Table 2.7 and Figure 2.1) relative to the isoclines. Points to the left of an isocline would represent a declining population ( $\lambda < 1$ ), and points to the right of an isocline would represent a growing population ( $\lambda > 1$ ).

# CHAPTER 3

# PLETHODON POPULATION DYNAMICS ARE STRONGLY

# LINKED TO FINE SCALE PRECIPITATION <sup>1</sup>

<sup>&</sup>lt;sup>1</sup> Howard, J.S., J.C. Maerz, and K.D. McEntire. To be submitted to *The Journal of Herpetology* 

#### <u>Abstract</u>

Models are important for predicting how animal populations may respond to environmental change. Rigorous models depend on reliable estimates of vital rates, which often requires long-term or spatially extensive data that often are logistically challenging for many animal species. Consequently, for many amphibians and reptiles, adequate demographic models are lacking. For example, salamanders within the genus *Plethodon* are abundant, ecologically influential, and among the most studied amphibian species; yet we have few reliable estimates of *Plethodon* survival rates that could be used to model their population dynamics (Chapter 2). Additionally, though variation in precipitation and soil moisture are known to be key drivers of salamander performance and abundance, no published studies have directly linked weather variables or climate variation to spatial or temporal variation in individual activity, growth, survival, or reproduction. We conducted a robust, capture-mark-recapture study of *Plethodon* within the Coweeta Basin in western North Carolina to (1) estimate fecundity and size-classspecific survival, (2) determine how survival varies with precipitation, and (3) parameterize a stage-based matrix model to project population growth across the landscape under current and future climate scenarios, and (4) compare projected population growth across the Coweeta Basin to abundance estimates from count data collected over the same area. We found that 28-day survival estimates were highly sensitive to mean daily precipitation, and that sensitivity of survival to precipitation declined with increasing body size. Total estimated abundance increased with site-specific annual mean daily precipitation, and size-class-specific abundance estimates indicated populations in dry areas are dominated by adults, while populations in wetter areas are dominated by hatchlings and juveniles. Estimates of fecundity based on estimated clutch size, clutch frequency, mean published hatch rate estimates, an assumed sex ratio of 0.5, and mean

adult survival from the capture-mark-recapture data was nearly identical to precipitationdependent reproductive rate calculated from abundance estimates for the same location. Landscape projections of population growth rate suggest growing populations are only present in the southwest and southeast corners of Macon County, NC, however this result may be an artifact of the 800 m<sup>2</sup> scale of the precipitation raster layers used in the projection model, which do not account for fine scale microhabitat variation that could produce a complex pattern of source and sink populations across the landscape.

#### Introduction

Climate has long been recognized as a major driver of the distribution and abundance of organisms. At larger extents, climate can interact with physiological tolerances to determine the range limits of a species (Grinnell, 1917; Molles, 2010). Within the climatic boundaries of a species' tolerances, variation in climate can drive variation in life history and abundance (Gurevitch et al., 2016). Weather, which constitutes the predictable manifestations of climate, can directly affect individual performance and regulate both intra- and interspecific interactions among individuals (Elton, 1927; Clark et al., 2011). Understanding the effects of climate and weather on individual performance, life history, and biological interactions has become a resurgent focus as ecologists seek to predict and manage for anthropogenic climate change. Climate change has already been linked to altered phenology (Parmesan, 2006), changes in morphology (Caruso et al., 2014), species interactions (Dallalio et al., 2017), community composition, and range shifts in plants and animals (Walther et al., 2002; Chen et al., 2011). To reliably predict the potential effects of shifting climates on species distributions and abundance,

we need rigorous demographic models, which are themselves dependent on rigorous estimates of demographic processes and how those processes vary in response to weather (Jackson et al., 2009). For long-lived species, estimating demographic responses can require long-term data sets and spatially extensive studies that take advantage of naturally occurring climate gradients.

In many eastern deciduous forests salamanders are often the most abundant vertebrates in terrestrial and small order stream habitats. Because of their capacity to achieve remarkably high abundance and biomass (Hairston Sr., 1996), salamanders are potentially influential constituents of forest ecosystems (Davic and Welsh, 2004), and spatial or temporal variation in salamander abundance is likely to contribute to changes in ecosystem processes (Keitzer and Goforth, 2013; Semlitsch et al., 2014; Milanovich et al., 2015). The vast majority of salamander species including all species that account for the majority of forest biomass belong to the family Plethodontidae. Plethodontid salamanders are lungless and exchange gasses through their thin, moist skin. Therefore, terrestrial plethodontid performance and abundance is tightly governed by moisture (Feder, 1983; Feder and Londos, 1984; Peterman and Semlitsch, 2014).

Though variation in precipitation and soil moisture are believed to drive variation in salamander abundance, only a single study has demonstrated that relationship (Peterman and Semlitsch, 2014), and no published studies have directly linked weather or climate variation to spatial or temporal variation in individual activity, growth, survival, or reproduction. We are aware of only a single - at present unpublished - study estimating spatial and temporal sensitivity of salamander growth and survival rates to weather (Caruso and Rissler, in review). Therefore, our current ability to project the effects of spatial or temporal variation on salamander abundance is limited. Mechanistic models are needed for more rigorous projections of salamander

population responses to shifting climates, particularly if those models are to be used to confidently inform management actions (Jackson et al., 2009).

The objectives of this study were (1) to generate reliable estimates of survival and components of female fecundity and reproductive rate, (2) to determine how survival rates vary by size class, and with occasion- and year-specific precipitation, (3) estimate stage-specific abundance across spatial precipitation gradient and relate projected population growth to abundance and population structure across the Coweeta Basin, and (4) use the population model in combination with georeferenced precipitation data to project population growth rates across a larger landscape.

### Materials and Methods

*Study site* – The Coweeta Basin, located in the southern Appalachian Mountains of western North Carolina, is the site of the Coweeta Hydrologic Laboratory and has been managed by the USDA Forest Service since the 1930s. The basin contains some of the least disturbed terrestrial forest and stream habitat in the region. Annual total precipitation can vary significantly from year to year, but over the course of this study mean recorded total annual precipitation was 228.5 centimeters at the rain gauge nearest to our study plots. From a regional perspective, Macon County, representing the area immediately surrounding the Coweeta Basin, sits within a zone of particularly mean daily precipitation (Figure 3.1).

Within Macon County, the Coweeta Basin further represents a unique island receiving extremely high levels of precipitation (Figure 3.2), but also contains a steep precipitation gradient from very wet to moderately dry (Figure 3.3). This precipitation pattern is related to the shape of the Basin and its spatial orientation, as described by Daly et al. (2017). Specifically, there is a known strong elevation dependence of precipitation. There is a 'dump zone' of high precipitation below and to the lee (north) of the mountain ridge forming the southern border of the basin, and precipitation declines rapidly moving west to east on leeward slopes, as evidenced by well-known rain-shadow gradients.

Robust capture-mark-recapture – We sampled a population of salamanders that represents a hybrid zone between *Plethodon shermani* and *P. teyahalee*. We established six 100-m<sup>2</sup> plots at three locations between 840 to 935 meters along Ball Creek Road in the Coweeta Basin (Figure 3.3). We used a robust capture-mark-recapture design (Pollock, 1982), which consisted of approximately monthly primary periods each consisting of three consecutive nights (secondary periods) from approximately March to November for each year from 2010 to 2014, and then three seasonal primary periods per year each consisting of three consecutive nights from May 2015 to October 2017. Two primary periods contained only two secondary periods and one primary period contained four secondary periods. Overall, we sampled 40 primary periods consisting of 118 secondary periods over 8 years. During each secondary period, 2 or 3 individuals searched each plot for a minimum of 60 person-minutes and each searcher made at least two complete passes over the entire plot. We did not turn any cover objects or leaf litter, so our captures were limited to animals that were active on the surface (on the leaf litter, rocks, logs, or climbing plants) or partially out of burrows. Some salamanders that were partially out of burrows were lured before capture by gently moving a thin twig in front of the burrow to simulate a moving prey item. We captured salamanders by hand and placed them in individual plastic Ziploc bags with a small amount of moist leaf litter.

We measured each salamander's snout-vent length (from the tip of the snout to the posterior end of the vent, SVL), total length, and wet mass. We considered individuals sexually mature if they had an SVL of at least 60 mm or had clear primary or secondary sexual characters. We distinguished mature by the presence of a mental gland. We also positively identified mature females when eggs were visible through the ventral skin. We marked salamanders individually using visual implant elastomer (Northwest Marine Technology Inc., Shaw Island, Washington) injected under the skin on the ventral side at the joint of each limb (Heemeyer and Homyack, 2007). Beginning in 2013, we took a tissue sample from each animal the first time it was marked by pressing a sterile cotton swab approximately 5 mm from the tip of the tail to induce autotomy. We stored tissue samples in 70% ethanol. Salamanders were released near the center of the plot later the same evening.

*Survival estimation* – To estimate capture probability, temporary emigration, and survival, we developed a Bayesian model (Appendices 3.1 and 3.2) using program JAGS (Version 4.2.0, Plummer, 2017) run via program R (Version 3.4.2, R Core Team, 2016) with the 'rjags' package (Version 4, Plummer, 2015) (Appendix 3.1). The model is based on the Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965; Lebreton et al., 1992), which we expanded to accommodate our data collected under the robust design. The model conditions on first capture, estimates monthly survival and temporary emigration probability between primary periods, and detection probability at each secondary period.

We modeled the survival process as a Bernoulli trial with probability of success (surviving from t-1 to t) equal to the probability of survival from the previous primary period, given that the animal was alive at the previous primary period, that is, that the animal's z-state is

equal to 1. We modeled survival probability for each individual at each primary period as the logit-transformed probability of surviving from one primary period to the next, dependent on the snout-vent-length of the individual at that primary period, and one or both of the following: the mean daily precipitation over the interval since the previous primary period, or a random effect of primary period. In the following equation, a model with survival dependent on mean daily precipitation and snout-vent-length is depicted:

$$logit(phi[i, t]) = \beta_0 + \beta_1 * precip_{dailv}[t] + \beta_2 * svl[i, t]$$

where *t* is the primary period, *i* is the individual,  $precip_{daily}$  is the mean daily precipitation parameter, and *svl* is individual snout-vent-length. We assigned the  $\beta$  coefficients normally distributed priors with mean 0 and standard deviation 0.01.

We also modeled the observation process, whether an animal is detected or not, as a Bernoulli trial with probability of success (being detected) equal to the probability of detection, p, given that the animal is surface active (not temporarily emigrated), and alive. We modeled detection probability for each individual at each secondary period within each primary period as the logit transformed probability of being detected during a secondary period, dependent on the snout-vent-length of the individual and the short-term precipitation value associated with that secondary period:

$$logit(p[i, k, t]) = \alpha_0 + \alpha_1 * precip_{short} + \alpha_2 * svl[i, k, t]$$

where *t* is the primary period, *k* is the secondary period, *i* is the individual, and *precip<sub>short</sub>* is the total precipitation for seven days prior to the secondary period. We assigned the  $\alpha$  coefficients normally distributed priors with mean 0 and standard deviation 0.01. We modeled temporary emigration as either random or Markovian. In the random temporary emigration model, we set the probability of being surface active (as opposed to underground in a burrow) with an uninformative Uniform(0,1) distribution. We modeled the temporary emigration process as a Bernoulli trial based on the probability,  $\gamma$ , of being surface active. In the Markovian temporary emigration model, we used two temporary emigration parameters: the probability of being surface active given that an animal was surface active at the previous primary period,  $\gamma'$ , and the probability of being surface active given that an animal was not surface active at the previous primary period,  $\gamma''$ . We then modeled the temporary emigration process as a Bernoulli trial as follows:

$$s[i,t] \sim Bernoulli((s[i,t-1] * \gamma') + (1 - s[i,t-1] * \gamma''))$$

where s is availability (the binary temporary emigration state), the gamma parameters are as described above, i is the individual, and t is the primary period.

We used snout-vent-length measurements as a time-varying individual covariate. To predict snout-vent-length for each marked individual on the occasions when they were not captured and measured, we constructed a von Bertalanffy growth model (Figure 3.5) using an R protocol described by Ogle (2013), and the parameterization described by Beverton (1954) and Beverton and Holt (1957):

$$E[L|a] = L_{\infty} \left(1 - e^{-K(a-a_0)}\right)$$

where *E* is the expected length, *L*, at age *a*;  $L_{\infty}$  is the asymptotic length; *K* is the growth rate coefficient; and  $a_0$  represents the imaginary age when mean length is equal to zero (Ogle, 2013). We used measurement records for known-age individuals marked initially as hatchlings or first year juveniles and re-captured at least once to build this model.

During the active season, we sampled about every twenty-eight days for the years 2010 to 2014, while from 2015 to 2017 samples were more widely dispersed and we did not sample during winter (approximately October to March) when animals are generally not surface active. We accounted for difference between primary periods by calculating the approximate number of 28-day units between each primary period and using those intervals to estimate properly scaled survival rates between all primary occasions.

We used two time-varying precipitation covariates to model capture probability and survival. Because we know that rainfall has a positive effect on salamander surface activity, we used the total precipitation over the seven-day period prior to the secondary occasion to model capture probability. We used the mean daily precipitation during the interval between two primary periods to model survival between those two periods. We obtained daily precipitation data from a rain gauge located approximately 550 meters from the study plots (Figure 3.3). We did not include temperature as a model covariate for two reasons. First, when temperature data were graphed, it was strongly confounded with season and date (Figure 3.4). Second, during the active season for all eight years of this study, night temperatures were generally always within the optimal performance range and never approached or exceeded temperatures assumed to impeded metabolic performance of closely related species (Clay and Gifford, 2017). Therefore,
we had no reason to expect that temperature would impact survival and have any impact on detection independent of natural seasonal phenology in activity.

We also tested a set of season covariates which used a binary coding system to identify whether the interval between primary periods represented a transition from one season to the next, or was full within a single season, however, posterior distributions for the majority of the parameters associated with these covariates contained zero, indicating they were not producing a significant effect on the survival process. Additionally, we modeled survival based on the effects of snout-vent-length and primary period, but as with the season covariates, a majority of the parameters associated with primary periods had posterior distributions that included zero. We did not model detection based on secondary periods because to do so would have added 117 parameters to the model. All covariates, except binary covariates, were standardized by scaling to a mean of 0 and a standard deviation of 1.

We worked with three variants each of the random temporary emigration and the Markovian temporary emigration models, in which survival depended on the additive effects of snout-vent-length and mean daily precipitation over the interval from one primary to the next, on snout-vent-length alone, or on the additive effects of snout-vent-length and a random effect of primary period. In all models, detection probability was dependent on the additive effects of snout-vent-length and total precipitation over the seven-day period prior to each sampling occasion. For each model we ran 10,000 iterations with a burn-in period of 1000.

*Estimating Female Fecundity* - From April 2015 to October 2016, adult or sub-adult female salamanders were collected from twenty-eight sites located in the Coweeta Basin, as shown in Figure 3.3. Salamanders were kept no longer than forty-eight hours in individual plastic zipper

bags with leaf litter in a refrigerator, then weighed, measured for SVL and total length, and euthanized by submersion in 0.5% pH neutral buffered MS-222. Specimens were fixed in 10% buffered formalin and preserved in 70% ethanol until dissection. We dissected all specimens to determine whether a female was mature and to estimate final clutch size. All ovarian follicles over 0.5 mm in diameter were measured across two perpendicular planes (to account for physical distortion of the follicles) and counted.

From October 2015 to October 2017 we also opportunistically counted and measured eggs through the ventral skin of live gravid females captured at the demographic study plots and at six plots used for a separate study, and these follicle counts and diameters were included in the data set with the dissected females. However, our estimate of annual probability of reproduction does not include this group of gravid females because, due to the dark ventral pigmentation of many individuals, we were unable to determine the reproductive status of every female captured over the course of sampling.

We used a general linear model to estimate final clutch size at oviposition based on snout-vent-lengths, follicle counts, follicle diameters, and capture dates. We assumed June 1<sup>st</sup> to be the oviposition date and the 730<sup>th</sup> day of an average female reproductive cycle. We assigned a number between 1 and 730 to each female based on the size of her ovarian follicles and the date she was captured. For example, a female captured on May 11<sup>th</sup> with average follicle diameter near maximum size was given the reproductive cycle date 709 because we assumed she was in the end of the second year of her reproductive cycle (see Figure 3.6).

We ran four multiple linear regression models in R using package 'AICcmodavg' (Version 2.1-0, Mazerolle, 2016) to select the best model of the candidate set based on AICc values. Candidate models included final clutch size as a function of each possible additive and interactive combination of SVL, reproductive cycle date, and average follicle diameter. We used the 'predict()' function in R to estimate final clutch size for each gravid female collected by providing the SVL measurement of each observed gravid female, with egg diameter set to 4.0 millimeters, and reproductive date code set to 730, the final day before oviposition. We calculated an average final clutch size and standard deviation across all observed gravid females.

To calculate female fecundity four values must be known: annual adult female survival rate, average clutch size, proportion of females breeding annually, and hatch rate. From our data, we determined the first three of these values, but we did not observe any nests so we could not directly estimate hatch rate. Few studies have been able to estimate hatch rate satisfactorily because *Plethodon* typically nest in inaccessible locations such as underground burrows, rotting logs, crevices in rocks, or other places that are not easily accessible (Chapter 2).

*Estimation of spatial variation in abundance and reproductive rate* – We estimated site and sizeclass specific abundance from count data collected at 20 sites across the Basin's steep precipitation gradient (Figure 3.3) in 2016 to 2017. Counts were made over three consecutive nights in the spring, summer, and fall of each year in a robust design (Pollock 1982) structure resulting in 6 primary periods composed of 18 secondary periods. Completing a full seasonal sample of three nights at each site took four consecutive weeks. While sampling dates for individual sites varied between the two years of the study, the spring sample was always conducted in May, the summer sample in July, and the fall sample in September and October.

Each site had at least three 25 m<sup>2</sup> plots, some sites had four. In total, we counted salamanders at 72 plots. Sampling began approximately one hour after sunset and was completed between midnight and 4:00 AM depending on the number of salamanders captured and

processed. Each plot was searched for 20 person-minutes. Salamanders were captured by hand and contained individually in plastic Ziploc bags until the search time ended. Disturbance to leaf litter, downed woody debris, and other habitat features was minimized by collecting only animals active on the surface. Salamanders were sorted into four size classes by measuring their snout-vent-length (SVL) (hatchling: 30 mm or less; juvenile: 31 to 45 mm; subadults: 46 to 60 mm; adults: 61 mm and above). We determined the sex of adults and mature subadults by the presence or absence of a mental gland located on the chin of males, dark testes visible through the ventral skin of males, or eggs visible through the ventral skin of females if that skin was light in color. Females were considered gravid if they had visible eggs of any size. For these individuals, in addition to SVL, we recorded body mass and approximate diameter and number of eggs. Salamanders were released at the center of the plot before searchers moved to the next plot.

We used this count data to model abundance separately for each size class in R using package 'unmarked' (Fiske and Chandler, 2011). 'unmarked' employs binomial N-mixture models (Royle, 2004; Zipkin et al., 2014) of several varieties. We employed the gpcount() function for a general binomial N-mixture model for repeated count data collected using the robust design, which allows estimation of population size, availability (temporary emigration), and detection probability (Fiske et al., 2017). We examined several site-specific covariates that did not vary over time including mean total active season precipitation (from March through October), aspect, slope, topographic index (Tarboton et al., 2011), and heat-load index (McCune, 2007). We also examined covariates that varied among sites and by primary period including total precipitation over the 7-day period prior to a sampling occasion, the season (spring, summer, or fall) in which sampling occurred, and a binary covariate identifying the presence (1)

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or absence (0) of severe drought or early frost conditions, both of which produced abnormally low counts at the most productive sites. Site and primary period varying covariates were applied only to detection and availability parameters, while site-specific parameters were applied to all three parameters. Except for the above limitation, we tested a wide range of possible additive and interactive combinations of site-specific and site and primary period varying covariates, insofar as the combinations made biological sense. We selected the best model of the set using AIC values (Akaike, 1973).

The structure of our data reflects the fact that sites produce either high or low counts, with no sites producing mid-range counts. This pattern suggests a threshold effect of precipitation on abundance: some level above which abundance is high but below which abundance is very low. Given this highly nonlinear data structure, we were unable to produce any biologically realistic models that performed well in goodness-of-fit tests using the parboot() function to conduct a parametric bootstrap data simulation. Instead, we used the simulate() function which generates count data from the candidate model, and compared these simulated counts to the observed data. If simulated counts appeared similar to observed counts, we assumed model fit was adequate.

Once site- and size-class-specific abundance estimates were completed, we calculated the ratio of number of hatchlings to number of adults at each site. Because the gpcount() model accounts for detection probability and temporary emigration, because we modeled abundance for each size class separately (Williams et al., 2001), because adults are the only size class that produces offspring, and because estimates of adults and hatchlings were for a concurrent period representing approximately 1.5 years, using this ratio as an approximation of a 'post-birth' reproductive rate is appropriate.

*Sensitivity analysis* – Using a deterministic version of the matrix model, we conducted a sensitivity analysis of all mean annual vital rates using the R package 'popbio' (Stubben and Milligan, 2007). We also used this deterministic model to create isoclines examining the reciprocal relationships between the four most sensitive parameters while holding population growth equal to 1.0.

Landscape projection of population growth – Using a stochastic stage-based matrix model (Lefkovitch, 1965), we simulated salamander survival and reproductive recruitment for 100 iterations of a 50-year simulation. The matrix model predicts survival for each size class in each simulated year based on a logistic regression of survival estimates on mean daily precipitation generated using the Bayesian model. We used the 'nls()' function in R to determine the nonlinear weighted least-squares estimates of coefficients for a logistic curve (as described in Cheng, 2014) to conduct these regression analyses. We did not have any information about how the mean clutch size and clutch frequency estimates we produced from the fecundity study vary with variation in precipitation, nor were we able to produce an estimate of hatch rate. Therefore, we used an exponential regression of site-specific reproductive rates across the Coweeta Basin on mean daily precipitation to produce an equation which allowed us to incorporate precipitation-dependent reproductive recruitment into the matrix model.

We acquired a 30-year (1981 to 2010) mean total annual precipitation raster layer for the contiguous United States (The PRISM Climate Group, 2012), and used the 'Raster Calculator' tool in ArcMap (Esri Inc., 2016) to calculate mean daily precipitation for each 800 square meter cell within the extent of Macon County, North Carolina, and within the extent of the Coweeta

Basin. We chose the Parameter-elevation Relationships on Independent Slopes Model (PRISM) precipitation data because it has been topographically adjusted for the Coweeta Basin area (in response to Daly et al., 2017) to better match long term precipitation data collected on site.

We used the R package 'raster' (Hijmans et al., 2017) to run the model including precipitation data. We ran a baseline version of the model in which all years of all iterations used the 30-year mean daily precipitation data. Then, because climate change is likely to produce more variable conditions, particularly, an increased incidence of extreme weather events such as meteorological droughts (Walther et al., 2002; Shepherd, 2011), those droughts defined by the degree of dryness in comparison to average conditions and the duration of the dry period (Wilhite and Glantz, 1985), we ran twelve other versions of the model to examine the possible effects of droughts on salamander populations. In these twelve models, the precipitation raster layer was adjusted to be either 5, 15, 25, or 35% drier than the 30-year mean. Rainfall data recorded in the Coweeta Basin over the duration of our capture-mark-recapture study showed that 2012, 2014, and 2016 had 4%, 18% drier and 28% less rainfall than the 30-year average, respectively. We also adjusted the frequency of dry years to 24%, 32%, or 50% to simulate droughts occurring every fourth, third year, or second year, respectively.

During initialization, the model was assigned one probability of dry year occurrence and one of the four drier conditions raster layers, which determined how severe a drought year would be. Every year of the simulation, the model drew a random number between zero and one, and if this number was less than or equal to the dry year probability assigned during initialization, the model would use the assigned drought year precipitation raster, while if the number drawn was greater than the drought year probability, the model would use the 30-year mean raster.

To introduce stochasticity into the model, we added a rate-specific error term which is drawn each year from a uniform distribution defined by the standard deviations of the vital rate estimates. For the survival equations, standard deviation was calculated from the 28-day survival estimates produced by the Bayesian model. For reproductive rate, standard deviation was calculated from rates we calculated for each count data collection site. Values used in the model and the matrix structure are provided in Tables 3.1 and 3.2.

We set starting population density to two animals per square meter. At our three CMR sites, the average number of marks applied across 200 square meters of total plot area is 3.61 per square meter (range: 2.69 to 5.33), so we believe an estimate of two is conservative but reasonable. Because the matrix projects over raster layers of precipitation data with cell sizes equal to 800 square meters, we set starting population size in each cell to 1600 individuals. Across all CMR sites and sampling occasions, 14.9% of animals marked were adults, 18.2% were sub-adults, 25.6% were juveniles, and 41.2% were hatchlings. We used these proportions to divide the starting population in each cell among the four size classes, resulting in starting populations made up of 239 adults, 292 sub-adults, 410 juveniles, and 659 hatchlings. In subsequent years, matrix calculations were made using abundance values from the previous year.

The model calculated mean population growth rate across all iterations of a run. We used package 'raster' to convert this output data back into a raster which showed the mean stochastic predictions of precipitation-dependent population growth across the Coweeta Basin and the county.

*Comparison of projections with estimated abundance* – We compared the spatial pattern of population growth rates projected for the Coweeta Basin to the site and size-class specific

abundance estimates produced using count data collected at 20 sites across the Basin's steep precipitation gradient. We examined both total abundance and size class specific abundance in relation to projected population growth rates.

## <u>Results</u>

*Survival estimates* – Our dataset consists of 5,946 captures of 2,138 individually marked animals over a seven-year period from September 2010 to November 2017. As of 2017, 64.0% of marked individuals have been recaptured at least once, 12.7% have been recaptured twice, and 36.0% have never been recaptured. The most captured individual was recaptured 18 times, or on 16.2% percent of occasions. The longest time between captures for an individual was five years.

The Bayesian model produced the following mean annual survival estimates by size class: adults: 0.899, sub-adults: 0.829, juveniles: 0.755, hatchlings: 0.635. Twenty-eight-day survival estimates increased with mean daily precipitation within size classes (Figure 3.7), and 28-day detection probabilities increased with mean daily precipitation within size classes (Figure 3.8) and with snout-vent-length across size classes (Figure 3.9).

*Female fecundity estimates* - We collected and dissected 329 female salamanders, of which, 22 were determined to be immature based on the presence of underdeveloped ovaries and oviducts and the presence of very tiny eggs less than 0.5 millimeters in diameter. The smallest gravid female had an SVL of 51 millimeters, while the largest had an SVL of 87 millimeters. Of the 307 mature females, 128 (41.7 %) had eggs greater than 0.5 millimeters. We also observed eggs in 80 live gravid females. Follicle counts ranged from 9 to 106. In the female with 9 follicles, eggs averaged 6.0 millimeters, while in the female with 106 follicles, eggs averaged 0.6 millimeters.

The best model of final clutch size included the additive effects of SVL, reproductive cycle date, and egg diameter. This multiple linear regression model was:

$$C = -19.844 + 0.768(S) + 0.0142(R) - 6.541(D)$$

where C is clutch size, S is snout-vent-length, R is reproductive cycle date, and D is egg diameter. The adjusted  $R^2$  value for this regression is 0.385.

By setting *R* to the assumed oviposition date of 730, and *D* to the approximate egg diameter at oviposition of 4.0 millimeters, the equation allows for calculation of final clutch size based on the SVL of any gravid female collected at any point in time during the apparent two-year cycle of egg production. Mean estimated final clutch size was 17 eggs (range: 4 to 31, standard deviation: 5.346; Figure 3.10). Assuming mean hatch rate is 0.578 (see Table 2.7 in Chapter 2), and offspring sex ratio is 0.5, then with the mean adult survival rate produced by the Bayesian model, annual fecundity for the wettest part of the Basin, where most fecundity study specimens were collected, is equal to 1.864, or approximately 2 female offspring per adult female.

*Estimation of spatial variation in abundance and reproductive rate* – Across the 20 sites in the Coweeta basin where we collected size-class-specific count data, total estimated abundance ranged from 9 to 183 salamanders per 25 m<sup>2</sup> area (mean: 45, standard deviation: 49). The best model of the candidate set was the same for each size-class-specific analysis and included abundance dependent on mean total annual precipitation, and both availability (temporary

emigration) and detection probability dependent on 7-day total precipitation and the severe weather binary covariate. Estimated abundance increased with mean total annual precipitation.

The proportion of total abundance made up by each size class varied across the Basin's precipitation gradient. Most of the drier sites had similar proportions, with nearly 50% adults, approximately equal parts juveniles and sub-adults, and the smallest proportion made up by hatchlings. Most wetter sites had nearly equal proportions of each size class, however, the absolute wettest sites had the greatest proportion, approximately 33%, of juveniles, followed by a nearly equal proportion of hatchlings, and about half as many each of adults and sub-adults.

Because reproductive rates were calculated from hatchling and adult abundance estimates, the pattern of rate values across the Basin, which ranged from 0.240 to 1.635 (mean: 0.607, standard deviation: 0.430), closely matched the pattern of abundance estimates, with the lowest recruitment occurring in the driest sites, and the highest reproductive rate occurring in the wettest sites (Figure 3.14).

*Sensitivity analysis* – The most sensitive vital rates were adult survival, hatchling survival, and reproductive rate (as calculated from abundance estimates) Adult survival was also the most elastic rate, while all other rates had the same elasticity (Table 3.3). Isocline plots show that the mean survival estimates we used for hatchlings and adults in the matrix model (0.635 and 0.899 respectively) fall between isoclines for reproductive rate of 0.2, and reproductive rate of 0.5. This suggests relatively low values of reproductive rate may be sufficient to produce a stable *Plethodon* population (Figure 3.17).

*Landscape projections of population growth* – Projection across the extent of the Coweeta Basin using the 30-year mean precipitation raster produced stochastic population growth rates averaging 0.911 in the driest locations, and 1.280 in the wettest locations across the natural precipitation gradient in the Basin, with rates less than 1 over a little more than one third of the Basin (Figure 3.9). When the model alternated between a drought raster and the 30-year mean raster to simulate drought conditions in some years, mean population growth rates were reduced. The most extreme conditions we simulated, 35% drier conditions with 50% probability of drought, reduced the range of growth rates to an average of 0.870 at the driest locations, and 1.200 at the wettest, which extend the projected area with population growth rates to approximately two thirds of the basin (Figure 3.11).

Projections over the extent of Macon County point to the Coweeta Basin as a place with hyper-productive salamander populations, which may be able to sustain population growth under even the most extreme drought conditions we tested. Even under the 30-year mean precipitation scenario with no drought years, our model projected a majority of the county contains unsuitable salamander habitat where population growth rates are less than 1.0 (Figure 3.15). When the simple forest land cover versus non-forested land cover layer is superimposed on the county level projection, the Coweeta area, where suitable habitat is identified, appears to be highly contiguous, unfragmented forest habitat which supports the projection model's predictions. However, in the southeast corner of the county in the vicinity of the town of Highlands, the other place the projection model predicted suitable habitat, relatively large areas have non-forest cover, and the landscape appears more fragmented which may indicate that although precipitation levels are suitable, the habitat is not (Figure 3.16).

*Comparison of projections with estimated abundance* – We found that projected population growth rates correlate well with site-specific abundance estimates made with size-class-specific gpcount() models in package 'unmarked' in that total abundance is higher at sites where population growth projections are higher (Figures 3.12 and 3.13). Additionally, the proportions of each size class estimated to be present at these sites seem logical when compared to projected population growth rates. For example, in dry sites with declining population growth rates, populations are dominated by adults, which are more resistant to dry conditions (Ash et al., 2003; Peterman and Semlitsch, 2014), while in wet sites with increasing population growth rates, populations are dominated by hatchlings and juveniles, indicating that substantial recruitment is occurring.

## **Discussion**

This study has produced some of the first reliable estimates of size-specific plethodontid annual survival and how those survival rates vary temporally with precipitation (see Caruso and Rissler, in review). Additionally, we included an assessment of the plausibility of our estimates, which is rare among Plethodontid demographic studies (for the only other example we have found, see Lee et al., 2012). We tested the predictive ability of estimated rates in a matrix model we projected over the study area to examine how well the emergent population growth rates correlated with estimates of abundance from count data we collected at sites across the Coweeta Basin. We also developed a novel regression-based method to predict final clutch size from the range of ovarian follicle counts and sizes observed across the female reproductive cycle. This method substantially improves our ability to determine average population-specific clutch size by making any follicle observation, even of immature ova, more informative. Our Bayesian model estimates suggest salamander survival is sensitive to fine-scale temporal variation in environmental moisture levels, and that sensitivity increases with decreasing body size. This is consistent with expected relationships between body size and sensitivity to water loss among plethodontid salamanders (Feder, 1983; Feder and Londos, 1984) and another unpublished study (Caruso and Rissler, in review). We note that our study sites were located within a cove in an area of extremely high rainfall where one might expect populations to be buffered from short-term variation in precipitation. However, there were two meteorological droughts during our study including a drought in the fall of 2016 that was the most severe in terms of water deficit and duration ever recorded for the region. These events and other moderate dry periods likely allowed us to capture sensitivity to precipitation even in relatively wet habitat and illustrates the importance of long-term data to estimating relationships between demographic rates and weather variables (Jackson 2009).

Our matrix population projection model includes survival and reproductive rate that vary with precipitation, a key environmental variable for lungless plethodontid salamanders. Interestingly, the estimate of fecundity we made using clutch size and clutch frequency from the fecundity study, 1.864, is nearly identical to the reproductive rate calculated for the wettest part of the Basin, 1.635, where most fecundity specimens were collected. This level of agreement between estimates made from entirely separate data sets that suggests the reproductive rates used in the projection model are relatively reliable. To our knowledge, this is the first study to estimate the effects of precipitation on plethodontid reproduction and survival, which is critical in developing rigorous and realistic models of salamander population dynamics. Moisture determines the amount of time salamanders can be surface active to feed (Feder, 1983; Feder and Londos, 1984), and Peterman and Semlitsch (2014) showed that plethodontid salamander

activity levels are dictated by water loss. Because smaller hatchlings and juveniles have higher surface area to volume ratios and therefore lose water at faster rates, spatial variation in juvenile survival is likely a driving factor determining spatial variation in salamander abundance along soil moisture gradients. Gifford and Kozak (2012) suggest that climate-driven spatial variation in foraging opportunities and energetics may determine species distributions under current and future climates. However, none of these studies directly estimated the relationships between climate and vital rates to directly model population growth potential. Our results suggest that while the sensitivity of hatchling and juvenile survival to precipitation is steep, adult survival is relative robust to declining precipitation until precipitation levels are extremely low. Our results suggest stronger sensitivity of adult fecundity [reproductive rate] to precipitation. Despite high predicted sensitivity of population growth to adult survival, our results suggest that climatic sensitivity of juvenile survival and adult fecundity are likely to determine salamander population responses to climate.

At the wider landscape scale, we also projected growing populations on average in the vicinity of the Coweeta Basin, and the town of Highlands. However, projected growth rates were less than one for all other parts of the county. First, we caution that our estimate of reproductive rate as a function of precipitation spanned a short period that included the most significant drought recorded for our study region. Therefore, the relative abundance of hatchlings to adults, particularly among our driest sites, may be lower than average and our rate may represent a steeper negative relationship between precipitation and reproductive rate across sites than is representative during more average periods. In more average years, reproductive rates may be higher at drier sites, which would elevate the predicted population growth rates closer to a stable rate over a larger portion of our study area and Macon County. We also caution that estimates of

negative population growth rates do not imply the absence of potential salamander habitat in those areas. We know that salamander populations occur in areas where our models predict negative population growth [though we have also identified extensively forested areas of low precipitation where *Plethodon* appear to be absent, Abernathy, Maerz, and Hepinstall-Cymerman unpublished data]. Based on the 800 m<sup>2</sup> resolution of the downscaled climate data, the resolution of our model projections is too coarse to differentiate among microhabitats within areas of generally unsuitable climate for positive salamander population growth. It is likely that areas of forest where we predict low population growth are composed of sink habitats dependent on localized source habitats such as moist coves or ravines if salamanders are to occupy those sites. Early studies noted the importance of coves and other features as key habitats for terrestrial salamanders populations in Southern Appalachian forests (e.g., Hairston, 1949). Finer resolution climate data would allow for the projection of finer resolution population models such as ours to identify local habitat features key to local salamander population persistence. Identifying areas where climates may limit population growth and persistence is necessary for understanding the importance of source habitats in population persistence, the potential for local extinctions, and evaluating the risks of habitat fragmentation to local salamander persistence. This knowledge can be used to prioritize areas and resources for conservation of salamander populations under current and future scenarios.

A second limitation of the matrix projection model was that it did not include density dependent effects. Plethodontid salamanders are known to be territorial (for a review, see Jaeger and Forester, 1993) and intense competition can occur in terrestrial salamander populations (for example, Thurow, 1976; Nishikawa, 1985; Griffis and Jaeger, 1998), therefore, we would expect to see evidence of density dependence in Coweeta Basin populations. However, based on the exponential relationship between projected population growth rates and estimated site-specific abundance (Figures 3.12 and 3.13), there is no evidence of density dependence, which, if present, should produce a logistic relationship between growth and abundance. If density dependence is not regulating population growth, then some other mechanism must be responsible for limiting abundance to different degrees across the precipitation gradient. Given the apparent dependence of terrestrial salamander survival and fecundity on moisture, the most likely regulating factor is interannual variation in precipitation patterns, however, the issue of density dependence remains an outstanding uncertainty in our understanding of Plethodontid population dynamics.

Matrix projection models are only one way to approximate the realities of wildlife population dynamics, so further research in this region should seek to validate model projections. The best way to validate the projections of our model would be to conduct salamander sampling at a wide variety of previously unstudied locations in the county to assess whether the estimates abundance and stage structure are consistent with predictions. Such an endeavor could also consider large contiguous forests versus remnant or regenerated forest fragments, which may reveal interactions between climate-driven effects on population growth and habitat fragmentation effects on source-sink and metapopulation dynamics.

Long term and spatially extensive studies require significant investments of time and effort, but as we have shown, long term data is essential to rigorous mechanistic understanding and estimation of the links between environmental variables and wildlife population dynamics. These links permit us to project population dynamics under a variety of future change scenarios to make predictions about population responses to key processes, such as climate change, affecting conservation of plants and wildlife worldwide. Mechanistic, predictive models are critical tools to better understand the dynamics of wildlife populations and can provide key insights about how best to manage sensitive and influential species, and development of these models is an important part of wildlife conservation planning.

We thank the USDA Forest Service Coweeta Hydrologic Laboratory for use of daily precipitation data collected long-term near our capture-mark-recapture sites at Rain Gauge 55, and in particular, Chelcy Miniat and Patsy Clinton for approving this data usage and processing the raw data.

## Figures and Tables

**Table 3.1.** Vital rate estimates and equations used in the stage-based matrix population model of *Plethodon* in western North Carolina. Survival rate equations are raised to the thirteenth power because the original equation calculates 28-day survival and there are thirteen 28-day units in one year. In these equations, 'p' is mean daily precipitation, and 's' is total precipitation over the 7-day period prior to count sampling occasions.

	Rate or equation	Standard deviation
Annual hatchling survival	$(0.993 / (1 + e^{-(2.313 + 0.209^*p)}))^{13}$	0.0130
Annual juvenile survival	$(0.996 / (1 + e^{-(2.806 + 0.209^*p)}))^{13}$	0.00820
Annual sub-adult survival	$(0.997 / (1 + e^{-(3.215 + 0.209*p)}))^{13}$	0.00553
Annual adult survival	$(0.998 / (1 + e^{-(3.787 + 0.209^*p)}))^{13}$	0.00316
Reproductive rate	$0.00217 * e^{(0.957*s)}$	0.430

**Table 3.2.** Structure of the stage-based matrix model used to examine and project estimated vital rates for *Plethodon* in western North Carolina. In the body of the table, f stands for fecundity and is equal to the reproductive rate we calculated from hatchling and adult abundance estimates, while the  $\varphi_x$  are age specific survival estimates. Equations used in the model to calculate these rates are listed in Table 3.1.

	hatchlings	juveniles	sub-adults	adults
hatchlings	0	0	0	f* qa
juveniles	$\phi_h$	0	0	0
sub-adults	0	φj	0	0
adults	0	0	$\phi_{sa}$	$\phi_a$

**Table 3.3.** Results of the sensitivity analysis of the stage-based matrix population projection model for *Plethodon* in western North Carolina. These results indicate the most sensitive and elastic rate is adult survival, but that reproductive rate, and hatchling survival to the juvenile stage are also important aspects of *Plethodon* population dynamics.

Vital rate	Sensitivity	Elasticity
Adult survival	0.595	0.460
Hatchling survival	0.226	0.135
Reproductive rate	0.194	0.135
Juvenile survival	0.191	0.135
Sub-adult survival	0.174	0.135



**Figure 3.1.** Regional map of 30-year mean daily precipitation, with Macon County, North Carolina, and the Coweeta Basin in one of the wettest areas in the Southern Appalachians.



**Figure 3.2.** Map of Macon County, North Carolina, showing 30-year mean daily precipitation and a soil moisture index. The Coweeta Basin sits in the wettest area of the county.



**Figure 3.3.** Map of capture-mark-recapture, fecundity, and count data collection sites within the Coweeta Basin. The CMR sites are located at the base of steep slopes in the Ball Creek drainage. The soil moisture index layer (created after Iverson et al., 1997) in combination with the 30-year mean precipitation layer (The PRISM Climate Group, 2012) show that these sites are located in an area that both receives high levels of annual precipitation and significant soil water from surrounding areas which are higher in elevation (water movement through the soil layers is described by Hewlett, 1961). While it appears collection of females for the fecundity study occurred at the same locations as the repeated count sampling, in reality, we collected females in the general vicinity of plots used for count sampling, and never removed individuals found within 100 meters of those plots.



**Figure 3.4.** Average nightly salamander captures, which are indicative of relative activity levels, calculated for each month of the year correlate closely with 30-year mean monthly temperatures. Capture data is from the CMR plots, sampled between 2010 to 2017 (black line). Temperature data comes from The PRISM Climate Group (2012) (gray line).



**Figure 3.5.** von Bertalanffy growth curve for known-age, individual marked *Plethodon* at our CMR sites in the Coweeta Basin. Age is counted in months assuming hatching occurs in August. Asymptotic size is approximately 73 mm SVL. We did capture animals as large as 87 mm SVL, but these individuals were marked as adults so they could not be aged reliably and therefore, were not included in the growth curve analysis. The equation for this curve is  $S = 73.103 * e^{(-0.0280*(A+3.729))}$ , where S is snout-vent-length in millimeters, and A is age in months.



**Figure 3.6.** Diagram of the female reproductive cycle based on observed egg sizes at specific dates for *Plethodon* in western North Carolina. The outer orange ring tracks the month of year through two full years, the blue ring shows the approximate timing of reproductive cycle activities, and the inner green ring lists the range of follicle diameters corresponding to each point in the cycle. These salamanders are not actually obligate biennial breeders, instead they are capital breeders, producing a clutch of eggs when the right time of year to deposit eggs comes around and they have enough bodily resources to commit to the energetic costs of egg production and parental care during the brooding process. Therefore, this diagram does not represent an absolute reality, but is instead the interpretive model of our observations which we used in developing the regression function to predict final clutch size.



**Figure 3.7.** Size-class-specific 28-day survival estimates produced by the Bayesian model from *Plethodon* CMR data collected from 2010 to 2017. Survival is plotted against mean daily precipitation during the interval over which each survival value was estimated. Plot 'a' shows the estimates and 95% credible intervals for hatchlings, plot 'b' juveniles, plot 'c' subadults, and plot 'd' adults.



**Figure 3.8.** Twenty-eight-day detection probability estimates produced the Bayesian model of *Plethodon* CMR data from 2010 to 2017. Detection probability increases with total precipitation over the 7-day period prior to each sampling occasion, for all four size classes. Plot 'a' is hatchlings, plot 'b' is juveniles, plot 'c' is sub-adults, plot 'd' is adults. Gray regions represent 95% credible intervals.



**Figure 3.9.** Snout-vent-length-specific detection probabilities for *Plethodon* populations at the CMR sites in the Coweeta Basin. We predicted detection probabilities for four snout vent lengths, each representative of one size class. White represents hatchlings, light grey juveniles, dark grey sub-adults, and black adults. The exponential regression line is described by the equation  $p = 0.0381 * e^{(0.0241*S)}$ , where p is detection probability and S is snout-vent-length. The R<sup>2</sup> value for this regression is 0.9726. Overall, detection probability increases with snout-vent-length.

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**Figure 3.10.** Relationship between final clutch size and snout-vent-length for *Plethodon* in western North Carolina. As predicted by the multivariate regression analysis of observed follicle count on snout-vent-length, date of observation, and mean follicle diameter. The left-hand plot shows the predicted relationship between final clutch size and snout-vent-length for all observed female salamanders. The right-hand plot is a histogram showing the frequency with which each final clutch size was observed. We used this set of predicted clutch size values to calculate mean clutch size for the Coweeta Basin population. Because most observations came from females collected in the wettest parts of the Basin, this clutch size estimate is probably descriptive of stable or growing populations.



**Figure 3.11.** Mean projected *Plethodon* population growth rates for the Coweeta Basin. Precipitation scenarios include: the 30-year mean daily precipitation value applied to every year, and twelve combinations of 24, 32, or 50% probability of 5, 15, 25, or 35% drier conditions representing a wide range of drought intensity and severity combinations. Black pixels indicate the location of non-forest land cover.



■ adults ■ subadults ■ juveniles □ hatchlings

**Figure 3.12.** Correlation between the magnitude of projected population growth rates and estimated abundance at 20 count data collection sites located across the Coweeta Basin. These plots were sampled from 2016 to 2017. The population growth rate projections were made under the 30-year mean precipitation with no drought years scenario. Pie charts at each count data collection site show the estimated size-class-specific abundance proportions of the four size classes. The size of pie charts indicates the total abundance estimated at the site. Black pixels represent non-forested areas.



**Figure 3.13.** Plot of estimated abundance against mean projected population growth rate for the *Plethodon* count data collection sites in the Coweeta Basin. Pie charts show the proportion of total abundance made up by each size class. The color codes are: adults = black, sub-adults = dark grey, juveniles = light grey, hatchlings = white. The exponential regression line equation is  $A = 0.0004 * e^{(10.625*\lambda)}$ , where A is abundance and  $\lambda$  is mean projected population growth rate. The regression has an R<sup>2</sup> value of 0.819.



**Figure 3.14.** Reproductive rate for *Plethodon* in western North Carolina increased exponentially with annual mean daily precipitation. We calculated reproductive rate estimates from estimates of size-class-specific abundance across the natural precipitation gradient in the Coweeta Basin. The black line is an exponential regression, described by the equation  $R = 0.00217 * e^{(0.957*P)}$ , where *R* is reproductive rate, and *P* is annual mean daily precipitation in millimeters. The R<sup>2</sup> value of the exponential regression was 0.708.


**Figure 3.15.** Mean projected *Plethodon* population growth rates for the extent of Macon County, North Carolina. Precipitation scenarios include: the 30-year mean daily precipitation value applied to every year, and twelve combinations of 24, 32, or 50% probability of 5, 15, 25, or 35% drier conditions. While mean population growth rates do decline as simulated droughts increase in frequency and intensity, none of these scenarios produced mean population growth rates less than 1.0.



**Figure 3.16.** Mean projected *Plethodon* population growth rates for the extent of Macon County, North Carolina, with non-forest land cover. Precipitation scenarios include: the 30-year mean daily precipitation value applied to every year, and twelve combinations of 24, 32, or 50% probability of 5, 15, 25, or 35% drier conditions. While mean population growth rates do decline as simulated droughts increase in frequency and intensity, none of these scenarios produced mean population growth rates less than 1.0.



**Figure 3.17.** Stable population growth isoclines for *Plethodon* in western North Carolina. The black dot represents the pair of mean adult and hatchling survival rates we used in the Leslie matrix model, the error bars are the standard deviations of those rates. Each isocline represents a different value of reproductive rate, as calculated from abundance estimates, from 0.2 to 1.6.

### CHAPTER 4

# HOW DO LOCAL STAKEHOLDER PERCEPTIONS OF STEEP SLOPE DEVELOPMENT COMPARE WITH PERSPECTIVES OF THE SCIENTIFIC COMMUNITY? A CASE STUDY FROM THE SOUTHERN APPALACHIAN MOUNTAINS <sup>1</sup>

<sup>&</sup>lt;sup>1</sup> Howard, J.S. To be submitted to *Southeastern Geographer* 

#### <u>Abstract</u>

Natural systems and human systems are reciprocally connected through flows of energy and materials and by disturbance regimes. Consequently, efforts to understand and manage natural systems that do not consider human social values and perspectives can be ineffective in the long-term and potentially create conflict that can accelerate destruction rather than conserve natural resources. In the rapidly exurbanizing southern Appalachian region, steep mountain slopes are being developed for homes with scenic views. The scientific community has been concerned about the ecological and human safety effects of steep slope development for many years, however, it is residents and local conservation organizations in mountain communities who make up the largest and most diverse stakeholder group affected by steep slope development. I used targeted interviews, archival research, and a participatory mapping study to try to understand how local stakeholder values compare with that of the scientific community on issues surrounding the process of steep slope development. Archival research and interviews indicated that local stakeholders are more concerned about the economic impacts of steep slope development and its regulation than they are about ecological impacts or safety. All participants in the mapping study were exurbanites, the same demographic that is driving processes such as steep slope development through consumer demand. Surprisingly, participants consistently applied conservation-oriented land uses to higher elevations, and development uses to lower elevations, suggesting a possible cognitive disconnect between the home sites they purchase, and a desire to limit development on steep slopes.

#### **Introduction**

The coupled human and natural systems (CHANS) perspective is based on the understanding that natural systems and human systems are reciprocally connected through flows of energy and materials and by disturbance regimes (Alberti et al., 2011). The idea of reciprocal connection is key conceptually: changes in human systems necessarily produce responses in the natural systems to which they are coupled, and vice versa. Consequently, efforts to understand and manage natural systems that do not consider human social values and perspectives can be ineffective in the long-term and potentially create conflict that can accelerate destruction rather than conserve natural resources. For example, in Madagascar, top-down patterns of natural resource governance consisted of total bans on slash and burn agriculture for over a century. Native people relied on this subsistence farming method for their livelihoods and perceived fire bans as an attack on their traditional way of life as well as a threat to their survival. For them, burning the forests became an act of resistance and rebellion, thus, conservation efforts that disregarded local perspectives resulted in increased loss of sensitive forest resources (Kull, 2002; Raik, 2009).

Many effective methods exist for learning about stakeholder values and perspectives. Targeted interviews seek out individuals from specific backgrounds who possess key knowledge about the system, from social, cultural, ecological, or other perspectives. Archival research involves data collection from publicly available sources inherent to the community of study, and can include newspapers, online news sources, and public records such as court proceedings, among other artifacts. Participatory mapping can be thought of as a spatially explicit interview process that elicits individuals' values and perspectives on land ownership or land uses. Participatory mapping is commonly used to collect stakeholder perspectives for community planning, and wildlife and land management efforts (examples in Beverly et al., 2008; Eadens et al., 2009; Fagerholm and Käyhkö, 2009; Dwamena et al., 2011; Cox et al., 2014).

The southern Appalachian Mountains of western North Carolina, a topographically complex region with high endemism and biodiversity, represents an important example of a coupled human-natural system. The Appalachians are among the most ancient mountain chains in the world and have served as region of high species radiations during warm episodes (Vieites et al., 2007), and as biodiversity reservoirs during repeated glaciations. These processes have resulted in both high levels of endemism and the presence of many range margin species that generally occupy more northern latitudes (Pittillo et al., 1998; Pickering et al., 2003; Gragson and Bolstad, 2006b; Scott, 2006; Kozak and Wiens, 2010). In the Southern Appalachians, complex montane topography creates steep environmental gradients and high microclimatic heterogeneity which are buffered against fine scale climate variation by forest land cover (Gragson et al., 2013). Ecologists recognize that these steep climate gradients and finer-scale habitat mosaics allow for high densities of species across the region. Additionally, the Southern Appalachian region serves as a critical water source for the southeastern US (Weidner and Todd, 2011). Thus, the steep, higher elevation, forested slopes of Southern Appalachia are a key conservation priority for biodiversity and ecosystem services.

Southern Appalachia also has a rich human history and is a region of rapid anthropogenic transformation. The forests and rivers make the region a recreation destination for residents of nearby metropolitan centers, and thereby drive a substantial tourism economy (Pickering et al., 2003). Human settlements including intensive agriculture, have been a dominant and continuous feature of the river valleys since at least AD 800, with temporary hunting camps established on mountain slopes (Gragson and Bolstad, 2006b). Permanent home building on slopes, however, has occurred in just the last sixty years, as residents from surrounding cities began seeking second homes and retirement properties in this scenic rural landscape (Wear and Bolstad, 1998; Webster et al., 2012). The process of exurbanization, the movement of urban dwellers to rural areas (Egan and Luloff, 2000), has created a market for properties with mountain views and, therefore, pressure to develop and build on steep slopes.

Landslides are a relatively common occurrence in the region (Pittillo et al., 1998), and an issue of high social concern linked to steep slope development. Soil saturation by heavy rains is the usual catalyst for landslides in the region and elsewhere (Neary and Swift, 1987; McCandless, 2010b; Lewis, 2014; Bogaard and Greco, 2016; Gill and Malamud, 2017). Historically, because people did not build on steep slopes, landslides were viewed as a relatively limited threat to human safety (Gragson and Bolstad, 2006b). However, Wooten et al. (2017) reports that 89% of landslides in the region between 1990 to 2016 happened on slopes modified by human activities, and that slides on modified slopes were triggered by less intense rainfall events than slides on unmodified slopes. The frequency of heavy precipitation events is expected to increase with climate change, which has led to a forecast of increasing steep slope landslides in the region (Band et al., 2012).

Slope destabilization also has significant ecological consequences as it can result in erosion and sedimentation of streams (Douglass, 1975; Radeloff et al., 2010), which can severely reduce water quality (McNulty and Sun, 1998) and reduce habitat suitability for aquatic organisms (Price and Leigh, 2006; Cecala et al., 2018). Despite these risks, zoning and land use regulations are limited and often unpopular in Southern Appalachian communities (Gragson and Bolstad, 2006a). For example, Macon County, North Carolina experienced intense conflict over steep slope development regulations drafted by the County Planning Board in 2011 (McCandless, 2011a). Due to opposition from many local officials and some individuals in real estate and home construction industries (McCandless, 2011c; 2011f), the proposed ordinance was ultimately tabled, landslide hazard maps produced by the North Carolina Geological Survey were removed from the County Planning Office website (McCandless, 2010a; 2011a), and development of steep slopes in Macon County remains almost completely unregulated today (for example: Macon County Soil Erosion and Sedimentation Control Ordinance 2008; Macon County Subdivision Ordinance 2013).

The scientific community has been concerned about the ecological and human safety effects of exurban development, including road and building construction on steep slopes, for many years (for example: McNulty and Sun, 1998; Cho et al., 2005; Chamblee et al., 2009; Bauer et al., 2012; Webster et al., 2012; Wooten et al., 2017). However, it is residents and local conservation organizations in mountain communities who make up the largest and most diverse stakeholder group affected by steep slope development. Additionally, they are the individuals and groups whose values are likely to have the greatest impact on western North Carolina's future through on-the-ground decisions about land use and conservation (examples in Giegerich, 2016; Gilbert, 2016; Hanchett, 2016). I wanted to understand how local stakeholders perceive the potential risks and benefits of steep slope development, and how their perceptions compare to the research priorities of the scientific community working in the region. I used a combination of archival research, targeted interviews, and participatory mapping to compare the perspectives and values of stakeholders on the issue of steep slope development in one western North Carolina county.

#### <u>Methods</u>

*Study area* – I focused this study on Macon County, North Carolina, a rural community with two major towns, and a resident population of approximately 34,000 people (United States Census Bureau, 2016b), located in the Blue Ridge Physiographic Province. The county is 520 square miles, of which 57.9% is privately owned, 41.2% is owned by the USDA Forest Service within the Nantahala National Forest, 0.503% is owned by the State of North Carolina, and 0.322% is owned by the County, the Town of Franklin, or the Town of Highlands (Hall and Hall, 2010).

*Archival research* – I use this term broadly to describe several methods of collecting information about recent (approximately within the last 10 years) land use conflicts. The primary source was the Franklin Press newspaper, which has a readership of 3900 (The Franklin Press Subscriptions Desk, 2017). This periodical is an effective clearing-house for local news, and because Macon County is a rural community with limited internet access, the paper still serves as an important information source for many residents. Back issues of the paper are not available online, so I relied on the collection of physical copies maintained by the Macon County Library in Franklin, NC. I also reviewed back issues of the Cherokee One Feather, the official newspaper of the Eastern Band of Cherokee Indians, which is published in Cherokee, NC and available online, and has print readership of 1400 and approximately 30,000 website views per week (McKie, personal communication).

I sorted all collected articles into broad topical categories based on the central theme of each article. Categories focused on natural resources, social, and economic issues and perspectives surrounding land use and development. Categories included Forest Service management of National Forests, Wildlife Resources Commission management, State Game Lands, Wilderness Area designation, invasive species, tourism (importance, impacts), friction between locals and newcomers, poverty and economic problems, reports of environmental destruction, disputes over climate change, land protection efforts, farming and agricultural issues, development and land use and community planning, anti-regulation sentiments, perspectives on fracking, regulation of flood plain development, and steep slope development (issues/impacts/perspectives).

Because I decided to focus on the most populous of these categories, steep slope development, I added a secondary coding system to quantify the frequency with which specific concerns about steep slope development were expressed by the community. Codes included: economic impacts, real estate market impacts, emergency services impacts, tourism impacts, aesthetic concerns, water quality concerns, ecological concerns, concerns for/impacts of naïve newcomers, negative impacts (usually of proposed regulation) on development, anti-regulation sentiments, evidence or claims of local officials acting in self-interest, private property rights, and distrust of science. I developed this list from the artifacts themselves, not *a priori*.

*Interviews* – Interview subjects were identified by Dr. Nik Heynen of the Coweeta Listening Project at the University of Georgia, given his experience conducting social science research in Macon County. Interviewees were members of the conservation, land use planning, and scientific communities who were, or had been, employed by a conservation organization or a state agency, or who had served in public office. I conducted interviews between February 2015 and December 2017. Each interview lasted 30 to 60 minutes and was open ended: the interviewer had a list of questions (Table 4.1), but interviewees were notified that they could decline to answer any question and were encouraged to expand on questions about which they had more information to share. I focused on past and present conflicts over land use, and asked questions about the social background of those conflicts. To quantify the relative importance of these conflicts, as perceived by interviewees, I tracked the order in which conflicts were discussed in each interview. I assumed that the sooner a topic was broached, the more important it was to the interviewee. Interviewees were precluded from participatory mapping activities.

I decided that maintaining the anonymity of interviewees was important given the sensitive nature of opinions they expressed or observations they shared about land use conflicts, and the small size of the Macon County community. I will not publish complete interview transcripts, and the citations of the interviews presented in this paper do not include interviewees' names. Additionally, I have maintained interview transcripts as electronic files in which interviewees' names have been redacted.

*Participatory mapping* – I limited participants to full- or part-time residents of Macon County, who were over age 18. Part-time residents were defined as persons who own or rent property in the county but do not live there year-round, though I did not ask for proof of residency status. I solicited participation in several ways, and our strategy evolved over time. Mainspring Conservation Trust, a local land trust, shared an invitation to participate in the mapping project with their volunteer roster. Staff at the Highlands-Cashiers Land Trust shared an invitation with specific individuals in the Highlands area (south-eastern Macon County) who they believed would be interested in the project. I advertised participatory mapping events in guest editorials written for two local newspapers and posted notices in a local event calendar available on the website for the Macon County Public Library, where several events were held. Librarians also put up flyers for mapping events at the library. The Coweeta Listening Project, an organization based at the University of Georgia and focused on conducting sociological research in Macon County, shared contact information for local social groups which I approached directly.

I held five mapping sessions between February 2015 and December 2016, and each lasted approximately one hour. When participants arrived at the mapping session, I offered them refreshments, and invited them to examine large scale maps of the county posted on the walls while waiting for the presentation to start. At the time set for the session to begin, I provided each participant with a hand-out containing information and helpful resources intended to supplement the presentation and provide a way to find out more about the topics covered. The presentation lasted twenty minutes, and described the factors affecting biodiversity within the region; the regulatory framework at the federal, state, county, and municipal levels; a list of actions residents can take to influence land use in their community; and a list of management strategies land owners can use to improve wildlife habitat quality in their own backyards. I dedicated the rest of the time to the mapping activity.

I asked participants to select their top ten priority uses for forested land from a predetermined list (Table 4.2), and then rank them from most to least important. Participants selected one (or more) of eleven sub-maps of the county, each map consisting of a single township (example in Figure 4.1). Most townships function as units with their own community groups and are of a manageable size for a single person to analyze spatially in a short period of time. On the front of the map, participants wrote down their five, highest-priority land uses, and color coded them with markers. Using those five colors, they marked the places they wanted to see specific land uses prioritized. On the back of the map, participants completed a short demographic survey in which they were asked about their place of origin, and their racial, educational, and financial background. During the activity, I described the step to be completed

and then actively facilitated by checking in with participants and answering questions. I monitored the progress of the room and continued to the next step only when most of the participants had completed the first step. After the process was completed, I invited participants to add their email address to a mailing list to receive updates about the progress of the research. No personal identifiers were associated with the maps or surveys to avoid any risk of reputation damage to participants based on the information they provided. Mapping event participants could only participate once and could only submit one completed map per township and one demographic survey.

I georeferenced and digitized maps completed in participatory mapping sessions using the GIS program ArcMap (Esri Inc., 2016). I created a separate shapefile was created for each map and maintained demographic survey responses as metadata in the shapefile.

For each township with completed maps, I made the following comparisons between all possible participant pairs within a township:

(1) To determine whether participants who chose the same land use agreed about where that land use should be located within the township, I calculated the amount of overlap between the areas each person assigned to that shared land use.

(2) To determine whether participants agreed about the uses that should occur at high elevations where steep slopes are prevalent, I calculated the average elevation of areas assigned to each land use selected by each participant and compared the results.

(3) To determine whether participants agreed about the uses that should occur in forested areas, I calculated the acreage of forested land cover included in the areas assigned to each land use selected by each participant and compared the results.

(4) To determine the apparent importance of land uses across townships, for each participant I calculated the ratio of acreage assigned to each land use to the total acreage of the township, which produced a value I could compare across townships.

(5) To determine whether participants' land use designations on the physical landscape matched their initial land use valuation rankings, I calculated total acreage assigned to each land use for each participant and compared these area values to the initial rankings.
(6) To examine how human land use values intersect with predicted locations of suitable salamander habitat (Chapter 3), I overlaid a composite map of the land use assignments made by all participants with on top of the map of suitable habitat.

#### <u>Results</u>

*Archival research* – I examined every issue of the bi-weekly Franklin Press newspaper from January 2010 through July 2017, and every story posted in the 'news' category at the Cherokee One Feather newspaper website from January 2010 through February 2018. In total, I collected 494 articles, letters to the editor, survey results, and anonymous quotes related to land use directly, and to the social and ecological issues surrounding land use. The percentage of articles in each category was as follows: 23.3% steep slope development (issues/impacts/perspectives), 16.0% development and land use and community planning, 10.7% perspectives on fracking, 7.9% land protection efforts, 6.3% Forest Service management of National Forests, 6.1% Wilderness Area designation, 4.0% reports of point-source pollution, 3.6% regulation of flood plain development, 3.4% Needmore State Game Lands management, 3.0% anti-regulation sentiments, 2.8% disputes over climate change, 2.6% tourism (importance, impacts), 2.0% regional poverty and lack of employment opportunities, 1.8% friction between locals and newcomers, 1.0% farming and agricultural concerns, 0.6% North Carolina Wildlife Resources Commission activities, and 0.6% invasive species.

Within the steep slope category, I assigned from zero to six secondary codes per artifact. Artifacts that received no secondary codes contained information about steep slope issues, but not evidence about local perspectives on the impacts of steep slope development. The most commonly assigned code was economic impacts (34 times), followed by local officials acting in self-interest (25 times), anti-regulation sentiments (19 times), and private property rights (17 times). Ecological concerns appeared in seven artifacts, and water quality concerns appeared in only four artifacts (Figure 4.2).

*Interviews* – I attempted to interview five individuals but was only able to schedule interview time with four of them. One person provided a follow-up interview to expand on a specific topic, the other three were interviewed once. One interviewee was born and raised in Macon County and was a descendent of a multi-generational farming family; two were current residents who were not born in the County and did not grow up there; and the fourth had lived and worked in the county in the early 2000s but was neither born there nor currently living there. One interviewee works for a non-governmental conservation organization based in the county; one works for a university in the region and is involved in natural resources based scientific research in the county; one served as a county planner in the past and still works in a planning capacity as a consultant for a regional non-profit based in the county; and the fourth worked for a nongovernmental conservation organization the seconty resident, but now lives and works elsewhere. While the interview questions did not specifically address steep slope development, all four interviewees brought this topic up as one of the primary sources of conflict over land use, and land use regulation in Macon County. When asked to describe important land use conflicts in the recent past, two interviewees brought up steep slope development first. The third interviewee discussed six other topics before mentioning steep slope development, while the fourth discussed steep slope development second. Two interviewees came back to this topic repeatedly during their interviews, one returned to it three times, the other returned twice. Interviewees also articulated the presence of several 'tension points' between certain values which have affected the debate over regulation of steep slope development: the perceived push-pull between land use regulation and economic growth (one interviewee), between land use regulation and private property rights (two interviewees), and between land use regulation and development interests (two interviewees).

*Participatory mapping* – I held five mapping sessions between February 2015 and December 2017. In total, seventeen individuals participated in a mapping session and completed a map of one or more townships, yielding twenty-three maps in total (Figure 4.3). Macon County consists of eleven townships, and the number of maps completed per township ranged from zero to four, with no completed maps for two townships (Figure 4.4).

The results of the demographic survey indicated that mean income among participants was approximately \$58,000 per year, however 29% of participants had an annual income over \$100,000. Census data indicates mean household income in Macon County is \$56,298, and 12% of households report income over \$100,000 (United States Census Bureau, 2016a). Sixty-four percent of participants were over 60 years of age, while only 35% of county residents are over 60 (United States Census Bureau, 2016b). All participants who completed surveys identified themselves as white. The county's population is 93% white (United States Census Bureau, 2016c). None of the participants were born in Macon County, and average years of residence was 13 (range: 0 to 64). According to Evans (2013), based on the number of Macon County landowners filing out-of-state taxes in the 2012 tax record, about 50% of landowners are from places outside the county. Thus, participants in this mapping project made up an older, wealthier, whiter, less 'native' (where natives are those born and raised in the county) subset of the county's population. I found that eliciting participation in this project was challenging despite the multiple channels through which I advertised mapping events and the different locations at which I held events.

Participants only rarely agreed exactly in the land uses they assigned to specific areas within the same township, despite often prioritizing some or even all of the same land uses. However, they often assigned commensurable uses to the same areas within the same township. Commensurable uses are defined here as those that would likely or could possibly occur in the same location. For example, national forest and extractive recreation are not identical, but they are commensurable uses since hunting, fishing, and collecting of biotic and abiotic materials is allowed in national forests. Overlap of incommensurable uses also occurred, for example, agriculture and residential development are incommensurable because farming would be impossible in a subdivided suburban neighborhood. Across the nineteen within-township participant pairs, one pair had two agreement overlaps, in which the overlapping assignments were for exactly the same land use, and nine pairs had a single agreement overlap. Among these pairs with agreement overlaps, the ratio of overlapping area to area assigned to the uses making up the overlap from 0.00443 to 0.427 (Table 4.3). Fifteen pairs had at least one, and up to

four, commensurable overlaps, in which the overlapping assignments were for non-identical but commensurable land uses. Among these pairs with commensurable overlaps, the ratio of overlapping area to area assigned to the uses making up the overlap ranged from 0.000342 to 0.309 (Table 4.4). All but three pairs had at least one incommensurable overlap, in which the overlapping assignments were for non-identical and incommensurable land uses, and one of these pairs had no overlaps of any kind. Across all nineteen pairs, the ratio of overlapping area to area assigned to the uses making up the overlap ranged from 0.00189 to 0.191 (Table 4.5).

Some participants assigned multiple uses to one area which made disagreements more difficult to assess. For example, participant 13 (P13) and participant 8 (P8) both assigned land uses in Highlands Township, but P13 assigned some areas three uses: 'preserve – public,' 'recreation – passive,' and 'recreation – extractive,' and one of these areas overlapped with an area P8 had designated 'recreation – passive' (Figure 4.5). In this case, one of P13's use assignments agreed with P8's single use assignment, but the other two uses P13 assigned did not. As P13's two non-identical uses would be suitable companion uses to P8's assignment, I determined this to be a commensurable overlap.

The average difference between mean elevation of areas assigned to the same land use, but not to the same location, by participant pairs in the same township was 130 meters (range: 11 to 504). On average, participant pairs assigned residential and recreational development to an elevation of 832 meters (range: 657 to 1161). Nature preserve without public access was assigned to the highest mean elevation of 1036 meters (range: 849 to 1223). The lowest mean elevation, 647 meters (range: 624 to 671), described areas assigned to the wild and scenic river designation, probably because rivers lie in the lowest parts of valleys (Figure 4.6 and 4.7). The average difference between percent forest cover of areas assigned to the same land use by participant pairs in the same township was 16.3% (range: 0.285 to 50.3%). On average, participant pairs assigned development to areas that were 91.8% forested (range: 85.0 to 90.4%). This was the highest mean percent forest cover of any assigned land use. The lowest mean percent forest cover, 70.5% (range: 40.7 to 91.0%), described areas assigned to nature preserves with public access (Figure 4.8).

Across participants and townships, the three land uses with the greatest percentage of total township acreage assigned were national forest: 38.6% (range: 6.05 to 56.9%), nature preserve with public access and passive recreation: 32.4% (range: 1.95 to 62.8%), and development of unspecified variety: 30.4% (range: 30.4 to 30.4%). The smallest percentage of total township acreage was assigned to commercial development: 0.540% (range: 0.436 to 0.348%) (Figure 4.9). However, the uses selected the greatest number of times were passive recreation (11 selections), conservation easement (10 selections), and nature preserve with public access (10 selections), while the following uses were chosen only once: Native American tribal ownership, nature preserve with unspecified access, nature preserve with public access and both passive and extractive recreation, recreation of unspecified variety, national forest with passive recreation, planted and pasture agriculture, national wildlife refuge, and development of unspecified variety. Most of these singly-designated uses are multiple use designations and designations in which the participant failed to specify the variety, or sub-type, of the use.

Only two participants' initial land use valuation (ranked in importance from 1 to 5) matched the ranking I gave to their land uses based on the number of acres assigned to each use, while four participants had no match between initial valuation ranking and my ranking by

number of acres assigned. Across participants, rank by acres assigned was different from valuation ranking 68.4% of the time.

I overlaid the salamander habitat map with the composite map of all participants' land use assignments and found that participants typically almost universally assigned conservationoriented land uses to the Coweeta Basin area, and the vicinity of the town of Highlands which are the two places projected to be able to support stable or growing salamander populations (Figures 4.10 and 4.11).

#### Discussion

My archival research suggests there is coarse-scale agreement between local stakeholders and published scientific research as both are concerned about the impacts of steep slope development, but a finer-scale disconnect in terms of the primary issues for stakeholders and the risks as reported by scientists. While water quality and habitat degradation, as well as human safety are common themes in the peer-reviewed literature on steep slope development, my archival data suggests stakeholders in Macon County are more focused on other issues related to steep sloped development. The four most commonly encountered through my archival research are: the potential economic impacts of regulating steep slope development, the possibility that local officials stopped efforts to pass regulation because they stood to gain financially from unregulated development, the mentality of resistance to regulation on principle, and the importance of protecting private property rights.

Interviews supported these findings, as interviewees pointed to two values and one powerful stakeholder group at the root of the conflict in the county-wide debate over steep slope development regulation: increasing economic growth, protecting private property rights, and influential or powerful individuals with development interests. Interviewees did not cite the ecological or water quality effects of steep slope development as primary concerns in public discourse on this issue, instead, two of them stated that garnering support for conservation and regulation in the county requires arguments crafted around the economic costs of not protecting land or not regulating development, instead of focusing exclusively on ecological impacts. One possible reason for stakeholder focus on economic growth is the relative poverty of the region compared to the rest of the country. American Community Survey 5-year Poverty Status data estimate that in 2016, 18.4% ( $\pm 2.1\%$ ) of Macon County's residents were living below poverty level, compared to 15.1% ( $\pm 0.1\%$ ) nationally (United States Census Bureau, 2016e; 2016f).

Although the participatory mapping study engaged only participants from a single demographic group (exurbanites who are white, older, generally wealthier, generally better educated), this particular group has already impacted the county in highly significant ways through consumer demand for homes built on steep mountain slopes, for recreation-related natural amenities, by increasing demand for emergency services and critical infrastructure such as wastewater treatment facilities, roads, etc. The finding that participants generally avoided assigning development uses to high elevation areas, where steep slopes are common, suggests a possible disconnect between where exurbanites want to build their own homes, and where they think homes should be located when faced with the challenge of making spatially explicit land use assignments.

Participants also rarely assigned acreage quantities to land uses in a way that reflect the way they ranked their chosen land uses prior to drawing on maps. Most participants assigned more acres to uses that not listed as their number one preferred land use, which suggests that the way people think about land use in the abstract is disconnected from the way they value land

when they must apply uses to specific places in a real landscape. Several participants stated that they chose land uses based not only on what they hoped would happen but also on a desire to have some control over future locations of the land uses they found undesirable. However, not every participant with a mismatch between land use valuation and total-area-assigned to that land use expressed this strategy, so some mismatching may represent a true cognitive disconnect between the land uses participants value in an abstract sense and the land uses they value on a real landscape.

Despite their apparent lack of interest in the ecological effects of steep slope development, Macon County's property owners and other stakeholders are the individuals most likely to directly experience negative impacts resulting from degraded ecosystem functions and services. Reduced water quality and aquatic biodiversity should be areas of concern for local stakeholders, especially given their interest in economic impacts of steep slope development because the county's economy relies heavily on tourists and second home buyers who come for both scenic views and outdoor recreation opportunities, both of which rely on the maintenance of relatively pristine natural amenities. Additionally, local stakeholders are the people who will pay the price of increased risk to their lives and properties from increased landslide frequency.

Human communities should strive for sustainability, both ecological and economic, yet the focus in Macon County seems to be mostly upon the latter. This lack of concern for ecological issues may be part of a nation-wide trend toward distrust of science. As Eden (1998) describes the situation, "public irrationality about environmental science and risk" is the product of societal prioritization of expert contributions over those of lay people, which effectively removes the public from participation in most scientific debate. Directives to educate the public through outreach as part of conservation initiatives are ubiquitous, however, serving up suitablysized portions of ecological knowledge to stakeholders is not sufficient to increase trust in science and scientists. Eden (1998) notes that, "people are not passive in the face of science, they actively construct their own environmental knowledge and their own ignorance." In other words, simply exposing people to the information we think they should know is not enough. People will learn more about what they are already interested in, and they will persist in ignorance of those things they would rather not know or which they believe have no bearing on their own lives.

One strategy for dealing with this problem is initiating reciprocal forms of communication between scientists and the public. The Coweeta Listening Project was a group of researchers from the University of Georgia working in Macon County from 2010 to 2016 with the goal of integrating scientific knowledge collected at the Coweeta Long Term Ecological Research Site located in the county, with the interests and information needs of county residents (Coweeta Listening Project, 2015). Instead of holding lectures, the researchers facilitated 'translational dialogues' in which citizens were invited to ask for the information that they wanted, and then a scientist who could provide that information would prepare a presentation in response to the questions asked. This strategy was intended to build trust and increase communication between scientists and the public, and to increase public awareness of the complexities of the issues about which people already wanted to know more. This kind of twosided communication around science is one way to make scientific knowledge more relatable and accessible for the public, though the process can be slow.

Another way to accomplish resource protection goals in a place where top-down governance of natural resources is rejected by stakeholders as it has been in Macon County, is the development of trusted institutions at the local level that can better interact with the public and engage them in conservation activities. In Macon County, Mainspring Conservation Trust, a non-governmental land trust, has been working since 1997 (as the Nikwasi Land Trust and The Land Trust for the Little Tennessee prior to 2016) to promote conservation and stewardship of land in private ownership in response to rapid development in the region. The organization receives donated conservation easements from property owners, purchases and manages land, aids in protecting sites with cultural significance to people of both Cherokee and European descent, restores impaired stream reaches, engages in youth outreach through hands-on restoration and monitoring projects, and supports a citizen science stream monitoring program that has been ongoing since 1990 through the efforts of local aquatic conservation biologist Dr. William McLarney. According to project descriptions on the organization website, Mainspring has helped conserve nearly 10,000 acres of land in Macon and surrounding counties as of 2017 (Mainspring Conservation Trust, 2018a).

Mainspring was a key partner in conservation of a property known as the Hall Mountain Tract, which was purchased by the Eastern Band of Cherokee Indians with additional help from the Wilderness Society, and one of the first grants given by the US Forest Service's Community Forest and Open Space Preservation Program (McRae, 2012; Flannick, 2013; Mainspring Conservation Trust, 2018b). The Program aims to support community-based management of forest resources through grant funding, a public access requirement, and by helping the community develop a forest management plan (McRae, 2012; USDA Forest Service, 2018). Community-based resource management has been proposed in several forms and attempted with varying levels of success elsewhere in the world (examples in: Grumbine, 1994; Kellert et al., 2000b; Armitage et al., 2009). In some cases, when people depend on forest resources for their livelihoods, community management can work well to improve socio-economic issues facing local people, but can result in reduced emphasis and effort put into meeting conservation goals, though this may be less of a risk in developed counties with effective legal support for management agreements (Kellert et al., 2000a), such as those under the Forest Service's Community Forest Program.

Coupled human and natural systems are inherently complex and conducting effective conservation and management of natural resources necessarily requires us, as conservation practitioners, to understand that most systems on Earth are reciprocally connected webs of human activities and ecological processes. Strategies such as communicating science through dialogues instead of lectures, building trusted local conservation institutions, and facilitating community-based natural resource management can be effective ways to reduce the distance between ecological science and local stakeholder values.

## Figures and Tables

Table 4.1.	Example	es of inter	rview a	uestions	used.

	Sample interview questions			
1.	What are some common themes, as you see them, of land use conflicts in Macon County?			
2.	In these disagreements over land use are there certain demographic or business groups, or segments of local government that seem always to be in opposition to one other?			
3.	Are there industries or land uses in the area that seem to make people more upset than others, or that have caused environmental problems in the past?			
4.	Where do farmers and agriculture fit into conflicts over land use?			
5.	How do you think the average citizen in Macon County views timber harvest on public and/or private lands?			
6	How do you think the average citizen in Macon County views regulation of land use?			
7.	Do you think recent migrants to the county view development pressures differently than people who were born here or are the children of multigenerational local families?			
8.	Do you think recent migrants to the county are more, or less, likely to have environmentalist or conservationist values than people who were born here or who are the children of multigenerational local families?			
9.	What do you think the future looks like for Macon County in terms of land use?			

Land uses and land management regimes	Additional descriptors or allowed uses
Agriculture – planted crops	
Agriculture – pasture land	
Agriculture – intensive livestock	feedlots, fowl or swine facilities, horse farms, etc.
Conservation easement	
Development – residential	
Development – commercial	
Development – industrial	
Development – recreation	sports fields, zip line facilities, boat launches, campgrounds, parking areas, landscaped parks, etc.
Development – transportation	new or expanded highways, railroad lines and/or stations, bus stations, etc.
Indian reservation or Tribal landholding off reservation	such as land containing significant cultural resources
Mineral mining	
Rock or gravel quarrying	
Timber harvesting/logging	
Wildlife/nature preserve – public access	
Wildlife/nature preserve – closed to the public	
Recreation – passive uses	hiking, wildlife viewing, biking, camping, kayaking, swimming, horseback riding, etc.
Recreation – extractive uses	fishing, hunting, foraging, etc.
Recreation – motor vehicle	OHV/ATV, motor boats, etc.
National Forest (USDA Forest Service)	Logging – access granted through permits, Mining – prospecting/exploration claims sometimes allowed with permits, patent moratorium in effect since 1994, Grazing – most forests sell grazing rights, Timber and stone collection – allowed for residents (those with property within national forest boundaries) who have appropriate permits, Hunting/fishing/trapping – allowed by permit or license obtained from the State DENR, OHV/ATV – typically allowed on marked trails, Mountain biking/horseback riding – typically allowed on marked trails, Hiking, Camping – some forests allow camping only at designated camp sites, some areas require a permit to camp, campfires may be permitted depending on current fire risk, usually no entrance or use fees

Table 4.2. List of land uses and land use regimes used in the mapping activity.

National Park (National Park Service)	No removal of any natural products from the park, typically no collection of wood for campfires, campfires only in specific areas, typically no hunting, trapping or fishing, camping in specific areas, horses on designated trails, some motor vehicle access restrictions, many parks have entrance fees, no fireworks, no grazing
National Wildlife Refuge (US Fish and Wildlife Service)	Sightseeing, nature observation, hunting and fishing, boating, camping, swimming, water skiing, and other similar activities allowed; Most refuges have site-specific regulations
State Game Land (State of North Carolina)	Hunting/fishing/trapping – allowed with appropriate state licenses/permits and additionally a Game Lands license; Collection of bait animals, reptiles, amphibians, pinestraw, and firewood for personal use is allowed with written permission; Non-protected edible plants for personal use may be collected; Some game lands allow camping, others allow only game-related activities; Motor vehicles – allowed only on roads; OHV/ATV – only in specially designated areas
Wilderness Area designation (typically USDA Forest Service)	No commercial businesses, no motorized or mechanical transport (except in emergency situations), no temporary or permanent roads, no mining claims or patents, no buildings/structures; Prospecting for minerals, water or other resources is allowed; Grazing is allowed only where it was established prior to the effective date of the Wilderness Act; Camping typically allowed only by permit, a limited number of permits are issued during a given time period
Wild and Scenic Rivers designation (federal, state, or private ownership)	Residential development, agriculture, and recreation are allowed – no control over private land; Hunting and fishing on public land with this designation is allowed if the public land is of a type that allows hunting and fishing (for example, a national park with a wild and scenic river designation is not open to hunting or fishing because no national park allows hunting or fishing); No mining allowed on federally owned land under this designation for up to two miles from the banks of the river, on the banks, or in the riverbed; Dams cannot be built with federal support, though the designation does not affect already existing water rights

Participants	Township	acres of overlap between pairs of	total acres assigned to pairs of identical	ratio of overlap to total acres assigned
		identical uses	uses	
P5, P3	Burningtown	23	5244	0.00443
P7, P6	Cartoogechaye	0	0	0
P3, P6	Cowee	134	7418	0.0180
P3, P8	Cowee	296	7835	0.0377
P6, P8	Cowee	67	1311	0.0511
P10, P11	Ellijay	428	1659	0.258
P12, P6	Franklin	0	0	0
P13, P14	Highlands	0	0	0
P13, P8	Highlands	749	6252	0.120
P14, P8	Highlands	0	0	0
P16, P17	Millshoal	35	3918	0.00885
P17, P15	Millshoal	0	0	0
P16, P15	Millshoal	0	0	0
P4, P2	Smithbridge	284	29926	0.00950
P4, P1	Smithbridge	0	0	0
P4, P18	Smithbridge	155	28017	0.00555
P18, P1	Smithbridge	0	0	0
P1, P2	Smithbridge	0	0	0
P18, P2	Smithbridge	22286	52187	0.4270

Table 4.3. Overlaps between identical land uses in within-township participant pairs.

Participants	Township	acres of overlap between pairs of	total acres assigned to pairs of	ratio of overlap to total acres assigned
		commensurable uses	commensurable uses	
P5, P3	Burningtown	1951	13052	0.149
P7, P6	Cartoogechaye	17961	58136	0.309
P3, P6	Cowee	0	0	0
P3, P8	Cowee	596	11849	0.0503
P6, P8	Cowee	20	1860	0.0110
P10, P11	Ellijay	161	9023	0.0179
P12, P6	Franklin	295	2844	0.104
P13, P14	Highlands	0	0	0
P13, P8	Highlands	144	8657	0.0167
P14, P8	Highlands	0	0	0
P16, P17	Millshoal	0	0	0
P17, P15	Millshoal	35	174	0.199
P16, P15	Millshoal	93	3422	0.0272
P4, P2	Smithbridge	6442	33524	0.192
P4, P1	Smithbridge	1	2943	0.000342
P4, P18	Smithbridge	7698	51052	0.151
P18, P1	Smithbridge	1269	41065	0.0309
P1, P2	Smithbridge	1064	28241	0.0377
P18, P2	Smithbridge	5260	50267	0.105

Table 4.4. Overlaps between commensurable land uses in within-township participant pairs.

Participants	Township	acres of overlap between pairs of	total acres assigned to pairs of	ratio of overlap to
		incommensurable	incommensurable	total acres assigned
		uses	uses	
P5, P3	Burningtown	4145	21721	0.191
P7, P6	Cartoogechaye	4855	62582	0.0776
P3, P6	Cowee	100	3879	0.0258
P3, P8	Cowee	1459	18533	0.0787
P6, P8	Cowee	50	1956	0.0255
P10, P11	Ellijay	536	9223	0.0581
P12, P6	Franklin	0	0	0
P13, P14	Highlands	0	0	0
P13, P8	Highlands	78	10886	0.00721
P14, P8	Highlands	7	3939	0.00189
P16, P17	Millshoal	570	7506	0.0759
P17, P15	Millshoal	0	0	0
P16, P15	Millshoal	493	9910	0.0498
P4, P2	Smithbridge	1275	34029	0.0375
P4, P1	Smithbridge	0	1751	0
P4, P18	Smithbridge	3252	57284	0.0568
P18, P1	Smithbridge	491	22018	0.0223
P1, P2	Smithbridge	110	29327	0.00376
P18, P2	Smithbridge	1177	74120	0.0159

Table 4.5. Overlaps between incommensurable land uses in within-township participant pairs.



Figure 4.1. Example of a blank township map prepared for a participatory mapping activity.



Figure 4.2. Comparison of the number times each value code was applied to articles in the steep slope development category.



Figure 4.3. Map showing all land use valuations made by all participants.


Figure 4.4. Number of completed maps per township.



**Figure 4.5.** Example of overlapping use designations. Here, one participant applied multiple uses, one of which agrees with the single use applied by a second participant. I determined this case to be a commensurable uses overlap.



Figure 4.6. Mean elevation of areas assigned to the same land use, but not the same location, by participant pairs in the same township.



**Figure 4.7.** Chart showing the elevational placement of land uses on average across all participants. Uses that are commensurable with conservation are marked with green bars, and those incommensurable with conservation are marked with blue bars. Overall, the chart shows a trend toward conservation-commensurable uses being assigned to higher elevations where steep slopes occur.



**Figure 4.8.** Percent forest cover of areas assigned to the same land use, but not the same location, by participant pairs in the same township.



Figure 4.9. Mean percentage of townships acreage assigned to each land use, across participants and townships.



**Figure 4.10.** Map of Macon County, North Carolina, showing both spatially explicit stakeholder values and projected salamander population growth rates. Projected growth rates are based on the modeled response of survival and fecundity to variation in precipitation (Chapter 3). Spatially explicit stakeholder values were obtained through the participatory mapping study. Black represents non-forest land cover, while all other areas are forested. The most suitable area for salamander habitat (blue/green) appears in the lower portion of the map, a little left of center. This area also has predominantly unfragmented forest cover, and stakeholder values are mostly conservation-oriented (blue tones). The lower right corner of the map also contains suitable habitat but has a greater quantity of non-forest land cover. Stakeholder values are quite patchy in that area, but they are generally conservation oriented. The inset map shows the location of Macon County in the state of North Carolina.

## **CHAPTER 5**

## CONCLUSIONS

Understanding coupled human and natural systems requires conservation researchers and practitioners to accept and engage pluralistically with knowledge acquired through methods native to diverse academic disciplines, and through interactions with individuals and communities outside of academia. In this dissertation I collected information about both wildlife population dynamics and vital rates, and about the land use values of human stakeholders. Because both kinds of information were georeferenced, I was able to integrate this knowledge in a visual, spatially explicit way at a landscape scale. The resulting map of Macon County, North Carolina (Figure 5.1), depicts both the perceptions of a representative sample of the exurbanite population regarding land use, and the locations in the county where suitable salamander habitat exists under current mean precipitation patterns, and where it may persist under several potential future precipitation regimes. The intersections between conservation-oriented stakeholder valuations and suitable salamander habitat appear common: both large areas of suitable habitat are associated with assignments for recreation uses, national forests, wilderness areas, nature preserves and conservation easements. Stakeholders applied development and agricultural uses, the two uses least commensurable with salamander habitat, only at the margins of suitable habitat areas, not within them (Figure 5.1). The non-forest land cover layer showed that one area of suitable habitat, centered on the Coweeta Basin, appears to be situated in an area of relatively continuous forest cover. The other area, in the vicinity of the city of Highlands in the lower right

corner of the map, has a significant quantity of non-forest land cover, which reduces the amount of suitable habitat present in that area (Figure 5.1).

Local land trusts and other grass roots conservation groups in the region compensate somewhat for the regional lack of oversight of development, through land protection, conservation, and management. The map I created may serve as a useful guide for these groups in identifying conservation priorities while remaining mindful of stakeholder values and perspectives regarding land use, particularly considering that the land uses assigned by stakeholders to places I projected to contain suitable habitat for salamanders are largely compatible with salamander conservation priorities.

In Chapter 2, I reviewed the current knowledge of vital rates and population dynamics for temperate, direct-developing Plethodontinae. I showed that some published estimates of clutch size and clutch frequency may be reasonably transferrable among species when size and age at maturity and population latitude is known. This is important because it provides confidence that some vital rates can be approximated in population models when direct estimates are not available. However, I demonstrated the likely implausibility of many of the limited estimates of salamander survival and failed to identify any pattern among survival estimates in relation to size or age at maturity or study design and duration. Survival estimates varied widely among species and studies, so the fact that we found no apparent pattern across that variation suggests it may be an artifact of the logistical and quantitative difficulty of robustly estimating these rates for terrestrial salamanders. Terrestrial salamanders are abundant, but individuals have low capture probability and spend significant amounts of time in inaccessible portions of the habitat. Those high rates of temporary immigration, low capture probability, and longevity make it difficult to estimate survival rates with confidence. I advocate that future studies, which are needed for

many species and locations, should employ a robust sampling design (Pollock, 1982), should endeavor to be multi-year efforts that approximate at least time to maturity if not generation time, and should include analyses of the plausibility of survival estimates using projection matrices or comparable approaches to produce predictions which could then be tested by sampling where predictions were made. It is important that implausible estimates be challenged by investigators and not published without adequate critique.

I addressed the need for size-specific estimates of weather-dependent salamander survival. I demonstrated reasonable mean estimates and measures of uncertainty for size-specific survival dependent on mean daily precipitation. My ability to model survival and measure sensitivity to precipitation was only possible because of relatively long-term data that captured two drought events including the driest and longest drought ever recorded for our study area. Prior to this study, the longest duration study used to estimate survival was a currently unpublished, 5-year study of *Plethodon montanus* (Caruso and Rissler, in review). That study also generated size and weather dependent survival rates comparable to our estimates. Collectively, these two contemporary studies demonstrate the critical need for long-term studies to provide robust models of population responses to weather, particularly for relatively longlived species. Such studies are rare because they are time, labor and resource intensive, and generally receive little priority for research support. Nonetheless, they are essential to generating the rigorous estimates and robust models needed to predict how populations will be impacted by climate or other anthropogenic changes and for evaluating potential management actions (Jackson et al., 2009).

My mechanistic matrix population model projections suggest that many salamander populations in the county may exist in places that will not be suitable for them in the future if climate change produces increased frequency and intensity of meteorological droughts. On the other hand, some places, such as the wettest portions of the Coweeta Basin, may possess surplus population growth capacity that can absorb some projected increases in drought frequency with limited impacts on salamander population viability. Gifford and Kozak (2012) used a mechanistic model to demonstrate potential surplus capacity for energy gain by salamanders (Plethodon jordani) throughout significant portions of their range under a warming scenario. Their models suggest relatively widespread capacity for habitats to continue to support positive population growth under warmer or drier future conditions. Our projections for the Coweeta Basin, and that of Gifford and Kozak (2012) are more optimistic projections than have been put forward using correlative models that predict dramatic loss of suitable habitat for salamanders under future climate scenarios (e.g., Milanovich et al., 2010). However, we did project declining population growth rates for the great majority of places in Macon County, even under the 30year mean precipitation scenario in which no years were drier than average. The fecundity proxy we used in the projection model was calculated from size-class-specific abundance estimates made across a steep precipitation gradient, using data that was collected in 2016 and 2017. 2016 was a severe drought year, and this may have skewed the abundance estimates lower than average. Thus, our projections under the 30-year mean precipitation scenario may in fact be the equivalent of projections based on fecundity under severe drought conditions. If this is the case, then our projections under a scenario such as 25% drier conditions and 50% drought probability would be testing an extreme situation that may be far beyond the realm of possibility under future climate regimes. Increased study duration is the best way to assess whether the reproductive rates we estimated are artifacts of the bad first year of the study or an accurate approximation of salamander fecundity on average in relation to precipitation variation.

Our ultimate goal was to link projections of habitat suitability, measured by estimates of current and future population growth potential, with stakeholder priorities for land use and conservation. Towards that end, we engaged local stakeholders in Macon County, North Carolina who own land and are therefore likely to impact land use policies and practices, to identify their land use priorities in a spatially explicit framework. We found that consistent with much of the ecological research focus in the region, residents are deeply concerned about steep slope development. However, while scientific research is focused extensively on the impacts of steep slope development on ecosystem services including biodiversity, water resources, carbon sequestration, and nutrient cycling, local residents are more concerned about the economic impacts of steep slope development and regulation. Given this finding, conservation practitioners and natural resources managers may want to adjust their initial focus in dialogues with local stakeholders, as people appear most likely to respond to information addressing the economic and safety impacts of steep slope development. Nevertheless, participants in the participatory mapping study did select more preservation and conservation-oriented land uses for higher elevation areas of the county, and more development uses for lower elevation areas, which suggests that when faced with spatially explicit decision-making scenarios, stakeholders may have an otherwise unexpressed preference for protecting steep slopes. This finding suggests that the participatory mapping strategy may be particularly valuable in assessing stakeholder values as it may either be able to elicit preferences that stakeholders are reluctant to express in other ways or provide a way to identify cognitive disconnects between the way stakeholders think about land use in the abstract versus in explicit contexts.

Some of the original goals of this dissertation were not reached as originally outlined, however, the adjusted outcomes of the project proved insightful in surprising ways. In particular, I intended to compare a large, spatially explicit dataset of diverse human perspectives on land use to a spatially explicit dataset of projected suitable habitat for salamanders under changing climate conditions. However, participation in the mapping project proved difficult to elicit, and the resulting spatial dataset contains the perspectives of 17 individual stakeholders representing a relatively homogeneous, exurbanite (white, often wealthier, older) subset of Macon County's population instead of a representative sample. Because the participant sample was so uniform and smaller than I had intended, I extended the project to include substantial archival research and interviews with community members who were knowledgeable about land use issues in the county. The addition of this data made clear the importance of steep slope development issues in the community, which provided a framework through which to interpret the results of the mapping project. Exurbanites are the demographic creating economic demand for homes on steep slopes, so it is particularly interesting that the participatory mapping results suggest the exurbanites I encountered preferred non-development uses be applied to steep slopes.

Ideally, perspectives of non-exurbanite residents would also be part of the mapping dataset. One interviewee stated that the pervasive culture among people born and raised in the region is to avoid getting involved in issues of local governance or expressing their opinions on contentious issues, and this is a substantial hurdle to increasing participation in this kind of research. Because of this basic unwillingness to participate, some alternative strategy is needed to elicit the perspectives of this particular group. Working with a trusted boundary organization in the community or with a respected individual could enable contact with this more reluctant group.

Moving forward, the participatory mapping research could be improved by engaging with key organizations and individuals to gain access to reclusive demographic groups, but also by making specific changes to the maps used by participants during the mapping activity.

Topographic relief was not included on the maps, yet one of the primary issues for stakeholders in the county is how land on steep slopes is used, and participants appeared to apply some uses more frequently in high elevation areas than others. Adding topography would make it easier for participants to identify steep areas and could lead to stronger relationships between elevation and land use assignments. The maps focused heavily on delineating private and publicly owned parcel boundaries as a way to identify units within each township for which I could calculate some measure of the level of conflict over land use. In practice, participants largely ignored these boundary lines and drew their own shapes over them. Therefore, maps could be greatly simplified by simply breaking the county into large unbroken blocks of private and publicly owned land, with perhaps a distinction between finely subdivided and developed private land and relatively open blocks of privately owned fields or forests. Additionally, some participants expressed interest in cultural and historical resources present in the landscape, such as the ancient mounds marking the sites where Native American villages were located, so inclusion of these resources on maps could be useful for participants to orient themselves to another layer of landscape complexity. Finally, the small scale individual maps provided to participants may simply have been too small to contain enough detailed information for participants to make precise decisions about where to place specific land uses. Future mapping efforts should consider using larger maps and perhaps having participants create maps jointly in small groups. This process would require a greater level of facilitation by the person running the mapping event, and ideally, multiple facilitators would be present to monitor the activities of small groups and ensure that all group members were able to express their perspectives. This modified activity format might also include presentations of completed maps by each group and an open discussion or

dialogue portion to process the outcomes of the mapping activity. This kind of mapping event would be significantly more interactive and could produce more synergistic outcomes than when individuals map their values in relative isolation from one another.

The primary future direction for the salamander demographic research is undeniably to develop a model that can simultaneously incorporate both streams of data collected in the Coweeta Basin. Integrated population models provide a way to combine multiple data sets to improve both demographic estimates and understanding of population dynamics (Kery and Schaub, 2012). The key to these models is linking information about population size to information about demographic rates, so one of the data sets must be a series of counts over time, and the second data set can be capture-mark-recapture, or mark-recovery. The integrated model will contain individual likelihoods for each dataset, as well as a joint likelihood for the overall model (Kery and Schaub, 2012). One limitation of integrated models has been the difficulty of accounting for spatial variation in demographic parameters and of making spatially explicit predictions of vital rates (Chandler et al., 2014). Chandler et al. (2014) describe a method that accounts for these limitations by "adopting a spatial population dynamics model upon which both the survey data and the capture-recapture data are conditioned." This version of the integrated population model would be particularly well suited to our salamander data sets, considering that the count data was collected over a spatial precipitation gradient.

This dissertation has provided a rich foundation of preliminary data on stakeholder perspectives and values in Macon County, and an important modeling effort to elucidate the connections between plethodontid survival rates and temporal variability in precipitation. My hope is that these foundational elements will represent a key contribution to the conservation of biodiversity in the southern Appalachian region.

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**Figures** 



**Figure 5.1.** Map of Macon County, North Carolina, showing both spatially explicit stakeholder values and projected salamander population growth rates. Black represents non-forest land cover. The most suitable area for salamander habitat (blue/green) appears in the lower portion of the map, a little left of center. This area also has predominantly unfragmented forest cover, and stakeholder values are mostly conservation-oriented (blue tones). The lower right corner of the map also contains suitable habitat but has a greater quantity of non-forest land cover. Stakeholder values are quite patchy in that area, but they are generally conservation oriented. The inset map shows the location of Macon County in the state of North Carolina.

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## **APPENDIX 3.1**

## CODE FOR THE BAYESIAN MODEL

```
model {
### priors ###
beta0 ~ dnorm(0, 0.01)
beta1 ~ dnorm(0,0.01)
beta2 ~ dnorm(0, 0.01)
alpha0 \sim dnorm(0, 0.01)
alpha1 ~ dnorm(0, 0.01)
alpha2 \sim dnorm(0, 0.01)
gamma ~ dunif(0,1)
### survival probability ###
for (i in 1:M) { #individuals
for(t in 1:(T-1)) { #primaries
logit(phiMonthly[i,t]) <- beta0 + beta1*precip[t] +</pre>
      beta2*svl[i,t]
phi[i,t] <- phiMonthly[i,t]^nMonths[t] #because of unequal intervals between
primaries, each 28-day (phiMonthly) estimate must be raised to the power
equal to the number of 28-day units that have elapsed since the previous
sample. nMonths is a vector of these values.
}#t
}#i
### detection probability ###
for (i in 1:M) { #individuals
for(t in 1:T) {
                      #primaries
for(k in 1:K[t]) {
                     #secondaries within primaries
logit(p[i,k,t]) <- alpha0 + alpha1*precipSS[k,t] +</pre>
      alpha2*svl.ss[i,k,t]
}#k
}#t
}#i
### survival, availability, and detection processes ###
for(i in 1:M) {
                           #individuals
```

```
for(t in (first[i]+1):T) { #primary periods
z[i,t] ~ dbern(z[i,t-1]*phi[i,t-1])
#is the individual alive? depends on whether it was alive last time and the
probability of survival last time
a[i,t] ~ dbern(gamma)
#is individual available to be detected?
for(k in 1:K[t]) { #secondary periods
y[i,k,t] ~ dbern(z[i,t]*p[i,k,t]*a[i,t])
#is the animal detected? depends on being alive, the probability of
detection, and the probability of being available
}#k
}#t
}#model
```

## APPENDIX 3.2

## STRUCTURE OF INPUT DATA AND NOTES ON RESHAPING DATA

Often the most challenging part of adapting a model developed for another project is attempting to replicate the structure of input data used in that model. Because this model is relatively simple, we hope that it will be used and adapted frequently. To that end, we have included this appendix on the structure of our data and some useful code snippets for reshaping data.

*Capture histories* – The initial format of this data was one row for each marked individual, and one column for each secondary period. The column names were coded as, for example, f12\_26\_2, indicating the fall of 2012, the 26<sup>th</sup> primary period, and 2<sup>nd</sup> secondary period of that primary. The body of this matrix consists of ones and zeros denoting capture or no capture, respectively. We converted the matrix to an array, with each slice of the array corresponding to one primary period, each row representing an individual, and each column representing a single secondary period:

#remove the secondary period code from the column names
ppc <- sapply(strsplit(colnames(y.mat), "\_"), function(x)
 paste(x[1],x[2], sep="\_"))
#create a list containing one copy of each primary period code
ppcu <- unique(ppc)
#create the empty array
y.0 <- array(NA, c(n00, max(K), T))
#fill the array
for(t in 1:T) { #loop over primary periods
 pp.i <- ppc %in% ppcu[t]
 y.0[,1:K[t],t] <- y.mat[,pp.i]</pre>

where n00 is the number of rows (individuals) in the capture history matrix, K is a vector of the number of secondaries in each primary period, and T is the number of primary periods. Next, we identified the primary period of first capture for each individual and removed all individuals that were only captured during the final primary period as the model cannot estimate survival from that period to the next:

#identify the first primary of capture for each individual first0 <- apply(apply(y.0, c(1,3), sum, na.rm=TRUE)>0, 1, function(x) min(which(x))) #identify the last primary of capture for each individual last0 <- apply(apply(y.0, c(1,3), sum, na.rm=TRUE)>0, 1, function(x) max(which(x))) #remove individuals from the array that were first detected in the #final primary y <- y.0[first0<T,,] first <- first0[first0<T] last <- last0[first0<T]</pre>

*Covariates* – Because we applied the snout-vent-length covariate to survival and detection, we had to create two versions of this covariate, one on the primary period scale, and one on the secondary period time scale to reflect how each rate is estimated. We also created two precipitation covariates, one applied to estimation of survival and one applied to estimation of detection. Survival depended on mean daily precipitation between primary periods, and detection depended on total precipitation for 7 days prior to the sampling occasion. The mean daily precipitation covariate was formatted on the primary period time scale and the 7-day precipitation covariate was formatted on the secondary period time scale. The original input data for snout-vent-length was identical to that of the capture histories except that instead of ones and zeros, the capture history string for an individual consisted of zeros until the occasion of first capture and then switched to time-varying snout-vent-lengths, both those actually measured and

}#t

those predicted by the von Bertalanffy growth model we applied to known-age individuals. Because the snout-vent-length covariate for detection included each secondary period, we structured this data as an array, using the same process as for the capture histories. Because the snout-vent-length covariate for survival included only each primary period, it was formatted as a matrix in which each column was a primary period, and each row was an individual. The mean daily precipitation covariate was formatted as a simple vector of values in the order of the primary periods. The 7-day precipitation covariate was formatted as a matrix with each column corresponding to a primary period and each row corresponding to a single secondary period. Because primary periods had different numbers of secondary periods, NA was used to fill spaces representing a greater number of secondaries than occurred in a particular primary. The snoutvent-length and precipitation covariates were standardized to have a mean of zero and a standard deviation of one.

We also created matrices of the known values of z, the true state of each individual, and a, the true availability of each animal. From the time an individual was first captured to the time of its final capture, z was equal to 1. At all other occasions, z was equal to zero. On the first occasion the animal was captured, a was equal to 1, but we allowed a to be unknown, equal to 0, at all other occasions.

Code for queueing up the model – Another helpful piece of code is the one we used to bundle the

data, set initial values, initialize the model, run the model, collect basic outputs, and extract

posterior predictions:

```
jd5 <- list(y=y.cjs.binary, M=nrow(y.cjs), K=K, T=T, first=first, z=zdat,
      a=adat,precipSS=precip.ss.s, precip=precip.pp.s, svl=svl.tvic.pp,
      svl.ss=svl.tvic, nMonths=nMonths$nMonths)
jp5 <- c("beta0", "beta1", "beta2", "alpha0", "alpha1", "alpha2", "deviance",</pre>
         "gam0", "gam1")
library(rjags)
load.module("dic")
ji5 <- function() list(beta0=rnorm(1), beta1=rnorm(1), beta2=rnorm(1),
                       alpha0=rnorm(1), alpha1=rnorm(1), alpha2=rnorm(1),
                       gam0=rnorm(1), gam1=rnorm(1))
ji5()
### initialize the model
jm5 <- jags.model("CJS phi-prcp-svl p-prcp-svl gamma-precip teR.jag",
                  data=jd5, inits=ji5)
### run the model
jc5 <- coda.samples(jm5, jp5, n.iter=10000)</pre>
### get basic model outputs
plot(jc5, ask=TRUE) #shows traces of the parameters you tracked (jp5)
sum.jc5<-summary(jc5)</pre>
sum.jc5
### extract predictions
mc5 <- as.matrix(jc5)</pre>
#we wanted to know survival and detection for a sub-set of snout-vent-lengths
svl.s <- c(-2.534129043,-1.243536734,-0.168043143,1.337647885)
#we tested a sub-set of precipitation values - only one of these is applied
#to the extraction script at a time, so to get estimates of phiMonthly for
#each of these precipitation values, you'd have to run the following script 9
#times.
precip <- 1.696665746
precip <- -1.809075915
precip <- 0.494563408
precip <- -0.843724627
precip <- -1.493560096
precip <- -0.168080124
precip <- -0.772687432
precip <- -0.669766996
precip <- 0.365380316
for(i in 1:iter) {
```

```
for (j in 1:length(svl.s)) {
            phiMonthly.pred[i,j] <- plogis(mc5[i,"beta0"] +</pre>
                   mc5[i,"beta1"]*precip + mc5[i,"beta2"]*svl.s[j])
      }#i
}#i
#calculate the mean phiMonthly for each SVL tested
for (i in 1:ncol(phiMonthly.pred)) {
      mean.phiMonthly[i] <- mean(phiMonthly.pred[,i])</pre>
      sd.phiMonthly[i] <- sd(phiMonthly.pred[,i])</pre>
}#i
#get confidence intervals for each svl-specific mean estimate
for (i in 1:ncol(phiMonthly.pred)) {
  quant.phiMonthly[1,i] <- quantile(phiMonthly.pred[,i], probs = c(0.025))</pre>
  quant.phiMonthly[2,i] <- quantile(phiMonthly.pred[,i], probs = c(0.25))</pre>
  quant.phiMonthly[3,i] <- quantile(phiMonthly.pred[,i], probs = c(0.5))</pre>
  quant.phiMonthly[4,i] <- quantile(phiMonthly.pred[,i], probs = c(0.75))</pre>
  quant.phiMonthly[5,i] <- quantile(phiMonthly.pred[,i], probs = c(0.975))</pre>
}#i
```

mean.phiAnnual
sd.phiAnnual
quant.phiAnnual