INTEGRATION OF BEHAVIOR INTO BIOPHYSICAL MODELS TO ESTIMATE SALAMANDER SENSITIVITY TO CLIMATE AND MIDSTORY FOREST MANAGEMENT

by

KIRA DANIELLE MCENTIRE

(Under the Direction of John C. Maerz)

ABSTRACT

Developing rigorous ecological models is a fundamental goal of ecologists in order to forecast biotic responses to environmental change. A limitation of many models is they are a-mechanistic and lack integration of behavior, which is integral to animal biology. Woodland salamanders (family Plethodontidae) are small, lungless animals known to be sensitive to climate, and often abundant across a wide range of forest conditions. In this dissertation, I reviewed plant climbing among plethodontid salamanders and discuss hypotheses for this commonly observed, but underappreciated, behavior. I integrated biophysical and agent-based models (ABM) to examine how climbing behavior could affect the sensitivity of Plethodontid salamander activity time to climate by using a temperature differential to stimulate plant climbing, allowing salamanders to alter their evaporative water loss rates. I used observations of Plethodontids in the southern Appalachian mountains to evaluate the model predictions. Finally, I used three approaches – a biophysical agent-based model, a field experiment, and spatially replicated surveys - to estimate the potential effects of *Rhododendron* and its management on terrestrial salamander activity time, survival, and abundance.

The model predicted that climbing increased salamander activity time with greater soil temperature relative to air temperature and increased time since rain. Model predictions were confirmed by field observations. The applied biophysical model predicted a negligible effect of *Rhododendron* on salamander activity time, and capture-recapture analyses showed no short-term effects of *Rhododendron* management on salamander survival. Estimated abundances from comparative surveys indicated little to no effect of *Rhododendron* on salamander abundance across a rainfall gradient. By using multiple approaches, our results suggest that *Rhododendron* has a negligible effect on salamander performance or abundance, and cutting *Rhododendron* and burning the forest floor had no short-term effect on apparent survival.

Including compensatory behaviors, like climbing, in models is important because they have the potential to moderate the effects of broader environmental changes - such as climate change - on animal performance and abundance.

INDEX WORDS: Agent-based modeling, Plethodontidae, salamander, southern Appalachian mountains, wildlife populations, compensatory behavior, Rhododendron, midstory canopy, arboreality

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KIRA DANIELLE MCENTIRE

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KIRA DANIELLE MCENTIRE

Major Professor:	John C. Maerz
Committee:	Kristen C. Cecala
	C. Rhett Jackson
	Kamal J. K. Gandhi

Electronic Version Approved:

Suzanne Barbour
Dean of the Graduate School
The University of Georgia
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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

The development of rigorous distribution, population, or performance models is a major focus of ecologists with renewed importance as we attempt to forecast population responses to environmental change. Most models relating animal performance to climate rely on correlations between known occurrences of a species and relatively coarse environmental variables (Buckley et al. 2010). These models rely on the assumption that mechanisms driving the relationship between an organism and its environment are captured indirectly within the correlations. Explicit integration of mechanisms into predictive models is being improved, largely through the integration of quantitative ecophysiological relationships; however, such efforts are limited for most species. These biophysical-based models lack integration of biotic interactions and key behaviors (Peterson et al. 2015). Behavior is a key component of animal biology, but is seldom integrated as a key mechanism in models of how animals interact with environmental changes such as climate change (Beever et al. 2017). The absence of behavior is seldom acknowledged as a limitation of models of animal relationships to climate, despite the knowledge that - on a finer scale - animals interact with patchily distributed microclimates within structural complex of environments (Porter et al. 2002; Kearney and Porter 2009; Sears et al. 2011; Scheffers et al. 2014; Hall et al. 2016). This ability to move among microclimates may buffer species exposure to climates that might otherwise limit their ability to occupy a site (Scheffers et al. 2014; Hall et al. 2016).

Because behavior permits flexibility and is the most proximate means by which most animals remain relatively homeostatic despite environmental heterogeneity, the absence of behavioral mechanisms likely results in models that overestimate animal sensitivity to climate. For example, animals engage in thermoregulatory behaviors in response to extreme temperatures such as seeking warmer microhabitats when conditions are cold, and cooler microhabitats when conditions are hot. These compensatory behaviors allow animals to occupy a wider range of climates at higher abundances than might be predicted by physiological tolerances alone. Consequently, a physiological model that integrates behavioral processes may predict lower sensitivity to an environmental gradient than is predicted by the physiological model alone. Of course, while behaviors may allow animals to occupy a wider range of climates, there are likely performance costs associated with behavioral compensation. Identifying how behaviors interact with physiological processes to allow animals to occupy a broader range of environments while potentially constraining performance within some environments is key to understanding how animals may respond to future novel environments.

I propose that plant climbing behaviors or facultative arboreality by Plethodontids may be – at least in part - a behavior that permits salamanders to regulate operant temperatures and evaporative water loss (McEntire 2016, Chapter 2). Though frequently disregarded as an esoteric behavior, reports of plant climbing are quite prevalent in the literature and, based on conversations with other scientists, commonly observed. The high frequency of reports suggests facultative arboreality is potentially important, though only a few studies have evaluated the potential benefits or costs of this behavior (reviewed by McEntire 2016).

Individual or agent-based models (hereafter, ABMs) provide a platform for integration of behavior into ecophysiological models. For example, recent physiological models of lizard performance incorporated behavior (Sears and Angilletta 2015; Sears et al. 2016). Although ABMs have been used to model recruitment in fish populations and for a variety of animal species related to movement or migration behavior (summarized in DeAngelis and Grimm, 2014), ABMs otherwise remain an underutilized tool in ecological research. The ABM structure allows the integration of flexible or responsive decision rules that permit emergent population level patterns from direct interaction between individual organisms and their environment. ABMs also create a means to measure how sensitive ecophysiological or population models are to behavioral processes.

In chapter 3, I integrated ecophysiological models into an agent-based modeling framework to estimate the potential effect of climbing on the sensitivity of Plethodontid salamander activity to variation in climate. Because plethodontid salamanders are lungless, they are dependent on moist skin for gas exchange, which makes them vulnerable to evaporative water loss. Consequently, plethodontid activity and performance are strongly linked to moisture and limiting water loss (Feder 1983). Plethodontid salamanders are known to retreat from the surface to below ground refugia to avoid water loss, though this comes at the expense of foraging time (Fraser 1976). The Southern Appalachian Mountains are a global hotspot for Plethodontid diversity, and within the topographically complex region, species occupy landscapes with steep natural gradients in rainfall and temperature. The region is expected to experience increased temperature and more variable precipitation over the coming century, prompting a growing number of efforts to forecast how plethodontids will respond to future climate scenarios (Milanovich et al. 2010; Gifford and Kozak 2012; Riddell et al. 2018). Other recent models of salamander activity or energetics have included surfacing and retreating behaviors (Gifford and Kozak 2012; Peterman et al. 2013; Caruso et al. 2014; Peterman and Gade 2017; Riddell et al.

2018), but no prior models have considered other compensatory behaviors like plant climbing. As a test of this model's predictions, in chapter 4, I used repeated field samples to test whether differences between ground and air temperatures affect the probability of climbing, confirming that the behavior is a compensatory mechanism for reducing evaporative water loss.

Finally, in chapter 5, I applied the model along with a spatially extensive comparative survey and a field manipulation to estimate the effect of *Rhododendron* and its management on terrestrial salamanders' performance, abundance, and survival across a broad rainfall gradient. *Rhododendron* alters the local microclimate, typically causing reduced variation in temperature and relative humidity (Clinton 2003). First, I applied the agent-based ecophysiological model from chapter 3 to estimate salamander activity in the presence and absence of *Rhododendron* across a gradient of rainfall probability. I included plant climbing as a compensatory behavior and used data from chapter 4 to parameterize the climbing probability relative to simulated temperature. Second, we estimated salamander survival on experimental forest plots before and after cutting of *Rhododendron* and burning to remove the dense leaf litter. Finally, we used repeated counts of salamanders in plots with and without *Rhododendron* present across an extensive rainfall gradient (same sites as in chapter 4) to determine whether the presence of *Rhododendron* was associated with greater or lower salamander abundance, and whether this effect varied with annual rainfall. We expect that *Rhododendron* might have no effect or a slightly negative effect on salamander abundance in areas of high rainfall because of the effects on soil acidity and soil moisture availability; however, in areas of low rainfall, *Rhododendron* may have a net positive effect on abundance by increasing forest floor humidity, stabilizing temperatures, and providing a substrate for climbing.

CHAPTER 2

ARBOREAL ECOLOGY OF PLETHODONTIDAE: A REVIEW[1]

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[1] McEntire, K. D. Copeia, 2016(1): 124-131, reprinted here with permission of publisher

ABSTRACT

Lungless salamanders in the family Plethodontidae are widely distributed and the most diverse lineage of caudates. Plethodontids occupy forested and freshwater habitats, where they can achieve remarkable abundance and biomass. The majority of tropical plethodontids are arboreal. Though generally considered ground dwelling, a large proportion of temperate species have been observed climbing shrubs, trees, and herbaceous vegetation. Approximately 45% of terrestrial and semi-aquatic (not including permanently aquatic) plethodontid species are known to obligately or facultatively climb vegetation; yet, with the exception of tropical plethodontids, the importance of arboreal habits is generally underappreciated. The potential benefits of arboreality vary based on life history and geography but may include improved olfaction, increased foraging potential, shelter and nesting, and predator avoidance. Constraints on arboreality include increased water loss rates and morphological limitations. Recognition of arboreal habits as a relevant component of salamander ecology is important in rapidly changing landscapes with anthropogenic alterations to midstory and canopy communities.

INTRODUCTION

The caudate family Plethodontidae is widely distributed and the most diverse lineage of salamanders in the world. There are 448 known species within Plethodontidae, which account for 66% of all known salamander species worldwide (AmphibiaWeb, 2015). All except nine of those species occur in temperate North America and the New World tropics. Plethodontids are the only salamanders known to occur in the Southern Hemisphere. Although plethodontids are found in a variety of terrestrial and freshwater habitats, the majority of species are associated with forests (Petranka 1998; Blankers et al. 2012). Many tropical plethodontids are generally or exclusively arboreal (Blankers et al. 2012), whereas North American plethodontids commonly frequent forest floor and streamside habitats (Petranka 1998). Because there is not a term to distinguish between climbing exclusively on trees and climbing on multiple types of vegetation, for this paper, the term ‘arboreal’ refers to climbing all types of vegetation. With this definition, many temperate plethodontids are facultatively arboreal. However, because most temperate plethodontids spend a significant amount of time on and are primarily associated with the forest floor, observations of arboreal habits are often treated as peculiar or trivial behaviors. Ignoring the arboreal habits of many plethodontids may skew our perspective on the prevalence and potential importance of these habits and the importance of vegetation as a component of plethodontid habitats.

The goal of this review is to 1) describe and characterize the prevalence and distribution of arboreality in Plethodontidae, 2) discuss the evolution and economics of plant climbing behaviors, and 3) explore the relevance of arboreality to our understanding of salamander ecology in a rapidly changing world.

DESCRIPTION AND DISTRIBUTION OF ARBOREALITY

Despite many anecdotal reports, one might infer that arboreality is rare among salamanders based on the paucity of published literature on this behavior. The absence of published reports of arboreality and explicit studies of climbing behavior for many species reflects the perception or implicit belief that arboreality is an esoteric behavior or restricted to specialist species in tropical America. Yet integration of anecdotal and published reports suggest at least 45% of non-permanently aquatic, plethodontid salamanders have been observed climbing plants. For the remainder of this paper, all references to plethodontid salamanders as a group refer to non-permanently aquatic species. A list of all arboreal plethodontid species based on these reports was deposited in the Dryad Digital Repository (DRYAD; McEntire, 2015). The overwhelming majority (95%) of obligately arboreal salamanders occur in tropical forests and spend the majority of their lives in the canopy (e.g., Wake 1987). At least 22% of tropical species are obligately arboreal (Fig. 2.1), and this estimate is likely conservative given limited information on the habits of many enigmatic tropical species. Canopy communities within the tropics are the centers of biodiversity, and many tropical plethodontids are associated with epiphytic plants such as bromeliads that provide moist microclimates in which to shelter, forage, and nest (Wake 1987; Benzing 1998; Bruce 1998; Nadkarni and Solano 2002).

The only temperate plethodontid genus that includes obligate (or near obligate) arboreal species is *Aneides* (Diefenbacher 2008). Seasonal weather shifts and freezing temperatures in temperate zones force salamanders to periodically seek shelter away from the canopy. In most areas, these shelters are underground or in deep rock crevices, where temperatures remain above freezing. In the absence of freezing temperatures, tropical salamanders can exclusively utilize the many humid shelters located in the canopy. Therefore, obligate arboreality would be predicted less frequently in temperate compared to tropical regions. The three temperate plethodontid species found frequently in trees, and believed to dwell there, occur in temperate rainforests, where moss mats provide shelter and food resources. One of these species, *Aneides ferreus*, has been found inside the nests of Western Gray Squirrels (*Sciurus griseus*), where temperatures were higher than the surrounding air (Spickler et al. 2006). A fourth species, *Aneides aeneus*, can be classified as facultatively arboreal as it extensively climbs high into trees during the summer and has been found up to 21 m in the canopy (Waldron and Humphries 2005; Thigpen et al. 2010) but retreats to rock outcrops in the winter. It has been speculated that *A. aeneus* was once highly arboreal, but the loss of American Chestnut (*Castanea dentata*) trees, which may have provided superior shelter compared to other tree species, restricted their current distribution to rock outcrops (Dodd 2004).

In addition to the obligately arboreal species, 28% of tropical salamanders and 33% of temperate plethodontid species are facultatively arboreal (Figs. 2.1, 2.2). These species spend much of their time on and under the ground but emerge to climb plants under favorable conditions. Although arboreality is seldom reported in species descriptions for temperate species, a rigorous literature search and personal communication with experts has revealed that arboreality is common among temperate species. Arboreal behavior has been observed for 19 species of *Plethodon*, 13 species of *Desmognathus*, four species of *Eurycea*, four species of *Batrachoseps*, *Gyrinophilus porphyriticus*, *Hydromantes italicus*, *Ensatina eschscholtzii*, and *Pseudotriton ruber*. If arboreality is extended to include other climbing surfaces (rock faces and cave walls), the proportion of animals known to climb grows to 51% of temperate species. Whether salamanders distinguish between these two vertical surfaces remains unstudied, but several species known to climb plants are also frequently found on rock faces (Huheey and Brandon 1973; Petranka 1998; Lannoo 2005; Casali et al. 2005).

The proportion of known species with arboreal behaviors changes slightly if temperate species with and without an aquatic larval stage are examined separately. This separation facilitates comparison of direct developing temperate and tropical species. Given this distinction, 47% of species with an aquatic larval stage and 31% of direct developing species have been observed displaying arboreal behaviors (17 of 36 and 31 of 100, respectively). These proportions are not significantly different (Fisher's Exact test $P = 0.1039$; GraphPad Quick Calcs, GraphPad software Inc., 2015).

Little information exists about facultative arboreality in tropical regions. High endemism and natural rarity combined with recent declines for many species has resulted in relatively little ecological or behavioral research on tropical species. Much of the published literature in this region focuses on phylogeography and species descriptions. Additional studies measuring the frequency of plant climbing would be useful in determining the utilization of plants as a microhabitat across the family. Currently, our knowledge of arboreality across plethodontid species, as measured by the number of species in an area that are reported as arboreal, is concordant with overall patterns of species richness (Fig. 2.3). This suggests that arboreality is common among all plethodontids that have terrestrial life stages, and that the form (facultative versus obligate) but not the prevalence of arboreal species varies geographically. However, populations or species may vary geographically in the prevalence of individual plant climbing depending on local climate and other environmental factors.

There have been few efforts to quantify the prevalence or amount of time individuals spend climbing and whether that varies geographically. Among 11 studies that quantified arboreal behavior, rates of plant climbing ranged from 0 to 88% of individuals (Table 2.1). Climbing rates may vary locally with weather and among populations or species depending on climate, which makes it difficult to characterize the extent to which individuals or species are facultatively arboreal. Because plethodontid activity is strongly governed by water loss (Jaeger 1978; Feder and Lynch 1982; Feder 1983), one would expect higher percentages of individuals to climb plants during wetter conditions. Though most studies report observations from wet nights, it is notable that Jaeger (1978) observed 13% of surface-active *Plethodon cinereus* and Trauth et al. (2000) observed 23% of *P. caddoensis* climbing plants on relatively dry nights (Table 2.1).

EVOLUTION AND ECONOMICS OF ARBOREALITY

The prevalence of arboreality among species across temperate and tropical ecosystems suggests arboreality among Plethodontidae is either conserved or has evolved multiple times. Regardless of whether this behavioral trait is highly con- served or evolved repeatedly, its prevalence across plethodontid species suggests arboreality has adaptive benefits. This raises several important questions: (1) what fitness benefits would select for obligate or facultative arboreality; (2) what fitness costs limit arboreality; and (3) among facultatively arboreal species, what local factors determine whether individuals climb vegetation?

Economics of obligate arboreality.—In rainforests, arboreality offers sites for nesting and shelter (Wake 1987; Bruce 1998; Spickler et al. 2006) and foraging opportunities (Wake 1987; Spickler et al. 2006). Tropical forest canopies support diverse and productive communities largely because epiphytic plants and moss mats provide abundant prey. Epiphytic plants (e.g., bromeliads) extract moisture from the atmosphere in cloud forests (Benzing 1998). In turn, these plants provide ideal shelter for salamanders by retaining moisture, stabilizing temperature, and providing habitat for prey (Wake 1987; Benzing 1998). The temperate rainforests of the Pacific Northwest of the U.S. also offer wet, moderate, maritime climates that support moss mats in the canopy, providing shelter and foraging for *Aneides* (Spickler et al. 2006).

The dominant physiological constraint for obligate arboreality is water loss, as lungless plethodontids require moist skin for cutaneous gas exchange (Jaeger 1978; Feder and Lynch 1982). Abundance of moist shelters within the canopy of tropical and some temperate rainforests alleviates much of this pressure and facilitates obligate arboreality. In the absence of these shelters, salamanders climbing on vegetation may be exposed to lower relative humidity and greater wind speed than on the surface of the ground. Arboreal salamanders in the tropics have more robust bodies than non-arboreal species (Blankers et al. 2012). This difference in body shape may reduce water loss rates by reducing their surface area to volume ratios. However, increased robustness may be limited as a way to reduce water loss because mass acts as a limiting factor for climbing ability, and, consequently, larger animals tend to be less arboreal than smaller ones (Alberch 1981).

Arboreality also requires morphological adaptations that may trade off with adaptations for using underground retreats. Obligately arboreal plethodontids frequently have highly specialized morphologies, especially in their foot shape and toe webbing (Alberch 1981). Wake (1987) described a general morphology of bromeliad-dwelling (specialist) salamanders as having a small overall size, long prehensile tails, long limbs, widely spread digits, and frontally directed eyes. All of these traits contribute to the salamanders' ability to cling to and forage on slippery, vertical surfaces (Alberch 1981). Cave and rock associated plethodontids frequently have similar morphological adaptations for climbing such as wider toe tips, webbing, prehensile tails, and projectile tongues (Diefenbacher 2008; Saunders 2009).

Most tropical plethodontid salamanders also have free projectile tongues, whereas most temperate species have attached protrusible or attached projectile tongues that are effective only at close range and require more bodily movement to search for and capture prey (Lombard and Wake 1986). The more robust bodies of some tropical plethodontids may accommodate the musculature needed to retract a projectile tongue. Similarly, highly arboreal *Aneides* have broad toe tips and prehensile tails, although their tongues are attached at the anterior margin instead of freely projectile.

In contrast to arboreal forms, fossorial plethodontids generally have slender bodies with shorter legs that facilitate retreat into small underground crevices and burrows (Petranka 1998). *Oedipina* and *Batrachoseps* have short legs, small feet, and an elongated body, which allows them to easily navigate fossorial habitats (Wake 1987). There are naturally some exceptions to these generalizations, but the patterns among tropical plethodontids suggest a morphological trade-off between effective use of arboreal and fossorial habitats.

Economics of facultative arboreality.—Temperate zones are less likely to support obligate arboreality because seasonality dictates a need to seek shelters that remain above freezing. In addition, some temperate zone forests may be too dry to allow animals to remain in arboreal habitats, and the general absence of epiphytic plants limits the availability of moist refuges within the canopy. Nonetheless, many temperate plethodontids climb vegetation opportunistically and with high frequency, suggesting advantages to facultative arboreality within temperate systems. Several hypotheses about the benefits of plant climbing within the temperate zone have been proposed, including increased prey quality or abundance (Jaeger 1978), increased detection of olfactory cues (Madison and Shoop 1970), and avoidance of predators (Roberts and Liebgold 2008).

Increased foraging potential was commonly assumed to be the reason for plant climbing behaviors and has been explored in four studies of two species of *Plethodon*. A foundational study for this hypothesis was conducted on *Plethodon cinereus*. That study attributed increased volumes of food in the stomachs of animals collected on plants (compared to individuals collected on the ground) to increased foraging success when climbing (Jaeger 1978). A dietary study on another species, *P. shermani*, found arboreal invertebrates present in the diet, which also suggested that salamanders forage when climbing (Mitchell and Taylor 1986). However, a later study on *P. shermani* found similar diets and volume of prey between individuals collected on plants and those collected on the ground (Lewis et al. 2014). Additionally, Roberts and Liebgold (2008) estimated that potential prey items for *P. cinereus* were less abundant on plants compared to the ground, suggesting better foraging potential on the ground.

There are a number of potential reasons for the equivocal findings among these four studies. Jaeger (1978) suggested that prey may be easier to capture on plants than in the complex matrix of leaf litter, and therefore, arboreal prey may be more available to salamanders even though it may be less abundant than forest floor-dwelling prey. Further, differences in the abundance or types of vegetation among sites may affect arboreal prey availability, and the relative availability of arboreal versus leaf litter prey may vary seasonally. A potential limitation of all these studies are the assumptions that prey found in a salamander's stomach were captured in the microhabitat where the animal was captured and that there are distinct arboreal and ground-dwelling taxonomic groups of prey (Jaeger 1978; Mitchell and Taylor 1986; Roberts and Liebgold 2008; Lewis et al. 2014). Salamanders may capture litter-dwelling prey before ascending plants and plant-dwelling prey before descending back to the ground. Some common invertebrates in salamander diets occur in both habitats, either because those invertebrates also climb vegetation (e.g., ants and spiders) or because they drop from plants into the leaf litter (e.g., caterpillars that are pupating or fall during storms). The movement of potential prey between habitats may confound the use of diets to study salamander arboreality, but it may also be a reason that salamanders are facultatively arboreal. Salamanders may alter their climbing behavior in response to variation in the availability of litter versus arboreal prey.

Plethodontids frequently use chemosensory information to interact with their surroundings, and salamanders may be able to more efficiently detect or orient toward the sources of olfactory cues when climbing. Above the ground there is less disruption of airflow, and climbing was proposed to increase their detection of olfactory cues and influence homing behavior (Madison and Shoop 1970). *Plethodon jordani* use olfactory cues to home when displaced (Madison 1969), and displaced salamanders were frequently observed climbing plants when homing. It is not clear whether detection of olfactory cues explains arboreality when salamanders are not homing. Plethodontids use olfactory cues to remain within territories (Jaeger et al. 1995), locate mates (Marco et al. 1998), and identify predators (Maerz et al. 2001; Madison et al. 2002; Sullivan et al. 2002), but no study has linked arboreality to chemical ecology in any of these contexts. Roberts and Liebgold (2008) proposed predator avoidance as a benefit of plant climbing when they found that *P. cinereus* climbed higher on vegetation following tail autotomy compared to individuals with their tails left intact.

The primary motivator for plethodontid salamanders to cease activity is water loss (e.g., Feder 1983; Peterman and Semlitsch 2014), so facultative arboreality should also be proximately and ultimately governed by water loss. Jaeger (1978) demonstrated that *Plethodon cinereus* lose water at a faster rate while climbing plants but suggested salamanders would need to spend a smaller amount of time hunting on vegetation because of improved foraging success. However, Hairston (1949) described activity patterns for *Desmognathus wrighti* and *D. carolinensis* and observed both species on vegetation later in the evening for several hours (it is not known if these were the same individuals). Additionally, individual *D. ocoee, P. teyahalee,* and *P. shermani* have been observed remaining on leaves for several continuous hours at mid and upper elevations in North Carolina (pers. obs.). These observations suggest the potential for water loss may not always be significantly higher on vegetation, or that salamanders are using other means such as behaviorally positioning themselves on vegetation to reduce water loss. Some species may have developed greater resistance to water loss that permits prolonged plant climbing. A recent study found elevation differences in resistance to water loss with animals from lower elevations having a higher resistance to water loss allowing estimated activity time to closely resemble higher elevation populations (Riddell and Sears 2015). This geographic variability suggests plasticity or local adaptation to the environment and may also apply when animals are climbing.

Morphological tradeoffs may also explain facultative arboreality in some temperate plethodontids. A study comparing morphology and microhabitat use found no distinct relationship among temperate species (Blankers et al. 2012) but did not include information about temporary use of arboreal microhabitats. Nonetheless, many temperate plethodontid species are morphologically intermediate to the highly arboreal and fossorial forms seen in tropical climates. The need to use subterranean burrows to escape winter temperatures, frost, and periodic droughts likely requires a relatively slender form that constrains the evolution of more robust body forms that are associated with climbing and reduced water loss. Temperate species, while generally intermediate in form, do vary in size, limb length, and robustness (Adams et al. 2009), which may be related to relative differences in arboreal tendencies (but this has not been evaluated). Similarly, in the tropics, salamanders typically found in moss mats have a less distinct overall morphology but generally are slender with short legs (Wake 1987). This intermediate morphology may reflect more facultative tendencies and the prevalence of moss mats in both ground level and arboreal habitats. Different body forms may also use different strategies to maintain arboreal behaviors. For example, the few species of *Oedipina* (elongate salamanders with reduced limbs) known to climb may use surface tension to cling to branches rather than specialized limbs and feet (Wake 1987).

As previously mentioned, cave and rock associated plethodontids have similar morphologies to obligately arboreal species (Diefenbacher 2008; Saunder, 2009). This suggests potential for salamanders with these morphologies to facultatively climb on different substrates, including vegetation, depending on availability. *Hydromantes* salamanders in Italy and California are known to inhabit caves and have specialized morphologies associated with climbing (Adams and Nistri 2010). Many of these habitats are devoid of vegetation, thus restricting any tendency for arboreality. When arboreal habitat is available, at least one species (*Hydromantes italicus*) is known to frequently climb vegetation as well as cave walls (Casali et al. 2005). Similarly, *Aneides aeneus* utilizes both arboreal habitats and rock outcrops, further suggesting potential translation of form to multiple habitats.

Extensive facultative climbing also exists in tropical areas. This behavior is less well studied in tropical climates, but many of the aforementioned constraints and benefits may also apply to tropical species. A large part of tropical diversity and biomass exists in the canopy, making arboreality a beneficial behavior for increased foraging potential. Climbing ability related to morphology may restrict the capacity for species to remain in the canopy permanently. Tropical species may also facultatively climb plants due to chemo- sensory information. Predator avoidance is unlikely to be a motivating factor for arboreality in the tropics, as Wake (1987) reported higher rates of tail loss in arboreal animals compared to other species. Further research would greatly enhance our understanding of facultative arboreality in tropical forests.

An understudied aspect of facultative arboreality is its potential relationship to interspecific interactions. Montane forests within southern Appalachia and Neotropical cloud forests harbor a high density and diversity of species. Interspecific competition and intra-guild predation have been proposed as structuring mechanisms for temperate salamander communities (Hairston 1987; Hairston et al. 1987; Bruce 2008). Facultative arboreality may influence the community structure through habitat partitioning if certain species or ages climb at different frequencies. Climbing also may change the frequency of direct interactions simply by increasing the potential surface area of a habitat by adding vertical surfaces. Future studies about differential climbing ability and propensities among species could help under- standing of possible intra-guild salamander interactions.

ARBOREALITY AND CHANGING FOREST ENVIRONMENTS

Recognition of the prevalence of arboreality and its potential importance to many plethodontids has pertinent applications to conservation and management. One of the primary drivers of global amphibian declines is the degradation of remaining forest habitats (e.g. Collins and Storfer 2003). Widespread logging, species invasions, and land development are altering the composition and structure of many forests and have been linked to declines in salamander populations (e.g. Herbeck 1998; Maerz et al. 2009; Connette and Semlitsch 2013; Wood and Williams 2013). The observed declines can be directly linked to loss of shelters and leaf litter (e.g., Maerz et al. 2009) and indirectly influenced by altered microclimates (e.g. Fetcher et al. 1985). Many of these processes result in simplified landscapes with reduced leaf litter and downed woody debris. This simplification has a negative impact on salamanders (see Clipp and Anderson 2014).

Less attention has been given to human alteration of the vertical complexity of forests. The loss of historically dominant tree species with particular structural effects on forest habitats such as the American chestnut (*Castanea dentata*) has been proposed as a contributing factor to declines in highly arboreal species such as *Aniedes aeneus* (and possibly a decline in their arboreal habits; Cupp 1991; Dodd 2004; Waldron and Humphries 2005). Invasions of Hemlock Wooly Adelgid (*Adelges tsugae*) have opened the canopies of Appalachian cove forests, resulting in the rapid expansion of midstory shrubs such as *Rhododendron* (e.g. Spaulding and Rieske 2010). The presence or absence of these midstory plants in gaps created by tree death influence local humidity, air temperature, soil temperature, and soil moisture (Clinton 2003). These microhabitat differences influence salamander activity and therefore fitness (Feder 1983). Midstory vegetation has an increasingly patchy distribution resulting from high levels of deer (*Odocoileus virginianus*) browse and the deliberate actions associated with residential development. Invasive species such as earth- worms are altering understory and midstory forest communities in northeastern North America, including shifting native shrub cover to non-native species such as Japanese barberry (*Berberis thunbergii*; Nuzzo et al. 2009). The influences of these changes in the vertical structure on salamander fitness are currently unknown but become an increasingly interesting topic in the light of facultative arboreality. Research on the use of this vertical habitat in a variety of vegetative structures and the influence of arboreality on fitness may help elucidate this relationship. Research on the indirect effects of changes to forest structure on microclimatic variables and the relationship of those changes to salamander fitness would also be pertinent.

In tropical regions, widespread land use change has had documented negative effects on many fauna, primarily through overall habitat degradation (i.e. Turner 1996; Foley et al. 2005). Deforestation directly removes shelters and foraging potential for highly arboreal animals. Indirectly, deforestation alters microclimate because trees themselves provide increased local humidity and reduce temperatures (Fetcher et al. 1985). Additionally, climate change is already linked to the lifting of cloud cover and declines in the bromeliads (Kessler 2002; Tabarelli 2006) that are essential to supporting arboreal amphibians including many plethodontids. The epiphytic diversity and dependence on cloud formation makes cloud forests one of the habitats most at risk to climate change (Benzing 1998).

CONCLUSION

It is challenging to draw meaningful linkages between the importance of arboreality, particularly facultative arboreality, and the ecology of plethodontids when the prevalence of the behavior is not recognized and often relegated to incidental and anecdotal observations. Nonetheless, the literature has accumulated a sufficient number of accounts to illustrate the widespread and frequent use of arboreal habitats by plethodontid salamanders. Vegetative structure should be considered an integral part of salamander habitat, and arboreal ecology should be incorporated into future studies. Considering the prevalence of arboreality among plethodontids, learning more about arboreal ecology for salamanders may be essential for conservation in a rapidly changing landscape.

TABLES

Table 2.1. The reported percent values are overall averages, ranges, or multiple values based on what was documented in the study. If known, exact number of individuals is also reported in parentheses. If reported in the study, a wet or dry designation is given in brackets to reflect the weather at the time of observation (NA if not reported). ‘‘Wet’’ refers to receiving rainfall within 24 hours prior to observation or other description of vegetation being wet (see Hairston, 1949), and ‘‘dry’’ refers to longer than 24 hours since the last rainfall.

Species	*Frequency of climbing*	*Location*	*Source*
Desmognathus carolinensis	22% (7 of 32) [wet]	Black Mountains area, Clingman’s Peak, North Carolina	(Hairston 1949)
Desmognathus wrighti	88% (7 of 8) [wet]	Black Mountains area, Clingman’s Peak, North Carolina	(Hairston 1949)
Eurycea bislineata	58% (11 of 19) [wet]	Canada	(LeGros 2013)
Hydromantes italicus	77% [overall, wet and dry]	Italy	(Casali et al. 2005)
Plethodon caddoensis	21% (11 of 52) [dry]	Ouachita National Forest, Montgomery County, Arkansas	(Trauth et al. 2000)
Plethodon cinereus	13 to 60% [dry and wet nights, respectively]	Blackrock Mountain, Shenandoah National Park, Virginia	(Jaeger 1978)
Plethodon cinereus	23% [wet]	Mountain Lake Biological Station, Salt Pond Mountain, Giles County, Virginia	(Roberts and Liebgold 2008)
Plethodon glutinosis	0-65% and 4-87% [NA]	Smokey and Balsam mountains, North Carolina	(Hairston et al. 1987)
Plethodon hubrichti	76% [wet]	Virginia	(Kramer et al. 1993)
Plethodon idahoensis	0.20% [overall, wet and dry]	Lincoln County, Montana	(Wilson Jr and Larsen Jr 1988)
Plethodon jordani	0-65% and 4-87% [NA]	Smokey and Balsam mountains, North Carolina	(Hairston et al. 1987)
Plethodon shermani	15% [wet]	North Carolina	(Lewis et al. 2014)

FIGURES

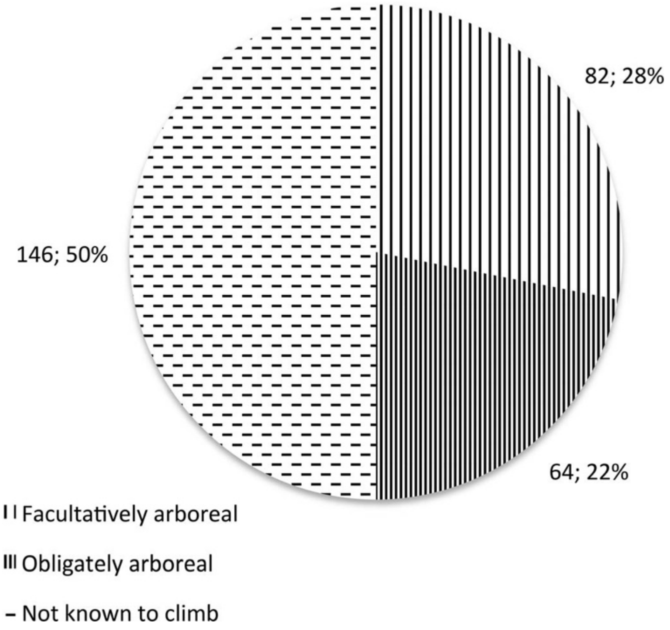

Fig. 2.1. **Frequency of plant climbing among tropical species** - The pie chart shows the number of tropical plethodontid species and the proportion of species split into three categories. The horizontal bars represent animals not known to climb, the wider vertical lines represent facultatively arboreal species, and the denser vertical lines represent obligately arboreal species.

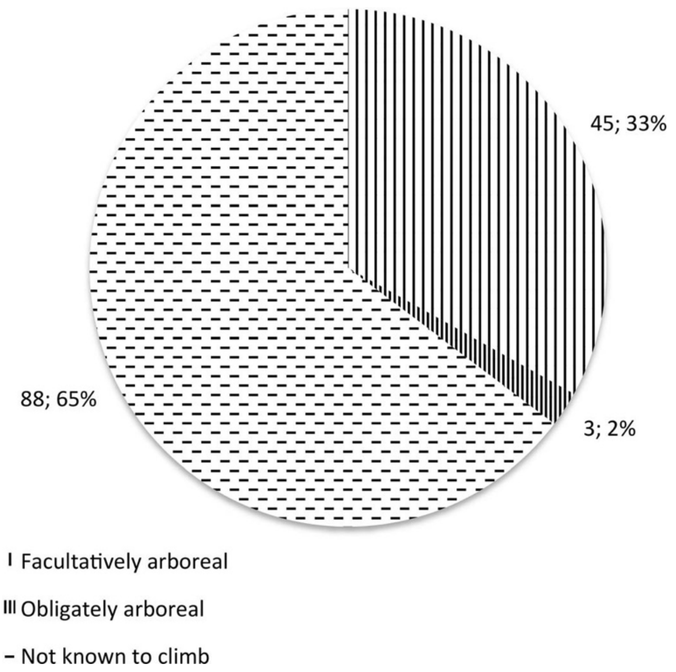

Fig. 2.2. **Frequency of plant climbing among temperate species** - The pie chart shows the number of temperate plethodontid species and the proportion of species split into three categories. The horizontal bars represent animals not known to climb, the wider vertical lines represent facultatively arboreal species, and the denser vertical lines represent obligately arboreal species.

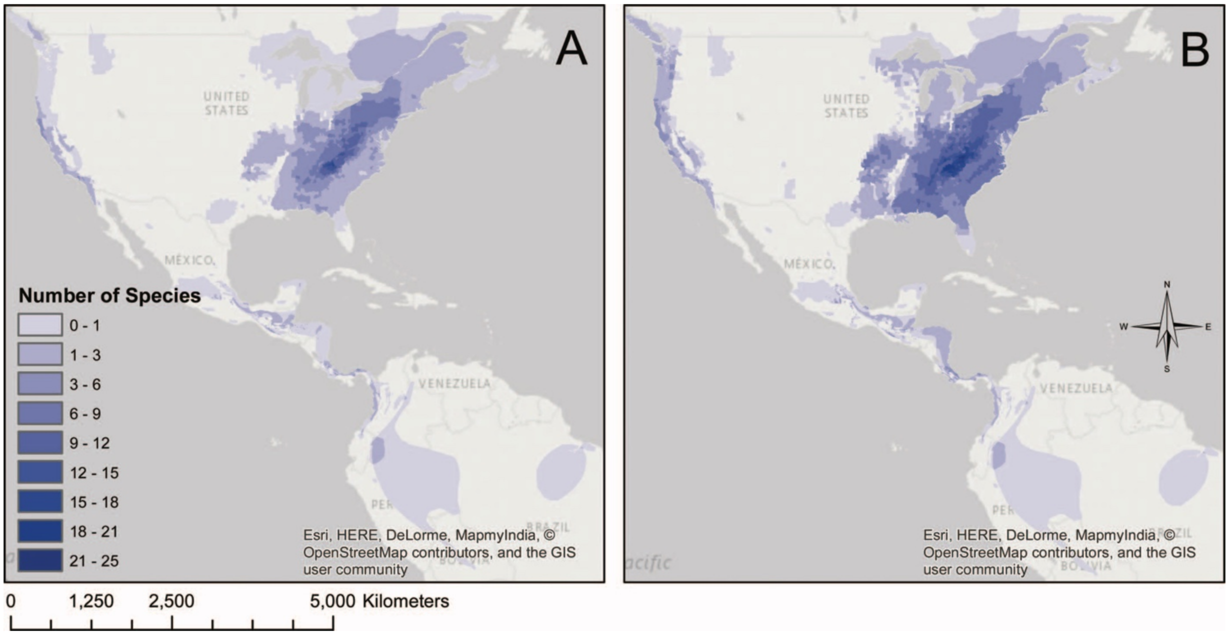

Fig. 2.3. Map (A) shows the number of species with known arboreal tendencies (both facultatively and obligately arboreal species); (B) shows the number of plethodontid salamanders found in the Americas based on ranges for 375 species of salamander (174 of 193 known to climb and 164 of 233 non-aquatic species not known to climb). These ranges were obtained through the IUCN and are limited to species in the Americas where all but nine species occur and to current IUCN species designations (some species have been split following genetic information, but this is not yet reflected in the distributions from IUCN).

CHAPTER 3

INTEGRATING ECOPHYSIOLOGICAL AND AGENT BASED MODELS TO SIMULATE HOW BEHAVIOR MODERATES SALAMANDER SENSTIVITY TO CLIMATE[2]

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[2] McEntire, K.D. and J.C. Maerz; To be submitted to *Behavioral Ecology*

ABSTRACT

Developing rigorous ecological models is a fundamental goal of ecologists in order to forecast biotic responses to climate change. A limitation of many models is they are amechanistic and lack integration of behavior, which is integral to animal biology. We integrated biophysical and agent-based models (ABM) to examine how behavior could affect the sensitivity of Plethodontid salamander activity time to climate. Specifically, our model used a temperature differential to stimulate plant climbing, a widely observed behavior among salamanders, which would allow salamanders to reduce body temperatures and associated dehydration rates. Consistent with expectations, predicted activity time was positively correlated with precipitation. The model showed that climbing plants increased activity time in drier conditions, particularly for smaller salamanders. The predicted importance of climbing behavior, a form of behavioral plasticity, was highly sensitive to assumptions about the threshold of water loss an individual was willing to tolerate. Because activity time is associated with fitness, increased activity time as a consequence of climbing behavior could moderate overall sensitivity to shifts in weather patterns. Our results demonstrate the potential and importance of integrating behaviors into ecophysiological models when judging a species potential sensitivity to climate.

INTRODUCTION

Models are important tools for understanding ecological systems and predicting how those systems may change across spatial and temporal gradients. The development of rigorous distribution, population, or performance models has reemerged as a major focus of ecologists attempting to forecast population responses to environmental change (Guisan et al. 2006; Araújo and New 2007; Jackson et al. 2009; Urban et al. 2016). Due to relative ease of data accessibility, distribution models based on correlations between species presence data and environmental attributes are commonly used to make predictions about how species distributions may change under future environmental conditions (Pearson and Dawson 2003; Araújo et al. 2005; Buckley et al. 2010). Criticisms of these bioclimatic models include the assumption that key mechanisms are captured within the correlations, missing other key parameters such as dispersal, migration, or biotic interactions, and concerns about extrapolation to future novel environments (Pearson and Dawson 2003; Hampe et al. 2004; Araújo et al. 2005; Soberon and Peterson 2005; Peterson et al. 2015). Mechanistic models address the assumption outlined above and are potentially more robust than correlative bioclimatic models. For example, ecophysiological models are a type of mechanistic model that uses mathematical models and basic laws of physics to predict an how an organism's performance (e.g., metabolic rate, energy acquisition, activity, survival) varies in response environmental variation (i.e. Peterman and Gade, 2017). Assuming that variation in individual performance correlates with spatial or temporal variation in abundance, ecophysiological models can be particularly useful for modeling species responses to environmental change (Kearney and Porter 2009). The development of mechanistic distribution models remains inaccessible for many species because key relationships between organisms and environmental factors are poorly understood (Kearney and Porter 2009; Buckley et al. 2010). Even for well-studied species, mechanistic models may not be robust for predicting changes in species distribution or abundance if those models do not account for other key processes such as physiological plasticity, biotic interactions, or compensatory behaviors (Buckley et al. 2010).

Behavior is a key process that – when missing - may limit the predictive capacity of ecophysiological models (Beever et al. 2017; Riddell et al. 2018). Behavior permits flexibility and is the most proximate means by which most animals remain relatively homeostatic despite environmental heterogeneity. Importantly, behaviors interact with an animals' physiology to determine performance. For example, animals engage in thermoregulatory behaviors in response to extreme temperatures such as seeking warmer microhabitats when conditions are cool, and cooler microhabitats when conditions are hot. These compensatory behaviors allow animals to occupy a wider range of climates at higher abundances than might be predicted by physiological tolerances alone. Of course, while behaviors may allow animals to occupy a wider range of climates, there are likely performance costs associated with behavioral compensation. For example, choosing to bask in the sun to increase motor function consequently requires increased caloric intake to compensate for a higher metabolic rate. Identifying how behaviors interact with physiological processes to allow animals to occupy a broader range of environments while potentially constraining performance within some environments is particularly relevant to understanding how animals may respond to future novel environments. Novel environments provide additional complexity for predicative models (Williams and Jackson 2007), and using mechanistic models that address behavioral and physiological plasticity can yield more realistic projections about species performances in those novel environments. A few recent studies have integrated behavioral plasticity into predictive, bioclimatic models in an effort to provide more realistic projections of species' distributions and performance under current and future climates (Gifford and Kozak 2012; Sears and Angilletta 2015; Peterman and Gade 2017; Riddell et al. 2018).

Individual or agent-based models (hereafter, ABMs) provide a useful platform for integration of behavior into ecophysiological models. This use of ABMs was first applied to model recruitment in fish populations and has been subsequently used for a variety of animal species, primarily focused on movement or migration behavior (summarized in DeAngelis and

Grimm, 2014). Sears and Angiletta (2015) and Sears et al. (2016) integrated behavior and physiology into an ABM to model of how use of local thermal heterogeneity might affect lizard performance. Those studies highlighted the importance of behavioral plasticity and local environmental heterogeneity to determine lizard energetics. Beyond this example, ABMs remain an underutilized tool in ecological research seeking to understand how behavior may influence animal responses to environmental change.

We integrated ecophysiological models into an agent-based modeling framework to explore the influence of two behaviors – surfacing and plant climbing – on the sensitivity of Plethodontid salamander activity to variation in air temperature, soil temperature, and relative humidity. Because Plethodontid salamanders are lungless, they are dependent on moist skin for gas exchange and vulnerable to water loss. Consequently, Plethodontid activity and performance are strongly linked to moisture and limiting water loss (Feder 1983). The Southern Appalachian Mountains are a global hotspot for Plethodontid diversity, and within the topographically complex region, species occupy landscapes with steep natural gradients in rainfall and temperature. The region is expected to experience increased temperature and more variable precipitation over the coming century, prompting a growing number of efforts to forecast how plethodontids will respond to future climate scenarios (Milanovich et al. 2010; Gifford and Kozak 2012; Riddell et al. 2018). We simulated weather and environmental conditions based on field measurements, and estimated the effects of the threshold of water loss on surfacing activity and climbing behavior on nightly and seasonal activity times. Plethodontid salamanders are known to retreat from the surface to below ground refugia to avoid water loss, though this comes at the expense of foraging time (Fraser 1976). Other recent models of salamander activity or energetics have included surfacing and retreating behaviors (Gifford and Kozak 2012; Peterman et al. 2013; Caruso et al. 2014; Peterman and Gade 2017; Riddell et al. 2018), but no prior models have considered other compensatory behaviors like plant climbing. When active above ground, plethodontids will routinely move between the ground and climbing on vegetation, which may allow animals to alter dehydration rates by altering their body temperature (McEntire 2016). We also included multiple size classes of animal in our model, which has only been included in one prior model (Riddell et al. 2018).

METHODS

Model Overview- The model estimated activity time using salamander dehydration rates. Although increased surface activity could make salamanders more vulnerable to predators, surface activity is directly correlated with foraging activity (Jaeger 1972; Fraser 1976; Jaeger 1980), which serves a as a good proxy for fitness (Adolph and Porter 1993). Correlations between higher predicted activity time and higher estimated density in the field (Peterman and Semlitsch 2013; Peterman and Semlitsch 2014), supports activity time as a good proxy for fitness despite any altered predation risk. We based our model on prior ecophysiological models of salamander activity and dehydration rates (Feder 1983; Gifford and Kozak 2012; Caruso et al. 2014; Peterman and Gade 2017). As an additional compensatory behavior, we modeled plant climbing effects on activity, through its relationship to thermal-dehydration regulation. We varied the probability of rainfall to examine how surfacing and climbing behavior affected the sensitivity of salamander activity time to variation in precipitation patterns.

Model Landscape Development- Detailed methods and explanations of model structure are presented in the form of an “ODD” (Overview, Design concepts, and Details) protocol (Grimm et al. 2006; Grimm et al. 2010) in Appendix 3.1. We used NetLogo (Version 6.0.2, U. Wilensky, 1999) to simulate salamander activity on a 50 X 50 tile landscape, with each tile representing one square meter of forest habitat. Daily probability of rainfall ranged from 0.3 to 0.9 and was consistent for the entire landscape to create a gradient from relatively wet to dry climates among simulations. The simulations ran 20 times for each set of parameters and a single simulation lasted for one active season (April through October) with alternating day and night time steps (428 total steps) and a minute-long sub-time step to calculate dehydration. The code is available in Appendix 3.2.

We simulated weather events, including rainfall events and nightly temperature, once every "24 hours" (two time steps) for the entire virtual landscape. Rainfall events occurred based on a probability ranging from 0.3 to 0.9 (in 0.05 increments). These events were assumed to be large enough to saturate the ground surface, but rainfall amounts were not directly modeled. Because rainfall events were used to regulate relative humidity, the amount of rainfall would not be as important as frequency of events in this simulation. During rainfall events the relative humidity was set at 100%. Relative humidity is the result of a large number of interacting factors including cloud cover, temperature, air pressure, and rainfall events. For simplicity, when not raining, the humidity decreased slowly based on the amount of time since the last rain (Appendix 3.1). Though a simplification of how relative humidity fluctuates, it created variability within the virtual environment, and comparable values to those observed during field studies (Howard 2018) The model simulated seasonal changes in air temperature by generating temperatures from a random-normal distribution using the monthly average and standard deviation for nightly temperature data recorded at the Coweeta Hydrologic Laboratory at 5 stations spread over an area of 25 square kilometers from 2013 to 2014 (Miniat et al. 2017). Soil temperature was set to the average monthly soil temperature at 5 cm (Miniat et al. 2017). We used temperature data collected during this time period, because it was all that was available at the time of model development. Directly modeling vapor pressure deficit rather than calculating it may have been more efficient, but it is more challenging to model over time as it depends on relative humidity which is also difficult to simulate. Although a simplification of reality, vegetation surface temperature was set nightly to an average between the soil and air temperature (Geiger 1965). Because air temperatures are typically measured higher than the level of the plants, plant temperatures are intermediate between soil and air temperatures (Geiger 1965). Hours of daylight were set for each month to the monthly average for the latitude of the Coweeta Hydrologic Laboratory (35° 3'35.70"N, http://aa.usno.navy.mil/data/docs/Dur_OneYear.php).

Agent Simulation- The agents were modeled as salamanders in the genus *Plethodon*, specifically members of the *Plethodon jordani* species complex. We included three size classes of individuals: hatchlings (snout-vent-length (SVL) < 32 mm), juveniles (SVL 32 to 42 mm), and adults (SVL 43 to 72 mm). We simulated 1000 agents of each size class for a total of 3,000 agents randomly distributed across the uniform landscape, and we did not include any density-dependent affects.

Resistance to water loss is a critical value for estimating activity time using biophysical models. Some studies found amphibians' skin acts as a free water surface (Spotila and Berman 1976), meaning their resistance value is very close to zero. However, other studies have found species-specific differences and variable resistance values based on environmental conditions with values greater than zero (Littleford et al. 1947; Cohen 1952; Ray 1958; Spotila 1972;

Riddell and Sears 2015; Riddell et al. 2017). We used data for *P. jordani* reported in (Spotila 1972) to create a function of predicted resistance to water loss based on soil temperature [1].

$$[1]\ R = 0.425T_S + 0.8136$$

Where R is the resistance to water loss in seconds per centimeter and T_s is the soil temperature in Celsius. While recent physiological models suggested the importance of including calculations of boundary layer resistance as part of the estimate of salamander's resistance to water loss (Riddell et al. 2017), we used literature values for skin resistance based on field-recorded water loss, which effectively included the boundary layer resistance in the value of skin resistance to water loss. Riddell et al. (2018) recently demonstrated seasonal plasticity in skin resistance, suggesting the monthly changes in water loss resistance in our model were appropriate.

We assumed body temperature was equivalent to the surface the salamander was sitting on. This deviates from previous studies that estimated operative body temperature using mathematical equations (Gifford and Kozak 2012; Peterman and Gade 2017). Body temperatures measured in the field were equivalent to the temperature of the substrate upon which they were found (Chapter 4, Fig. 4.2a) and were on average 2.38 ± 1.04 °C cooler than the air temperature (Chapter 4, Fig 4.2b). These relationships, along with previous studies using the temperature of the substrate beneath the salamander as the body temperature (Feder and Lynch 1982), suggest it was reasonable to assume modeled soil temperature as the agents' initial body temperature. If a salamander remained on the ground, they maintained the soil temperature as their body temperature; when a salamander climbed on vegetation, they adopted the temperature of the plant as their body temperature.

When air temperatures were cooler than soil temperatures, agents had a 0.50 probability of climbing once they were surface active. This value was not chosen to represent natural climbing rates, which remain unknown. By setting a fixed probability of climbing, this resulted ~ 50% of the agents climbing on any given evening, which allowed us to compare differences in activity time between those agents that climbed and those that did not. We did not allow salamanders to climb when soil temperatures were cooler than air temperatures because we assumed that this would create conditions where dehydration was always faster for climbing animals. This was not to imply that real animals would not climb under such conditions in the field (see Chapter 4).

Model Process- We constrained to surface activity based on field observations and other published studies to times when: (1) the relative humidity was above 45% and (2) the animal's water deficit was less than 4% (Feder and Londos 1984). Simulated body temperatures did not fall out of the range of active temperatures used in previous studies (Peterman and Gade 2017; Riddell et al. 2018), so this restriction was not included. Nightly foraging time in minutes was calculated based on dehydration rate [2]

$$[2]\ EWL = \frac{\rho_{sal} - \rho_{air}}{R}$$

where EWL is evaporative water loss (g cm^{-2} sec^{-1}); R is the resistance value of the salamander to dehydration (sec cm^{-1}); ρ_{sal} is the vapor pressure density at the surface of the salamander and is assumed to be equal to the saturation vapor pressure density (Tracy 1976); ρ_{air} is the vapor pressure density of the air given the relatively humidity. We estimated these values based on standard equations related to temperature (Appendix 3.1). We multiplied the evaporative water loss rate by an agent's surface area (cm^2) to estimate grams of water lost per minute. The agents remained active until they lost 3 to 10% of their body mass, which is the threshold range observed in dehydration studies and used in other models (Ray 1958; Feder and Londos 1984; Gifford and Kozak 2012; Caruso et al. 2014; Peterman and Gade 2017; Riddell et al. 2018). For each simulation, the percentage of water lost was held constant and consistent among all individuals, but we compared 3, 5, 7, and 10% water loss thresholds because previous models suggested high sensitivity to this value (Peterman and Gade 2017).

When simulated salamanders were inactive, they rehydrated on a minute-by-minute basis as determined by soil temperature and soil moisture [3] (Spotila et al. 1992):

$$[3]\ r = (\varphi_{sal} - \varphi_{soil}) \times K$$

Where rehydration is measured in grams per cm^2 per minute, φ_{sal} is the water potential of the salamander in pascals, φ_{soil} is the soil moisture tension in pascals, and K is the hydraulic conductance, set at 0.00000013 g cm^{-2} min^{-1} pa^{-1} as calculated for Leopard frogs (Tracy 1976). The water flux of the salamanders was estimated using the following equation [4] established for Leopard frogs (Tracy 1976).

$$[4]\ \varphi_{sal} = (-284.802\theta^3 + 773.427\theta^2 - 703.223\theta + 0.0214809) \times 100$$

Where θ is the hydration level of the salamander (1 - percent of mass lost to water loss). These parameters are currently unavailable for salamanders; however, the leopard frog values produce reasonable rehydration rates reflective of those found in previous studies with salamanders (Cohen 1952; Spight 1967a,b; Spotila 1972; Feder 1983). Soil moisture was modeled simply and remained well above the minimum water potential for salamanders to rehydrate (-2 atm, Spight 1967a,b; Spotila 1972) as modeling soil moisture dynamics went beyond the scope of this study.

Agents recorded their nightly foraging time, which allowed for comparison of nightly activity with simulated environmental factors. At each 'night' time step, we recorded the average nightly activity time of each size class. When climbing occurred, we divided the agents into 'climbers' and 'non-climbers', then recorded the average nightly time for each size class in both categories.

Sensitivity analysis- We conducted a sensitivity analyses for the assigned threshold for water loss. We did not conduct sensitivity analyses on ecophysiological model values that have been validated by previous studies or were based on the best available published values (Table 3.1; Whitford and Hutchison, 1967; Spotila, 1972; Tracy, 1976; Peterman and Gade, 2017). There were 52 possible simulations combining possible rainfall probabilities and thresholds for water loss.

Data analysis — We limited comparison of nightly activity between climbing and non-climbing salamanders to simulated nights when air temperature was cooler than soil temperature. We subtracted the recorded average activity time of non-climbing agents from the time for climbing agents to determine any difference in nightly activity time associated with the behavior. We visually examined the effects of weather, body size class, and threshold for water loss on differences in nightly activity time between climbing and not climbing salamanders. We used general additive models with smoothing to make patterns more easily visible. To evaluate the effects of climbing on sensitivity of salamanders to 'climate', we summed the nightly activity times for each size class and rainfall probability per simulation across the rainfall probability gradient. We assumed animals were active every night of the simulation, so the absolute values do not reflect true estimates of seasonal activity for salamanders.

RESULTS

As part of the model structure, climbing only occurred on nights when simulated air temperature was lower than soil temperature. This resulted in approximately 85 climbing nights out of 214 nights per simulation. The maximum potential difference in nightly activity time between climbing and non-climbing animals ranged from 6.1 to 7.0 hours. There were a few instances when climbing resulted in lower activity times than remaining on the ground, with those differences not exceeding 22 minutes. During rainy nights with only slight differences between soil and air temperature, there was little to no difference in activity time between climbing and non-climbing salamanders (Fig. 3.1). As the temperature difference between the ground and air increased, the benefits of climbing increased for all size classes of salamander and all thresholds of water loss (Fig. 3.1). Hatchlings were the most responsive to very small temperature differences regardless of water loss threshold or time since last rainfall (Fig 3.1c). Importantly, as conditions dried [days since rain increased], the advantages of climbing manifest with a smaller temperature difference between the ground and air, though days since rain also constrained the realized activity time because of the negative relationship to relative humidity.

The general patterns of increased activity among climbing animals with increasing temperature difference did not vary with the threshold of water loss; however, the benefits of climbing manifest at a lower temperature difference as the threshold for water loss declined (Fig. 3.1). The unimodal patterns of differences in activity time as a function of temperature differences during rainy nights reflected other constraining conditions. Specifically, in our observed weather data used to simulate weather in the model, we observed air temperatures ~5 °C or greater cooler when cold fronts moved in creating near freezing air temperatures while soils remained relatively warm (Fig.3.2). These cold conditions constrained salamander activity independent of other factors. Total seasonal activity time increased with increasing probability of rainfall, and the benefit of climbing was consistent across the rainfall probability gradient (Fig. 3.3). Overall, climbing had the largest benefit for hatchlings across the rainfall probability gradient (Fig 3.3).

DISCUSSION

Inclusion of climbing behavior increased activity time of salamanders under the specified conditions and acted as a compensatory behavior when interacting with both time since last rain and differences in air and soil temperatures. As a compensatory behavior, climbing may decrease the predicted sensitivity of salamanders to climate change compared to models that do not including climbing. This is broadly consistent with other recent models that show the inclusion of behavioral and physiological plasticity reduces the predicted impact of climate warming on the performance and distribution of salamanders (Riddell et al. 2018) and other taxa (Sears et al. 2011; Sears and Angilletta 2015). An interesting outcome of our model results is the demonstration that the addition of climbing behavior creates a mechanism by which salamanders that occupy areas with lower rainfall probabilities can realize comparable amounts of activity time to salamanders that occupy areas with a higher rainfall probability. Of course, variation in rainfall likely affects productivity and food availability independent of activity time, and we are assuming that equivalent activity time translates to equivalent food intake rates regardless of whether the salamander is climbing or not. This assumption has not been validated in the field. Jaeger (1978) found that eastern red-backed salamanders (*P. cinereus*) had larger, higher-quality prey in their stomachs compared to animals found on the ground; and Mitchell and Taylor (1986) reported arboreal invertebrates in the diets of red-legged salamanders (*P. shermani*), which is among our model species, suggesting climbing salamanders can access specific prey. However, a more recent study of *P. shermani* found similar diets and volume of prey between individuals collected on plants and those collected on the ground (Lewis et al., 2014), and Roberts and Liebgold (2008) estimated that potential *P. cinereus* prey were actually less abundant on plants compared to the ground. Therefore, it remains to be determined whether salamanders that climb are able to translate increased activity time to equal or greater intake of prey or some other fitness benefit.

Assuming that climbing is adaptive, particularly in areas with less frequent rainfall, our model results would suggest a shallower relationship between rainfall gradients and salamander abundance than would be predicted by models that exclude climbing or other plastic traits. Our predictions are consistent with other studies that find hatchling salamanders should be most sensitive to drier conditions (created by either declining precipitation or increased temperature, Riddell et al. 2018). We currently lack empirical data that can be used to test this prediction. *Plethodon albagula* were observed to increase movement in drier areas as a compensatory behavior for water loss (Peterman et al. 2014). Increased horizontal movement has been positively correlated with vertical movements (arboreality) in Australian vertebrates, including amphibians (Scheffers et al. 2017). Model predictions are generally consistent with two studies that demonstrate both reduced spatial abundance of salamanders in relation to mean annual precipitation (Howard 2018) or soil moisture (Peterman and Semlitsch 2013). In both studies, the largest contributor to declining abundance was the decline in hatchling or juvenile abundance, which is also consistent with model predictions. Howard (2018) estimated salamander abundance and population structure across the Coweeta basin, which served as the context for our simulation model and was the source of our weather data in simulations. Her results demonstrate a rather shallow decline in abundance over a large range of mean annual precipitation until condition become very dry. Qualitatively, the shape of this relationships is similar to our modeled estimates of activity time across the rainfall probability gradient.

One powerful use of models is to examine and estimate latent processes that cannot be observed. It is currently not practical (or likely even possible) to directly measure salamander activity time in the field, yet it is widely accepted as a critical currency in salamander fitness. One emergent pattern in our model was that the benefits of climbing increase as time since rain decreases. This contradicts earlier characterizations of this behavior. Jaeger (1978) hypothesized that dehydration during plant climbing would restrict the behavior to rainy nights. Our model results, across a range of weather conditions and thresholds for water loss, suggest the benefits of climbing increase with time since rain and are instead likely to be determine by differences in temperature between the ground and air rather than rain events. In fact, at higher water loss thresholds, which have been demonstrated for our model *Plethodon* species (Riddell et al. 2018), our model predicts little to no advantage in terms of activity time for climbing during rainy nights unless extreme temperature differences occur.

There are some important limitations to our model in terms of predicting the advantages of climbing or when we expect to see increases of climbing in the field. In addition to regulating water loss, salamanders may be selecting among thermal microhabitats to optimize metabolic rate and may be balancing increases in activity time with metabolic efficiency (Riddell et al. 2018). Though our model can integrate metabolic rates and efficiencies, we did not evaluate that parameter in these simulations. In our model, we strictly evaluate the benefits of climbing on activity time as a function of water loss. Our results suggest that – generally – the benefits of climbing increase as the air becomes progressively cooler compared to the ground. In reality, weather data indicate that this occurs most frequently during cooler seasons when the ground is warm but the air is particularly cold. Under these conditions, it is reasonable that a salamander would remain on the ground where temperatures are more metabolically optimal even though their dehydration rate would be greater and their activity time shorter. Ultimately, field studies that can directly or indirectly relate activity time to behavior as a function of weather are needed to validate our and other models and the importance of behaviors in determining salamander fitness and demography.

Another outstanding issue in ecophysiological models of salamanders is the issue of the threshold for evaporative water loss before an animal will cease activity and retreat into moist refugia. An early laboratory study on *Desmognathus ochrophaeus* suggested salamanders will "give up" activity at much lower levels of water loss than they can tolerate before becoming impaired, and that water loss thresholds may be plastic depending on the dehydration potential of the environment (Feder and Londos 1984). A model by Peterman and Gade (2017) estimated similar high sensitivity for *Plethodon*. However, field measures of *Plethodon metcalfi* water deficits recorded by Riddell et al. (2018), suggested the species may tolerate higher water loss thresholds than has been demonstrated in the lab or through other models. The sensitivity of our and other model estimates to an assumed water loss threshold (e.g. Gifford and Kozak, 2012; Peterman and Gade, 2017; Riddell et al., 2018) illustrates the importance of better understanding this parameter, particularly for climate change projections. Moreover, differences in water loss resistance and threshold water loss tolerances among size classes and species would aid in understanding behavioral differences in the field and comparing the relative sensitivity of species to spatial and temporal climate change. For example, our model predicts that size classes or species with reduced water loss resistance or lower water loss thresholds or greater surface area to volume ratios would realize a greater benefit from climbing at a lower temperature differential. We would expect these size classes or species to show a greater propensity to climb compared to larger size classes or species with greater skin resistance to water loss.

Another limitation of our model, and all models to date, was our inability to deal with natural variation in soil moisture and soil tension. Our models does include some variability in soil moisture, but we were unable to provide additional insights about this poorly understood relationship. During model development, when soil moisture dropped below -0.2 atm, the majority of animals would “die” from an inability to rehydrate in the soil. However, Spotila (1972) and Spight (1967a) demonstrated that *Plethodon* could rehydrate at up to a soil moisture of -2 atm. Salamanders are also known to create a “wetting front” to slow water loss in dry soils (Spotila 1972), but the mechanism and the conditions under which this front is formed along with the hydraulic conductance or water flux rates for salamanders remains undescribed. This indicates that current rehydration models for salamanders [and other amphibians] are incomplete. This also illustrates that while salamanders spend a large portion of their time underground or in retreats, all current models of salamanders’ interactions with climate have focused only on their time above ground (i.e. Walls 2009; Milanovich et al. 2010; Gifford and Kozak 2012; Ficetola et al. 2016, Peterman and Gade, 2017, Riddell et al. 2018). Part of this knowledge gap stems from the inaccessibility of the belowground habitats of these animals; however, until this knowledge gap is filled, our models of these organisms will remain incomplete and prone to error. This illustrates a wider problem with the development of mechanistic models. Plethodontid salamanders are a group that are extensively studied and for which there is a relatively rich physiological literature, and yet our current knowledge is still insufficient to construct a full working physiological model of how these animals interact with their environment (Gifford 2016). Many other species are even more knowledge deficient, which will limit the ability to develop and apply mechanistic models to understanding the performance and distributions of those species in current or future novel environments.

Because of the heterogeneous nature of most environments, most animals use behaviors to compensate for less suitable conditions that might otherwise limit their performance and ability to occupy a site. Behavioral and physiological plasticity and acclimation are one of the fastest phenotypic responses of animals to environmental change, and compensatory behaviors and plasticity in physiology act as key mechanisms for acclimatization to seasonal climates or short-term changes in weather, food availability, predation (Muñoz et al. 2016; Beever et al. 2017). These compensatory traits, therefore, shape the potential sensitivity of animals to longer-term environmental changes (Beever et al. 2017). By including multiple behaviors and physiological processes into mechanistic models, we can make more robust predictions about how organisms might respond to future novel environments. Although recent models are incomplete, the demonstration by several recent studies that the integration of behavioral and physiological plasticity dramatically reduces the projected impacts of climate change on some species is heartening and should have important ramification for how we think about threats and conservation actions.

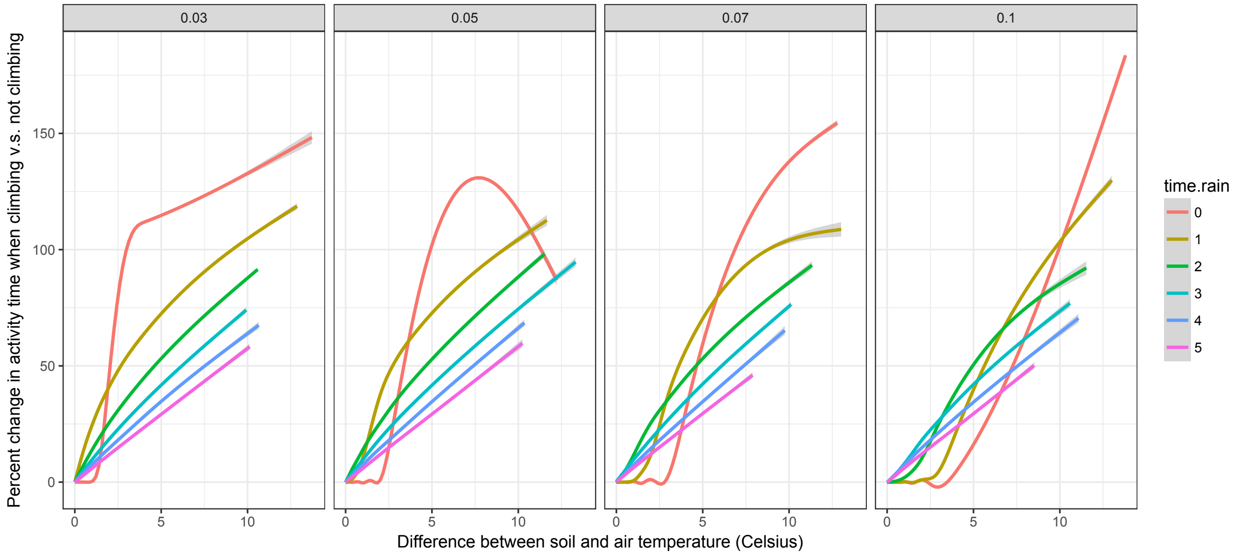
TABLES

Table 3.1: Simulated abiotic factors, and biophysical parameters and functions used in the model. Additional details can be found in Appendix 3.1.

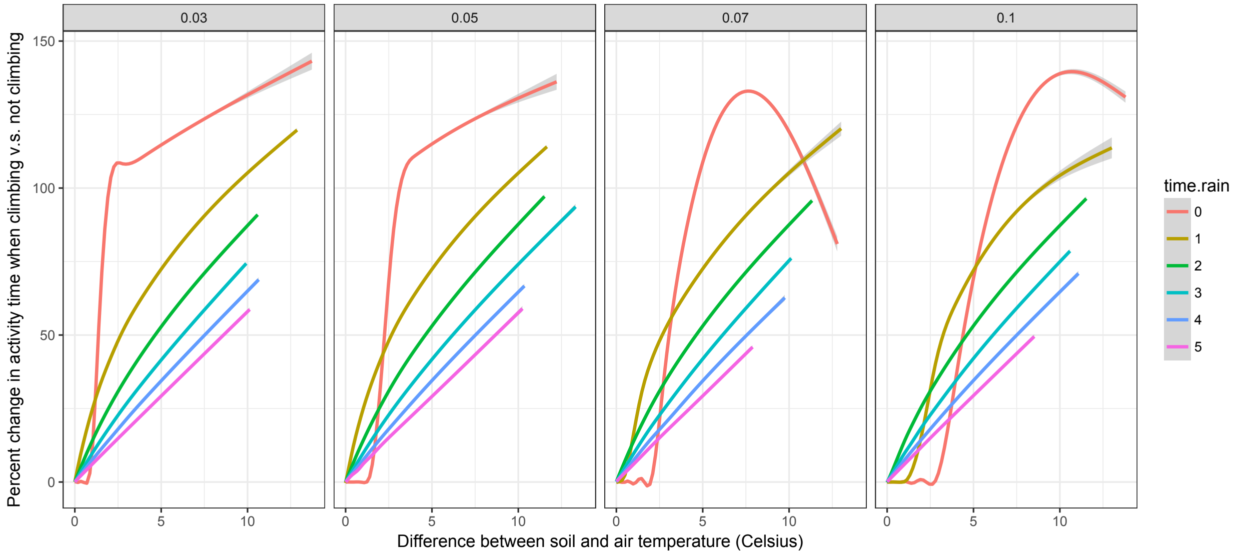
Parameter name	Parameter Value	Source
hour	9.5 to 13	http://aa.usno.navy.mil/data/docs/Dur_OneYear.php
Air temperature	Random normal draw from:	Average nightly temperatures recorded between 2013 and 2014 at the Coweeta LTER (± 1 SD) (Miniat et al 2017)
April	11.89 ± 1.85	
May	15.00 ± 1.83	
June	18.57 ± 0.70	
July	19.07 ± 0.95	
August	19.15 ± 1.01	
September	17.36 ± 1.94	
October	12.07 ± 3.00	
Soil temperature		Average nightly temperatures recorded between 2013 and 2014 at the Coweeta LTER (Miniat et al 2017)
April	11.64	
May	14.17	
June	17.44	
July	18.61	
August	18.62	
September	17.95	
October	14.13	
Probability of climbing	0 or 0.5	For model evaluation
Rainfall probability	0.3 to 0.9 at 0.05 increments	For model evaluation
Water loss threshold	0.03, 0.05, 0.07, 0.10	Peterman and Gade 2017
Resistance to water loss	$0.425 * T_{soil} + 0.8136$	Derived from Spotila 1972
Snout-vent length (mm)	$32.8 * mass^{0.34}$	Howard 2018
Surface area	$8.42 * mass^{0.694}$	Whitford and Hutchison 1967
Hydraulic conductance	1.3×10^{-7}	Tracy 1976

FIGURES

(A)


0.03
0.05
0.07
0.1
Percent change in activity time when climbing v.s. not climbing
0
50
100
150
0
5
10
Difference between soil and air temperature (Celsius)
time.rain
0
1
2
3
4
5

(B)


0.03
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Percent change in activity time when climbing v.s. not climbing
0
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5
10
Difference between soil and air temperature (Celsius)
time.rain
0
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(C)

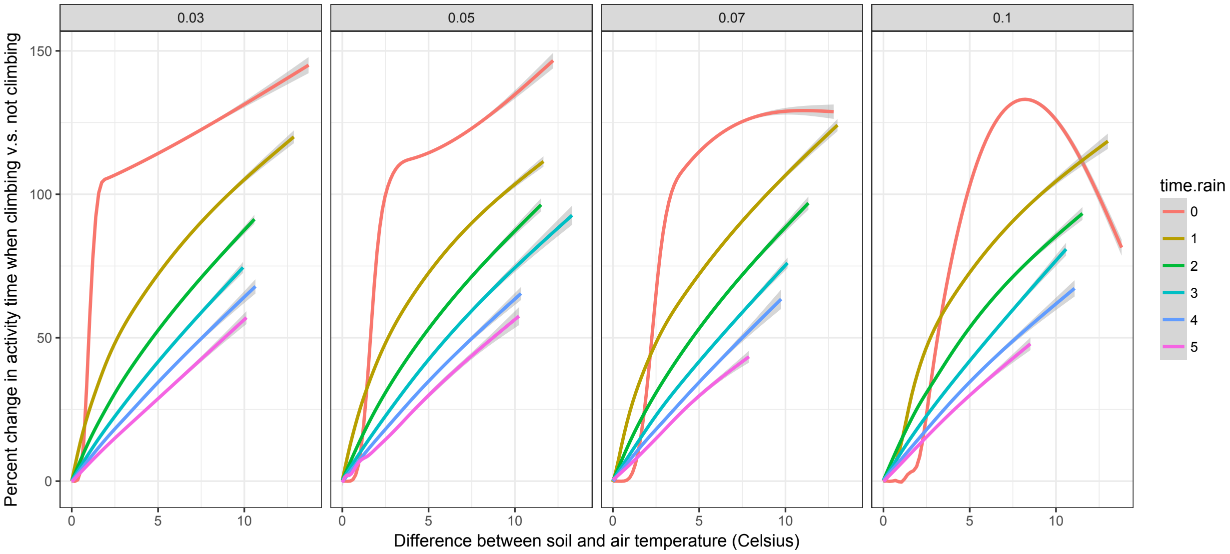

Fig. 3.1. Percent change in activity time of climbing compared to non-climbing salamanders as a function of the difference between air and ground temperature, days since last rain, water loss threshold, and body size class. Shown is the generalized additive model of the percent increase in mean activity time for non-climbing salamanders compared to the mean activity time of climbing salamanders on the same simulated night. Positive value indicates greater activity time among climbing salamanders. The grey area around each line represents a 95% confidence interval.(A) adult salamanders, (B) juvenile salamanders, and (C) hatchling salamanders.

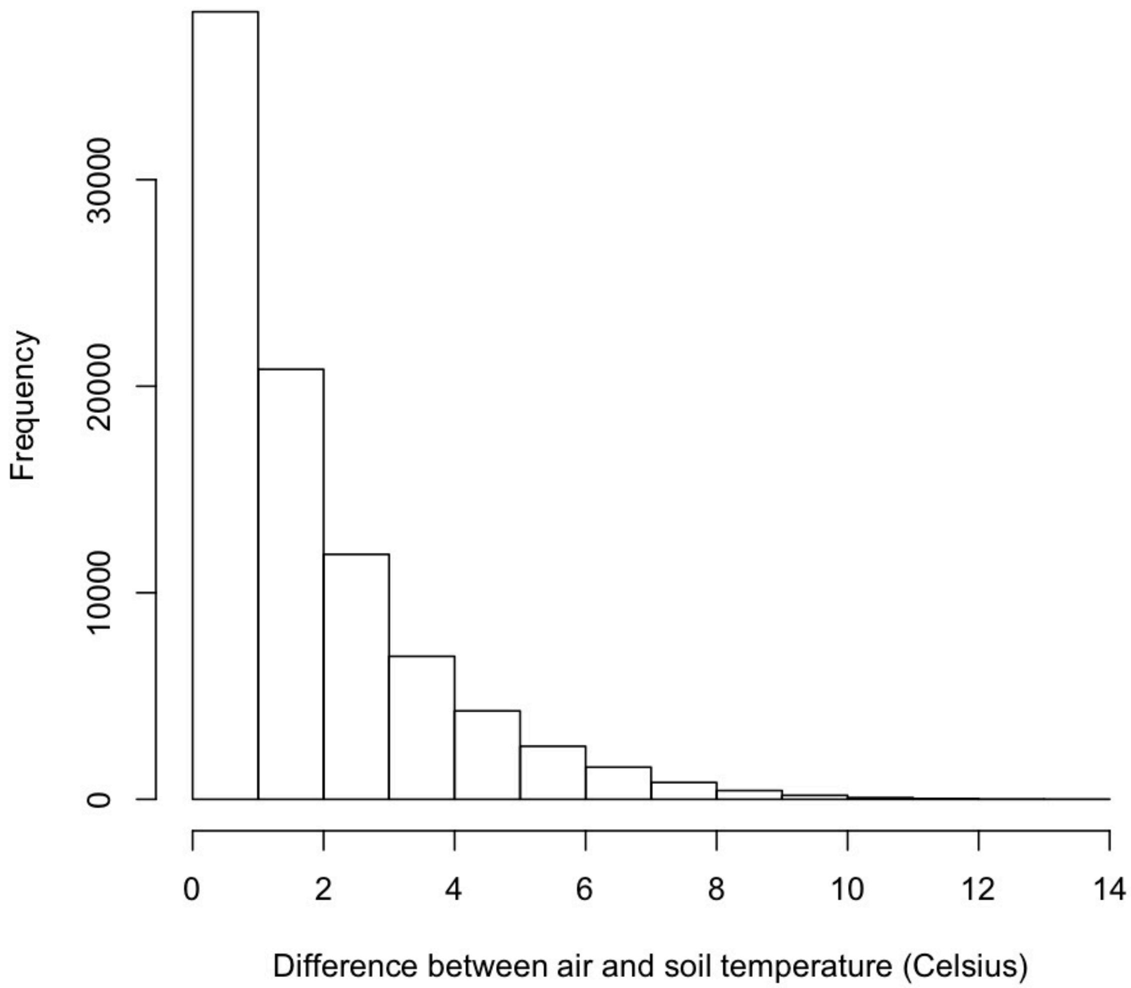

Fig. 3.2. Histogram of differences between simulated air and soil temperature.

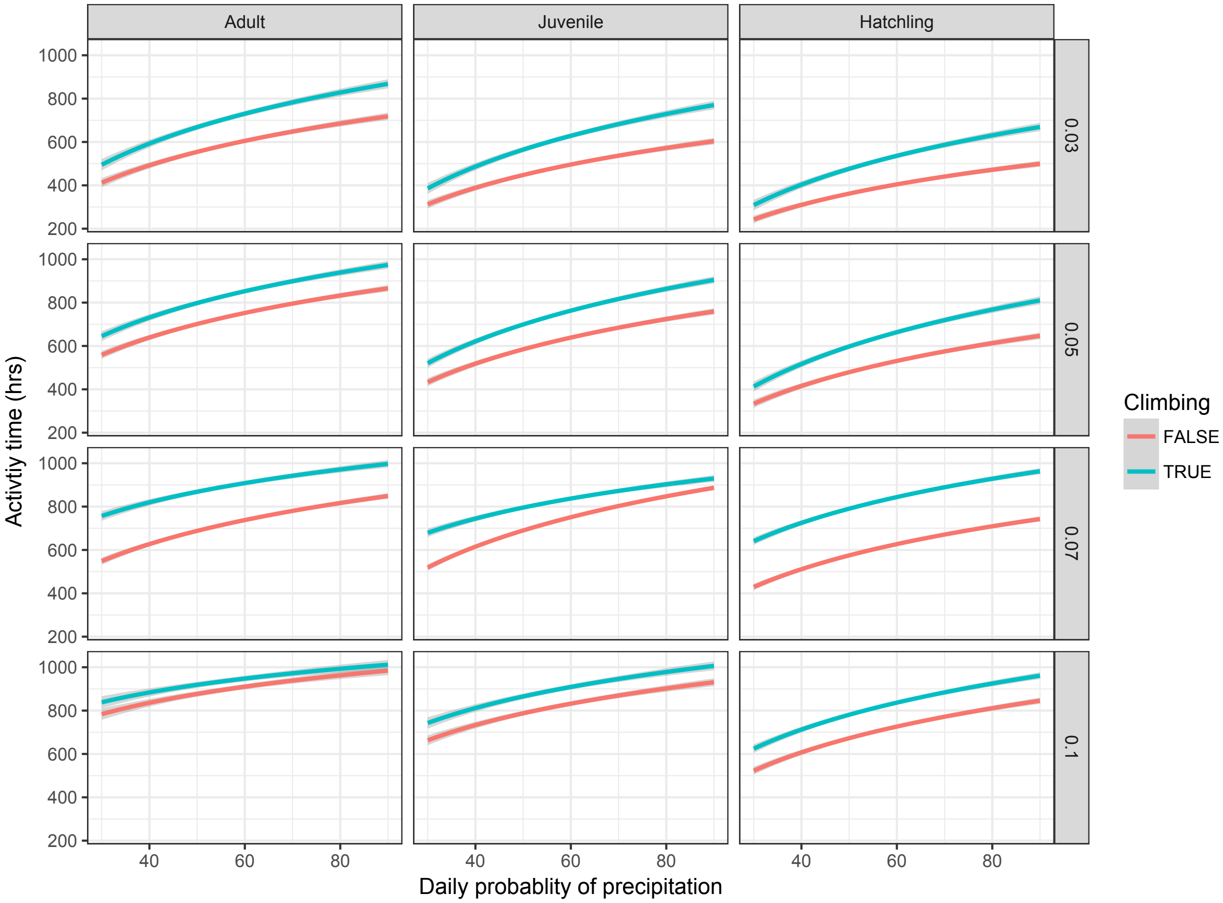

Fig. 3.3. Estimated mean total seasonal activity time, restricted to nights when climbing occurred, for climbing and non-climbing adult, juvenile, and hatchling salamanders as a function of the probability of precipitation and water loss threshold in the model simulation. The lines were smoothed using a logarithmic linear model fit to the data, grey bands surrounding each line indicate a 95% confidence interval.

CHAPTER 4

PLANT CLIMBING BY SALAMANDERS PREDICTED BY AIR TO GROUND TEMPERATURE DIFFERENTIAL EFFECTS ON EVAPORATIVE WATER LOSS: A TEST OF A MODEL HYPOTHESIS[3]

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[3] McEntire, K.D., J.S. Howard, and J.C. Maerz; To be submitted to *Behavioral Ecology*

ABSTRACT

Behavioral plasticity is increasingly recognized as an important adaptive mechanism for species interactions with climate change. Plant climbing has been proposed as a compensatory behavior for Plethodontid salamanders to reduce their water loss rates and increase their activity time during cooler weather. We collected repeated count data on terrestrial salamanders in the southern Appalachian mountains across a range of microhabitats and weather conditions to test whether thermal gradients between the ground and air predicted plant climbing. The probability that a salamander was observed climbing increased with greater soil temperature relative to air temperature, which was consistent with model predictions that plant climbing is a compensatory behavior to reduce water loss and extend activity. Smaller *Desmognathus* species also had a higher probability of climbing. Compensatory behaviors, like climbing, have the potential to moderate the effects of weather on salamander activity and fitness, which may dampen population sensitivity to climatic variation in rainfall or soil moisture.

INTRODUCTION

Predicting ecological responses to climate change is a grand ecological challenge of this century. Critical to that endeavor are mechanistic models of how species or processes respond to climate variation (Kearney and Porter 2009; Buckley et al. 2010; Martinez et al. 2015; Lapiedra et al. 2016; Urban et al. 2016). Ultimately, the robustness of a of model is measured by its capacity to predict observations. Ideally such model outputs would be compared directly to observations; however, for some systems, the desired model outputs are latent. In such cases, comparing model outputs to analogous field observations may be necessary.

For animals, behavioral and physiological plasticity are the most proximate means by which animals respond to fine scale environmental variation. In most cases, plasticity serves to compensate for local stressors. For example, an animal may move into a sunny area to increase its body temperature, allowing the animal to remain active longer in an otherwise cool climate. A number of recent models have included plasticity and its influence on sensitivity to climate (Gifford and Kozak 2012; Sears et al. 2016; Peterman and Gade 2017; Riddell et al. 2018). The outputs of physiology-based models are often energy gain or activity time, which are proxies for fitness (Adolph and Porter 1993). These models are then used to project how animal "fitness" may vary spatially or under future novel climates (Buckley et al. 2010; Denny and Benedetti-Cecchi 2011; Gifford and Kozak 2012; Peterman and Semlitsch 2014; Riddell et al. 2018). The premise of this approach is that the greater mechanistic realism of these models will yield more realistic projections of species responses to environmental change; however, that assumes the model is sufficiently robust to begin with. That is, the model is able to predict observable patterns by including the most appropriate mechanisms. For many species, measuring activity time or energy acquisition in the field is untenable and therefore remains a latent prediction of these models. However, evaluation of such models can be achieved through analogous field-based predictions such as survival, abundance, or the probability of observing an animal in a particular state.

In the previous chapter, we modeled the potential for climbing to act as compensatory behavior among terrestrial salamanders (McEntire, Chapter 3). Specifically, our model predicted that climbing when the air was cooler than the ground would increase salamander activity time, and that the benefits of climbing would occur at smaller temperature differentials with smaller body size or lower relative humidity. While it is not practical, if at all possible, to measure salamander activity time in the field, if salamanders are using climbing to maximize their potential activity time or fitness we expect to see an increased probability a salamander will climb with increasing temperature differential between the ground and air (ground temp. – air temp.), smaller body size, and lower relative humidity (until relative humidity is too low for any above-surface activity). We used observations of climbing from repeated, spatially-extensive field counts of salamanders and measures of weather variables to determine whether temperature differentials, relative humidity, body size, and species are drivers of plant climbing behavior among Plethododntid salamanders in southern Appalachia.

METHODS

Study System and Site- Our study system consisted of several terrestrial salamander species, the most abundant being *Plethodon shermani* and *P. teyahalee*, which form a wide hybrid swarm across a wide rainfall gradient at the U.S.D.A. Forest Service Coweeta Basin, home to the Coweeta Hydrologic Laboratory (Hairston 1973; Hairston et al. 1992). Despite large scale manipulations of certain watersheds within the basin, it remains one of the least disturbed areas in the region. The Coweeta basin receives more annual rainfall than the surrounding region and exists along a steep precipitation gradient described by Daly et al. (2017). The gradient is driven by the shape of the basin, ranging from moderately dry on the western edge to very wet on the eastern edge, encompassing both north and south facing slopes.

Field methods - We identified 20 sites within the Coweeta Hydrological Laboratory distributed across three microclimate gradients (Fig. 4.1); rainfall, aspect, and slope. At these 20 sites, we placed three or four 5-m X 5-m plots, approximately 20 m apart generally along the same elevational contour (72 subplots total).

In 2015, we conducted nocturnal visual encounter surveys of all sites four times (in May, June, July, and September/October). Sampling for all sites was conducted once per site within two weeks of the first sampling period. Surveys started approximately an hour after dusk and were completed between midnight and 5 am depending on the number of animals encountered and the distance between sites surveyed each night. Each plot was searched for 20 person-minutes for surface active salamanders of any species. We hand captured salamanders and placed them in individual plastic Ziplock bags until the end of sampling.

At each site, we recorded temperature, relative humidity, and wind speed using a Kestrel 3500 Pocket Weather Meter (Kestrel Instruments). We recorded this information at the first and last subplot sampled at each site, resulting in two measurements per site per night sampled. We also recorded leaf litter surface temperature, ground surface temperature, and vegetation temperature at four locations in each sub-plot using an Etekcity Lasergrip 774 Non-contact Digital Infrared Thermometer. When possible, we recorded body temperature of salamanders at the point of capture using the same device. We hand captured active salamanders of all species and recorded size class based on snout-vent-length (SVL), sex, and climbing behavior. For most species, size classes consisted of adult and juvenile. *Desmognathus ocoee* with an SVL less than 25 mm were classified as juvenile and larger were considered adults (Huheey and Brandon, 1973, pers. obs.). *Eurycea wilderae* with an SVL greater than 27 mm were classified as an adult, any smaller were called juveniles (pers. obs.). For *Plethodon* spp. we included additional size classes; hatchling: less than 30 mm SVL; juvenile: between 31 and 45 mm SVL; sub-adult: between 46 and 60 mm SVL; and adult: greater than 60 mm SVL. These values were based on demographic analysis (Howard 2018). We considered salamanders climbing if they were fully suspended off the ground on downed woody debris, a tree trunk, herbaceous vegetation, or a shrub.

Statistical Analysis –We used a generalized logistic regression model in Program R (version 3.5.0.) to estimate the effects of temperature differential (soil – air), relative humidity, wind speed, species, size class, and presence of *Rhododendron* on the probability a salamander was observed while climbing. We included the presence of *Rhododendron* in the model because it forms a dense architecture that may increase substrates for climbing and because the importance of Rhododendron on salamander activity and abundance was the focus of a subsequent study (see Chapter 5). Because temperature differential, relative humidity (represented by time since last rain in the model in Chapter 3), and size class were all important for the model in Chapter 3, we included these factors as covariates in the model. We also included wind speed, species, and presence of *Rhododendron* (an evergreen shrub) as covariates. For analysis, we clustered *D. aeneus* and *D. wrighti* adults, and *D. ocoee* and *E. wilderae* juveniles into the “Plethodon hatchling” size class and *D. ocoee* and *E. wilderae* adults into “Plethodon juvenile” size class because they were more comparable in size and this allowed us to separate species from size class effects. We constructed a full covariates model, additional models containing all possible combinations of subsets of these covariates, and a null model, and we used AIC to select the top models among all candidate models (Burnham and Anderson, 2002; Akaike, 1973).

RESULTS

In 2015, we observed 885 salamanders, of which 155 were observed climbing. This included 671 observations of *Plethodon,* 13 were *Desmognathus aeneus*, 22 were *D. wrighti*, 3, 133 were *D. ocoee*, and 46 were *Eurycea wilderae*. Of these observations, we recorded body temperature 57 times for adult *Plethodon*, 79 times for sub adult *Plethodon*, 88 times for juvenile *Plethodon*, and 27 times for hatchling *Plethodon*. We were able to measure salamander body temperature in relation to proximate soil temperature and air temperature 326 times spanning 17 of 21 sampling occasions; however, the majority of these body temperature measurements were taken during 2 summer samples, and almost half of these observations occurred at the three wettest sites where a majority of animals were observed. Whether climbing on plants or on the ground, the body temperatures of salamanders were equivalent to the temperature of the substrate upon which they were found (Fig. 4.2a) and were on average 2.38 ± 1.04 °C cooler than the air temperature (Fig 4.2b).

Temperature differential between the soil and air, relative humidity, and species were the most significant predictors of salamander climbing (Table 4.1). Increased difference in air and soil temperature (with positive values representing cooler air temperatures) sharply increased the probability of climbing for all species and size classes (Fig. 4.3). Relative humidity also had a positive effect on the probability of climbing, though this relationship was shallower than the effect of the temperature differential (Fig. 4.4). Among species for a given combination of weather conditions, *Plethodon* had a lower probability of climbing compared to *Desmognathus* and *Eurycea* species. Size class, wind speed, and the presence of *Rhododendron* had no effect on the probability of salamander climbing.

DISCUSSION

This study provides the first field evidence suggesting plant climbing – also referred to as facultative arboreality - in salamanders is a compensatory behavior using temperature gradients to extend activity time. This supports the hypothesis from simulations using a mechanistic, agent-based biophysical model (Chapter 3), which estimated increased activity time among climbing salamanders as air temperatures became cooler than soil temperatures (Chapter 3). Even though we cannot directly measure activity times of climbing and non-climbing salamanders, the higher probability of observing a salamander climbing during conditions predicted to be most beneficial by the model provides reasonable support for the model's mechanism driving the behavior. Collectively, we provide the first robust, adaptive explanation for this widely observed behavior among temperate plethodontid salamanders (McEntire 2016).

This field study also provided some of the first estimates of climbing frequency for different Plethodontid species. Prior studies largely describe the occurrence of climbing among salamanders as a binary anecdote [species does or does not climb]. We detected species-specific propensities to climb. Specifically, *Plethodon* had lower probability of climbing for a given set of weather conditions. There are several possible mechanisms driving these species differences. First, *Plethodon* are fully terrestrial while *Desmognathus* and *Eurycea* more typically occupy stream riparian zones (Hairston 1949; Barbour et al. 1969; Camp et al. 2007; Connette et al. 2016). *Plethodon* were also larger than the *Desmognathus* and *Eurycea* species we observed. Though we did not observe a direct effect of size class on climbing probability, we might expect the larger size and more terrestrial habits of *Plethodon* are linked to greater resistance to water loss. Qualitatively, *Plethodon* have thicker, sticky secretions compared to *Desmognathus* and *Eurycea*. Increased resistance to water loss reduces the relative benefit of climbing until much higher temperature differentials (Chapter 3). Thus, the species-specific differences may reflect underlying morphological and physiological differences that drives sensitivity to water loss (Spight 1968). Unfortunately, there are few estimates of species-specific water loss rates or measures of resistance to water loss (Gifford 2016). Early studies assumed water loss of salamanders was equal to a free water surface (Spotila and Berman 1976; Peterman et al. 2013), however more recent studies suggest this is not the case and salamanders may even have some plasticity in their resistance to water loss (Feder and Londos, 1984; Winters and Gifford, 2013; Peterman and Gade, 2017; Riddell and Sears, 2015; Riddell et al., 2017; Riddell et al., 2018).

It is also possible that species specific differences in climbing propensity are related to differences in movement among species. Among vertebrates, species that make larger horizontal movements have been shown to exhibit increased vertical movements (Scheffers et al. 2017). Because *Desmognathus* and *Eurycea* have aquatic larval phases, they regularly –sometimes up to hundreds of meters – between terrestrial habitats and streams for breeding. In contrast, Plethodon do not migrate and have relatively small home ranges on the scale of tens of square meters or less (Nishikawa 1990).

Finally, we cannot rule out the possibility that the smaller salamander species increase climbing in response to reduce competition or predation by the larger *Plethodon*. Competition and intra-guild predation are important factors structuring salamander communities (Hairston, 1996; Hairston, 1987; Adams, 2007), and escape from predation has been proposed as a mechanism driving climbing behavior (reviewed by McEntire 2016).

We note that the model described in Chapter 3 simulated greater differences in temperature than those recorded in the field (Appendix 4.1). Model simulated temperature differences were generated using weather records from the site and differences between soil and air reached 10°C. In contrast, the largest differences we observed during our study was 2°C. The model simulations were parameterized using extensive temperature data collected continuously in 2013 and 2014, whereas our observations studies were on a total of 16 occasions between 2015 and 2017. Therefore, we likely missed the full range of temperature differences due to sampling on a relatively small number of nights compared to weather records used in the simulated data, and the two weather data sets occurring during different years. We also note that in our original model (Chapter 3), climbing only occurred – by rule – on nights when air temperatures were lower than ground temperatures. While our field observations showed relatively low rates of climbing when air temperatures were warmer than soil temperature, some climbing did occur under those conditions. This suggests that our initial model is overly strict by not allowing climbing to occur under conditions when air temperatures are warmer than soil temperatures. This also suggests there may be some randomness or error associated with climbing or that other factors such as predation, competition, prey availability, or navigation also motivate climbing (Jaeger, 1978; Roberts and Liebgold, 2008; Cote et al., 2015;Mezebish et al. 2018).

It is also important to note that our original model and field data only consider the value of temperature from the perspective of evaporative water loss. It is likely that if salamanders move among microhabitats including climbing on vegetation to regulate body temperatures, then adaptive decisions to climb may be related to other processes such as metabolic efficiency. Optimal temperatures for the *Plethodon* hybrids observed in this study are not available, but similar species and one of the parent species' (*Plethodon teyahalee*) have optimal metabolic temperatures between 22.2 to 22.9°C (Clay and Gifford 2017). Both modeled and field measurements of soil temperatures were always below this range. Therefore, it is possible that salamanders may climb on some nights when air temperatures are warmer than soil temperatures because it improves their metabolic rate. A recent study found that salamanders with shortened tails selected warmer temperatures, presumably to increase metabolic efficiency for regeneration (Bliss and Cecala 2017). Recent models of salamander plasticity and activity have demonstrated that behavioral plasticity can mediate trade-offs between activity and metabolic rate to optimize when to be active and when to remain inactive underground (Riddell et al. 2018). Future models could integrate our measured relationships between temperature and climbing to optimize among both water loss, activity time, and metabolic rate to better forecast how climbing behavior compensates for weather and climate.

Contrary to predictions from the model, we did not observe any effect of size class on the probability of climbing independent of species effects. Our model predicted greater benefit to hatchling and juvenile *Plethodon* at smaller temperature differential compared to adults. Therefore, we would have expected a higher probability of climbing among hatchlings and juveniles. One explanation for this is that while there is a larger proportional benefit for climbing among hatchlings and juveniles, overall activity times of those smaller size classes are significantly shorter than for adults – particularly as conditions get drier. Therefore, the probability of observing any hatchling or juvenile during drier conditions or at drier sites is low. Indeed, Howard (2018) found that hatchling and juvenile capture probability was lowest among all size classes, that capture probability declined with increasing time since rain, and hatchling and juvenile abundance dropped significantly with reduced annual rainfall.

Our field results provide some confirmation of our agent-based biophysical model through the use of an analogous observation process. We cannot directly measure animal activity time, which is predicted by the model, but model predictions conformed to probabilities of observing salamanders in a state of climbing. This confirmation validates the underlying mechanism of the model, which is that salamanders use climbing to capitalize on thermal differences between the ground and plants, which allows them to reduce their evaporative water loss rates and extend activity. Salamanders may also use these thermal gradients between the ground and plants when ground temperatures are less metabolically optimal. That hypothesis remains to be tested. A robust, mechanistic model linking salamander activity and performance to weather can facilitate better predictions of how salamanders will respond to spatial and temporal gradients in climate, including forecasts of how they may perform in future novel climates (Riddell et al. 2018).

TABLES

Table 4.1: Model selection results for generalized logistic regression of climbing behavior by salamanders. "Temp diff "refers to the difference between soil and air temperature. "RH" refers to the relative humidity. "Rhodo" refers to Rhododendron presence. "Sp" refers to species . "No Par" refers to the number of parameters. For space efficiency, only models within 4 AICc are presented. Only models within 2 AICc were considered equally parsimonious.

Temp Diff	RH	Wind speed	Sp	Size class	Rhodo	NoPar	R^2	AICc	delta_ AICc	wt
X	X		X			7	0.173	691.545	0	0.202
X	X		X		X	8	0.175	691.638	0.093	0.193
X	X		X	X		8	0.175	691.954	0.409	0.165
X	X		X	X	X	9	0.177	692.210	0.664	0.145
X	X	X	X			8	0.173	693.283	1.737	0.085
X	X	X	X		X	9	0.175	693.451	1.906	0.078
X	X	X	X	X		9	0.175	693.722	2.177	0.068
X	X	X	X	X	X	10	0.177	694.043	2.497	0.058

FIGURES

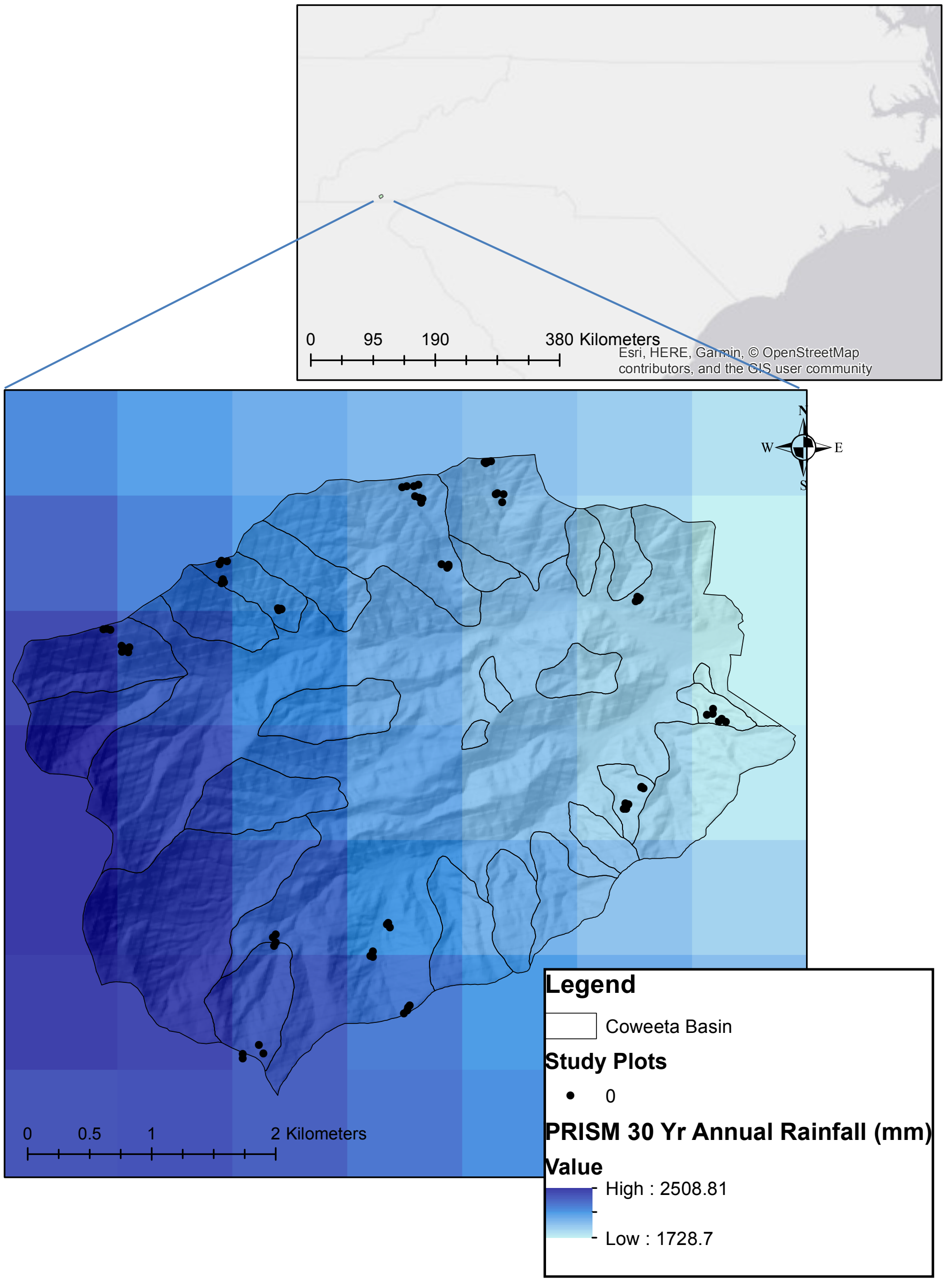

Fig 4.1: Study plots distributed across the mean annual precipitation gradient within the Coweeta basin. Darker blue bands that indicate increased annual rainfall. Black circles mark the locations of study plots.

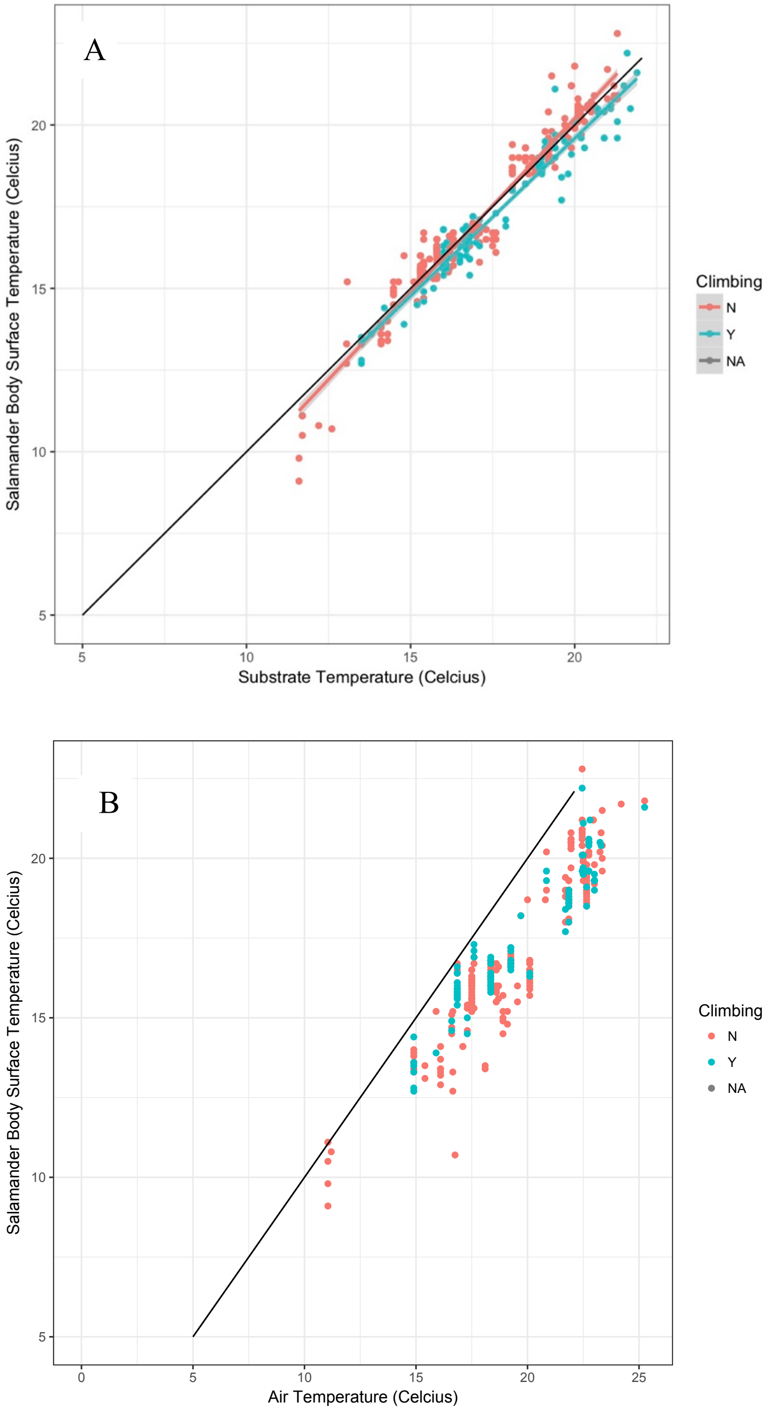

Fig. 4.2: Relationship between substrate (A) or air temperature (B) and salamander body temperatures. The solid line represents a 1:1 relationship. The lines represent a linear model of the relationship between substrate and salamander body temperature, colors reflect climbing o non-climbing animals.

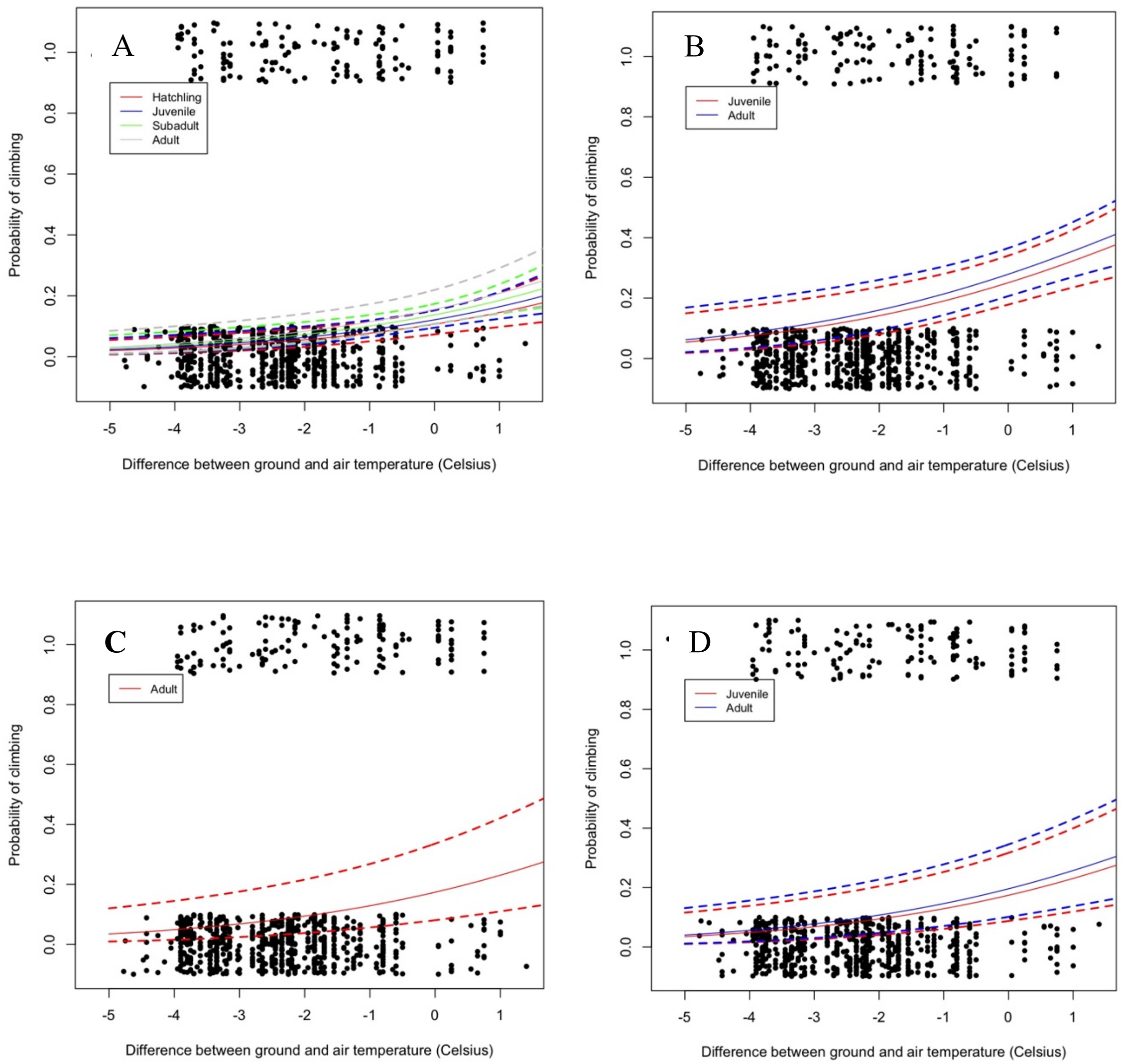

Fig. 4.3: The relationship between the difference between soil surface temperature and air temperature and the probability of a salamander climbing for each species. The colors correspond to the size class designations for (A) *Plethodon* spp., (B) *Desmognathus ocoee*, (C) *D. wrighti* and *D. aeneus*, and (D) *E. wilderae*. Dashed lines are 95% confidence intervals.

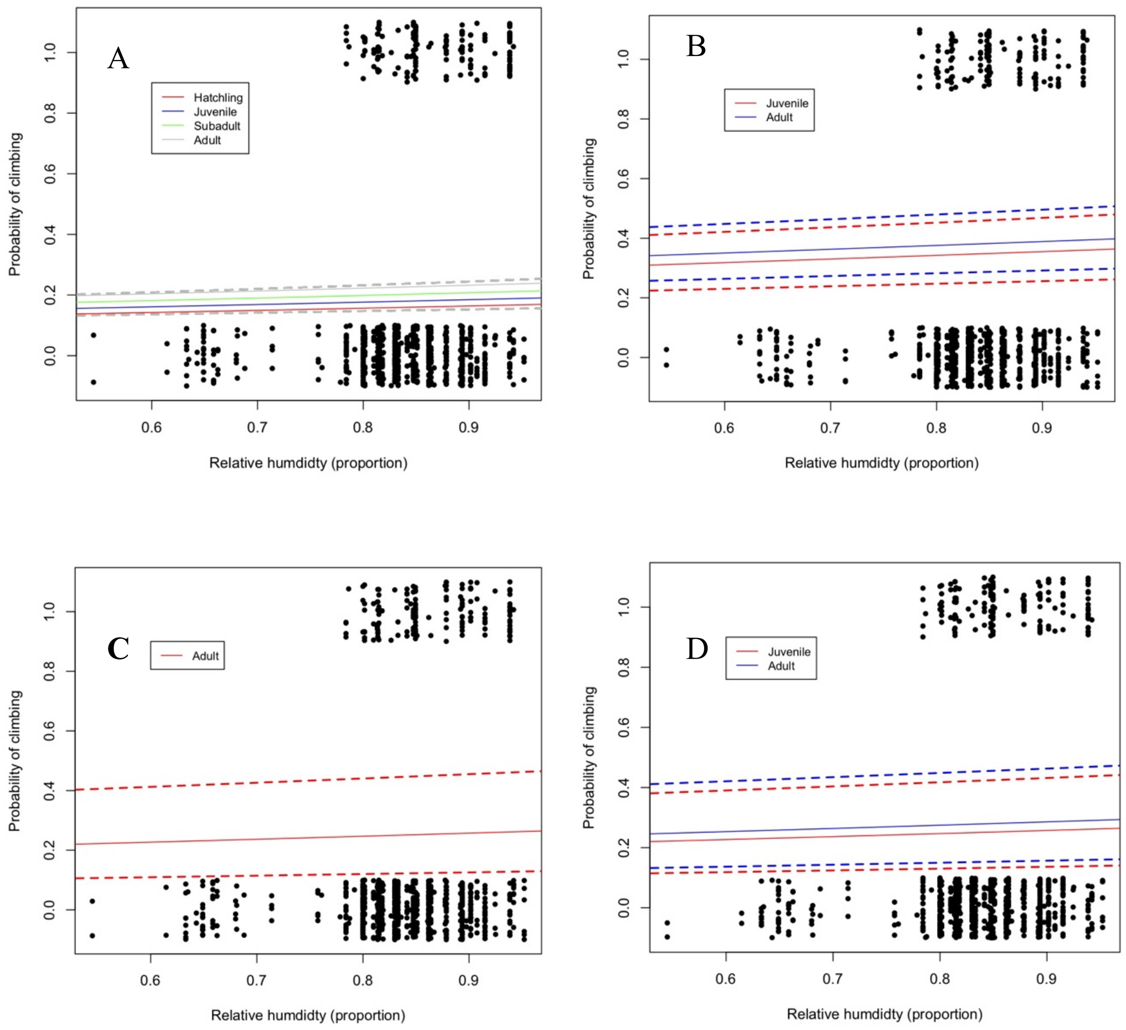

Fig. 4.4: The relationship between relative humidity and the probability of a salamander climbing for each species. The colors correspond to the size class designations for (A) *Plethodon* spp., (B) *Desmognathus ocoee*, (C) *D. wrighti* and *D. aeneus*, and (D) *E. wilderae*. Dashed lines are 95% confidence intervals.

CHAPTER 5

ESTIMATING THE INFLUENCE OF *RHODODENDRON* ON TERRESTRIAL SALAMANDER PERFORMANCE, SURVIVAL, AND ABUNDANCE[4]

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[4] McEntire, K.D., J. C. Maerz, C. Minat, and K. J. Elliot; To be submitted to *Forest Ecology and Management*

ABSTRACT

Forests are intentionally managed to provide a range of ecosystem services including the maintenance of biodiversity. One challenge in forest management is often a lack of information on the non-target effects. In the Appalachian mountains, dense thickets of *Rhododendron,* an evergreen shrub, have become a management target because of concerns over hardwood recruitment and other forest processes. There is a need to inform *Rhododendron* management efforts about non-target impacts on wildlife. Here we use three approaches – a biophysical agent-based model, experimental removal of Rhododendron, and spatially replicated surveys - to estimate the potential effects of this plant and its management on terrestrial salamander activity time, survival, and abundance. Biophysical models predicted a negligible effect of *Rhododendron* on salamander activity time, and capture-recapture analyses showed no short-term effects of *Rhododendron* cutting or burning on salamander survival. Estimated abundances from comparative surveys indicated little to no effect of *Rhododendron* on salamander abundance across a rainfall gradient. By using multiple approaches, our results suggest that *Rhododendron* has a negligible or slightly deleterious effect on salamanders, and that salamander survival – at least over the two years following action - is not impacted by cutting or the use of fire.

INTRODUCTION

Forests are managed for a range of natural services including timber and fuel production, water quality and yields, soil management, carbon sequestration, game species, and biodiversity (i.e. Patric, 1976; Douglass, 1983; Sohngen et al., 1999; Birdsey et al., 2006). As stressors ranging from land use, shifting disturbance and climate regimes, and introduced species change the composition of forests, new interventions may be needed to preserve or restore important functions. Management actions need to be informed by rigorous understanding of the drivers of change, the impacts of forest change, the responsiveness of forests to management actions, and non-target effects of management.

The montane, temperature forests of the eastern United States have undergone significant transitions in composition and coverage over the past 150 years (Van Lear et al. 2002; Birdsey et al. 2006; Elliott and Vose 2012). Forests were cleared extensively during the 19h century, with a partial rebound with the decline of agriculture in the eastern United States by the latter half of the 20th century (Birdsey et al. 2006). Forest composition was dramatically altered by post-agricultural succession that included extensive colonization by nitrogen fixing locust trees (*Robinia* spp.), altered fire regimes, and the introduction of invasive pests that decimated the American chestnut (*Castanea dentata*), Dogwood (*Cornus florida*), and most recently Eastern hemlock (*Tsuga canandensis*) (Van Lear et al. 2002; Elliott and Swank 2008).

In response to chestnut blight, more than 50 years of fire suppression, and the recent decline of hemlock, cover and biomass of midstory forest species, such as *Rhododendron* spp., have expanded (Spaulding and Rieske 2010; Elliott and Vose 2012; Ford et al. 2012). *Rhododendron* can alter forest structure and forest floor and soil conditions in ways that may affect the recruitment of other species (Clinton and Vose 1996; Baker and Van Lear 1998; Nilsen et al. 2001; Clinton 2003; Wurzburger and Hendrick 2007; Elliott and Vose 2012). *Rhododendron* creates a thick midstory layer, and its dense thickets are associated – along with Eastern hemlock – with acidic soils and the relative absence of understory herbaceous vegetation (Elliott and Vose 2012), and inhibition of seedling establishment (Clinton and Vose 1996) and reduced hardwood tree species recruitment (Wurzburger and Hendrick 2007). *Rhododendron* may also have effects on nutrient cycling, water yields, and habitat quality for native biota (Baker and Van Lear 1998; Nilsen et al. 2001; Wurzburger and Hendrick 2007; Webster et al. 2012). In rapidly human developed regions such as the southern Appalachian mountains, the expansion of *Rhododendron* has led to actions by individuals and agencies. Some land owners clear *Rhododendron* to improve forest access and aesthetics and their views, while larger agencies such as the U.S. Forest Service are exploring large scale management of *Rhododendron* to improve hardwood recruitment on public lands. To better inform *Rhododendron* management decisions, agencies need information on additional positive and negative, short and long-term system responses to *Rhododendron* removal.

The importance of forest midstory shrubs, particularly *Rhododendron*, to wildlife is relatively poorly studied. *Rhododendron* dramatically increases the structural complexity of forest environments, and is known to be an important nesting substrate for migratory songbirds (Stodola et al. 2013). *Rhododendron* is also known to modify local microclimates by decreasing variability in soil and air temperature, and soil water content compared to surrounding areas (Clinton 2003). As mentioned previously, *Rhododendron* is also contributes to soil acidification and reduced cover of herbaceous vegetation (Elliott and Vose 2012). Collectively, these changes in forest understory environments may affect wildlife.

Salamanders make up a large portion of the vertebrate biomass in North American montane forests (Burton and Likens 1975a; Semlitsch et al. 2014; Milanovich and Peterman 2016). Ecologically, these highly abundant amphibians are important components of nutrient cycling and nutrient standing stock (Burton and Likens 1975b; Davic and Welsh 2004; Semlitsch et al. 2014; Milanovich and Peterman 2016). As predators of forest floor invertebrates, salamanders indirectly regulate leaf litter decomposition (Best and Welsh, Jr. 2014; Hickerson et al. 2017). Because of their ecological significance and known sensitivity to microclimate (Spotila 1972; Feder 1983), salamanders are of interest in conservation and forest management. Nothing is known about the influence of *Rhododendron* on salamander performance and abundance. Some research exists in relation to the impact of clear cutting, selective logging, and general forest management (Pough et al., 1987; Petranka et al., 1993, 1994; reviewed in deMaynadier and Hunter Jr., 1995; Messere and Ducey, 1998), but the results of those studies and their relevance to predicting the effects of *Rhododendron* or its removal are equivocal (Petranka et al. 1993). Salamanders show resilience to small scale or low intensity management practices that limit effects on soil temperatures and moisture (Pough et al. 1987; Messere and Ducey 1998; Semlitsch et al. 2009) which are the largest determinants of salamander performance and fitness (Feder 1983). Qualitatively, one might expect *Rhododendron*'s effects on relative humidity reducing temperature variability may be beneficial to salamanders. In addition, *Rhododendron* serves as a substrate for climbing, which can help salamanders reduce evaporative water loss and extend surface activity during periods without rainfall. On the other hand, more acidic soils and reduced soil moisture availability (Nilsen et al. 2001) may increase salamander dehydration and limit rehydration sufficiently to constrain salamander activity and fitness (Frisbie and Wyman, 1991,1992,1995). These paradoxical predictions highlight the need estimate or directly measure the influence of *Rhododendron* presence and management on salamander populations.

We utilized three approaches to estimate the effect of *Rhododendron* and its management on terrestrial salamanders. First, we used an agent-based ecophysiological model to estimate salamander activity in the presence and absence of *Rhododendron* across a gradient of rainfall probability. Because they are mechanistic, agent-based models (hereafter ABM) can provide realistic predictions of how animals will respond to habitat change (McEntire, Chapter 3), and have been used to predict the outcome of disease management decisions (e.g. Smith and Harris, 1991), evaluate different land management strategies (Railsback and Johnson 2014), and define suitable habitat (Kühn et al. 2008; Westervelt et al. 2013). Second, we estimated salamander survival on experimental forest plots before and after cutting of *Rhododendron* and burning to remove the dense leaf litter. Finally, we used repeated counts of salamanders in plots with and without *Rhododendron* present across an extensive rainfall gradient to determine whether the presence of *Rhododendron* was associated with greater or lower salamander abundance, and whether this effect varied with annual rainfall. We expect that *Rhododendron* might have no effect or a slightly negative effect on salamander abundance in areas of high rainfall because of the effects on soil acidity and soil moisture availability; however, in areas of low rainfall, *Rhododendron* may have a net positive effect on abundance by increasing forest floor humidity, stabilizing temperatures, and providing a substrate for climbing.

METHODS

Model: *Overview*- We applied a modified form of the mechanistic model presented in Chapter 3 to estimate salamander activity time with presence of and absence of *Rhododendron*. Additional methods and explanations of model structure are available in the form of an "ODD" (Overview, Design concepts, and Details) protocol (Grimm et al. 2006; Grimm et al. 2010) in Appendix 5.1. To simulate the effect of *Rhododendron* on salamander activity, we adjusted the microclimate to reflect values found under a *Rhododendron* canopy. By comparing those values to simulations without a midstory canopy, we estimated the relative importance of *Rhododendron* mediated microclimate on salamander fitness. We included plant climbing as an important mediator for microclimate interactions (Ch 3) and based climbing propensity on frequencies recorded in the field (Ch 4). We used the relationship between climbing probability and difference in air and soil temperature of *Plethodon* spp. described in Chapter 4 to estimate individual probability of climbing on any given night.

We used NetLogo (Version 6.0.2, U. Wilensky, 1999) to simulate salamander activity on a 50 X 50 tile landscape. We used daily probability of rainfall to create a gradient from relatively wet to dry climates among simulations. The simulations ran 20 times for each set of parameters and a single simulation lasted for one active season (April through October) with alternating day and night time steps (428 total steps) and a minute-long sub-time step to calculate dehydration. The code is available in Appendix 5.2.

We simulated weather events, including rainfall events and nightly temperature, once every "24 hours" (two time steps) for the entire virtual landscape. The presence of midstory canopy altered the relative humidity and temperature of a tile based functions developed using empirical data from the Coweeta Hydrologic Laboratory, Macon Co., NC (Miniat and Elliott, unpublished data; Appendix 5.1).

Agent Simulation- The agents were modeled as salamanders of the *Plethodon jordani* species complex. We included three size classes of individuals: hatchlings (snout-vent-length (SVL) < 32 mm), juveniles (SVL 32 to 42 mm), and adults (SVL 43 to 72 mm). We simulated 1000 agents of each size class for a total of 3,000 agents randomly distributed across the uniform landscape, and we did not include any density-dependent effects. Agents emerged if the relative humidity was greater than 45% and they had a water loss deficit smaller than 4%. The agents remained active until they lost 3 to 10% of their mass to water loss, depending on the simulation. Agents adopted soil temperature as their body temperature when active on the ground and plant temperature when climbing (Ch. 3). We estimated climbing probability of each agent on each night based on the difference between soil and air temperature. This relationship was derived from field data (Ch 4) and generally increased with increasing difference between air and soil, when the air was cooler than the soil. Plant climbing interacts with temperature gradients and may compensate for environmental variation (Ch 3). Agents recorded their daily foraging time for the entire simulation (one active season).

Data analysis- We visually examined the effects of Rhododendron on nightly and seasonal activity time with respect to probability of rainfall, time since last rainfall, air temperature, water loss threshold, and size class. We used generalized additive models to visualize the relationships between the data. To estimate seasonal activity, we summed the nightly activity times for each size class and rainfall probability per simulation across the rainfall probability gradient. We assumed animals were active every night of the simulation, so the absolute values do not reflect true estimates of seasonal activity for salamanders.

Field Studies: *Study System and Site*- Our study system consisted of two terrestrial salamander species, *Plethodon shermani* and *P. teyahalee*, which form a wide hybrid swarm across a wide rainfall gradient at the U.S.D.A. Forest Service Coweeta Basin, home to the Coweeta Hydrologic Laboratory (Hairston 1973; Hairston et al. 1992). Despite large scale manipulations of certain watersheds within the basin, it remains one of the least disturbed areas in the region. The Coweeta basin receives more annual rainfall than the surrounding region and exists along a steep precipitation gradient described by Daly et al. (2017). The gradient is driven by the shape of the basin, ranging from moderately dry on the western edge to very wet on the eastern edge, encompassing both north and south facing slopes.

Field Experiment –Sixteen, 20 X 20 meter plots were established within relatively unmanipulated watersheds with dense *Rhododendron* cover. Adjacent to eight of the 16 plots, we established a 5 m X 20 m plot that was included in the treatment area. Two treatments, physical removal and removal of the O-horizon through burning, were applied alone and in combination in a factorial design with four replicates of each treatment. The four possible treatments included "reference", "cut only", "cut and burn", and "burn only". The reference plots were not altered during the course of this study. The "cut" refers to physical removal of Rhododendron shrubs through cutting and application of herbicides. The fallen branches in the "cut only" plots were removed and placed into piles outside of the study areas. In the "cut and burn" treatments, the branches were left where they fell and allowed to dry before burning occurred. Removal of the O-horizon through burning was proposed to facilitate hardwood recruitment because *Rhododendron* leaves suppress decomposition and alter soil chemistry (Hladyz et al. 2011). The 8 plots included in the "cut only" or "cut and burn" treatments were cut in February 2015. Controlled burns used to remove the O-horizon were performed in early May 2016.

We conducted 24 monthly capture-mark-recapture surveys between April 2014 and October 2017. We only had time for four pre-treatment capture periods on control, cut, and cut & burn treatments, and 11 capture periods on burn only treatments. Two people each searched the entire plot area twice and hand-captured surface active salamanders. The salamanders were placed in individual plastic bags for processing. We recorded species, sex, snout-vent length (SVL), total length, and mass. We uniquely marked salamanders by injections of visible implant elastomer (VIE; Northwest Marine Technologies, Inc.). We did not mark hatchling salamanders deemed too small to safely inject.

Comparative Surveys – We identified 20 sites within the Coweeta Hydrological Laboratory distributed across three microclimate gradients (Figure 1); rainfall, aspect, and slope. At these 20 sites, we placed three or four 5-m X 5-m plots, approximately 20 m apart generally along the same elevational contour (72 subplots total). When present, we placed one or two sub-plots within thickets of *Rhododendron* spp.

In 2016 and 2017, we conducted nocturnal visual encounter surveys in a robust design (Pollock 1982) with three primary periods (spring, summer, and fall) and three secondary periods within each primary period. Spring samples occurred between April and mid-May, summer samples occurred between mid-June through August, and fall samples occurred between September and October. At each site, we recorded temperature, relative humidity, and wind speed using a Kestrel 3500 Pocket Weather Meter (Kestrel Instruments). We recorded this information at the first and last subplot sampled at each site, resulting in two measurements per site per night sampled. Surveys started approximately an hour after dusk and were completed between midnight and 5 am depending on the number of animals encountered and the distance between sites surveyed each night. Each plot was searched for 20 person-minutes for surface active salamanders. We hand captured salamanders and placed them in individual plastic Ziplock bags until the end of sampling. For each salamander, we recorded size class based on snout-vent-length (SVL), sex, and climbing behavior. We used four size classes; hatchling: less than 30 mm SVL; juvenile: between 31 and 45 mm SVL; sub-adult: between 46 and 60 mm SVL; and adult: greater than 60 mm SVL. These values were based on prior demographic analysis (Howard

2018). Among adults, sex was determined by the presence or absence of a mental gland on the chin and visible testis or ovaries through underside skin for sexually mature individuals.

Statistical Analysis – We estimated apparent survival of salamanders pre and post treatment application using a Cormack-Jolly-Seber model (Kéry and Schaub, 2012) fit to the mark-recapture data. We modeled salamander survival as a function of treatment pre and post treatment application. Because treatments were not applied at the same time point and the cut and burn treatment involved the application of two treatments at two time points, we present estimated survival post the first and second treatment applications. Because treatments altered the structure among plots, we modeled capture probability as a random temporal variable within treatments. We fit the integrated model using a Bayesian framework with Markov chain Monte Carlo (MCMC) methods in Jags called from R (version 3.1.2, R Core Team, 2013) via the R2jags package (Su and Yajima, 2012). We assigned diffuse prior distributions for all fixed effect parameters and hyperparameters governing random effects in all models. For the integrated model, we generated three MCMC chains using 30,000 iterations where we retained the last 29,700 iterations with a thinning rate of 3 (Link and Eaton, 2012). We assessed convergence for all models by visually inspecting chain mixing in MCMC trace plots and Rhat values should be ~ 1 when convergence is acheived. We based parameter inferences on posterior means and 95% Bayesian credible intervals (BCIs; 2.5th–97.5th percentile of the distribution).

To test whether the presence of *Rhododendron* was positively associated with the abundance of salamanders across a rainfall gradient, we used generalized binomial N-mixture models in the R package ‘unmarked’ (Fiske and Chandler 2011) to estimate local abundance of *Plethodon* hybrids for each size class. We used the gpcount() function for repeated count sampling in the robust design. To model abundance in the presence and absence of *Rhododendron*, we modified the model described in Howard (2018) to include *Rhododendron* presence as a covariate for abundance, availability and detection probability. We also included average annual rainfall during the active season (March -October) for 2016 and 2017 as a site specific, non-time varying covariate of abundance. We included time varying covariates of total precipitation in the 7 days prior to sampling, and a binary variable indicating the presence of a severe drought for availability and detection probability. Previous analysis of this data suggested the importance of these variables (Howard 2018). The non-linear structure of the data prevented the models from performing well in parametric bootstrap goodness-of-fit tests (Howard 2018). We used the simulate() function to generate simulated count data to compare to observed data. We assumed the model fit was acceptable if these counts were similar to our field data.

RESULTS

Model Results –Nightly activity time decreased with increasing time since last rainfall, which directly correlated with declining relative humidity (Fig 5.1). The relationships between nightly activity time and time since last rainfall or water loss threshold was not affected by the presence of *Rhododendron* (Fig 5.1). Total seasonal activity increased with increasing rainfall probability, with the steepest increases at the lowest water loss threshold (Fig 5.2). As water loss threshold declined, *Rhododendron* presence had an increasingly positive effect on mean total seasonal activity time of salamanders, particularly among juveniles and hatchlings (Fig. 5.2); however, this effect was relatively small and resulted in negligible differences in total season activity time across a wide range of realistic water loss thresholds. The effect of *Rhododendron* presence on mean total seasonal activity time did not vary across the rainfall probability gradient (Fig. 5.2).

Field Studies Results – We marked 576 *Plethodon spp*., recaptured 59 at least one time, and did not mark 6 individuals. We also marked 84 *Desmognathus ocoee* and 12 *D. monticola*, of which we recaptured 14 and one individual, respectively. The *Desmognathus* spp. were not included in our survival analysis. We also encountered but did not mark 44 *D. aeneus*, 4 *D. quadramaculatus*, 43 *E. wilderae*, 2 *Gyrinophilus porphryticus*, and 1 *Notophthalmus viridesens*. Chains for all model estimates had reasonable convergence and, with the exception of our posterior estimate for pre-treatment capture probability on the control plots (Rhat = 1.30), posterior estimates achieved stationarity (Rhat < 1.07 for all posterior estimates; Fig. 5.3). With the possible exception of the cut and burn treatment, there were no significant differences between pre- and post-treatment mean posterior apparent survival estimates for any treatments (Fig. 5.4). For control, burn only and cut only treatments, credible intervals between pre- and post-treatment estimates were widely overlapping. For the cut and burn treatment, credible intervals for pre- and post-treatment apparent survival estimates barely overlapped, indicating a potentially lower survival rate pre-treatment compared to post-treatment (Fig. 5.4). However, among all treatments, mean posterior apparent survival estimates were lower and credible intervals wider owing to the relatively small number of pre-treatment sampling occasions. Overall, post-treatment posterior apparent survival estimates for control and all treatment plots were similarly high, ranging between 0.905 and 0.914 over the two or three years post-treatment.

Among the comparative study plots, we captured 2377 *Plethodon,* including 470 adults, 660 sub adults, 825 juveniles, and 422 hatchlings. *Rhododendron* presence had no significant influence on abundance estimates across all sites. (Fig. 5.5). Estimated abundance of all three size classes increased with mean annual rainfall, but the presence of *Rhododendron* had no effect on local abundance or the relationship between abundance and mean annual precipitation.

DISCUSSION

Using three complementary approaches, we estimated little to no effect of *Rhododendron* on salamander activity, survival, or abundance across a rainfall probability gradient. These results are consistent with Pursel (2012), who also found no relationship between *Rhododendron* presence and *Plethodon* abundance at a nearby site. These results suggest that – with one exception - *Rhododendron* is unlikely to have a measurable net effect on salamander activity, fitness, or abundance across a relatively wide range of climates. Our model did predict that *Rhododendron* could have a positive effect on salamander activity at lower water loss thresholds, particularly for smaller salamanders such as hatchlings. We know that water loss thresholds are plastic (Feder and Londos, 1984; Winters and Gifford, 2013; Peterman and Gade, 2017; Riddell and Sears, 2015; Riddell et al., 2017; Riddell et al., 2018), but we still understand relatively little about variation in water loss thresholds among salamander species, size classes, and weather conditions. At the lower end of the water loss threshold that we explored, hatchling salamanders would realize a net benefit in activity time from the presence of *Rhododendron*, and as a proportionate change in activity time, that benefit would increase with reduced probability of rainfall. We can imagine that water loss threshold might be lower and more sensitive among small salamanders that are more prone to evaporative water loss. Moreover, our study are ranges from average to well above average rainfall probability for the region. Therefore, it is possible that *Rhododendron* does act as buffer and facilitate increased activity of small salamanders in drier habitats; suggesting it may be an important habitat feature for salamanders in drier climates. Future studies are needed to test this hypothesis.

Our study highlighted the great potential for rigorous ABMs to simulate – mechanistically – the unknown effects of habitat variation and management on a focal taxa. Our model predicted a relatively negligible net effect of *Rhododendron* on salamander activity time, which was consistent with patterns of abundance among sites with and without *Rhododendron* across a wide rainfall gradient. In other words, the model could reasonably estimate an effect – or lack thereof – in the absence of direct comparative or experimental approaches. Moreover, comparative and experimental approaches have limits in their capacity to inform management decisions, particularly in the short-term. Comparative surveys are confounded by the possibility that patches with and without *Rhododendron* cover are not random, but rather the result of other underlying processes. Experimental studies such as ours are cost and labor intensive, which leads to limited replication. This in turn can lead to high uncertainty in estimated responses to treatment, and – at least within the short-term – responses may be to the application of treatments such as cutting *Rhododendron*, rather than a response to the longer-term absence or reduction of *Rhododendron*.

Our model did employ some assumptions that may affect inferences about the importance of *Rhododendron* on salamander activity. The most important limitation was our inability to integrate information about soil moisture and rehydration rates of salamanders. This restriction is discussed in more detail in Chapter 3. If, as some studies suggest, available soil moisture under *Rhododendron* is lower than comparable areas without *Rhododendron* (Boettcher and Kalisz 1990; Clinton and Vose 1996; Nilsen et al. 2001; Clinton 2003; Beier et al. 2005; Wurzburger and Hendrick 2007), then salamander water budgets and activity time may in fact be reduced under *Rhododendron* thickets. In addition to soil moisture, soil temperature might increase and pH might decrease (Boettcher and Kalisz 1990; Clinton and Vose 1996; Nilsen et al. 2001; Clinton 2003; Beier et al. 2005; Wurzburger and Hendrick 2007). Soil temperature will affect salamander metabolic rates, which can affect animal decisions to be active (Riddell et al. 2018).

Our model does not directly integrate this process. Soil pH also affects salamander water balance, which can also constrain salamander activity (Frisbie and Wyman, 1991,1992,1995). Studies about the influence of *Rhododendron* on soil moisture and drying rates, soil temperature, and pH in addition to a better understanding of salamander rehydration processes are needed before such information could be integrated in our simulation model. Nonetheless, our model assumptions highlight that the effects of *Rhododendron* on forest floor environments may have antagonistic and net neutral effects on salamander performance. We note that the effects of *Rhododendron* on soil moisture and pH appear variable and uncertain (Boettcher and Kalisz 1990; Clinton and Vose 1996; Nilsen et al. 2001; Clinton 2003; Beier et al. 2005; Wurzburger and Hendrick 2007). If *Rhododendron* effects on soil conditions vary in response to other environmental factors, then the net effects of *Rhododendron* on salamanders may differ between positive, neutral, and negative among sites.

Though it was not incorporated into the design, we note that our treatments in field experiments were distributed across a 10% change in mean annual rainfall gradient, with one cut site receiving the lowest mean annual rainfall of any replicate. We do not know whether this gradient was sufficient to affect our ability to detect treatment effects on survival, but we suspect not. We did observe a phenotypic change among salamander hybrids between the wetter and drier replicates (McEntire and Maerz, unpublished data) that was consistent with patterns of hybrid phenotype distributions in relation to mean annual precipitation (Maerz et al. unpublished data). We also know that salamander abundance varies across the basin as a function of mean annual precipitation, and we know that survival rates of Plethodon within the basin are positively correlated with the amount of rainfall (Howard 2018). However, our post-treatment apparent survival estimates were high among all treatments and consistent with independent reference estimates from high rainfall sites (Howard 2018). Therefore, we doubt that the rainfall gradient confounded any estimates of short-term responses to treatments.

For our comparative surveys, because we included plots with and without *Rhododendron* at nearly ever site across the rainfall gradient in our observational study, we were better able to limit confounding effects and examine the local effects of *Rhododendron* across a range of climates. Nonetheless, it was not uncommon for some of our non-*Rhododendron* plots to be nestled within large patches of *Rhododendron* and vice versa. Therefore, our comparative studies may have limited ability to detect local effects on salamanders if the effects from the surrounding habitat conditions overwhelm the local plot level conditions. Collectively, the limitations of all three approaches reinforces the rigor of using three different approaches to address the same question. That all three of our approaches yield similar inferences about the small potential effects of Rhododendron on salamanders gives us greater confidence that decisions to manage Rhododendron will not have substantial non-target effects on these species.

An encouraging result of our study suggests that *Plethodon* should be relatively resilient to the short-term impacts of *Rhododendron* management – specifically cutting and burning. Previous studies estimating the impact of forest management – broadly - on salamanders found mixed responses depending on the intensity of the management and the time since disturbance (Pough et al., 1987; Petranka et al., 1993, 1994; reviewed in deMaynadier and Hunter Jr., 1995; Messere and Ducey, 1998). Smaller scale management practices such as selective harvest that leave parts of the overstory canopy intact found salamander abundance was relatively resilient to the disturbance, at least in the short term (Pough et al. 1987; Messere and Ducey 1998). This type of harvest is most similar to the physical removal of *Rhododendron*, because the overstory canopy is left intact. The controlled burns on our plots were relatively low impact, in terms of maintaining the overstory canopy. Our results are consistent with other studies that found salamanders were relativity tolerant of prescribed fires in the Appalachian mountains (Ford et al. 1999; Ford et al. 2010). It is likely that salamanders are resilient to these lower impact forest management practices because they are nocturnal, therefore not likely to be active why actions are going on, and salamanders spend significant amounts of time underground where they can stay for protracted periods. Therefore, as long as *Rhododendron* management actions limit disturbance to the soil and the leaf litter remains intact or recovers quickly, our results predict negligible impact to salamander populations resulting from *Rhododendron* management.

Intentional management of any ecosystem is prone to unexpected impacts and using large scale experimental manipulations to monitor the outcome of these effects is wise but challenging. Taking a multi-faceted approach, as we did here, provides multiple lines of information for making inferences and judgements about management actions. In particular, agent-based models have been used previously to inform management decisions, (i.e. Smith and Harris 1991; Kühn et al. 2008); however, they remain an underutilized tool for simulated desired and non-target outcomes of forest management.

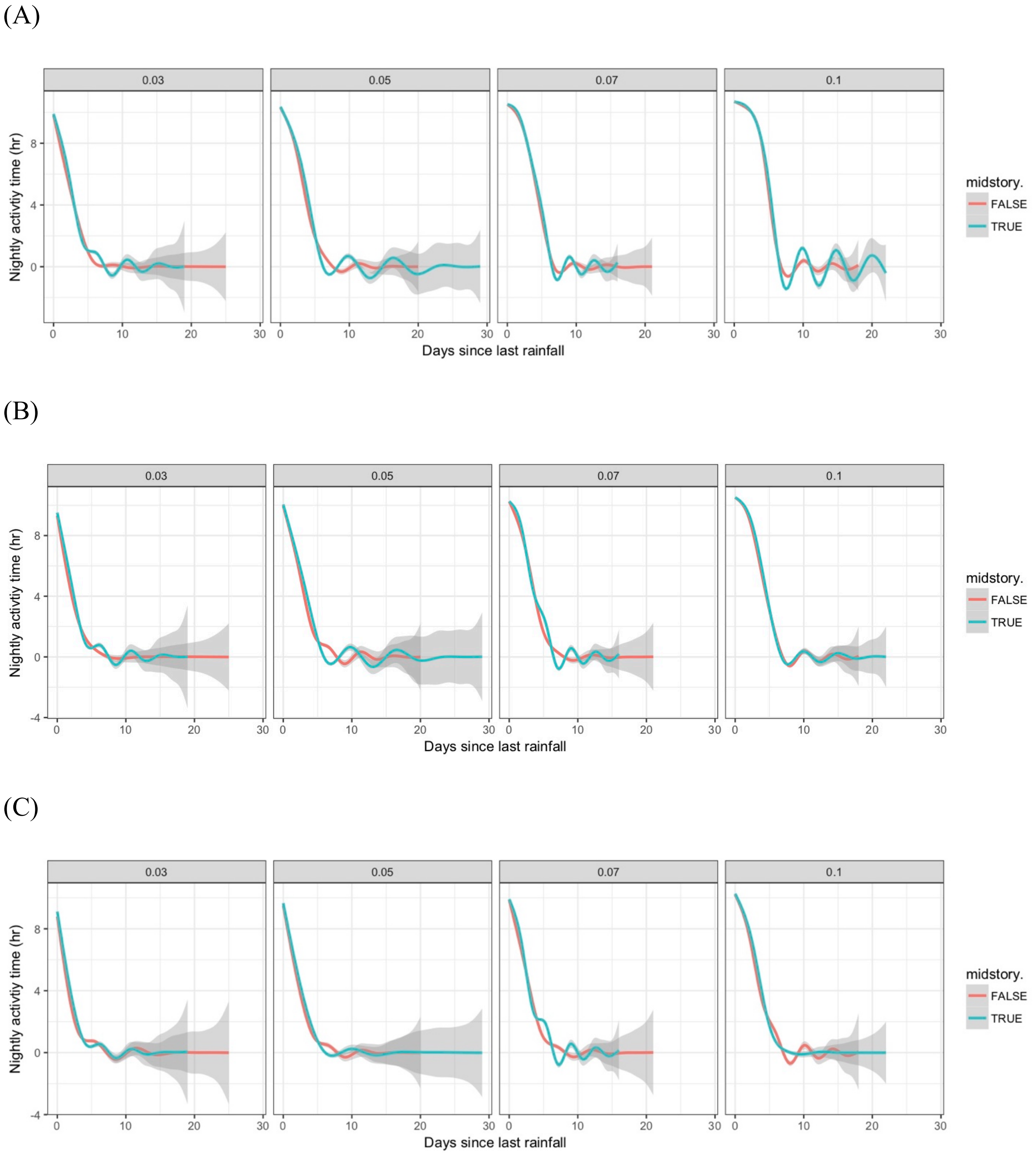

Fig. 5.1: Nightly activity time compared to time since last rainfall for areas with Rhododendron present (true, in teal), and absent (false, in orange). The three size classes (A) adults, (B) juveniles, and (C) hatchlings are paneled by water loss threshold, with increasing threshold from left to right. Grey bands represent 95% confidence intervals.

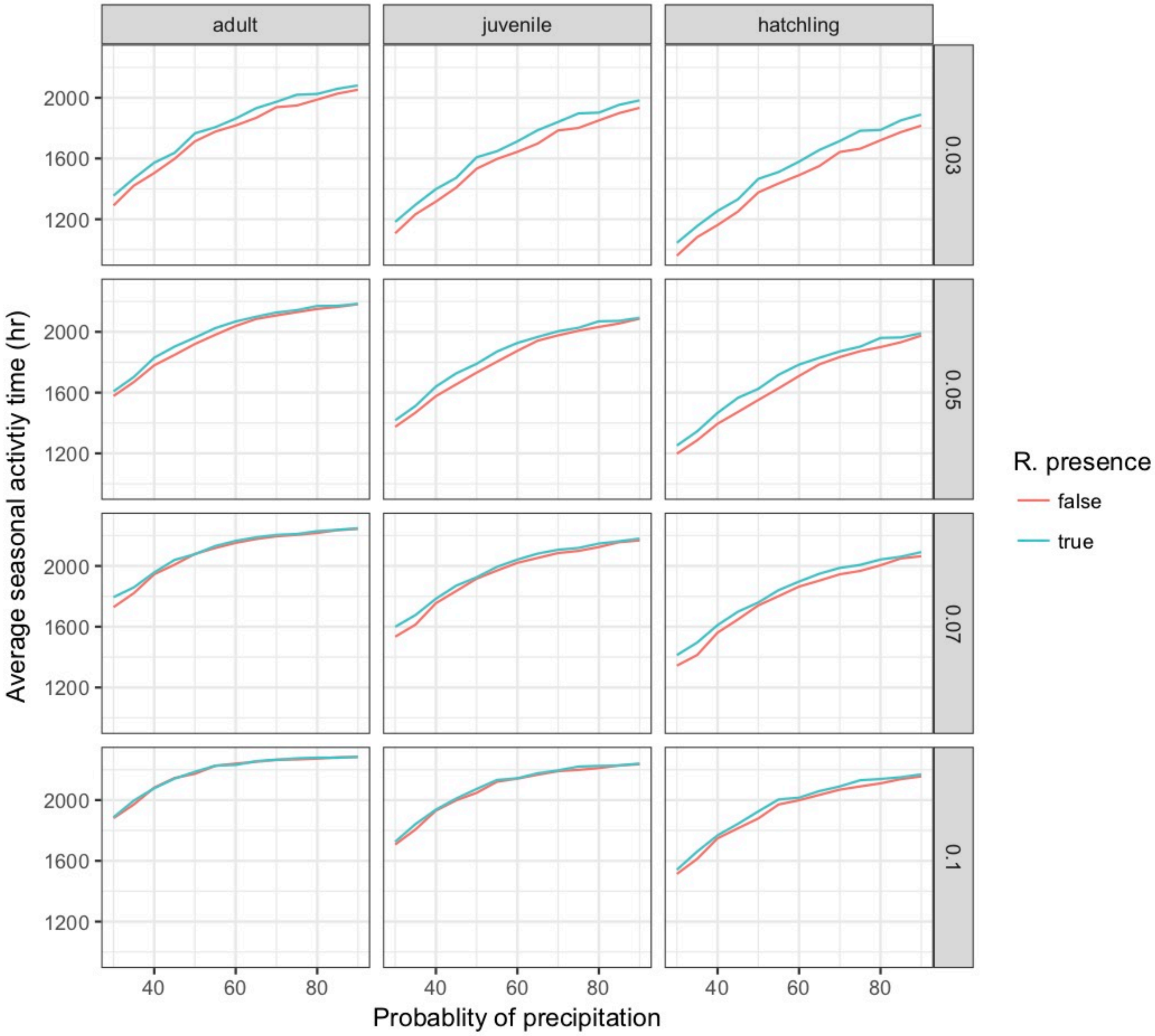

Fig. 5.2: Mean salamander seasonal activity time plotted against probability of rainfall and as a function of water loss threshold and size class.

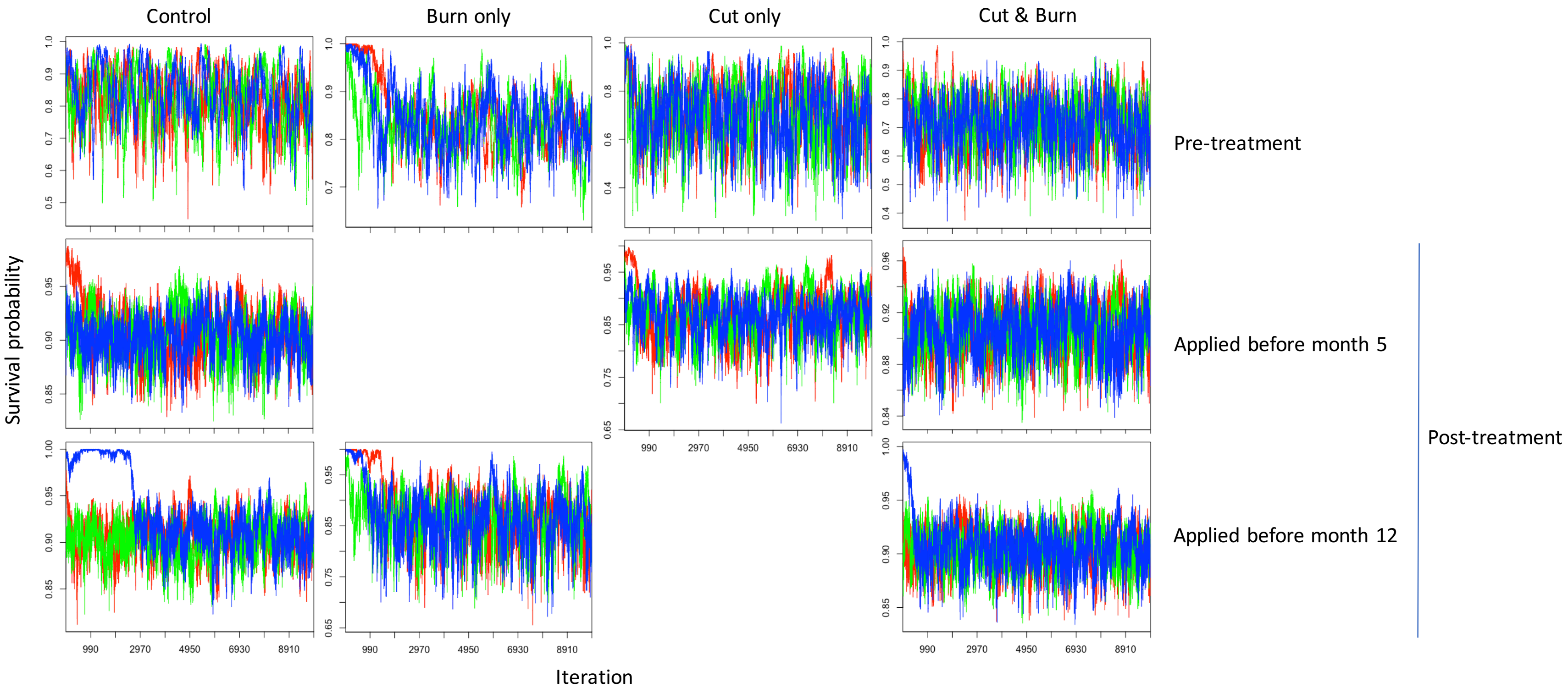

Fig. 5.3: Convergence of three Markov chain Monte Carlo (MCMC) simulations for salamander apparent survival estimates, pre and post treatment, over 30,000 iterations with a thinning rate of 3.

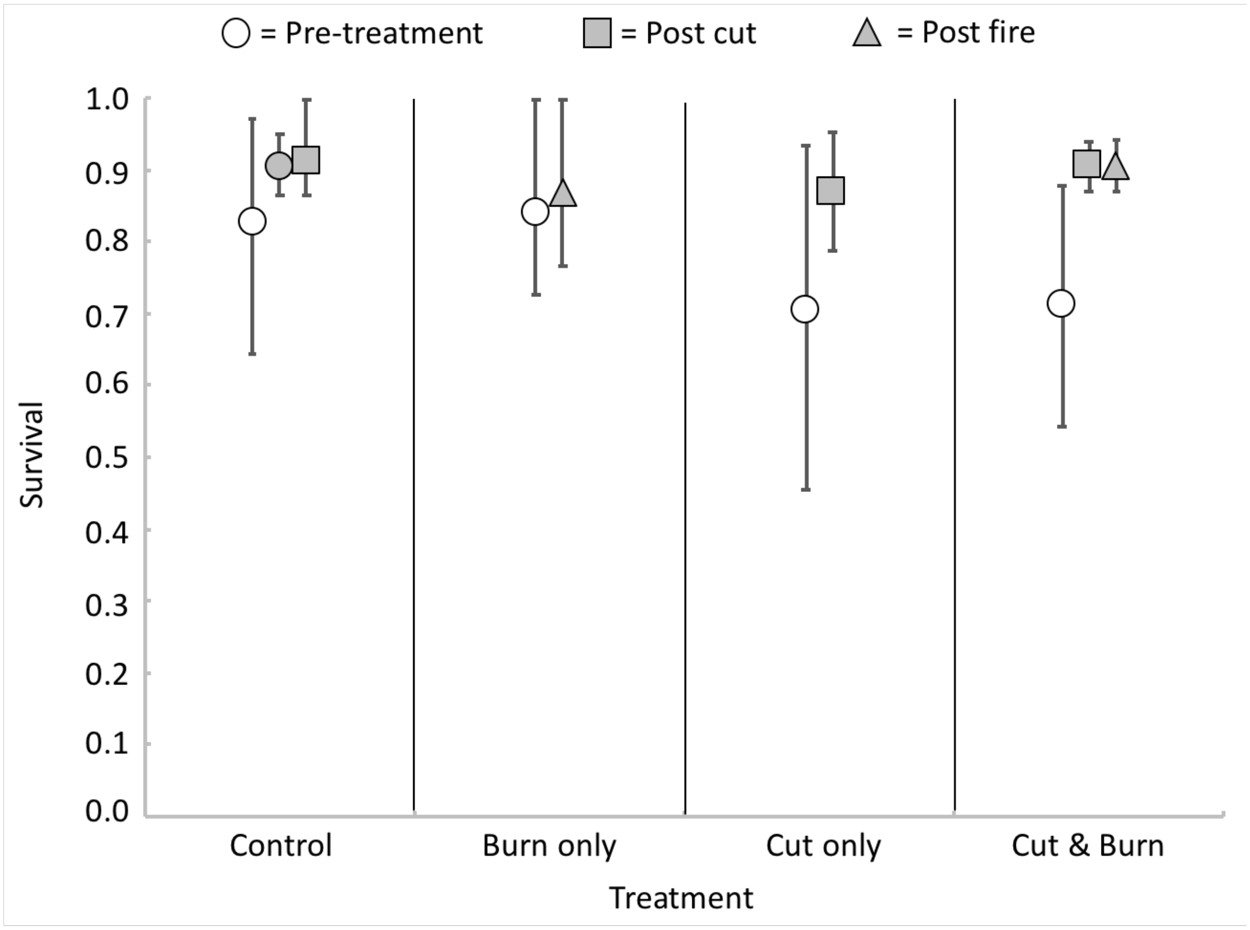

Figure 5.4: Mean posterior apparent survival estimates (± 95% credible intervals) of *Plethodon shermani X teyahalee* hybrid salamanders on experimental *Rhododendron* management plots. White symbols indicate pre-treatment estimates, which cover 4 capture periods for control, cut, and cut & burn treatments, and 11 capture periods for burn only treatments. Shaded symbols are post-treatment estimates.

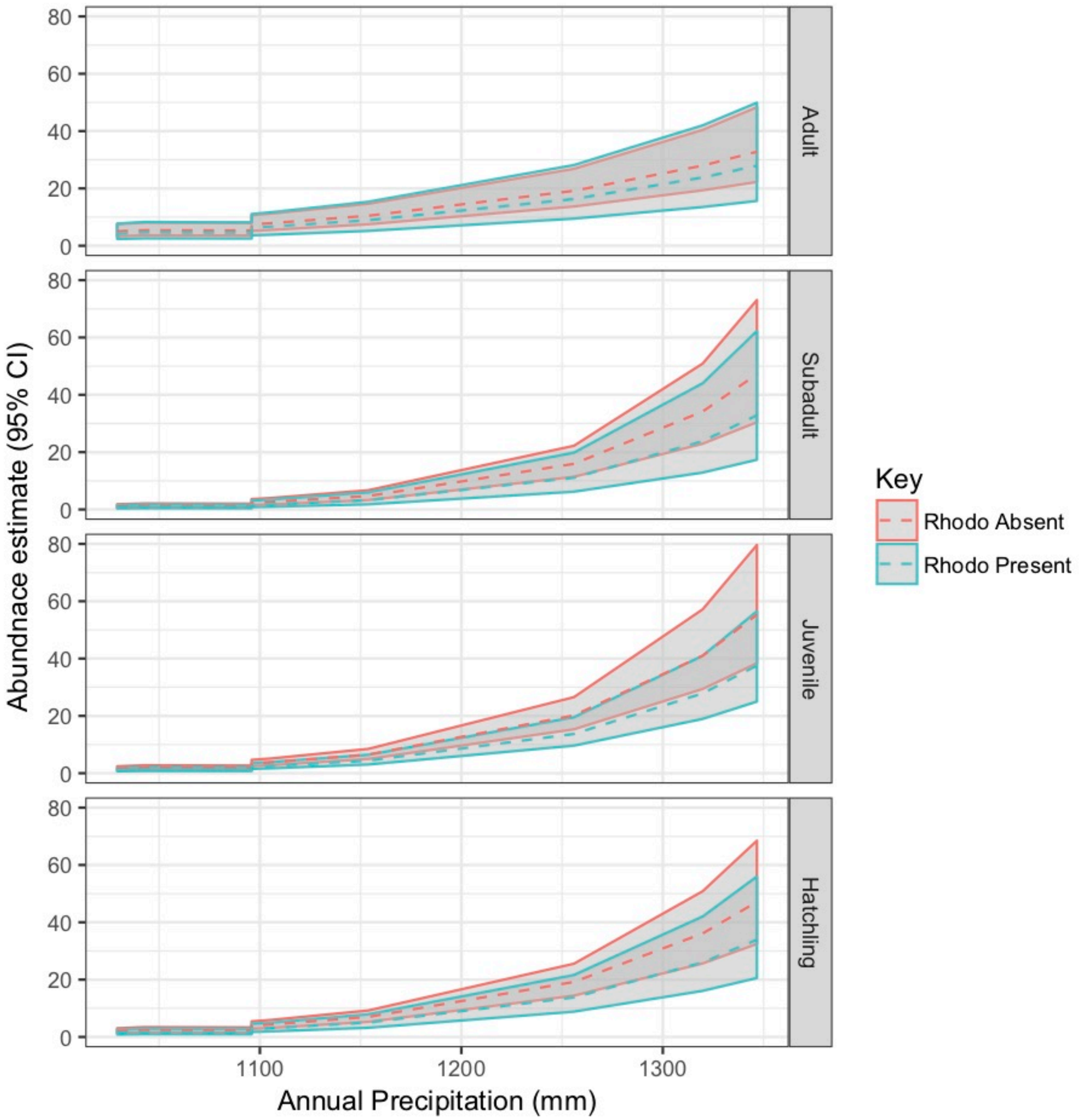

Fig. 5.5: Estimated *Plethodon spp*. abundance by size class as a function of mean annual precipitation and the presence or absence of *Rhododendron*. Grey ribbon outlined in corresponding colors indicate 95% confidence intervals.

CHAPTER 6

CONCLUSION

Models are important tools for understanding ecological systems and predicting how those systems may change across space and time. Robust predictive models are especially helpful to address management questions in the face of climate change. The ongoing challenge with predictive models is ensuring they are robust. Here, I demonstrated the value of incorporating compensatory behaviors within ecophysiological models as a robust approach to understanding and making predictions about ecological systems. After discovering conflicting and poorly supported hypotheses for facultative arboreality in salamanders, I proposed a new hypothesis based on the fundamental physics of evaporative water loss. Because salamander activity is governed by water loss more, I proposed that climbing behavior was means for animals to alter their body temperature to reduce their evaporative water loss rate. Previous papers proposed salamanders would only climb on wet nights (Jaeger 1978) and some studies found higher incidence of climbing on wetter nights (Chapter 2, Table 2.1). But none of the studies on plant climbing explored the influence of temperature on climbing behavior and how that might be related to water loss rates.

I used this idea along with known ecophysiological relationships between salamanders and environmental variables to estimate water loss rates and activity times for climbing and non-climbing animals. Using temperature differentials as the mechanism driving climbing behavior, I found inclusion of climbing as a compensatory behavior increased salamander activity times across a broad range of rainfall probability (Chapter 3). Moreover, the benefits of climbing increased at smaller temperature differentials with increasing time since rain and at a smaller salamander body size. These results predict that the relative benefits of climbing may be greatest in areas with the lowest probability of rainfall, and that climbing may be a compensatory behavior that increases the performance of salamanders in areas that receive lower amounts of rainfall.

In contrast to many other predictive models, in this dissertation I explicitly connected model predictions with field data. Similar models for salamanders have been field validated only twice (Gifford and Kozak 2012; Peterman and Semlitsch 2014). Because the ecophysiological model estimates latent predictions, I had to use analogous field observations for evaluation. Specifically, the model predicted increased activity time when climbing, if the air was cooler than the soil. Though I could not measure activity time in the field, I that increased activity would results increased probability of detecting salamanders in the state of climbing. Consistent with the model, I found a strong correlation between temperature differentials and plant climbing frequency (Chapter 4). I saw an increase in climbing probability with cooler air temperatures compared to soil temperatures, which was consistent with patterns in the model and therefore provides support for the behavioral mechanism in the model. Collectively, the model and field data provide the first robust, adaptive explanation for this widely observed behavior among temperate plethodontid salamanders (McEntire 2016). Specifically, salamanders use climbing to exploit temperature gradients to reduce evaporative water loss. We hypothesize that salamanders may also use climbing to exploit temperature gradients for other purposes such as optimizing metabolic rates. Because the evidence strongly indicates that climbing is an adaptive compensatory behavior for weather and climate, it should be considered integrated with other behavioral and physiological plasticity into future models applied to studies of salamander responses to climate change (Riddell et al. 2018).

There were some important limitations to our model in terms of predicting the advantages of climbing or when we expect to see increases of climbing in the field. In addition to regulating water loss, salamanders may be selecting among thermal microhabitats to optimize metabolic rate and may be balancing increases in activity time with metabolic efficiency (Riddell et al. 2018). Though our model can integrate metabolic rates and efficiencies, we did not evaluate that parameter in the model simulations. Estimation of energy budgets is relatively straight-forward, but requires a an understanding or algorithm for the probability a salamander emerges to be active on a given night. Different values have been used in other studies to estimate emergence probability including a function of time since last rain event (Peterman and Gade, 2017) and based on metabolic cost of being active (Riddell et al., 2018). These values remain poorly understood and would benefit from additional field research.

An important limitation of our model, and all models to date, was our inability to deal with natural variation in soil moisture and soil tension. Our model does include some variability in soil moisture, but we were unable to provide additional insights about natural variation in soil moisture and how that relates to salamander rehydration rates and activity time. During model development, when soil moisture dropped below -0.2 atm, the majority of animals would “die” from an inability to rehydrate in the soil. However, Spotila (1972) and Spight (1967a) demonstrated that *Plethodon* could rehydrate at up to a soil moisture of -2 atm. Salamanders are also known to create a “wetting front” to slow water loss in dry soils (Spotila 1972), but the mechanism and the conditions under which this front is formed along with the hydraulic conductance or water flux rates for salamanders remains undescribed. This indicates that current rehydration models for salamanders [and other amphibians] are incomplete. This also illustrates that while salamanders spend a large portion of their time underground or in retreats, all current models of salamanders' interactions with climate have focused only on their time above ground (i.e. Walls 2009; Milanovich et al. 2010; Gifford and Kozak 2012; Ficetola et al. 2016, Peterman and Gade, 2017, Riddell et al. 2018). Part of this knowledge gap stems from the inaccessibility of the belowground habitats of these animals; however, until this knowledge gap is filled, our models of these organisms will remain incomplete and prone to error. This illustrates a wider problem with the development of mechanistic models. Plethodontid salamanders are a group that are extensively studied and for which there is a relatively rich physiological literature, and yet our current knowledge is still insufficient to construct a full working physiological model of how these animals interact with their environment (Gifford 2016). Many other species are even more knowledge deficient, which will limit the ability to develop and apply mechanistic models to understanding the performance and distributions of those species in current or future novel environments.

By using three approaches to explore the relationship between *Rhododendron* and salamander performance, survival, and abundance, I am confident in concluding *Plethodon* should be relatively resilient to the short-term impacts of *Rhododendron* management – specifically cutting and burning. Previous studies estimating the impact of forest management – broadly - on salamanders found mixed responses depending on the intensity of the management and the time since disturbance (Pough et al., 1987; Petranka et al., 1993, 1994; reviewed in deMaynadier and Hunter Jr., 1995; Messere and Ducey, 1998). Smaller scale management practices such as selective harvest that leave parts of the overstory canopy intact found salamander abundance was relatively resilient to the disturbance, at least in the short term

(Pough et al. 1987; Messere and Ducey 1998). This type of harvest is most similar to the physical removal of *Rhododendron*, because the overstory canopy is left intact. Controlled burns were also relatively low intensity in terms of impact on the forest floor and retention of the overstory canopy. Other studies also found that salamanders were relativity tolerant of prescribed fires in the Appalachian Mountains (Ford et al. 1999; Ford et al. 2010). It is likely that salamanders are resilient to these lower impact forest management practices because they are nocturnal, therefore not likely to be active why actions are going on, and salamanders spend significant amounts of time underground where they can stay for protracted periods. Therefore, as long as *Rhododendron* management actions limit disturbance to the soil and the leaf litter remains intact or recovers quickly, our results predict negligible impact to salamander populations resulting from *Rhododendron* management.

This dissertation highlights the great potential for rigorous ABMs to simulate – mechanistically – the unknown effects of habitat variation and management on focal taxa or processes. One of the challenges of ABMs are their need for specific data on mechanistic relationships. On the flip side, constructing ABMs often draws out critical knowledge gaps or identify novel mechanisms or key processes. Because the nature of ABMs focuses on individual agents, it requires that ecological processes be scaled to how individuals interact with their proximate environment; which is fundamentally how ecological systems work. Species don't interact with other species respond to climate, individuals interact with other individuals or respond to weather events. Therefore, ABMs provide a means to understand how larger relationships and processes emerge from fine-scale interactions among individual agents. Moreover, any uncertainty in those processes is naturally propagated through the model to outputs of interest. ABMs also have the potential to integrate individual differences and evolutionary processes, which are increasingly recognized as integral to our understanding and ability to model the dynamics of natural systems (Grimm et al. 2017). Finally, ABMs allow for estimation of latent states or processes that are critical to understanding a system. For example, there was no feasible way for us to estimate salamander activity time or energy gain in the field, yet those are central to salamander fitness. Models allow us a means to estimate those important parameters of performance that should underlie observable parameters such as growth, survival, fecundity, abundance, occupancy.

Because of the heterogeneous nature of environments, most animals use behaviors to compensate for less suitable conditions that might otherwise limit their performance and ability to occupy a site. Behavioral and physiological plasticity and acclimation are one of the fastest phenotypic responses of animals to environmental change, and compensatory behaviors and plasticity in physiology act as key mechanisms for acclimatization to seasonal climates or short-term changes in weather, food availability, and predation risk (Muñoz et al. 2016; Beever et al. 2017). These compensatory traits, therefore, shape the potential sensitivity of animals to longer-term environmental changes (Beever et al. 2017). Indeed, several recent studies show that accounting for behavioral and physiological plasticity dramatically reduces the projected impacts of climate change on some species, which is both heartening and should have important ramification for how we think about threats and conservation actions. By including multiple behaviors and physiological processes into mechanistic models, we can make more robust predictions about how organisms might respond to future novel environments and make better informed management decisions.

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APPENDIX 3.1

ODD PROTOCOL

1. Modeling Approach

An agent-based model (ABM) of salamander activity in a variable environment with behavioral variation was developed using ecophysiological models and pattern-oriented modeling. We ran 20 simulations of each model.

2. Modeling Description

The model description below follows the ODD protocol (Grimm et al. 2010), a standard format for communicating the concepts and methods used in individual- or agent-based models.

2.1. Purpose

The primary purpose of this of model is to determine the relative importance of compensatory behaviors on salamander fitness across environmental variability represented by a realistic range of rainfall probabilities. A secondary purpose of this model is to evaluate active regulation of water loss rates as driver of salamanders' plant climbing behaviors. The model estimates activity time using salamander dehydration. These estimates are influenced by plant climbing as a temperature regulation mechanism. All model versions were run in the context of a rainfall probability gradient and assumed a uniform vegetative structure and simple behavior (surfacing).

2.2. Programing

The model was built in the program NetLogo (Version 6.0.2, U. Wilensky, 1999). Simulations and sensitivity analyses were run repeatedly during development of the model to ensure proper function of the ecophysiological models within the ABM. The exact code can be obtained by contacting the authors (Appendix 3.2).

2.3. Entities, State Variables, and Scales

The mobile agents were based on salamanders in the genus *Plethodon,* especially *Plethodon jordani* (complex) when available. The *Plethodon jordani* complex represents a mid-size *Plethodon* salamander found throughout Southern Appalachia. The agents consisted of three size classes. All individuals had the same fixed attributes, including 'size class', 'mass', 'snout-vent-length' (SVL), 'surface area', and 'hydraulic conductance'. The three size classes included hatchling (mass < 1 g, SVL < 3.2 cm), juvenile (mass between 1 and 2 g, SVL between 32 and 42 cm), and adult (mass between 2 and 10 g, SVL > 4.2 cm, up to 7.2 cm) to reflect different life phases. Mass (*m*) was randomly generated at set up of the model, and SVL (in cm) was calculated from the mass (in grams) based on a relationship derived from our long-term capture mark recapture data (Howard 2018).

$$[1]\ SVL = 32.8m^{0.34}$$

Surface area was calculated from the mass based on an empirical formula (Whitford and Hutchison 1967), copied below. Where *SA* is equal to surface area in cm^2 and *m* is equal to mass of the salamander in grams:

$$[2]\ SA = 8.42m^{0.694}$$

The hydraulic conductance for leopard frogs (Tracy 1976) was used as the hydraulic conductance for the modeled salamanders, as it is the only reported value for amphibians (Table 1). Climbing propensity was set to 50% for all agents, meaning when conditions were appropriate they had a 50% chance of climbing vegetation. We used 50% because individual propensities are unknown and this offered the ability to compare activity of individuals on any given night.

The variable attributes of the mobile agents included 'resistance to water loss', 'body temperature', 'nightly foraging time', 'water level', 'nights without attempting to forage', and 'overall foraging time', which change over time. Resistance to water loss was calculated nightly from soil temperature, using an equation derived from data for *P. jordani* (Spotila 1972).

$$[3]\ r = 0.425T_S + 0.8136$$

Where r is the resistance to water loss per second and T_s is the soil temperature in Kelvin. We assumed body temperature was equal to soil temperature except when climbing where it was equal to plant temperature. Nightly foraging time in minutes was calculated based on the dehydration model described below and reset at the end of each night. Water level recorded the mass lost due to water lost via the dehydration model during the night. Overall foraging time recorded the total minutes an individual salamander spent foraging during all the nights of the simulation.

The variable patch attributes included 'local relative humidity', 'air temperature', and 'vegetation temperature'. Relative humidity was estimated based on the amount of time since the last rainfall, assuming an even decline of 10% for every day since rain. This is a simplification but effectively functioned to reduce relative humidity when rainfall probabilities were low. Because estimating soil moisture tension (SMT) over time requires extensive knowledge of soil structure, plant composition and density, and throughfall rainfall, we assumed two possible states: (1) 10 kilopascals when raining and (2) 20 kilopascals when not raining. Although, it has been suggested that full drainage occurs after 3 days and SMT is equal to 33 kilopascals (Richards and Weaver 1944), this value resulted in dehydration of salamanders and SMT is generally not well documented in the study area. Stable populations (personal observation) in our simulated area suggest an ability to rehydrate, so we maintained SMT above the absorption threshold for salamanders (T. Spight 1967; Spotila 1972). Plant temperature was set to an average between the soil and air temperature (Geiger 1965).

Global variables included ‘air temperature’, ‘soil temperature’, ‘raining’, ‘time since last rainfall’, and ‘hours of daylight’. Air temperature was set at the beginning of each night, generated from a random-normal distribution using the monthly average night-time temperature and standard deviation for data recorded at Coweeta from 2013 to 2014s (Miniat 2017). Soil temperature was set monthly to the average monthly soil temperature recorded at Coweeta at a depth of 5 cm from 2013 to 2014 (Miniat 2017). Rainfall was simulated randomly with the probability in 24 hours ranging from 30-90% in 5% increments. Hours of daylight were set for each month to the monthly average for the latitude of the Coweeta Hydrologic Laboratory (35° 3'35.70"N, http://aa.usno.navy.mil/data/docs/Dur_OneYear.php).

2.4. Process Overview and Scheduling

The model alternated through day and night time steps and ran for one active season (April through October, 428 time steps total). During ‘day’ time steps, rainfall was simulated based on a probability of rain. Rainfall then affected the soil moisture, immediately setting to -10 kPa, then decreasing to -20 kPa after 6 time steps (3 days and 3 nights) with no rain (see above for justification). Next, salamander agents rehydrated based on soil moisture and temperature. Rehydration rates were calculated on a minute-by-minute basis and could result in dehydration if the soil moisture was too low. If salamander agents lost 50% of their mass due to dehydration, they died. This level of water loss is higher than would be physiologically possible, but allows for unknown factors relating to rehydration, such as the creation of a wetting front, which is recognized but poorly understood (Spotila 1972).

'Night' time steps began with temperature selection by drawing a value from a month-specific normal distribution of average nightly temperatures at Coweeta. These temperatures were recorded at 5 stations over 2 years. The duration of each night was set to the month-specific average number of night-hours. Vegetation temperature was set to the average of the soil and air temperature (Geiger 1965). We use a set value of 40% (a value chosen during model development) probability of emergence; an intermediate value used (Peterman and Gade 2017).

Once a salamander agent surfaced, it lost water based on a ecophysiological model described in the Submodels section. The model calculated water loss based on surface area, temperature, and relative humidity every minute. Salamanders lost water until their body mass had decreased by 3-10% depending on the model run. This model was run at 3, 5, 7, and 10% as part of sensitivity analysis, where all agents accepted the same water loss for each run. Though one study suggested salamanders retreat to burrows with as little water loss as 4% body mass (Feder and Londos 1984), previous estimates of activity time used a threshold of about 10% which is well below the lethal limit (Ray 1958; Feder and Londos 1984; Gifford and Kozak 2012; Caruso et al. 2014). Peterman and Gade (2017) found ecophysiological models were sensitive to this value. The salamander agents recorded their time spent foraging, both for each night individually and overall. For simulations including climbing, once the salamanders surfaced, they had an opportunity to climb based on the sub-model described below.

2.5. Design Concepts (basic principles, emergence, adaptation, objectives, ~~learning,~~ ~~prediction~~, sensing~~, interaction~~, stochasticity, ~~collectives~~, observation)

This model used formulas derived from physiological data and ecophysiological models to estimate potential foraging time for salamanders. Conventionally this is done with one or 2 specific-sized salamanders and one set of environmental variables. The ABM approach allows a wider range of sizes and climatic conditions for the ecophysiological model calculations and it allows individual plasticity in resistance to water loss. This approach also makes the addition of rehydration more feasible. The simulations included behavioral variability in emergence behavior and climbing as a compensatory behavior. The primary outputs for this model include the average nightly foraging time for each size class and overall, seasonal foraging time of each size class.

In the ABM framework, the interaction of spatial and temporal variation with individual physiological variability and behavior that cannot be accounted for in strictly ecophysiological models produces *emergent* patterns in foraging time and survival across the rainfall gradient and through the active season. The ecophysiological models do build in a certain part of the results, however the results ultimately emerge from individual 'decisions' to leave burrows, climb and retreat. Survival emerges from the salamanders' ability to leave burrows, forage, and rehydrate. The salamanders *sense* the air temperature and relative humidity on the patch when foraging and the soil temperature and moisture on a patch when rehydrating. In the climbing and full models, salamanders sense the difference between the soil and air temperature before deciding to climb vegetation. The temperature, relative humidity, and soil moisture are ultimately sensed through the ecophysiological models calculating water loss and gain.

The salamanders have *adaptive* behavior in the sense that they climb plants only when it might be beneficial to their foraging time. However, their propensity to climb is not adaptive in these models because individuals had a 50% chance of climbing on any night when the air temperature was cooler than the soil temperature. The *objective* of the salamanders is to maximize their fitness by increasing foraging time. The salamanders can do this indirectly under certain environmental conditions by climbing to reduce body temperature or by moving to an area of lower temperature or higher relative humidity. However, the scale of the model compared to the size of salamanders makes moving between patches to improve fitness by finding more humid areas unreasonable. Assuming no movement of the salamanders in the model is realistic considering that salamander home ranges are notoriously small (Madison and Shoop 1970).

The actual sizes of the salamanders were created *stochastically* within certain ranges for each size class at initialization. This created more realistic variability in size. The resistance values for water loss were plastic and responded to the soil temperatures. Environmental variables were generated pseudorandomly within given parameters on each 'night' time step. The temperature was drawn from a normal distribution with an average and standard deviation for the month (April-October) from data collected at the Coweeta LTER (SOURCE). During calibration of the ecophysiological models, individual water loss levels were monitored and compared to reported dehydration and rehydration rates. Plotting the nightly foraging time of salamanders allowed for monitoring of general activity patterns. The outputs mentioned above, (average nightly and total foraging time) allowed for comparison of overall trends between size classes, midstory canopy presence, climbing, and precipitation gradients and sensitivity to emergence probability and water loss acceptance.

2.6. Initialization

The generated landscape was uniform for each simulation. One thousand salamanders of each size class were created and randomly distributed for a total of 3,000 salamanders.

2.7. Input Data

The model did not use input data to represent time-varying processes (Grimm et al. 2010).

2.8. Submodels

2.8.1. Precipitation - The percent chance of rain over one 24-hour period was based on the amount of annual rainfall for the simulation run. A random number was generated from 0 to 1 and if it was below the percent chance of rain for each simulation then the night was set to "raining". If it was raining, then the humidity was set to 100%. If it was not raining, then the humidity decreased by 10% every 24 hours since the last rain based on the number of days since the last rain. This was a simplification of reality as relative humidity depends on a variety of factors but resulted in values representative of those recorded during previous work at the Coweeta LTER (unpublished).

2.8.2. Soil moisture - If it was raining then the soil moisture tension was set to 10 kilopascals, which reflected wet soil. A night of no rain increased the tension to 20 kilopascals. Although 33 kilopascals is the standard tension for saturated soil after water has time to drain (Richards and Weaver 1944), at this value salamanders started losing water to the soil with our ecophysiological models. Understanding of rehydration in soil is limited for amphibians, and salamanders in particular. Future models should include better rehydration functions and more accurately reflect soil type and vegetation and soil drying rates.

2.8.3. Salamander emergence - For the set value of emergence probability, a random number less than 1 was generated within the program, if the number was less than or equal to 0.4, the salamander had an opportunity to emerge, that is, to leave its burrow. After probability values were evaluated, the salamander would emerge only if (1) the relative humidity was greater than 45%, (2) its body temperature was greater than 5 degrees Celsius, and (3) its water loss level was less than 4% of its mass.

2.8.4. Dehydration - Once the salamander did emerge, it started to lose water. This procedure was set up to be a minute-long step and was repeated for the number of minutes in the night (average night duration for the month). Dehydration models followed published formulas for estimating dehydration rates. Salamanders were assumed to be saturated at their skin surface in terms of water vapor (Spotila and Berman 1976). Water vapor pressure of salamanders was estimated by calculating saturation vapor pressure (Pascals):

$$[4]\ \rho_{sat} = 611e^{\left(\frac{2{,}500{,}000}{461.5}\right)\left(\frac{1}{273}-\frac{1}{T}\right)}$$

Where ρ_{sat} is the saturation vapor pressure in Pascals, and *T* is the temperature in Kelvin. The water vapor pressure of the air was calculated using:

$$[5]\ \rho_{air} = \frac{Rh \times \rho_{sat}}{T \times 461.5} \times 0.001$$

Where ρ_{air} is the water vapor pressure of the air in grams per cubic centimeter, Rh is the relative humidity, and T is the temperature in Kelvin. Dehydration rates were calculated using:

$$[6]\ EWL = \frac{\rho_{sal} - \rho_{air}}{R}$$

Where R is the resistance value of the salamander to dehydration (sec/cm). The resistance values in this model were derived from published literature but in reality may vary geographically (Riddell and Sears 2015) and by species. These values should be adjusted for specific future applications of this model. The resistance value changed depending on temperature (using data from Spotila 1972). Activity time was estimated every minute by multiplying the above estimate of water loss by the surface area of the animal (cm^2) and by 60 seconds. This was repeated on a minute by minute basis until the salamanders reached their threshold to cease activity. When water loss reached 3, 5, 7, or 10% (depending on the simulation) the salamanders "retreated", meaning they stopped the dehydration procedure. In future versions or extensions of this model, the water level when salamanders abandon foraging may vary based on dehydration rate itself, as animals tend to abandon foraging earlier on drier nights (Feder and Londos 1984).

2.8.5. Rehydration - When salamanders retreat or remain in their burrow, they rehydrate at rates based on surface area, temperature, level of dehydration, and soil moisture tension. Since the soil moisture was sometimes very low, some salamanders dehydrated during this process (as observed in empirical studies) causing them to reach unrealistic water loss levels. If this happened, the salamander died when water loss was higher than 20% of its mass (18-26% is lethal, Feder and Londos 1984). Salamanders are unlikely to remain in areas where they would continue to lose water, but the model does not include this type of avoidance behavior. Rehydration rates were calculated as a minute-long step repeated each minute of the day or night when a salamander was inside a burrow. Rehydration rates were calculated using (Tracy 1976):

$$[7]\, r = (\varphi_{sal} - \varphi_{soil}) \times \ K$$

Where rehydration is measured in grams per cm^2 per minute, φ_{sal} is the water potential of the salamander in pascals, φ_{soil} is the soil moisture tension in pascals, and K is the hydraulic conductance, set at 0.00000013 g cm^{-2} min^{-1} pa^{-1} as calculated for Leopard frogs (Tracy 1976). The water flux of the salamanders were estimated using the following equation established for Leopard frogs (Tracy 1976).

$$[8]\ \varphi_{sal} = (-284.802\theta^3 + 773.427\theta^2 - 703.223\theta + 0.0214809) \times 100$$

Where θ is the hydration level of the salamander (1 - percent of mass lost to water loss). These parameters are currently unavailable for salamanders, however the leopard frog values produce reasonable rehydration rates reflective of those found in previous studies with salamanders (Cohen 1952; Spight 1967a,b; Spotila 1972; Feder 1983). The relationship between soil moisture and water loss rate is independent of species of salamander (Spight 1967), suggesting the formula would remain unchanged for any future applications of the model with other species.

2.8.6. Climbing – When climbing was modeled, once the salamanders have gone through the emergence sub-model, they had an opportunity to climb vegetation before dehydrating. The salamanders determined if their body temperature (equal to the soil temperature at the time of emergence) was cooler or warmer than the air. If the air temperature was cooler, then the salamander had an opportunity to climb. Climbing under such conditions would lower its body temperature and thus its dehydration rate as the salamander adopted the temperature of the plant. Salamanders had as 50% propensity to climb. If a randomly generated number was less than the salamander’s individual propensity to climb then it climbed. Salamanders do have an ability to sense and behaviorally regulate temperature (Feder 1982; Feder 1983; Strickland et al. 2016), but little is known about climbing propensities and this part of the model should be updated with information from additional field studies.

3. Field Validation

Field studies were conducted at the Coweeta Hydrologic Laboratory in Macon County, NC. This field site spans a steep natural precipitation gradient with patchily distributed *Rhododendron sp*. (midstory canopy). We selected 20 sites spanning the moisture gradient and placed sub-plots in areas with and without *Rhododendron* at these sites when possible. Sub-plots consisted of three or four 5 X 5 meter squares. The plots were surveyed using nocturnal visual encounter surveys for 20 person-minutes, and were visited four times between May and October 2015. The number of animals, size class, and observed climbing behavior were recorded for each plot.

4. Statistical analysis

The nightly foraging times were compared between models across the rainfall gradient and size classes using visual comparison with confidence intervals (graphs). The difference in nightly activity time between climbing and non-climbing salamanders was calculated for each time step in each simulation.. We also considered the magnitude of difference between the ground and air temperature as a factor driving the difference in fitness of climbers and non-climbers on any given night. By limiting the data to nights climbing occurred, we compared the average seasonal activity time between climbing and non-climbing animals. While the totals themselves are not informative, the relative differences reflect any pattern and differences.

APPENDIX 3.2

MODEL CODE

NetLogo language

;The World settings include origin located in the bottom left corner, with a max-pxcor and max-ycor of 49. View settings include patch size of 10. On the interface, there is a slider for “cease-forage” from 0.03 to 0.1 in increments of 0.01. A slider titled “p” reflects probability of rainfall and ranges from 0.1 to 1 in increments of 0.05. A switch for “climbing?” included climbing behavior when switched on and does not allow climbing when switched off. A switch for “midstory?” included the microclimate influence of Rhododendron when switched on.

```
globals[
  month
  hour              ;hours of night
   temp             ;average nightly temperature, set each night Celsius
   raining                ; if its currently raining
   time-rain        ;time since last rainfall (number of ticks=hours)
   str               ;average monthly soil temperature
   ;p                       ;probability of rainfall in 24 hrs
  ;cease-forage     ;percent water loss willing to accept now individualized, possibly will change
                    ;based on dehydration rate after each 30 minute tick
  output-file-name ;needs to be updated to reflect version (date)
```

```
 ]
patches-own [
  SMT                  ;soil moisture tension, negative pressure of water in soil, as gets greater,
                  ;more resistant to losing water from soil to object (Pa)
  soil-t          ;temperature of soil @ about 5 -10  cm in degrees C, monthly average,
  plant-t         ;temperature of plants
  rh              ;relative humidity
  atemp           ;local air temp
 ]
turtles-own [
  out             ;y/n if animal emerged on any given night to prevent emerging twice in one
                  ;night
  mass            ;in grams
 svl                   ;snout- vent length in cm
 sarea            ;surface area in sq cm
 class            ;H = hatchling, J = juvenile, A= adult
 water-loss       ;keep track of water level, sort of a reserve but as a record of water lost
 forage-time      ;keep track of total time spent foraging
 resist           ;whole body resistance to water loss ;;depends on size of animal,
                  ;temperature and relative moisture
 K                     ;hydraulic conductance
  body-temp       ;in degrees C
  time        ;nightly time spent foraging,  reset each day
```

```
  rtime          ;time inactive
  deficit        ;dehydration deficit proportion of water lost compared to mass
  outside         ;time since last emergence
  climbing        ;yes or no if climbing at night
  EWL             ;evaporative water loss per hour (after repeat 30 minutes * 2)
  emr            ;probability of emergence,
 ]
to setup
 ca               ;clear all
 reset-ticks      ;reset time counter
 set    sig          5.67 * 10 ^ -8
 set    emis    0.96
 set    wind    0.05     ;m/s
 ask patches
 [
  ifelse midstory?                        ;if rhodo is present
    [set midstory 1
     set pcolor 62]
    [set midstory 0                         ;rhodo is not present then set all patches to the same values
    set pcolor 66]
  ]
 weather                              ;set simulated air temperature on each patch
 rain                                  ;set rain
```

```
  ask   patches    [soil]      ;set relative soil temperature
  create-output                ;process to create output file to record data at multiple time steps
                              ;(end of each night)
  crt-sal                       ;create salamanders
end
to create-output
  ; Open the main output file
  ; Do not delete it instead of appending to it because we could be doing multiple model run
  ;experiments
  ; Instead- print headers only if the file is new, and put date and time
  ; as separator between model runs
set output-file-name (word "ClimbPhysics2Apr18" midstory? climbing? cease-forage ".csv")
;change date
ifelse (file-exists? output-file-name)
  [
    file-open output-file-name
    ; Print a header between model runs
    file-print date-and-time
  ]
  [
    file-open output-file-name
    file-print date-and-time
    file-type ","
```

```
file-type "midstory?,"              ;if version includes Rhododendron or not
file-type "climbing?,"              ;if version includes climbing or not
file-type "cease-forage,"           ;water-loss acceptance
file-type "month,"                  ;month
file-type "tick,"                   ;time step
file-type "temp,"                   ;air temperature in Celsius
file-type "time-rain,"              ;number of days since rainfall event
file-type "rain-probability,"       ;probability of rainfall in model run
;time foraging
file-type "time-A,"                 ;nightly hours of activity, adults
file-type "time-J,"                 ;nightly hours of activity, juvenile
file-type "time-H,"                 ;nightly hours of activity, hatchling
;time foraging climbing
file-type "time-Ac,"                ;nightly hours if climbing, adults
file-type "time-Jc,"                ;nightly hours if climbing, juvenile
file-type "time-Hc,"                ;nightly hours if climbing, hatchling
;time foraging notclimbing
file-type "time-Anc,"               ;nightly hours if not climbing, adults
file-type "time-Jnc,"                       ;nightly hours if not climbing, juvenile
file-type "time-Hnc,"               ;nightly hours if not climbing, hatchling
;proportion active
file-type "active-A,"                       ;proportion of adults active
file-type "active-J,"               ; proportion of juvenile active
```

```
  file-type "active-H,"                    ; proportion of hatchling active
  ;proportion climbing
  file-type "climb-A,"                     ; proportion of adults climbing
  file-type "climb-J,"               ; proportion of juvenile climbing
  file-print "climb-H,"                    ; proportion of hatchling climbing
 ]
 file-close
end
to crt-sal
 crt 1000                  ; hatchlings
 [
  set   shape   "salamander"
  set   color   grey
  set   size    0.5
  setxy random-xcor random-ycor
  set   mass r  andom-float 1                ;randomly assign mass to less than one gram
  set   svl (32.8 * mass ^ 0.34)       ;based trendline from actual observations (Maerz et al
                                       ;Unpublished, CMR)
  if    svl     < 10    [die]          ;if animal is too small, die
  set sarea 8.42 * (mass ^ 0.694)      ;surface area from formula found in Spotila 1972 for
                                       ;salamanders
  set class "H"                        ;hatchling salamander
  set water-loss random-float (0.15 * mass)   ;start water loss level greater than 0, at a
```

```
                                        ;maximum just below lethal level
  set   forage-time     0
  set   time     0
  set   resist    0.09                  ;sec/cm from Spotila and Berman for D. ochrophaeus,
                                        ;initial values, changes nightly
  set   K   0.00000013                    ;for leopard frogs from Tracy 1976 ; g/cm^2/min/pa
  set   deficit  0
  set   outside 0
  set   climbing "no"
  set   emr      0.4                            ;emergence probability for the  night
  ]
crt 1000                        ; juvenile
[
  set   shape   "salamander"
  set   color   grey
  set   size     0.7
  setxy random-xcor random-ycor
  set   mass    (random-float 1) +1     ;randomly assign mass to between 1 and 2 grams
  set   svl (32.8 * mass ^ 0.34)        ;based trendline from actual observations (Maerz et al
                                        ;Unpublished, CMR)
  set sarea 8.42 * (mass ^ 0.694)       ;surface area from formula found in Spotila 1972 for
                                        ;salamanders
  set class "J"                         ;juvenile salamander
```

```
  set water-loss random-float (0.15 * mass)   ;start water loss level greater than 0, at a
                                              ;maximum just below lethal level
  set   forage-time    0
  set   time    0
  set   resist   0.09                         ;sec/cm from Spotila and Berman for D. ochrophaeus,
                                              ;initial values, changes nightly
  set   K   0.00000013                          ;for leopard frogs from Tracy 1976 ; g/cm^2/min/pa
  set   deficit  0
  set   outside 0
  set   climbing "no"
  set   emr      0.4                                   ;emergence probability for the  night
  ]
crt 1000                          ; adults
[
  set   shape   "salamander"
  set   color   grey
  set   size     0.9
  setxy random-xcor random-ycor
  set   mass    (random-float 8)  + 2         ;randomly assign mass to between 2 and 10 grams
  set   svl (32.8 * mass ^ 0.34)              ;based trendline from actual observations (Maerz et al
                                              ;Unpublished, CMR)
  set sarea 8.42 * (mass ^ 0.694)             ;surface area from formula found in Spotila 1972 for
                                              ;salamanders
```

```
  set class "A"                           ;adult salamander
  set water-loss random-float (0.15 * mass)   ;start water loss level greater than 0, at a
                                          ;maximum just below lethal level
  set   forage-time    0
  set   time    0
  set   resist   0.09                     ;sec/cm from Spotila and Berman for D. ochrophaeus,
                                          ;initial values, changes nightly
  set   K   0.00000013                      ;for leopard frogs from Tracy 1976 ; g/cm^2/min/pa
  set   deficit  0
  set   outside 0
  set   climbing "no"
  set   emr     0.4                               ;emergence probability for the  night
  ]
end
to go
 if ticks < 60
 [ set month "april"    ;set month
  set hour 11           ;set number of hours of night
  set str 11.64 ]       ;set soil temperature to monthly average
 if ticks > 60 and ticks < 122
 [ set month "may"
  set hour 10
  set str 14.17 ]
```

```
if ticks > 122 and ticks < 182
[ set month "june"
  set hour 9.5
  set str 17.44 ]
if ticks > 182 and ticks < 244
[ set month "july"
  set hour 10
  set str 18.61 ]
if ticks > 244 and ticks < 306
[ set month "august"
  set hour 10.5
  set str 18.62 ]
if ticks > 306 and ticks < 366
[ set month "september"
  set hour 11.5
  set str 17.95 ]
if ticks > 366 and ticks < 428
[ set month "october"
  set hour 13
  set str 14.13 ]
tick
ifelse ticks mod 2 = 0          ;divides by 2, if remainder = 0 then 'night' process, if > 0 then
                                ;'day' process
```

```
 [night
 update-output]
 [day]
 if ticks >= 428 [stop]
end
to day
 ask turtles
 [
  set   climbing  "no"        ;reset
  set   color    grey
  set   out       "no"
  set   body-temp soil-t
  set   time     0               ;reset before start foraging again
  set   rtime    0              ;reset
  let   minutes (24 - hour) * 60
  repeat minutes [rehydrate]
  ]
end
to night
 weather              ;procedure to set temperature
 rain                 ;procedure to create rain events
 ask patches [
  soil                ;procedure to set soil moisture
```

```
if climbing? [
      ifelse midstory = 0
      [set plant-t ((temp + soil-t) / 2)]          ;average of near ground temp and air temperature
      [let mtemp 1.0009 * temp - 0.5970     ;if midstory is turned on, adjust air temperature
       set plant-t ((mtemp + soil-t) / 2)]]      ;based on general air temp adjusted for Rhodo
    ]  ask turtles
  [
    set   rtime    0                              ;reset
    set   body-temp      soil-t               ;set body temperature to soil temperature
    set   resist          0.425 * soil-t + 0.8136      ;based on trend line fit to temperature for
                                                         ;calculated resistance values from Spotila 1972 for
                                                         ;P. jordani, because at this temperature longer, so
                                                         ;time to adjust
    ifelse random-float 1 <= 0.4
      [emerge]                                           ;procedure for salamander to surface
      [set      body-temp      soil-t
            let       minutes      hour * 60                        ;number of minutes in night
       repeat      minutes     [rehydrate]          ;rehydration procedure
       set      outside      (outside + 1)]               ;keep track of how long since last emergence
  ]
end
to weather
;pull temperature value from random normal distribution centered around the monthly
```

```
;average night temperature
  if ticks < 60                                         ;April
  [ set temp random-normal 11.89 1.85]
  if ticks > 60 and ticks < 122                ;May
  [ set temp random-normal 15.00 1.83]
  if ticks > 122 and ticks < 182               ;June
  [ set temp random-normal 18.57 0.70]
  if ticks > 182 and ticks < 244               ;July
  [ set temp random-normal 19.07 0.95]
  if ticks > 244 and ticks < 306               ;August
  [ set temp random-normal 19.15 1.01]
  if ticks > 306 and ticks < 366               ;September
  [ set temp random-normal 17.36 1.94]
  if ticks > 366 and ticks < 428               ;October
  [ set temp random-normal 12.07 3.00]
  ask patches[
  ifelse midstory = 1           ;rhodo present
   [set atemp (1.0009 * temp - 0.5970)] ;adjust local temperature based on Miniat 2013
   [set atemp temp ]              ;set local temperature to simulated air temperature
end
to rain
  ifelse random-float   1 <= p           ;based on probability of rainfall
     [setraining      "yes"]
```

```
    [set     raining      "no"]
  ifelse     raining      =    "yes"
    [set     time-rain   0]
    [set     time-rain   time-rain + 1]            ;once every 24 hrs
  ask    patches      [ifelse  raining = "yes"
    [set     rh   1]                             ;if raining set relative humidity to 1
    [let           t     time-rain * 0.1
     set     rh   1 - t ]]            ;relative humidly declines 10% every day it does not rain, this is an
                                      ;over simplification but give variability
end
to soil                              ;set soil moisture and relative temperature
 ifelse raining = "yes"
   [set SMT 10000]
   [set SMT 20000]                ;if raining  = "no"


ifelse midstory = 1              ; rhodo present
   [set rh (1.0139 * rh + 0.0029)
   set soil-t (0.8921 * str + 1.0658)] ;adjust soil temperature and relative humidity Miniat 2013
  [set rh rh                              ;rhodo not present = no change
  set soil-t str]
end
to emerge ;now given multiple limits to emerge
  if water-loss >= 0.5 * mass [die]
```

```
  if      rh  <= 0.45  ;;don't emerge if less than 45% humidity (which rarely happens), just
rehydrate
    [set body-temp       soil-t
     let  minutes     hour * 60
     repeat  minutes     [rehydrate]
     set  outside       (outside + 1)
     stop]
;if body temperature is too high OR if water loss is about 4% of mass then do not emerge and
;rehydrate
;otherwise do the 'dehydrate' procedure every minute
   ifelse body-temp < 25 and body-temp > 5 and water-loss <= (0.04 * mass)
   [
      set      color    blue
      if  climbing?  [climb]              ;if switch is on , then do climbing procedure here, before
                                           ;calculating dehydration
      set      out       "yes"
      let minutes     hour * 60
     repeat  minutes [
          ifelse   water-loss >= cease-forage * mass    ;check water loss level
                 [set color grey
                  stop] ;to stop repeating the 'forage' model if water loss is too high
                [dehydrate]
       ]
```

```
    ]
    [ set body-temp       soil-t
      let  minutes     hour * 60
      repeat  minutes     [
        if water-loss = 0 [stop] ;do not continue if full rehydrated,
        rehydrate]
      set  outside       (outside + 1) ;one night since outside
    ]
end
to climb                                      ;simplified procedure, only based on temperature difference
  ifelse atemp < soil-t [               ;if air temp is cooler than the average of near ground temp
                                        ;and soil temp then have some probability of climbing
  ifelse random-float 1 < 0.5
          [set body-temp plant-t            ;if random number is less than 0.5
           set climbing "yes"
          set color red]
           [set climbing "no"               ;if random number is greater than 0.5
           set color blue]
end
to dehydrate             ;repeat multiple times in one tick for each 'minute' of potential foraging
 if water-loss >= cease-forage * mass [set color grey stop]
                ;if reached tolerance level then stop procedure
 let tem atemp + 273.15                          ;convert from C to Kelvin
```

```
  let btemp body-temp + 273.15                              ;convert from C to Kelvin
;vapor density of skin @ temperature, usually close enough to 1 that assume saturation vapor
;density (Campbell and Norman 1998), Tracy 1976
  let sal-sat (611 * exp ((2500000 / 461.5) * ((1 / 273) - (1 / btemp))))
                 ;Riddell Sears 2015 , vapor pressure in Pa water
  let wvapor-s ((sal-sat / (btemp * 461.5)) * 0.001)
           ;convert from pressure to water vapor density and to g/cm^3
  let saturation (611 * exp ((2500000 / 461.5) * ((1 / 273) - (1 / tem))))
                       ;Riddell Sears 2015 ; vapor pressure in Pa
;water vapor density of air = relative humidity * saturation vapor density which varies based on
temperature
  let wvapor-a (rh * saturation) / (tem * 461.5) * 0.001   ;convert to vapor density  and to g/cm^3
  let water-loss-out (sarea * 60 *  ((wvapor-s - wvapor-a) / resist))
   ;total water loss in grams for 1 minute (cm^2 * seconds * vapor deficit/resistance to water loss)
  ifelse water-loss-out < 0 [set water-loss water-loss]
  [set water-loss (water-loss + water-loss-out)]                          ;total water lost in grams
  set forage-time forage-time + 1      ;Keep a cumulative total of activity time, minutes spent out
  set time time + 1                                        ;nightly foraging time, reset each day step
  if water-loss >= cease-forage * mass
  [stop]                                                   ;if water deficit gets to range from 3-10%
  set deficit (water-loss / mass)
  set outside 0                                     ;this way it only resets if make it all the way through
end
```

```
to rehydrate
 set rtime rtime + 1                                          ;time inactive, assumed "rehydrating",
though may not make it through entire procedure
 if water-loss = 0 [set deficit 0 stop]
 if water-loss >= 0.5 * mass [die]          ;extreme value, would likely die well before this value
 if water-loss > 0 [set deficit (water-loss / mass)]
 let hydr 1 - deficit                      ;hydration level, proportion of water remaining
 let Swp  (-284.802 * (hydr ^ 3) + 773.427 * (hydr ^ 2) - 703.223 * hydr + 0.0214809) * 100
;salamander water potential, as a function of dehydration deficit,
;for now using leopard frog equation (Tracy 1976), converted to pa from assumed mb,
;converted from percent to proportion
 let water-gain-rate K * ((-1 * Swp) - SMT)                      ;hydraulic conductance *
;difference between salamander water potential and soil moisture tension
 let water-gain water-gain-rate * sarea                         ;should be grams / minute
 set water-loss (water-loss - water-gain)
 if water-loss <= 0 [set water-loss 0]      ;eliminate the negative numbers, which would be a
;water surplus
 set deficit (water-loss / mass * 100)                          ;reset new deficit
  if water-loss = 0 [stop]                                   ;stop procedure when fully rehydrated
end
to update-output
  ; First calculate outputs
  ;Split by size class
```

```
let adult turtles with [class = "A"]
let juv turtles with [class = "J"]
let hatchling turtles with [class = "H"]
let adult-out adult with [outside = 0]
let juv-out juv with [outside = 0]
let hatch-out hatchling with [outside = 0]

let adult-c adult-out with [climbing = "yes"]
let juv-c juv-out with [climbing = "yes"]
let hatch-c hatch-out with [climbing = "yes"]
let adult-nc adult-out with [climbing = "no"]
let juv-nc juv-out with [climbing = "no"]
let hatch-nc hatch-out with [climbing = "no"]
; Now write file output
;
file-open output-file-name
file-type "," ; Blank column for separator between runs
file-type (word midstory? ",")
file-type (word climbing? ",")
file-type (word cease-forage ",")
file-type (word month ",")
file-type (word ticks ",")
file-type (word temp ",")
```

```
file-type (word time-rain ",") ;;days (24 hrs) since last rainfall
file-type (word p ",")
;time foraging each night
ifelse count adult-out = 0
  [file-type (word 0 ",")]
  [file-type (word (mean [time] of adult-out / 60) ",")]
ifelse count juv-out = 0
  [file-type (word 0 ",")]
  [file-type (word (mean [time] of juv-out / 60) ",")]
ifelse count hatch-out = 0
  [file-type (word 0 ",")]
  [file-type (word (mean [time] of hatch-out / 60) ",")]
;time-climbing
ifelse climbing?
[
ifelse count adult-c = 0
  [file-type (word 0 ",")]
  [file-type (word (mean [time] of adult-c / 60) ",")]
ifelse count juv-c = 0
  [file-type (word 0 ",")]
  [file-type (word (mean [time] of juv-c / 60) ",")]
ifelse count hatch-c = 0
  [file-type (word 0 ",")]
```

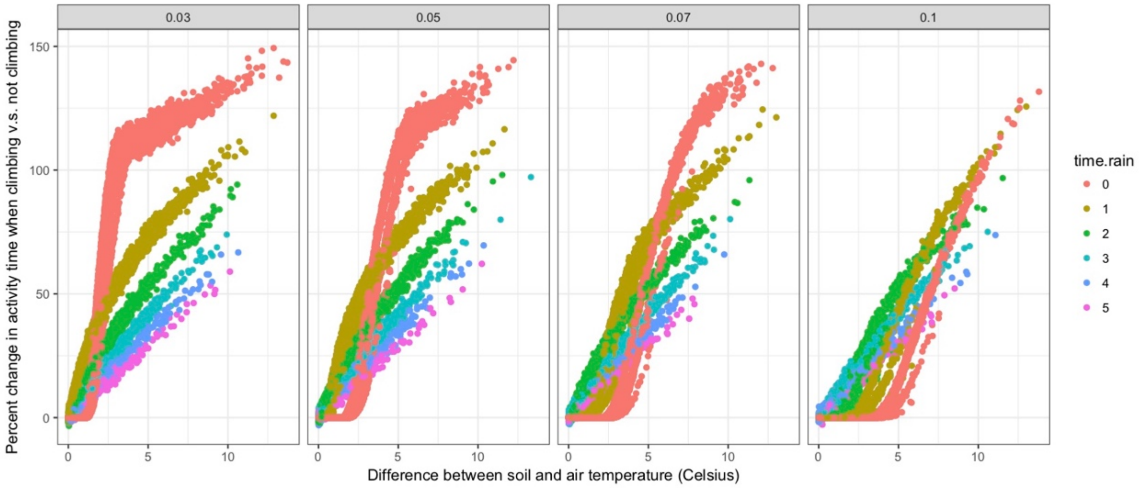
```
  [file-type (word (mean [time] of hatch-c / 60) ",")]
]
[file-type (word 0 "," 0 "," 0 ",")]
;time-not-climbing
 ifelse climbing?
[
ifelse count adult-nc = 0
  [file-type (word 0 ",")]
  [file-type (word (mean [time] of adult-nc / 60) ",")]
ifelse count juv-nc = 0
  [file-type (word 0 ",")]
  [file-type (word (mean [time] of juv-nc / 60) ",")]
ifelse count hatch-nc = 0
  [file-type (word 0 ",")]
  [file-type (word (mean [time] of hatch-nc / 60) ",")]
]
[file-type (word 0 "," 0 "," 0 "," )]
;porportion active
ifelse count adult-out = 0
  [file-type (word 0 ",")]
  [file-type (word (count(adult-out) / count(adult)) ",")]
ifelse count juv-out = 0
  [file-type (word 0 ",")]
```

```
    [file-type (word (count(juv-out) / count(juv)) ",")]
 ifelse count hatch-out = 0
    [file-type (word 0 ",")]
    [file-type (word (count(hatch-out) / count(hatchling)) ",")]
  ;proportion-climbing
  ifelse climbing?
  [
  ifelse count adult-c = 0 or count adult-out = 0
    [file-type (word 0 ",")]
    [file-type (word (count(adult-c) / count(adult-out)) ",")]
  ifelse count juv-c = 0 or count juv-out = 0
    [file-type (word 0 ",")]
    [file-type (word (count(juv-c) / count(juv-out)) ",")]
  ifelse count hatch-c = 0 or count hatch-out = 0
    [file-print (word 0 ",")]
    [file-print (word (count(hatch-c) / count(hatch-out)) ",")]
  ]
  [file-print(word 0)]
  file-close
end
```

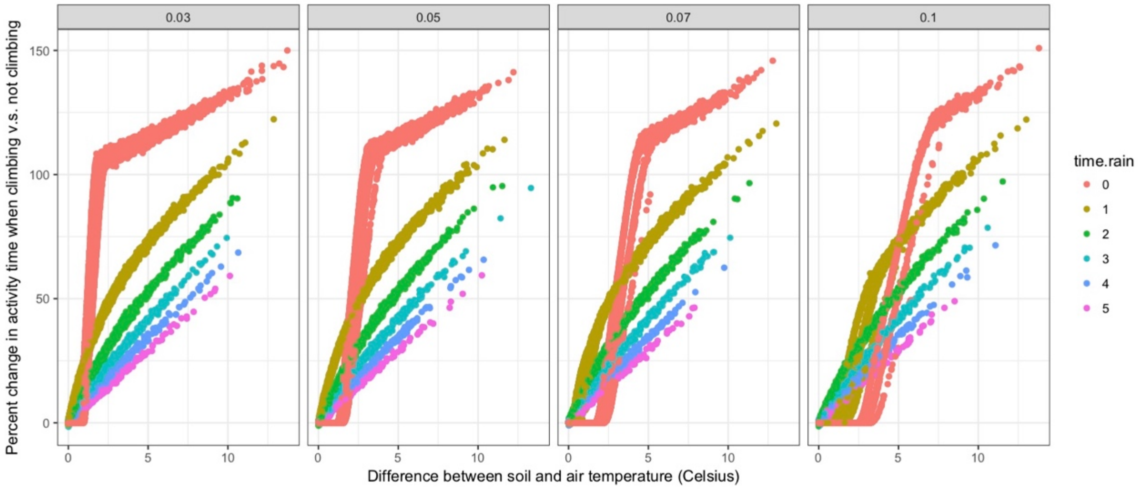
APPENDIX 3.3

SUPPLEMENTARY GRAPHS

(A)



(B)



(C)

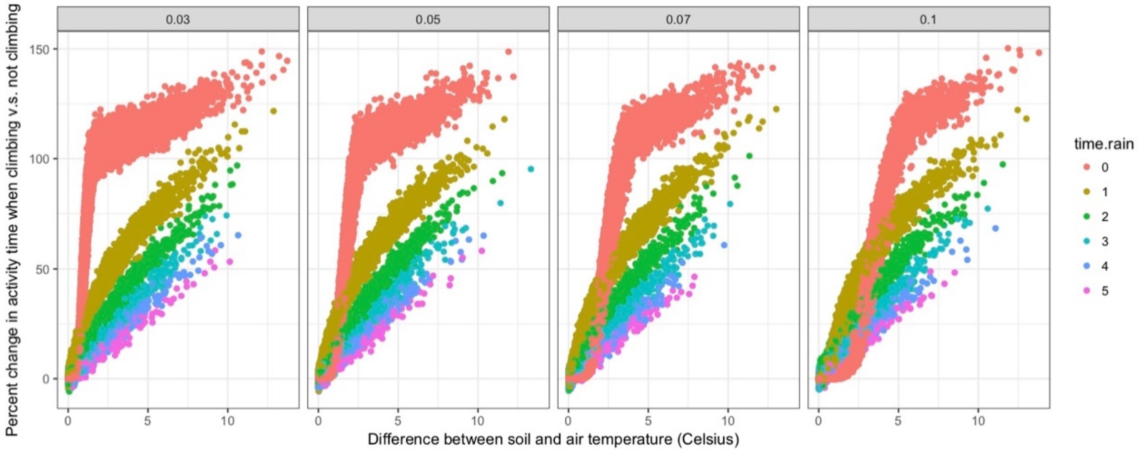


Fig. S3.1. Percent change in activity time of climbing compared to non-climbing salamanders as a function of the difference between air and ground temperature, days since last rain, water loss threshold, and body size class. Shown is the percent increase in mean activity time for climbing salamanders compared to the mean activity time of climbing salamanders on the same simulated night. Positive value indicates greater activity time among climbing salamanders.(A) adult salamanders, (B) juvenile salamanders, and (C) hatchling salamanders.

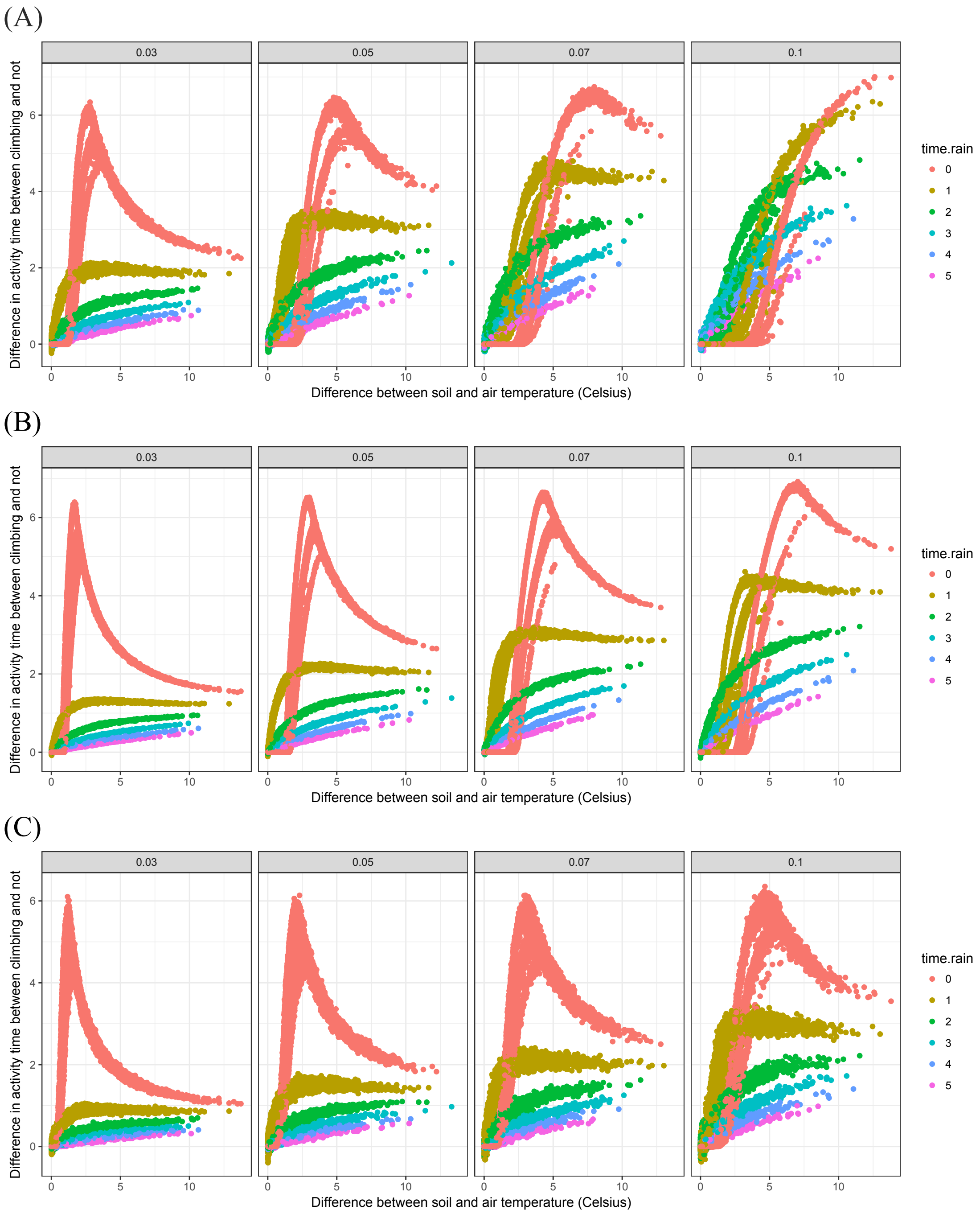


Fig. S3.2. Difference in mean activity time for climbing and non-climbing salamanders as a function of the difference between air and ground temperature, days since last rain, water loss threshold, and body size class. Shown is the mean activity time for non-climbing salamanders subtracted from the mean activity time of climbing salamanders on the same simulated night. Positive value indicates greater activity time among climbing salamanders. (A) adult salamanders, (B) juvenile salamanders, and (C) hatchling salamanders.

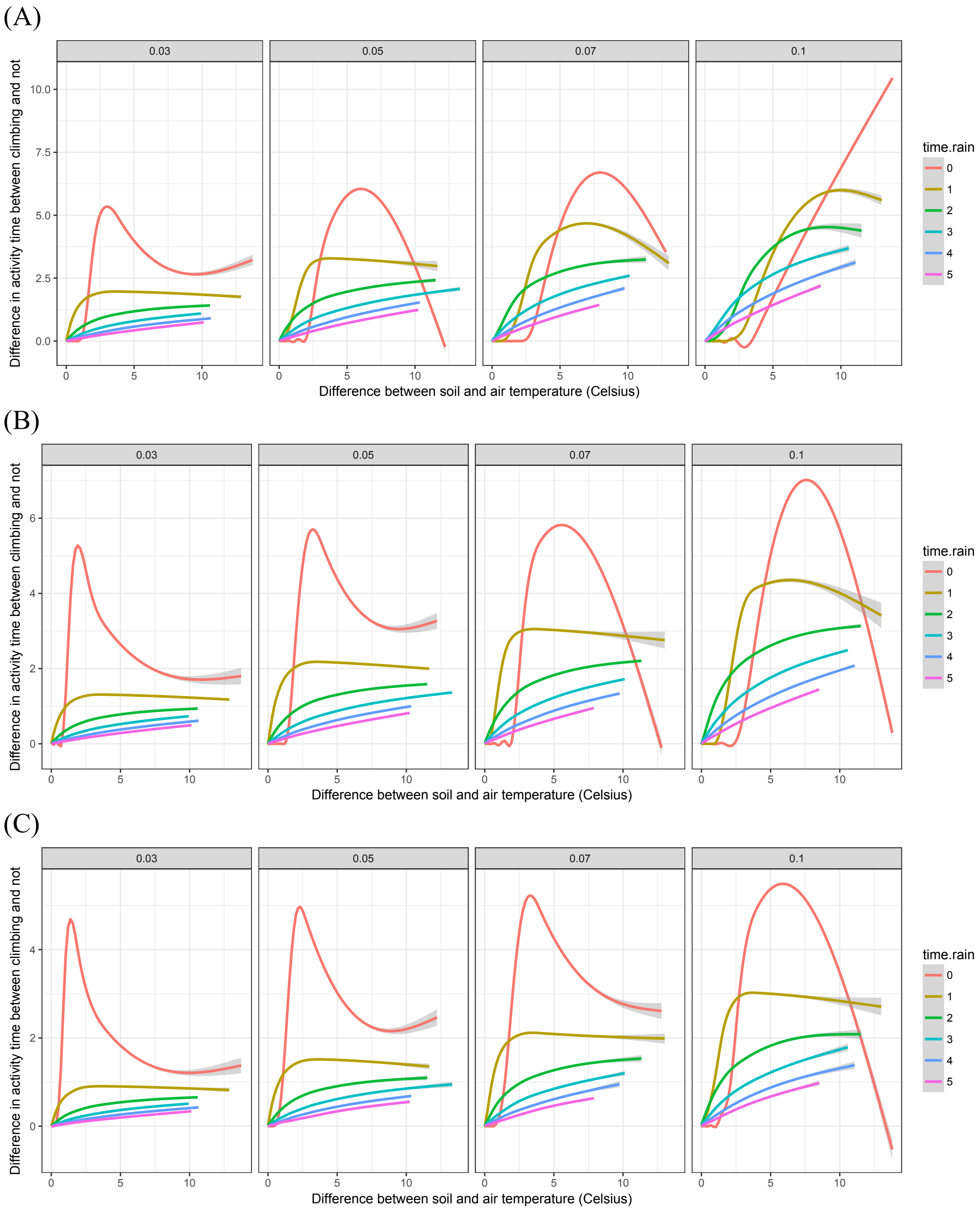
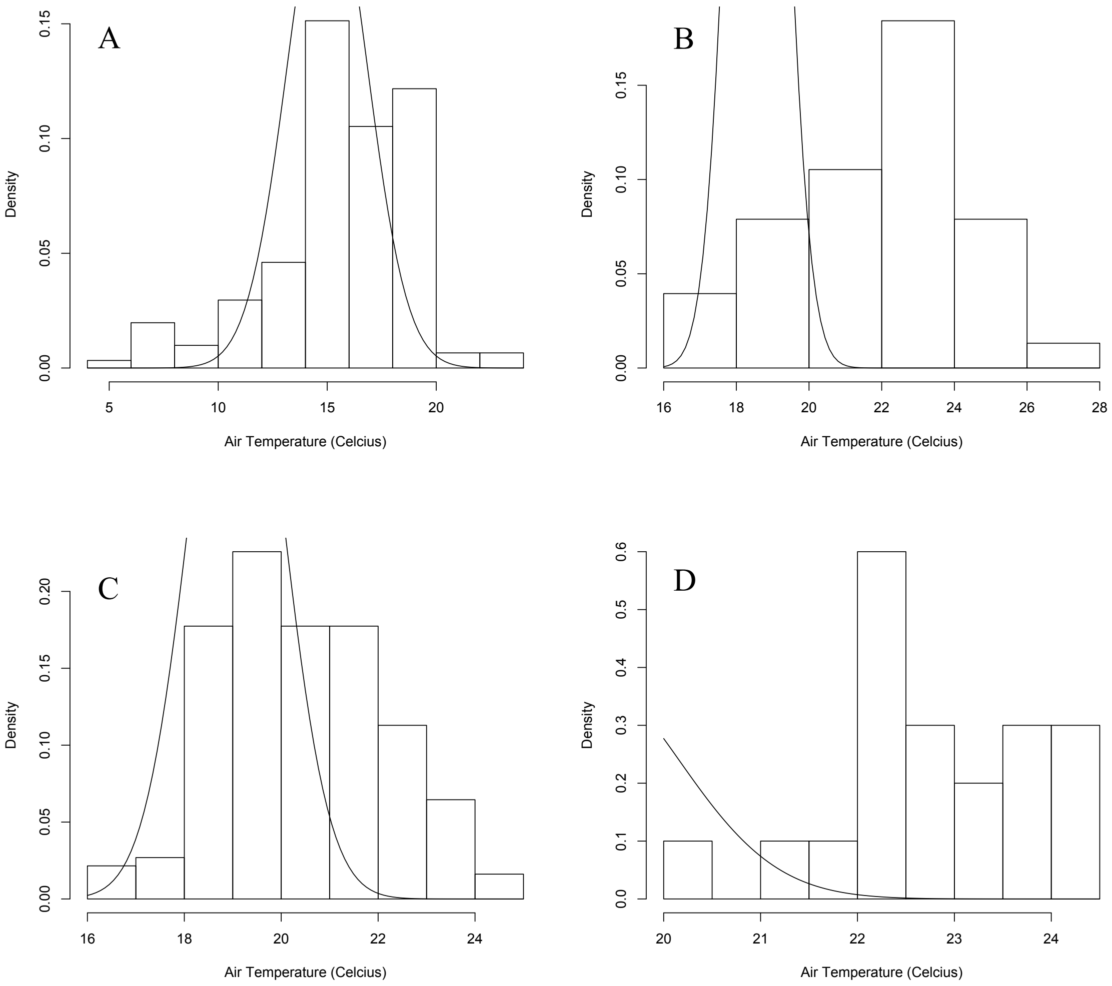


Fig. S3.3. Difference in mean activity time for climbing and non-climbing salamanders as a function of the difference between air and ground temperature, days since last rain, water loss threshold, and body size class. Shown is the generalized additive model of mean activity time for non-climbing salamanders subtracted from the mean activity time of climbing salamanders on the same simulated night. Positive value indicates greater activity time among climbing salamanders. Grey bars indicate a 95% confidence interval. (A) adult salamanders, (B) juvenile salamanders, and (C) hatchling salamanders.

APPENDIX 4.1

SUPPLEMENTARY GRAPHS



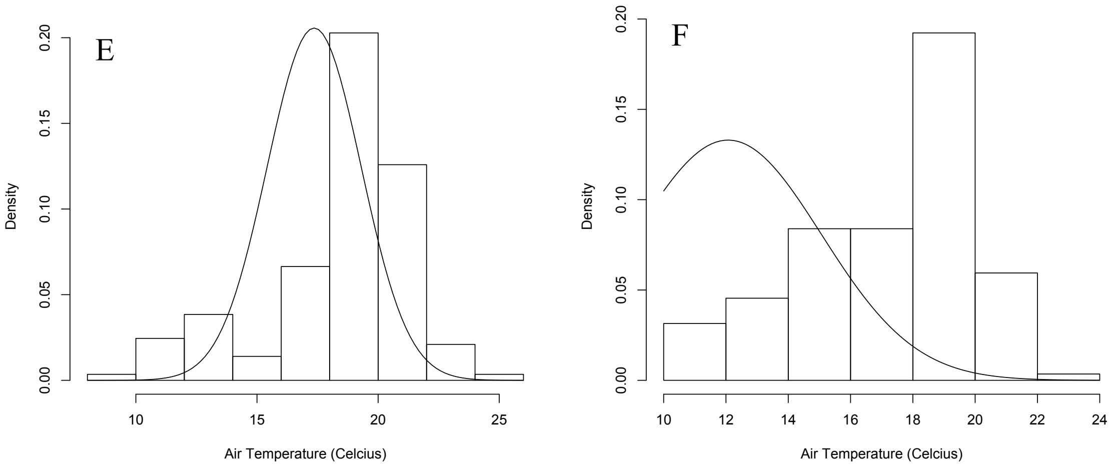


Fig. A4.1: Monthly modeled (Chapter 3) vs. observed temperatures (this chapter). Curves represent the modeled temperature for each month based on nightly average temperatures from 2013 to 2014. The bars represent the frequency (as a probability) of recorded air temperatures from 2015-2017. (A) May; (B) June; (C) July; (D) August; (E) September; (F) October.

APPENDIX 5.1

ODD PROTOCOL

1. Modeling Approach

An agent-based model (ABM) of salamander activity in a variable environment with behavioral variation was developed using ecophysiological models and pattern-oriented modeling. We ran 20 simulations of each model.

2. Modeling Description

The model description below follows the ODD protocol (Grimm et al. 2010), a standard format for communicating the concepts and methods used in individual- or agent-based models.

2.1. Purpose

The primary purpose of this of model is compare salamander fitness in areas with and without Rhododendron present. The model estimates activity time using salamander dehydration. These estimates are influenced by plant climbing as a temperature regulation mechanism. All model versions were run in the context of a rainfall probability gradient and assumed a uniform vegetative structure and simple behavior (surfacing). This model was applied to understand the importance of Rhododendron sp., an evergreen shrub, as a microclimate modifier on salamander activity and behavior.

2.2. Programing

The model was built in the program NetLogo (Version 6.0.2, U. Wilensky, 1999). Simulations and sensitivity analyses were run repeatedly during development of the model to ensure proper function of the ecophysiological models within the ABM. The exact code can be obtained by contacting the authors (Appendix 5.2).

2.3. Entities, State Variables, and Scales

The mobile agents were based on salamanders in the genus *Plethodon,* especially *Plethodon jordani* (complex) when available. The *Plethodon jordani* complex represents a mid-size *Plethodon* salamander found throughout Southern Appalachia. The agents consisted of three size classes. All individuals had the same fixed attributes, including 'size class', 'mass', 'snout-vent-length' (SVL), 'surface area', and 'hydraulic conductance'. The three size classes included hatchling (mass < 1 g, SVL < 3.2 cm), juvenile (mass between 1 and 2 g, SVL between 32 and 42 cm), and adult (mass between 2 and 10 g, SVL > 4.2 cm, up to 7.2 cm) to reflect different life phases. Mass (*m*) was randomly generated at set up of the model, and SVL (in cm) was calculated from the mass (in grams) based on a relationship derived from our long-term capture mark recapture data (Howard 2018).

$$[1]\ SVL = 32.8m^{0.34}$$

Surface area was calculated from the mass based on an empirical formula (Whitford and Hutchison 1967), copied below. Where *SA* is equal to surface area in cm^2 and *m* is equal to mass of the salamander in grams:

$[2]\ SA = 8.42m^{0.694}$

The hydraulic conductance for leopard frogs (Tracy 1976) was used as the hydraulic conductance for the modeled salamanders, as it is the only reported value for amphibians (Table 1). Climbing propensity was related to the difference between soil and air temperature and based on field data for *Plethodon shermani* X *P. teyahalee* hybrids(Ch 4).

$$[3]\ p = \frac{e^{B_1 T_{as} - B_0}}{1 + e^{B_1 T_{as} - B_0}}$$

First, B_1 was drawn from a normal distribution with an average of 0.4477 and a standard deviation of 0.1158. Then B_0 was drawn from a normal distribution with an average of 1.8587 and a standard deviation of 0.1229. T_{as} is the difference between air and soil temperature in Celsius. These probabilities were drawn for each individual agent once per night. The variable attributes of the mobile agents included 'resistance to water loss', 'body temperature', 'nightly foraging time', 'water level', 'nights without attempting to forage', and 'overall foraging time', which change over time. Resistance to water loss was calculated nightly from soil temperature, using an equation derived from data for *P. jordani* (Spotila 1972).

$$[4]\ r = 0.425T_S + 0.8136$$

Where r is the resistance to water loss per second and T_s is the soil temperature in Kelvin. We assumed body temperatures were the same temperature as surroundings. This resulted in bosy temperature being equal to soil temperature when rehydrating, and active but not climbing. Climbing agents adopted the plant temperature (described below) as their body temperature. Nightly foraging time in minutes was calculated based on the dehydration model described below and reset at the end of each night. Water level recorded the mass lost due to water lost via the dehydration model during the night. Overall foraging time recorded the total minutes an individual salamander spent foraging during all the nights of the simulation.

The only fixed attribute of the patches was the presence or absence of midstory canopy. The variable patch attributes included ‘local relative humidity’, ‘air temperature’, and ‘vegetation temperature’. Relative humidity was estimated based on the amount of time since the last rainfall, assuming an even decline of 10% for every day since rain. This is a simplification but effectively functioned to reduce relative humidity when rainfall probabilities were low. Relative humidity was also adjusted based on the presence of midstory canopy plants based the equations below from on data recorded at Coweeta in areas with and without *Rhododendron* (Miniat and Elliott, unpublished data). T_{ra} is the air temperature under *Rhododendron* in Celsius; T_a is the simulated air temperature before the adjustment in Celsius; RH_r is the relative humidity under *Rhododendron* as a decimal; RH is the simulated relative humidity before adjustment; T_{rs} is the soil temperature under *Rhododendron* in Celsius; and T_s is the simulated soil temperature before the adjustment in Celsius.

$$[5]\ T_{ra} = 1.009T_a - 0.5970$$

$$[6]\ RH_r = 1.0193RH + 0.029$$

$$[7]\ T_{rs} = 0.8921T_s + 1.0658$$

Because estimating soil moisture tension (SMT) over time requires extensive knowledge of soil structure, plant composition and density, and throughfall rainfall, we assumed two possible states: (1) 10 kilopascals when raining and (2) 20 kilopascals when not raining. Although, it has been suggested that full drainage occurs after 3 days and SMT is equal to 33 kilopascals (Richards and Weaver 1944), this value resulted in dehydration of salamanders and SMT is generally not well documented in the study area. Stable populations (personal observation) in our simulated area suggest an ability to rehydrate, so we maintained SMT above the absorption threshold for salamanders (T. Spight 1967; Spotila 1972). Plant temperature was set to an average between the soil and air temperature (Geiger 1965).

Global variables included ‘air temperature’, ‘soil temperature’, ‘raining’, ‘time since last rainfall’, and ‘hours of daylight’. Air temperature was set at the beginning of each night, generated from a random-normal distribution using the monthly average night-time temperature and standard deviation for data recorded at Coweeta from 2013 to 2014s (Miniat 2017). Soil temperature was set monthly to the average monthly soil temperature recorded at Coweeta at a depth of 5 cm from 2013 to 2014 (Miniat 2017). Rainfall was simulated randomly with the probability in 24 hours ranging from 30-90% in 5% increments. Hours of daylight were set for each month to the monthly average for the latitude of the Coweeta Hydrologic Laboratory (35° 3'35.70"N, http://aa.usno.navy.mil/data/docs/Dur_OneYear.php).

2.4. Process Overview and Scheduling

The model alternated through day and night time steps and ran for one active season (April through October, 428 time steps total). During ‘day’ time steps, rainfall was simulated based on a probability of rain. Rainfall then affected the soil moisture, immediately setting to -10 kPa, then decreasing to -20 kPa after 6 time steps (3 days and 3 nights) with no rain (see above for justification). Next, salamander agents rehydrated based on soil moisture and temperature. Rehydration rates were calculated on a minute-by-minute basis and could result in dehydration if the soil moisture was too low. If salamander agents lost 50% of their mass due to dehydration, they died. This level of water loss is higher than would be physiologically possible, but allows for unknown factors relating to rehydration, such as the creation of a wetting front, which is recognized but poorly understood (Spotila 1972).

‘Night’ time steps began with temperature selection by drawing a value from a month-specific normal distribution of average nightly temperatures at Coweeta. These temperatures were recorded at 5 stations over 2 years. The duration of each night was set to the month-specific average number of night-hours. Vegetation temperature was set to the average of the soil and air temperature (Geiger 1965).

Once a salamander agent surfaced, it lost water based on a ecophysiological model described in the Submodels section. The model calculated water loss based on surface area, temperature, and relative humidity every minute. Salamanders lost water until their body mass had decreased by 3-10% depending on the model run. This model was run at 3, 5, 7, and 10% as part of sensitivity analysis, where all agents accepted the same water loss for each run. Though one study suggested salamanders retreat to burrows with as little water loss as 4% body mass (Feder and Londos 1984), previous estimates of activity time used a threshold of about 10% which is well below the lethal limit (Ray 1958; Feder and Londos 1984; Gifford and Kozak 2012; Caruso et al. 2014). Peterman and Gade (2017) found ecophysiological models were sensitive to this value. The salamander agents recorded their time spent foraging, both for each night individually and overall. For simulations including climbing, once the salamanders surfaced, they had an opportunity to climb based on the sub-model described below.

2.5. Design Concepts (*basic principles, emergence, adaptation, objectives, ~~learning,~~ ~~prediction~~, sensing~~, interaction~~, stochasticity, ~~collectives~~, observation)*

This model used formulas derived from physiological data and ecophysiological models to estimate potential foraging time for salamanders. Conventionally this is done with one or 2 specific-sized salamanders and one set of environmental variables. The ABM approach allows a wider range of sizes and climatic conditions for the ecophysiological model calculations and it allows individual plasticity in resistance to water loss. This approach also makes the addition of rehydration more feasible. The simulations included behavioral variability in emergence behavior and climbing as a compensatory behavior. The primary outputs for this model include the average nightly foraging time for each size class and overall, seasonal foraging time of each size class.

In the ABM framework, the interaction of spatial and temporal variation with individual physiological variability and behavior that cannot be accounted for in strictly ecophysiological models produces *emergent* patterns in foraging time and survival across the rainfall gradient and through the active season. The ecophysiological models do build in a certain part of the results, however the results ultimately emerge from individual ‘decisions’ to leave burrows, climb and retreat. Survival emerges from the salamanders’ ability to leave burrows, forage, and rehydrate. The salamanders *sense* the air temperature and relative humidity on the patch when foraging and the soil temperature and moisture on a patch when rehydrating. In the climbing and full models, salamanders sense the difference between the soil and air temperature before deciding to climb vegetation. The temperature, relative humidity, and soil moisture are ultimately sensed through the ecophysiological models calculating water loss and gain.

The salamanders have *adaptive* behavior by changing their probability of climbing based on the difference between air and soil temperature and increasing their probability of climbing under the most advantageous conditions. The *objective* of the salamanders is to maximize their fitness by increasing foraging time. The salamanders can do this indirectly under certain environmental conditions by climbing to reduce body temperature or by moving to an area of lower temperature or higher relative humidity. However, the scale of the model compared to the size of salamanders makes moving between patches to improve fitness by finding more humid areas unreasonable. Assuming no movement of the salamanders in the model is realistic considering that salamander home ranges are notoriously small (Madison and Shoop 1970).

The actual sizes of the salamanders were created *stochastically* within certain ranges for each size class at initialization. This created more realistic variability in size. The resistance values for water loss were plastic and responded to the soil temperatures. Environmental variables were generated pseudorandomly within given parameters on each 'night' time step. The temperature was drawn from a normal distribution with an average and standard deviation for the month (April-October) from data collected at the Coweeta LTER (SOURCE). During calibration of the ecophysiological models, individual water loss levels were monitored and compared to reported dehydration and rehydration rates. Plotting the nightly foraging time of salamanders allowed for monitoring of general activity patterns. The outputs mentioned above, (average nightly and total foraging time) allowed for comparison of overall trends between size classes, midstory canopy presence, climbing, and precipitation gradients and sensitivity to emergence probability and water loss acceptance.

2.6. Initialization

The generated landscape was uniform for each simulation. One thousand salamanders of each size class were created and randomly distributed for a total of 3,000 salamanders.

2.7. Input Data

The model did not use input data to represent time-varying processes (Grimm et al. 2010).

2.8. Submodels

2.8.1. Precipitation - The percent chance of rain over one 24-hour period was based on the amount of annual rainfall for the simulation run. A random number was generated from 0 to 1 and if it was below the percent chance of rain for each simulation then the night was set to "raining". If it was raining, then the humidity was set to 100%. If it was not raining, then the humidity decreased by 10% every 24 hours since the last rain based on the number of days since the last rain. This was a simplification of reality as relative humidity depends on a variety of factors but resulted in values representative of those recorded during previous work at the Coweeta LTER (unpublished).

2.8.2. Soil moisture - If it was raining then the soil moisture tension was set to 10 kilopascals, which reflected wet soil. A night of no rain increased the tension to 20 kilopascals. Although 33 kilopascals is the standard tension for saturated soil after water has time to drain (Richards and Weaver 1944), at this value salamanders started losing water to the soil with our ecophysiological models. Understanding of rehydration in soil is limited for amphibians, and salamanders in particular. Future models should include better rehydration functions and more accurately reflect soil type and vegetation and soil drying rates.

2.8.3. Salamander emergence -The salamander would emerge only if (1) the relative humidity was greater than 45%, (2) its body temperature was greater than 5 degrees Celsius, and (3) its water loss level was less than 4% of its mass.

2.8.4. Dehydration - Once the salamander did emerge, it started to lose water. This procedure was set up to be a minute-long step and was repeated for the number of minutes in the night (average night duration for the month). Dehydration models followed published formulas for estimating dehydration rates. Salamanders were assumed to be saturated at their skin surface in terms of water vapor (Spotila and Berman 1976). Water vapor pressure of salamanders was estimated by calculating saturation vapor pressure (Pascals):

$$[8]\ \rho_{sat} = 611e^{\left(\frac{2,500,000}{461.5}\right)\left(\frac{1}{273}-\frac{1}{T}\right)}$$

Where ρ_{sat} is the saturation vapor pressure in Pascals, and T is the temperature in Kelvin. The water vapor pressure of the air was calculated using:

$$[9]\ \rho_{air} = \frac{Rh \times \rho_{sat}}{T \times 461.5} \times 0.001$$

Where ρ_{air} is the water vapor pressure of the air in grams per cubic centimeter, Rh is the relative humidity, and T is the temperature in Kelvin. Dehydration rates were calculated using:

$$[10]\ EWL = \frac{\rho_{sal} - \rho_{air}}{R}$$

Where R is the resistance value of the salamander to dehydration (sec/cm). The resistance values in this model were derived from published literature but in reality may vary geographically (Riddell and Sears 2015) and by species. These values should be adjusted for specific future applications of this model. The resistance value changed depending on temperature (Eq. 4, using data from Spotila 1972). Activity time was estimated every minute by multiplying the above estimate of water loss by the surface area of the animal (cm^2) and by 60 seconds. This was repeated on a minute by minute basis until the salamanders reached their threshold to cease activity. When water loss reached 3, 5, 7, or 10% (depending on the simulation) the salamanders "retreated", meaning they stopped the dehydration procedure. In future versions or extensions of this model, the water level when salamanders abandon foraging may vary based on dehydration rate itself, as animals tend to abandon foraging earlier on drier nights (Feder and Londos 1984).

2.8.5. Rehydration - When salamanders retreat or remain in their burrow, they rehydrate at rates based on surface area, temperature, level of dehydration, and soil moisture tension. Since the soil moisture was sometimes very low, some salamanders dehydrated during this process (as observed in empirical studies) causing them to reach unrealistic water loss levels. If this happened, the salamander died when water loss was higher than 20% of its mass (18-26% is lethal, Feder and Londos 1984). Salamanders are unlikely to remain in areas where they would continue to lose water, but the model does not include this type of avoidance behavior. Rehydration rates were calculated as a minute-long step repeated each minute of the day or night when a salamander was inside a burrow. Rehydration rates were calculated using (Tracy 1976):

$$[11]\, r = (\varphi_{sal} - \varphi_{soil}) \times K$$

Where rehydration is measured in grams per cm^2 per minute, φ_{sal} is the water potential of the salamander in pascals, φ_{soil} is the soil moisture tension in pascals, and K is the hydraulic conductance, set at 0.00000013 g cm^{-2} min^{-1} pa^{-1} as calculated for Leopard frogs (Tracy 1976). The water flux of the salamanders were estimated using the following equation established for Leopard frogs (Tracy 1976).

$$[12]\, \varphi_{sal} = (-284.802\theta^3 + 773.427\theta^2 - 703.223\theta + 0.0214809) \times 100$$

Where θ is the hydration level of the salamander (1 - percent of mass lost to water loss). These parameters are currently unavailable for salamanders, however the leopard frog values produce reasonable rehydration rates reflective of those found in previous studies with salamanders (Cohen 1952; Spight 1967a,b; Spotila 1972; Feder 1983). The relationship between soil moisture and water loss rate is independent of species of salamander (Spight 1967) suggesting the formula would remain unchanged for any future applications of the model with other species.

2.8.6. Climbing – Once the salamanders have gone through the emergence sub-model, they had an opportunity to climb vegetation before dehydrating. Individual probability of climbing was estimated based on the difference between soil and air temperature. If a randomly generated number was less than the salamander's individual propensity to climb then it climbed.

Salamanders do have an ability to sense and behaviorally regulate temperature (Feder 1982; Feder 1983; Strickland et al. 2016).

3. Data analysis

The nightly foraging times were compared between models across the rainfall gradient and size classes using visual comparison with confidence intervals (graphs). We compared the total seasonal activity time in relation to the probability of rainfall separated by the water loss threshold and size classes.

APPENDIX 5.2

MODEL CODE

NetLogo language

;The World settings include origin located in the bottom left corner, with a max-pxcor and max-ycor of 49. View settings include patch size of 10. On the interface, there is a slider for "cease-forage" from 0.03 to 0.1 in increments of 0.01. A slider titled "p" reflects probability of rainfall and ranges from 0.1 to 1 in increments of 0.05. A switch for "climbing?" included climbing behavior when switched on and does not allow climbing when switched off. A switch for "midstory?" included the microclimate influence of Rhododendron when switched on.

```
globals[
  month
  hour             ;hours of night
   temp            ;average nightly temperature, set each night Celsius
   raining               ; if its currently raining
   time-rain       ;time since last rainfall (number of ticks=hours)
   str              ;average monthly soil temperature
  c                ;climbing propensity, estimated based on difference in air and soil temperature
   ;p                    ;probability of rainfall in 24 hrs
  ;cease-forage    ;percent water loss willing to accept now individualized, possibly will change
                   ;based on dehydration rate after each 30 minute tick
  ;midstory?       ;presence or absence of Rhododendron
```

```
  output-file-name ;needs to be updated to reflect version (date)
 ]
patches-own [
  SMT                    ;soil moisture tension, negative pressure of water in soil, as gets greater,
                     ;more resistant to losing water from soil to object (Pa)
  soil-t             ;temperature of soil @ about 5 -10  cm in degrees C, monthly average,
  plant-t            ;temperature of plants
  rh                 ;relative humidity
  midstory           ;presence of midstory
  atemp              ;local air temp
 ]
turtles-own [
  out                ;y/n if animal emerged on any given night to prevent emerging twice in one
                     ;night
  mass               ;in grams
 svl                     ;snout- vent length in cm
 sarea               ;surface area in sq cm
 class               ;H = hatchling, J = juvenile, A= adult
 water-loss          ;keep track of water level, sort of a reserve but as a record of water lost
 forage-time         ;keep track of total time spent foraging
 resist              ;whole body resistance to water loss ;;depends on size of animal,
                     ;temperature and relative moisture
 K                       ;hydralic conductance
```

```
  body-temp        ;in degrees C
  time           ;nightly time spent foraging,  reset each day
  rtime          ;time inactive
  deficit        ;dehydration deficit proportion of water lost compared to mass
  outside        ;time since last emergence
  climbing        ;yes or no if climbing at night
  EWL            ;evaporative water loss per hour (after repeat 30 minutes * 2)
  emr            ;probability of emergence,
 ]
to setup
 ca               ;clear all
 reset-ticks      ;reset time counter
 ask patches
 [
  ifelse midstory?                        ;if rhodo is present
    [set midstory 1
     set pcolor 62]
    [set midstory 0                         ;rhodo is not present then set all patches to the same values
    set pcolor 66]
  ]
 weather                            ;set simulated air temperature on each patch
 rain                               ;set rain
 ask    patches     [soil]        ;set relative soil temperature
```

```
  create-output                    ;process to create output file to record data at multiple time steps
                                   ;(end of each night)
  crt-sal                          ;create salamanders
end
to create-output
  ; Open the main output file
  ; Do not delete it instead of appending to it because we could be doing multiple model run
  ;experiments
  ; Instead- print headers only if the file is new, and put date and time
  ; as separator between model runs
set output-file-name (word "ClimbPhysics2Apr18" midstory? cease-forage ".csv") ;change date
ifelse (file-exists? output-file-name)
  [
    file-open output-file-name
    ; Print a header between model runs
    file-print date-and-time
  ]
  [
    file-open output-file-name
    file-print date-and-time
    file-type ","
    file-type "midstory?,"          ;if version includes Rhododendron or not
    file-type "cease-forage,"       ;water-loss acceptance
```

```
  file-type "month,"                ;month
  file-type "tick,"                 ;time step
  file-type "temp,"                 ;air temperature in Celsius
 file-type “soilT”                  ;soil temperature in Celsius
 file-type “airSoil”                ;difference between air and soil temperature
  file-type "time-rain,"            ;number of days since rainfall event
 file-type “climb-prob”       ;climbing probability based on difference between air and soil
                              ;temperature
  file-type "rain-probability,"     ;probability of rainfall in model run
  ;time foraging
  file-type "time-A,"               ;nightly hours of activity, adults
  file-type "time-J,"               ;nightly hours of activity, juvenile
  file-type "time-H,"               ;nightly hours of activity, hatchling
  ;proportion active
  file-type "active-A,"                    ;proportion of adults active
  file-type "active-J,"             ; proportion of juvenile active
  file-type "active-H,"                    ; proportion of hatchling active
  ;proportion climbing
  file-type "climb-A,"                     ; proportion of adults climbing
  file-type "climb-J,"              ; proportion of juvenile climbing
  file-print "climb-H,"                    ; proportion of hatchling climbing
]
file-close
```

```
end
to crt-sal
 crt 1000                        ;number of hatchlings
 [
  set size 0.5
  set mass random-float 1                 ;randomly assign mass to less than one gram
  set svl (32.8 * mass ^ 0.34)            ;created this based trendline from actual observations
                                          ;(Maerz et al Unpublished, CMR)
  if svl < 10 [die]
  set sarea 8.42 * (mass ^ 0.694)          ;surface area from formula found in Spotila 1972 for
salamanders
  set class "H"                      ;hatchling salamander
  common-par
  ]
 crt 1000                        ;number of juvenile
 [
  set size 0.7
  set mass (random-float 1) + 1            ;randomly assign mass to between 1 and 2 grams
  set svl (32.8 * mass ^ 0.34)            ;created this based trendline from actual observations
                                          ;(Maerz et al Unpublished, CMR)
  set sarea 8.42 * (mass ^ 0.694)     ;surface area from formula found in Spotila 1972 for
;salamanders will adjust later for other species with different body shapes
  set class "J"
```

```
   common-par
   ]
  crt 1000                        ;total number of adults
  [
   set size 0.9
   set mass (random-float 8) + 2              ;randomly assign mass to between 2 and 10 grams
   set svl (32.8 * mass ^ 0.34)               ;created this based trendline from actual observations
                                              ;(Maerz et al Unpublished, CMR)
   set sarea 8.42 * (mass ^ 0.694)            ;surface area from formula found in Spotila 1972 for
;salamanders will adjust later for other species with different body shapes
   set class "A"
   common-par
   ]
end
to common-par
   set shape "salamander"
   set color grey
   setxy random-xcor random-ycor
   set water-loss random-float (0.15 * mass)   ;start water loss level greater than 0, at a maximum
just below lethal level
   set forage-time 0
   set time 0
   set resist 0.09                        ;sec/cm from Spotila and Berman for D. ochrophaeus, initial
```

```
                                      ;value, adjusted based on soil temperature
   set K 0.00000013                   ;for leopard frogs from Tracy 1976 ; g/cm^2/min/pa
   set deficit 0
   set outside 0
   set climbing "no"
   set emr 1                      ;emergence probability for the  night
   set energy 0                     ;Assume low because just emerged from hibernation
end
to go
  if ticks < 60
  [ set month "april"    ;set month
    set hour 11          ;set number of hours of night
    set str 11.64 ]      ;set soil temperature to monthly average
  if ticks > 60 and ticks < 122
  [ set month "may"
    set hour 10
    set str 14.17 ]
  if ticks > 122 and ticks < 182
  [ set month "june"
    set hour 9.5
    set str 17.44 ]
  if ticks > 182 and ticks < 244
  [ set month "july"
```

```
    set hour 10
    set str 18.61 ]
  if ticks > 244 and ticks < 306
  [ set month "august"
    set hour 10.5
    set str 18.62 ]
  if ticks > 306 and ticks < 366
  [ set month "september"
    set hour 11.5
    set str 17.95 ]
  if ticks > 366 and ticks < 428
  [ set month "october"
    set hour 13
    set str 14.13 ]
  tick
  ifelse ticks mod 2 = 0          ;divides by 2, if remainder = 0 then 'night' process, if > 0 then
                                  ;'day' process
  [night
  update-output]
  [day]
  if ticks >= 428 [stop]
end
to day
```

```
 ask turtles
 [
  set   climbing  "no"        ;reset
  set   color   grey
  set   out      "no"
  set   body-temp soil-t
  set   time     0              ;reset before start foraging again
  set   rtime   0             ;reset
  let   minutes (24 - hour) * 60
  repeat minutes [rehydrate]
  ]
end
to night
 weather              ;procedure to set temperature
 rain                 ;procedure to create rain events
 ask patches [
  soil                ;procedure to set soil moisture
   ifelse midstory = 0
   [set plant-t ((temp + soil-t) / 2)]          ;average of near ground temp and air temperature
   [let mtemp 1.0009 * temp - 0.5970     ;if midstory is turned on, adjust air temperature
    set plant-t ((mtemp + soil-t) / 2)]      ;based on general air temp adjusted for Rhodo
  ]
ask turtles
```

```
 [
  set   rtime    0                          ;reset
  set   body-temp      soil-t               ;set body temperature to soil temperature
  set   resist         0.425 * soil-t + 0.8136      ;based on trend line fit to temperature for
                                                   ;calculated resistance values from Spotila 1972 for
                                                   ;P. jordani, because at this temperature longer, so
                                                   ;time to adjust
  ifelse random-float 1 <= emr
    [emerge]                                       ;procedure for salamander to surface
    [set      body-temp      soil-t
         let        minutes      hour * 60                    ;number of minutes in night
     repeat       minutes     [rehydrate]          ;rehydration procedure
     set      outside      (outside + 1)]              ;keep track of how long since last emergence
 ]
end
to weather
;pull temperature value from random normal distribution centered around the monthly
;average night temperature
 if ticks < 60                                                ;April
 [ set temp random-normal 11.89 1.85]
 if ticks > 60 and ticks < 122                     ;May
 [ set temp random-normal 15.00 1.83]
 if ticks > 122 and ticks < 182                    ;June
```

```
  [ set temp random-normal 18.57 0.70]
  if ticks > 182 and ticks < 244                    ;July
  [ set temp random-normal 19.07 0.95]
  if ticks > 244 and ticks < 306                    ;August
  [ set temp random-normal 19.15 1.01]
  if ticks > 306 and ticks < 366                    ;September
  [ set temp random-normal 17.36 1.94]
  if ticks > 366 and ticks < 428                    ;October
  [ set temp random-normal 12.07 3.00]
  ask patches[
  ifelse midstory = 1              ;rhodo present
   [set atemp (1.0009 * temp - 0.5970)] ;adjust local temperature based on Miniat 2013
   [set atemp temp ]                ;set local temperature to simulated air temperature
end
to rain
  ifelse random-float   1 <= p             ;based on probability of rainfall
     [setraining       "yes"]
     [set      raining       "no"]
  ifelse       raining       =    "yes"
     [set      time-rain    0]
     [set      time-rain    time-rain + 1]            ;once every 24 hrs
  ask     patches      [ifelse  raining = "yes"
     [set      rh   1]                              ;if raining set relative humidity to 1
```

```
    [let         t    time-rain * 0.1
     set     rh  1 - t ]]          ;relative humidly declines 10% every day it does not rain, this is an
                                   ;over simplification but give variability
end
to soil                         ;set soil moisture and relative temperature
 ifelse raining = "yes"
   [set SMT 10000]
   [set SMT 20000]              ;if raining  = "no"


ifelse midstory = 1             ; rhodo present
    [set rh (1.0139 * rh + 0.0029)
    set soil-t (0.8921 * str + 1.0658)] ;adjust soil temperature and relative humidity Miniat 2013
  [set rh rh                       ;rhodo not present = no change
  set soil-t str]
end
to emerge ;now given multiple limits to emerge
  if water-loss >= 0.5 * mass [die]
   if     rh  <=  0.45  ;;don't emerge if less than 45% humidity (which rarely happens), just
rehydrate
     [set body-temp      soil-t
      let  minutes     hour * 60
      repeat  minutes     [rehydrate]
      set  outside      (outside + 1)
```

```
    stop]
;if body temperature is too high OR if water loss is about 4% of mass then do not emerge and
;rehydrate
;otherwise do the 'dehydrate' procedure every minute
  ifelse body-temp < 25 and body-temp > 5 and water-loss <= (0.04 * mass)
  [
    set      color    blue
    climb
    set      out      "yes"
    let minutes     hour * 60
    repeat  minutes [
        ifelse   water-loss >= cease-forage * mass    ;check water loss level
            [set color grey
             stop] ;to stop repeating the 'forage' model if water loss is too high
            [dehydrate]
     ]
  ]
  [ set body-temp      soil-t
    let  minutes     hour * 60
    repeat  minutes     [
      if water-loss = 0 [stop] ;do not continue if full rehydrated,
      rehydrate]
    set  outside      (outside + 1) ;one night since outside
```

```
   ]
end
to climb                                ;simplified procedure, only based on temperature difference
  let airSoil atemp - soil-t                      ;some probability of climbing based on the difference
                                                     ;between ground temp and soil temp
  let beta1 random-normal 0.4477 0.1158        ;based on field data
  let beta0 random-normal 1.8587 0.1229        ;based on field data
  set c (exp(beta1 * airSoil - beta0) / (1 + (exp(beta1 * airSoil - beta0)))) ;set individual
    ;probability for each animal based on field data related to diff between soil and air temp
  ifelse random-float 1.0 < c             ;generate random number between 0 and 1
                    [set body-temp plant-t
                     set climbing "yes"
                     set color red]
                    [set climbing "no"
                     set color blue]
end
to dehydrate            ;repeat multiple times in one tick for each 'minute' of potential foraging
  if water-loss >= cease-forage * mass [set color grey stop]
              ;if reached tolerance level then stop procedure
  let tem atemp + 273.15                              ;convert from C to Kelvin
  let btemp body-temp + 273.15                           ;convert from C to Kelvin
;vapor density of skin @ temperature, usually close enough to 1 that assume saturation vapor
;density (Campbell 1977 pg 29), Tracy 1976
```

```
  let sal-sat (611 * exp ((2500000 / 461.5) * ((1 / 273) - (1 / btemp))))
                ;Riddell Sears 2015 , vapor pressure in Pa water
  let wvapor-s ((sal-sat / (btemp * 461.5)) * 0.001)
           ;convert from pressure to water vapor density and to g/cm^3
  let saturation (611 * exp ((2500000 / 461.5) * ((1 / 273) - (1 / tem))))
                     ;Riddell Sears 2015 ; vapor pressure in Pa
;water vapor density of air = relative humidity * saturation vapor density which varies based on
temperature
  let wvapor-a (rh * saturation) / (tem * 461.5) * 0.001   ;convert to vapor density  and to g/cm^3
  let water-loss-out (sarea * 60 *  ((wvapor-s - wvapor-a) / resist))
   ;total water loss in grams for 1 minute (cm^2 * seconds * vapor deficit/resistance to water loss)
  ifelse water-loss-out < 0 [set water-loss water-loss]
  [set water-loss (water-loss + water-loss-out)]                      ;total water lost in grams
  set forage-time forage-time + 1      ;Keep a cumulative total of activity time, minutes spent out
  set time time + 1                                  ;nightly foraging time, reset each day step
  if water-loss >= cease-forage * mass
  [stop]                                             ;if water deficit gets to range from 3-10%
  set deficit (water-loss / mass)
  set outside 0                                ;this way it only resets if make it all the way through
end
to rehydrate
 set rtime rtime + 1                          ;time inactive, assumed "rehydrating",
                              ;though may not make it through entire procedure
```

```
 if water-loss = 0 [set deficit 0 stop]
 if water-loss >= 0.5 * mass [die]            ;extreme value, would likely die well before this value
 if water-loss > 0 [set deficit (water-loss / mass)]
 let hydr 1 - deficit                         ;hydration level, proportion of water remaining
 let Swp  (-284.802 * (hydr ^ 3) + 773.427 * (hydr ^ 2) - 703.223 * hydr + 0.0214809) * 100
;salamander water potential, as a function of dehydration deficit,
;for now using leopard frog equation (Tracy 1976), converted to pa from assumed mb, converted
;from percent to proportion
 let water-gain-rate K * ((-1 * Swp) - SMT)                    ;hydraluic conductance *
difference between salamander water potential and soil moisture tension
 let water-gain water-gain-rate * sarea                       ;should be grams / minute
 set water-loss (water-loss - water-gain)
 if water-loss <= 0 [set water-loss 0]                        ;eliminate the negative numbers,
which would be a water surplus
 set deficit (water-loss / mass * 100)                        ;reset new deficit
  if water-loss = 0 [stop]                                  ;stop procedure when fully rehydrated
end
to update-output
  ; First calculate outputs
  ;Split by size class
  let adult turtles with [class = "A"]
  let juv turtles with [class = "J"]
  let hatchling turtles with [class = "H"]
```

```
  let adult-out adult with [outside = 0]
  let juv-out juv with [outside = 0]
  let hatch-out hatchling with [outside = 0]


  let adult-c adult-out with [climbing = "yes"]
  let juv-c juv-out with [climbing = "yes"]
  let hatch-c hatch-out with [climbing = "yes"]
let air mean [atemp] of patches
let soilt mean [soil-t] of patches
  ; Now write file output
  ;
  file-open output-file-name
  file-type "," ; Blank column for separator between runs
  file-type (word midstory? ",")
  file-type (word cease-forage ",")
  file-type (word month ",")
  file-type (word ticks ",")
  file-type (word temp ",")
  file-type (word soilt ",")
  file-type (word (air - soilt) ",")
  file-type (word time-rain ",") ;;days (24 hrs) since last rainfall
file-type (word (exp(0.4477 * (air - soilt) - 1.8587) / (1 + (exp(0.4477 * (air - soilt) - 1.8587))))
",")
```

```
 file-type (word p ",")
 ;time foraging each night
 ifelse count adult-out = 0
   [file-type (word 0 ",")]
   [file-type (word (mean [time] of adult-out / 60) ",")]
 ifelse count juv-out = 0
   [file-type (word 0 ",")]
   [file-type (word (mean [time] of juv-out / 60) ",")]
 ifelse count hatch-out = 0
   [file-type (word 0 ",")]
   [file-type (word (mean [time] of hatch-out / 60) ",")]


 ;porportion active
 ifelse count adult-out = 0
   [file-type (word 0 ",")]
   [file-type (word (count(adult-out) / count(adult)) ",")]
 ifelse count juv-out = 0
   [file-type (word 0 ",")]
   [file-type (word (count(juv-out) / count(juv)) ",")]
ifelse count hatch-out = 0
   [file-type (word 0 ",")]
   [file-type (word (count(hatch-out) / count(hatchling)) ",")]
 ;proportion-climbing
```

```
 ifelse count adult-c = 0 or count adult-out = 0
   [file-type (word 0 ",")]
   [file-type (word (count(adult-c) / count(adult-out)) ",")]
 ifelse count juv-c = 0 or count juv-out = 0
   [file-type (word 0 ",")]
   [file-type (word (count(juv-c) / count(juv-out)) ",")]
 ifelse count hatch-c = 0 or count hatch-out = 0
   [file-print (word 0 ",")]
   [file-print (word (count(hatch-c) / count(hatch-out)) ",")]
 file-close
end
```