THE ROLE OF BEHAVIOR IN INFLUENCING HEADWATER SALAMANDER

RESPONSES TO ANTHROPOGENIC DEVELOPMENT

by

Kristen Kimberly Cecala

(Under the Direction of John C. Maerz)

ABSTRACT

Evolutionary theory predicts that animals have evolved to move in response to a suite of

cues that maximize animal survival and growth while minimizing risk of injury or

mortality. When humans modify environments, new conditions can suddenly yield

maladaptive behavioral responses to cues that were adaptive in undisturbed

environments. Changes in behavior can alter animal movement patterns impacting

patterns of occupancy among habitats and fragment populations. My objectives were to

determine which environmental features best predict salamander occupancy in an

exurban region of the southern Appalachian Mountains and describe the behavioral

mechanisms driving observed stream salamander distributions. Headwater streams

generally have dense canopy cover that limits direct light penetration and regulates

temperature and humidity known to affect salamander behavior. Therefore, I predicted

that canopy cover would be an important predictor of stream salamander occupancy and

behavior. A regional survey of stream salamander occupancy was conducted in the Little

Tennessee River basin with the Coweeta Long Term Ecological Research site. Of a

variety of factors and scales, upstream riparian forest and canopy cover were the two most important predictors of stream salamander occupancy. Because deforestation increases light penetration to streams, I performed controlled laboratory and field experiments to determine if salamanders exhibited consistent behavioral responses to light under a range of environmental conditions and experience with high-light environments. Salamander larvae generally exhibited negative phototaxis that was exacerbated by the absence of refuge. Individuals with prior experience with high-light conditions exhibited weaker responses to light suggesting that salamanders may be capable of adapting to high-light environments. Lastly, we tested whether negative phototaxis could negatively influence natural behaviors in a field environment by surveying homing behavior across canopy gaps. All salamander life stages were unwilling to cross even small canopy gaps. Because streams are bisected frequently by canopy gaps for a variety of purposes, the accumulation of these small land-use changes and their effects have the potential to profoundly reduce connectivity among populations even in the absence of additional habitat alteration. This dissertation demonstrates the importance of considering the consequences of behavior in determining how disturbance influences populations.

INDEX WORDS: amphibian, Appalachian Mountains, barrier, behavior, buffer, canopy cover, connectivity, deforestation, *Desmognathus quadramaculatus,* dispersal, *Eurycea wilderae,* exurban, fragmentation, habitat degradation, headwater, land cover, landscape, land-use, larvae, local, management, movement, Plethodontid, phototaxis, population, riparian, salamander, scale, sedimentation, stream, substrate

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B.S., Davidson College, 2007

A Dissertation Submitted to the Graduate Faculty of The University of Georgia in Partial

Fulfillment of the Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2012

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DEDICATION

To my family, your unwavering support and love have made all of this possible, and I am forever grateful. Who would have thought that all the time spent running around in streams as a kid would be what I ended up doing as an adult.

ACKNOWLEDGEMENTS

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

As human populations expand, development of natural areas to accommodate this growth

threatens the status of wildlife populations globally (Foley et al. 2005, Hamer and McDonnell

2008). In the United States, a "rural renaissance" has occurred where nonmetropolitan growth is

outpacing metropolitan growth to capitalize on natural amenities offered in rural and exurban

landscapes (Fuguitt 1985, Brown et al. 2005). Conversion of previously intact habitat

fundamentally alters the functions and services that these areas can provide (Grimm et al. 2008,

Radeloff et al. 2005). These shifts can impact animals by eliminating essential habitat, but the

impact of development is often found far beyond its footprint (Theobald et al. 1997). Land-

cover change can degrade adjacent habitat quality, subsidize non-native organisms, or increase

the isolation of suitable habitat patches making wildlife particularly susceptible to extirpation in

altered landscapes (McKinney 2006, 2008).

As humans modify environments, understanding and managing the impacts of land-use

conversion on animal populations requires attention to the evolutionary, physiological,

ecological, and behavioral mechanisms contributing to the effects of changing land use (Frid and

Dill 2002, Gordon 2011, Lima and Zollner 1996). Organisms experience physiological and

evolutionary constraints that limit their distribution, but ecological needs such as prey

availability or refuge from predators further restrict an animal's use of the landscape (Bernardo

and Spotila 2006, Brown et al. 1996, Cunningham et al. 2009, Guisan and Thuiller 2005).

Because these conditions serve to alter an animal's growth, survival, and reproduction, individuals should select habitat where fitness is maximized (Werner and Anholt 1993). To remain within suitable environmental conditions, individuals respond to cues in their environment that signify habitat quality (Williams and Nichols 1984). Ultimately, individual responses to cues can collectively yield observed distribution patterns.

Behavioral responses to environmental change can take several different forms where modification of the sensory environment inhibits individuals from exhibiting adaptive behaviors (Schlaepfer et al. 2002). Changes in prey and predator communities can reduce foraging success, survival, or reproduction to negatively influence population growth rates and potentially form population sinks (Battin 2004). Poor habitat conditions may also encourage individuals to disperse away from these habitats or to avoid immigrating into disturbed environments (Battin 2004). Alternatively, new habitat conditions can suddenly create potentially maladaptive responses to cues that were adaptive in the undisturbed environment (Schlaepfer et al. 2002). New cues or cues disconnected from their original meaning may attract individuals to poor-quality habitat forming an ecological trap (Schlaepfer et al. 2002). Lastly, natural behaviors that reduce predation risk or help individuals to remain within their physiological tolerances can interact with changing landscapes to reduce rates of successful immigration and emigration if animals chose to avoid matrix habitat formed by anthropogenic development (Farig 2003, Lima and Dill 1990). To fully appreciate the mechanisms behind animal declines, researchers need to understand how human influences in the environment alter and interact with animal behaviors to prevent further decline.

Southern Appalachian Mountains

The forests of the southern Appalachian Mountains have been identified as one of the most biodiverse temperate regions (Stein 2000). These mountains are unique due to their age, north-south orientation, high precipitation, and dense stream network (Stein 2000). Because of the general lack of regional planning and regulatory protection for streams and rivers and the limited buffering capacity of underlying geology, Appalachian stream systems are particularly sensitive to environmental changes occurring within their catchments (Sullivan et al. 2004). Regional changes to water resources influence local residents via a variety of ecosystem services including freshwater provisioning, cultural and recreational uses, and sediment and nutrient transport. Because this system also serves as a water tower to the rapidly expanding southeastern megapolitan area, the effects of changing water quality and quantity extend beyond the mountainous region (Viviroli et al. 2007). The southern Appalachian Mountains are close to southeastern cities and offer many amenities; therefore, the sprawl of expanding southeastern cities has reached into the region (Rasker and Hansen 2000, Radeloff et al. 2010, Kirk et al. 2012). Historically, river valleys have long been used for agrarian human settlement, but more recent development favors high-elevation hillslopes (Gragson and Bolstad 2007, Kirk et al. 2012, Wear and Bolstad 1998). Although this area was largely deforested for timber harvest in the early 1900s, federal land acquisition in the first half of the 20th century protected much of the southern Appalachians that has since re-grown and remains forested. For example, the Nantahala National Forest protects almost 50% of the land in Macon County, North Carolina, where these studies were conducted. Consequently, this region is a patchwork of forest, small-scale agriculture with increasing residential development and the services necessary to support this growth (Webster et al. 2012). Understanding how anthropogenic activity in pristine areas of

the southern Appalachian Mountains is affecting the behavior, trajectory, and distribution of stream animal populations is critical because this area harbors some of the highest diversity of stream organisms in the United States if not globally (Stein et al. 2000). Loss of biodiversity is a global issue, and understanding the mechanisms behind population declines or extinctions as a result of land-use conversion and other human activities is the first step in preserving this area as a global hot-spot of diversity (Foley et al. 2005).

Headwater Streams

Headwater streams are a common landscape features due to their high density. Despite headwater streams composing up to 75% of the total stream and river channel length in the United States, headwater streams have little legal protection from anthropogenic activities (Leopold et al. 1964, Lowe and Likens 2005). Streams are particularly susceptible to environmental change because they are sensitive to not only local changes but to changes occurring throughout their catchments (Uchida et al. 2005). Vegetation clearing for development reduces riparian canopy cover, detrital inputs, and increases sediment inputs due to erosion of graded surfaces and loss of ground cover (Allan 2004, Paul and Meyer 2001, Walsh et al. 2005). Increases in impervious surface area alter stream hydroperiods by increasing the magnitude and frequency of floods (Allan 2004, Paul and Meyer 2001, Walsh et al. 2005). Changes in hydroperiod and sediment inputs collectively simplify channel morphology and substrates (Leopold et al. 1964). Increased erosion and terrestrial runoff tends to increase the transport of nutrients and pollutants from anthropogenic activities to stream ecosystems (Allan 2004, Paul and Meyer 2001, Walsh et al. 2005). Lastly, reductions in riparian canopy cover and the thermal influences of impervious surfaces on terrestrial overland flow cause urban streams to have altered thermal regimes and greater daily temperature fluctuations (Beschta 1997, Caissie 2006,

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Sinkrot and Stefan 1994). When headwater streams persist in human-altered landscapes, these altered conditions create biological communities distinct from communities from nearby, unaltered, habitats (McKinney 2006).

Amphibian Declines and Stream Plethodontid Salamanders

Amphibians worldwide are experiencing wide-spread and rapid declines and is the most threatened vertebrate taxon (reviewed in Stuart et al. 2004). Researchers have identified a diverse set of causes of species declines that act independently, additively, or synergistically (Collins and Storfer 2003). Habitat loss and degradation is one driver repeatedly linked to amphibian declines and defines the context in which other more enigmatic drivers act (Collins and Storfer 2003, Stuart et al. 2004). Amphibians are hypothesized to be sensitive to environmental change for a variety of reasons related to their life histories and physiology. In particular, their complex life cycles requiring two high-quality habitats for successful recruitment suggests that degradation of either habitat would lead to population declines (Hamer and McDonnell 2008).

The family Plethodotidae is the fifth most threatened amphibian family with 28 genera, greater than 420 species, and is unique in that all species lack lungs (Stuart et al. 2004, Petranka 1998). Although many of these species are terrestrial or arboreal, the southern Appalachian Mountains harbor a high diversity of stream-associated Plethodontid salamanders (Petranka 1998). These species have a biphasic life history requiring aquatic environments to complete larval development before becoming terrestrial as adults, but species vary widely in larval period, adult size, and adult affinity for aquatic habitat (Petranka 1998). Because of their unique ecology and widespread and dense populations, stream-amphibian communities may contribute to stream processes by influencing predator-prey dynamics, downstream transport of nutrients,

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and increasing transfer of nutrients between terrestrial and aquatic environments (Davic and Welsh 2004, Milanovich 2010, Trice 2011).

Plethodontid salamanders are often small with highly permeable skin to promote respiration. Consequently, their activity patterns are largely driven by desiccation risk limiting their activity to nighttime periods of high humidity and moderate to low temperatures (Feder 1983, Spotila 1972). These requirements limit their dispersal capabilities, and they often maintain small territories (Camp and Lee 1996). Therefore, human activities that negatively influence local microhabitat quality can also impact their fitness. Stream-salamanders may be more sensitive to these changes because streams often integrate environmental changes occurring throughout their catchments making stream organisms susceptible to local changes and those occurring upstream.

Dissertation

This dissertation represents one attempt to identify important proximate mechanisms regulating regional stream-salamander distributions in a globally significant region of biodiversity threatened by exurban sprawl. Although the relationship between land-use change and wildlife populations have been well studied, the underlying mechanisms are rarely tested explicitly. By identifying mechanistic relationships between environmental change and population declines, management strategies can be targeted to allow for continued human use of the landscape while simultaneously preventing regional declines in stream salamander diversity and abundance. This research benefits from and contributes to extensive local knowledge of disturbances and their effects on stream processes at the Coweeta Long-Term Ecological Research site (Coweeta LTER). This dissertation represents an important baseline of stream

salamander populations in this region, and continued research using these protocols will yield the first long-term regional monitoring study of stream vertebrates as part of the Coweeta LTER.

In chapter two, I evaluate regional patch occupancy patterns of stream salamanders in the upper Little Tennessee River basin subject to a range of environmental conditions to determine the appropriate scale for prediction and management. Using an information theoretic approach to test multiple hypotheses, I identify the most important variables for predicting salamander patch occupancy (Burnham and Anderson 2002). By taking into account the variable scales at which these species perceive their environments, the influence of interacting variables, and the role of life history traits, this chapter identifies commonalities and differences among predictors for larval and adult life stages of the same species as well as between two commonly detected species. Commonalities among life stages and species provide targets for management and additional research into important mechanisms driving the relationships observed in this study.

Appalachian stream salamanders are adapted to forested streams that generally have dense overstory and midstory canopies that limit direct light penetration to streams (Clinton and Boring 1993, Kozak and Wiens 2010). Stream salamanders are also generally reclusive (Petranka 1998). Results from chapter two corroborate previous studies of Plethodontid salamanders showing that forest loss is a critical driver of stream amphibian declines (e.g. Peterman and Semlitsch 2008, Stoddard and Hayes 2005, Welsh and Lind 2002), but results from chapter two nor previous studies do not directly indicate a mechanism. In particular, local canopy cover is related to riparian forest cover and improved the fit of our models in chapter two. Therefore, I suggest that behavioral responses to altered canopy cover indicate an important mechanism behind stream salamander declines in disturbed streams. Chapter three seeks to test one proximate behavioral mechanism behind relationships among canopy cover, riparian forest,

and salamander occupancy. Because behaviors are often context-dependent, drawing ecological inferences from behavioral results can be difficult without testing a range of conditions (Stamps and Groothuis 2010). Specifically, I sought to identify behaviors driving low salamander patch occupancy in areas of low canopy cover. Canopy cover is directly responsible for reducing the quantity and intensity of light reaching stream surfaces and is often correlated with additional habitat alterations resulting from land-use change. Therefore, I examine habitat selection of larval blackbelly salamanders in response to a light gradient and substrate and refuge availability. I also determine if differences exist between behaviors of individuals captured from forested streams and those captured from canopy gaps. Differences among individuals with and without experience in high-light environments could indicate the potential for local adaptation to altered light environments, which could prevent extirpation following land-use conversion. Ultimately, local-scale behaviors in response to high-light environments could indicate that larger-scale movements such as dispersal could be influenced by losses in riparian canopy cover.

Population connectivity can be critical for maintaining populations through time particularly as the landscape context changes (Brown and Kodric-Brown 1977, Frankham 2005, Holland and Hasting 2008, Pulliam 1988). For organisms using stream channels to disperse, environmental changes that restrict movement can be particularly effective at fragmenting and isolating stream reaches (Fagan 2002, Grant et al. 2007). In chapter four, I conduct an experiment to determine if fine-scale behaviors observed in chapter three could interact with small and moderate landscape-level features to alter movement patterns of stream salamanders. Specifically, this study seeks to understand if small losses in riparian forest cover could negatively influence population connectivity along a stream. Because declines in population connectivity are known to increase a population's risk of extirpation, preventing fragmentation

of stream salamander populations in the face of additional stressors may be particularly

important for preventing large-scale declines.

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CHAPTER 2

ASSESSMENT OF MULTIPLE DRIVERS, SCALES, AND INTERACTIONS

INFLUENCING SOUTHERN APPALACHIAN STREAM SALAMANDER OCCUPANCY[1]

ABSTRACT:

Animal abundance can be influenced by environmental features occurring at local and landscape scales, but identifying these influences can be complicated by interactions with species traits, other environmental predictors, and spatial scale. Understanding the influence of natural and anthropogenic variables on the distribution of animals is particularly important in regions of high biodiversity subject to increasing residential development, such as the southern Appalachian Mountains. Our objective was to determine the best variables and spatial scale at which to predict the occupancy patterns of southern Appalachian stream salamanders in a mixed-use region. We surveyed 37 streams in the upper Little Tennessee River basin that experienced a gradient of human impacts from agriculture, residential, and commercial development. We modeled the patch occupancy probabilities of larval and adult blackbelly salamanders (*Desmognathus quadramaculatus*) and larval Blue Ridge two-lined salamanders (*Eurycea wilderae*) as a function of 17 different predictors representing a range of scales and types of anthropogenic effects on aquatic ecosystems. Combinations of landscape and local features best predicted both species' occupancy patterns. Our results indicated that patch occupancy patterns of both species were best predicted by forest cover, but the scale, strength, and direction of this relationship varied. *Desmognathus quadramaculatus* were positively associated with riparian forest cover, but *E. wilderae* were negatively associated with catchment forest cover. Of the eight local-scale predictors, canopy cover was positively associated with both species' occupancy patterns and highly correlated with riparian forest cover, suggesting that studies into the role of canopy cover on local population dynamics may describe the mechanism behind the effects of forest loss on stream-associated amphibian declines. Collectively, studies surrounding the distributions and responses of stream-associated amphibians to environmental change

demonstrate that populations exhibit natural variance in abundance and that responses to environmental predictors is often species- and context- specific.

INTRODUCTION:

Defining relationships between environmental heterogeneity and animal distributions are critical to conserving biodiversity during periods of global change, but understanding these relationships can be difficult due to interactions among species traits and environmental factors at various spatial scales (Turner 2005). At fine spatial scales, species often respond to cues indicative of food or refuge, but at broader, landscape scales, species often respond to much larger scale cues as they seek mates or disperse among habitat patches (Lima and Zollner 1996). Because environmental change occurs at broad spatial scales and influences multiple environmental features simultaneously, isolating the effects of a single environmental variable on species response is difficult (Kiesecker et al. 2001). The influences of changing micro- and macro- scale features on the behaviors and responses of species will impact their demographic rates culminating in observable patterns of abundance. Collectively, the variability associated with different behavioral states and multiple changing and interacting environmental variables dictate the ways that species will respond to environmental change. The challenge for researchers is to understand the complex ways that multiscalar environmental features interact to affect animal distribution patterns.

Because modern landscapes include anthropogenic activities, the integration of interactions among natural and anthropogenic drivers is needed to fully describe species distributions (Foley et al. 2005). Understanding the role of human influences and natural environmental heterogeneity on animal populations is particularly important in regions of high global biodiversity threatened by increasing development. The temperate forests of the southern

Appalachian Mountains are a region experiencing increased exurban development and is one of the most significant areas globally of salamander diversity (Kirk et al. 2012, Rasker and Hansen 2000, Stein et al. 2000). In this region, headwater streams are ubiquitous, productive environments sensitive to environmental change, and serve as habitat for a diverse group of stream-associated amphibians requiring high quality aquatic and terrestrial habitat (Lowe and Likens 2005, Peterman and Semlitsch 2008, Petranka 1998). These headwater streams are influenced by conditions within their entire catchments, but local conditions such as a maintained riparian buffer can mitigate these effects (Naiman et al. 2005). Similarly, changes in watershed forest cover are known to negatively influence local conditions such as sedimentation via land-cover cascades (Burcher et al. 2007). In exurban landscapes, streams can be expected to experience a multitude of degraded conditions due to residential, commercial, and agricultural land uses such as altered hydrographs and hydrologic connectivity, increased sediment loads associated with altered channel morphology, increased chemical and nutrient inputs, removal of local, riparian vegetation, and increased temperature fluctuations (Allan 2004, Paul and Meyer 2001). Ultimately, these changes work independently and synergistically to simplify the geomorphology of the channel and the biotic community. Amphibians have been hypothesized and demonstrated to have little resistance and resiliency to these changes at landscape and local scales due to their reliance on aquatic and terrestrial environments, limited dispersal abilities, philopatry, and apparent susceptibility to chemical changes due to their highly permeable skin and specialized physiology (summarized in Cushman 2006, Stuart et al. 2004).

Studies on the effects of anthropogenic activities on the distribution of stream-associated amphibians in the Appalachian Mountains have largely been restricted to the fine-scale effects of logging on salamander population dynamics (Crawford and Semlitsch 2007,

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Crawford and Semlitsch 2008a,b, Lowe and Bolger 2002, Peterman and Semlitsch 2008).

Studies in the Pacific Northwest have highlighted the associations between broad-scale forest

loss and fine-scale increases in sedimentation in predicting population and occupancy declines of

stream-associated amphibians in logged landscapes (Kroll et al. 2008, Sepulveda and Lowe

2009, Stoddard and Hayes 2005, Welsh and Lind 2002, Welsh and Olliver 1998). In the

Piedmont, the negative effects of urban development on the occupancy of stream-salamanders at

a landscape scale have been described, yet the specific factors influencing these declines have

not been described (e.g. Miller et al. 2007, Orser and Shure 1972, Price et al. 2006, but see

Barrett et al. 2010), and disagreement exists in identifying the best spatial extent at which to

predict declines in abundance due to forest cover loss (Price et al. 2006, Price et al. 2011,

Willson et al. 2003). Collectively, this literature suggests that stream-associated amphibians are

sensitive to both fine- and broad-scale predictors, but no study has evaluated a comprehensive set

of multiscalar factors affecting salamander populations across a broad spatial scale along a

gradient of human land-use.

Our objective was to identify the most important predictors of broad-scale patch

occupancy of stream-associated amphibians in a large region of the southern Appalachian

Mountains currently threatened by the expanding metropolitan areas of the southeastern United

States (Hansen et al. 2005, Radeloff et al. 2010, Stein 2000). We modeled the influence of 17

predictor variables, measured and/or derived at local and landscape scales, on patch occupancy

probabilities (Conroy et al. 2008, MacKenzie et al. 2005). These variables encompass

information about land cover, land use, physical features such as elevation, fine-scale physical

features such as substrate and canopy cover, and local water chemistry and were selected to

include effects from multiple forms of land-use change including forestry, agriculture,

residential, and commercial development. We used an information theoretic approach (Burnham and Anderson 2002) to identify which of these variables were most important in predicting larval and adult patch occupancy of the blackbelly salamander (*Desmognathus quadramaculatus*) and larval Blue Ridge two-lined salamanders (*Eurycea wilderae*). These species are distributed over a wide geographic area at high densities and allow us to examine inter- and intra- specific differences (Biek et al. 2002, Davic and Welsh 2004, Milanovich 2010).

METHODS:

Study Region

The southern Appalachian Mountains are one of the most biodiverse temperate regions (Stein et al. 2000), yet this region is also experiencing rapid development as a result of the close proximity of southern metropolitan cities and the amenities offered by this region (Kirk et al. 2012, Radeloff et al. 2010, Rasker and Hansen 2000). Mountainous river valleys in this region have long been used for agrarian human settlement (Gragson and Bolstad 2007), but more recent trends favor development on high elevation hillslopes where headwater streams are found (Kirk et al. 2012). Although the region was largely clearcut for timber harvest in the early 1900s, the majority of this area has experienced forest regrowth and federal protection in the Nantahala and Chattahoochee National Forests. The presence of two rural towns yields a patchwork of urban, residential, agricultural, and forested land cover. We surveyed 37 sites with variable land cover in the Little Tennessee River basin upstream of Fontana Lake, which encompasses 111,760 hectares and is located in Rabun County, Georgia, and Macon County, North Carolina (Figure 2-1). These sites were selected from a larger set of study locations by sampling all sites with drainage areas less than 1,700 hectares (Webster et al. 2012).

Focal Species

Our two study species (*D. quadramaculatus* and *E. wilderae*) of the family

Plethodontidae are endemic to the southern Appalachian Mountains and are the two most

frequently encountered species within the region (Milanovich 2010). *Desmognathus*

quadramaculatus is a large-bodied, powerful salamander that occurs immediately streamside as

an adult although foraging movements into the surrounding forest are common (Kucken et al.

1994, Peterman et al. 2008, Petranka 1998). Adults often use their heavily ossified skull to

maintain extensive burrow systems in stream banks. They spend 2 – 4 years as larvae before

transforming at 35 – 42 mm in snout vent length (SVL; Austin and Camp 1992, Bruce 1988,

Castanet et al. 1996). As part of the lungless salamander family, this species must respire

entirely through the skin as adults and as larvae because they lack vascularized gills. As a

consequence, the larvae of this species are often found in areas of cold, fast flowing water where

dissolved oxygen is high (Davic and Orr 1987, Hairston 1949, Organ 1961, Pope 1924).

Eurycea wilderae is a small salamander that remains in the forest from June – December before

returning to streams to breed, but the timing of these movements varies widely geographically

and with local climate (Bruce 1982a, Petranka 1998). As larvae, they remain in the stream for 1

– 2 years, transforming at 18 – 32 mm SVL (Bruce 1982a,b, Petranka 1998, Voss 1993). These

larvae have vascularized gills and can often be found in multiple stream habitat types due to the

ability to extract oxygen via their gills and skin.

Salamander Data Collection

Because stream salamanders in the Southern Appalachians are abundant and occupy

almost all sites within our study area, we used a rapid assessment protocol to determine the

probability of a species occupying a one m^2 patch within each stream after accounting for

incomplete detection (Conroy et al. 2008). We designated a 150 m stream reach at each study

site generally upstream of any nearby road crossings. At each site, 31 one m^2 patches were

created, each located five meters apart. We surveyed each patch using two different techniques

from May – July 2009 (Jung et al 2000, Marsh 2009). First, we set a 25 X 40 cm leaf-litter bag

in each patch. Leaf-litter bags were constructed with one cm^2 plastic mesh and filled with leaf

litter from stream banks. If leaf litter was not available, we used litter from the nearest upstream

source. After bags were set in the patches, they were allowed to soak for 48 hours before our

first sampling occasion. Secondly, we actively surveyed the one-m^2 patch by turning cover

objects and searching leaf litter.

To incorporate incomplete detection into estimates of patch occupancy, we surveyed each

patch for three consecutive days. On each sampling occasion, we actively surveyed the patch

and checked the leaf-litter bag. These leaf-litter bags were checked by placing them in a bin,

pouring water through the bag, and gently agitating the bag to remove any organisms. Water,

debris, and salamanders located in the bin were poured through a net for increased detection. We

then identified species and life stage for all captured individuals and released them back into

their capture patch ensuring that they were not swept out of the patch by the current. Leaf-litter

bags were removed from the streams following our final sampling occasion.

Predictor Variable Collection

We selected a series of variables to predict salamander patch occupancy based on

evidence from previous studies on salamanders and other stream-dwelling organisms. These

variables represent a variety of spatial scales and categories of factors. For example, we

included variables describing surrounding land use and land cover, landscape level abiotic

effects such as elevation, and local level abiotic variables such as substrate particle sizes and total dissolved phosphorus (Table 2-1).

We used a 10-m digital elevation model (DEM) to delineate catchment basins, using our sampling point as the pour point for the catchment, then used these basins for subsequent evaluation of land-use and land-cover variables. Stream salamanders are often found in low-order streams with small discharges (Petranka 1998, Sepulveda and Lowe 2009). Similarly, terrestrial salamanders are distributed along elevation gradients, and stream salamanders in other regions have shown positive associations with elevation (Grant et al. 2005, Kozak and Wiens 2010, Ward et al. 2008; Elevation; Table 2-1). Therefore, we measured drainage area and elevation to evaluate whether these variables explained the observed distribution patterns of these salamanders (Drainage Area; Table 2-1). Previous studies have demonstrated that stream salamanders may occupy streams with confluences with higher probabilities than streams with no upstream confluences (Network; Grant et al. 2009; Table 2-1). We used the 10-m DEM to develop a stream layer using the Arc Hydro tools in ArcGIS 9.3 (ESRI, Redlands, CA) from which the Shreve stream order was calculated for each sample location. Shreve stream order describes the number of confluences occurring upstream of our sample location.

Catchment land cover was obtained from the 2006 National Land Cover Dataset (NLCD, Fry et al. 2011). Land cover has repeatedly been demonstrated to influence stream-salamander occupancy and abundance (Barrett et al. 2010, Price et al. 2011, Stoddard and Hayes 2005, Willson and Dorcas 2003). Because land cover types within this region were correlated, we combined proportions of deciduous forest (41), evergreen forest (42), mixed forest (43), and scrub/shrub (52) as a proxy for the amount of forested land cover within a stream catchment to reflect the proportion of the catchment undisturbed by human activities such as commercial,

residential, and agricultural land cover. The forest cover proportion was used for all of our land-cover analyses and transformed using an arcsine transformation (Sokal and Rohlf 1995). Studies on salamander declines have demonstrated conflicting results about the scale at which forest cover is important (Peterman and Semlitsch 2008, Willson and Dorcas 2003). We compared the relative support for the influence of reduced forest cover in the whole catchment, within a 100m upstream network buffer (100m network buffer), and within a 100m point buffer to identify the scale at which forest cover loss was important in predicting salamander patch occupancy. We used ArcGIS to calculate land-cover proportions from our delineated scales. We included catchment land use in addition to land cover because concurrent studies indicate that land use may be a better predictor of other stream conditions (Webster et al. 2012). Similarly, these classifications allowed us to distinguish between the effects of commercial use from agricultural use on salamander patch occupancy (Table 2-1). We derived the proportion of catchment land use (commercial and agriculture use) and maximum building age within each sample catchment from Macon County, North Carolina, tax records. Proportion of the catchments in agriculture and commercial land use were then transformed using an arcsine transformation because initial tests revealed that residual values of linear models including these variables were non-normal (Kéry and Hattfeld 2003, Sokal and Rohlf 1995). Unified records were unavailable for sites located in Rabun County, Georgia, and these sites were excluded from analyses involving land use and maximum building age.

Additional measures were taken at each patch to describe local stream conditions. First, active channel width and depth were taken at each patch, and we identified the channel unit types located within the entire study reach. By using these measurements, we obtained estimates of the proportion of different microhabitat types for our site. For this study, we examined the

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percent riffle as a predictor variable, which included all channel units with fast flowing water (e.g. riffle, bedrock step, cascade, etc). Riffles are regions of increased dissolved oxygen content necessary for salamanders lacking vascularized gills, increased access to subsurface habitat, and have been demonstrated to be important in predicting occupancy of other stream-associated species (Cecala et al. in review, Stoddard and Hayes 2005, Welsh and Olliver 1998; Table 2-1). Similarly for the 150 m reach, we counted all large woody debris greater than 10 cm that could increase the availability of refuge for stream-dwelling salamanders and increase channel complexity (Kluber et al. 2009, Table 2-1). Canopy cover has been positively linked to stream fish and aquatic and terrestrial salamander occupancy and abundance (Ash 1997, Peterman et al. *in press*, Rieman et al. 1997, Ward et al. 2008). We measured canopy cover at each patch by taking digital photos of the canopy from one meter above the stream channel and quantifying the percent cover via visual analysis using a grid. Reductions in canopy cover are often linked to increases in temperature, which is known to affect salamander activity (Feder 1983, Nelson and Palmer 2007, Spotila 1972). Lastly, two or three HOBO Pendant® temperature/light data loggers (Onset Computer Corporation, Massachusetts, USA) were placed at the water surface to obtain water surface temperatures at 10 minute intervals. Data loggers were placed haphazardly in the site stream reach and allowed to collect data for at least 72 hours concurrent with our sampling. Mean canopy cover and mean daily variation in stream water temperature were used to characterize the sample reaches (Table 2-1).

To assess the local physical and chemical properties of these streams, we conducted synoptic sampling at each of our study sites during base flow. Associated with sedimentation is an increase in fine sediments that embed larger particles used by salamanders and invertebrates as refuge and has been implicated in gill fouling of fish (Barrett et al. 2010, Berkman and Rabeni

1987, Stoddard and Hayes 2005, Welsh and Olliver 1998; Table 2-1). Sampling included a Wolman pebble count that included 100 measurements in a representative riffle for the 150 m reach (Wolman 1954). We then calculated Φ (-$\log_2$ [Sediment β-axis]) to represent the median particle size in each stream. Smaller median particle sizes are indicative of greater sedimentation due to an increase in the frequency of small particle sizes. Secondly, we took three replicate grab samples for chemical analysis. Samples were filtered using a Whatman GF/F filter in the field and frozen before chemical analysis. Phosphorus concentrations in southern Appalachian headwaters tend to be low and limit ecosystem processes along with nitrogen (Rosemond et al. 2008, Scott et al. 2002). As phosphorus is added to an Appalachian stream, the biomass, production, and growth rates of stream invertebrates rises, which serve as the primary food resource for stream salamanders (Cross et al. 2005, Cross et al. 2006). Stream salamander growth rates were also observed to increase when phosphorus and nitrogen was added to a headwater stream (Johnson et al. 2006). Total dissolved phosphorus was obtained via a persulfate in-line UV digestion with a Lachat QuickChem FIA+ (Table 2-1, Webster et al. 2012). Calcium was selected as a predictor variable because although most salamanders lack ossified skeletons, *D. quadramaculatus* requires calcium for their heavily ossified skulls (Petranka 1998). Conversely, high sodium levels in this region typically indicate the presence and use of road salt in the catchment. In northern regions where the use of de-icing salts is high, Karraker et al. (2008) described significant pre-metamorphic amphibian mortality as a result of high salt (NaCl) concentrations likely to contribute to declines in stream salamander patch occupancy. Calcium and sodium concentrations were obtained from an atomic absorption spectrometer (Perkin Elmer Analyst300; Table 2-1; Webster et al. 2012).

Data Analysis

Because stream salamanders in the southern Appalachian Mountains are extremely

abundant, we were unable to conduct traditional site level occupancy surveys because most sites

would be occupied with a probability of one, but salamander abundances could vary greatly.

Stream salamanders are highly secretive requiring intensive capture-mark-recapture studies to

obtain reliable estimates of abundance (Milanovich 2010). Consequently, surveying abundance

at the scale of this study was logistically unfeasible. To address these issues, we sectioned the

stream into small patches to estimate the patch occupancy probability, which is the probability of

any one m^2 patch being occupied within our sample location. This patch size was selected as a

unit that we were likely to avoid supersaturation, or occupancy of all patches at a survey

location. Occupancy probabilities vary in response to detection probability and abundance

(MacKenzie et al. 2005). Because we had standardized collection techniques by using leaf-litter

bags and consistent personnel for active surveys, we assumed that variation in patch occupancy

probabilities would generally be due to variability in abundance among sample locations.

To determine which of our predictor variables best explained salamander patch

occupancy, we needed to account for incomplete detection of salamanders that could bias

parameter estimates and spatial correlations within watersheds that could underestimate

parameter variance (Snijders and Bosker 1999). Therefore, we developed single-species

occupancy models that estimated patch occupancy probability for each species and stage

combination at each sample site given selected predictor variables after accounting for

incomplete detection. Simultaneously, we used a normally distributed, random-effects ANOVA

to account for spatial variability among watersheds. Due to the complexity of this model and the

uncertainty associated with detection, we used the Monte Carlo Markov Chain (MCMC) method

to fit our models using WinBUGS (Spiegelhalter et al. 2000). We used the Gelman-Rubin

diagnostic to test for convergence of our models using non-informative priors (Gelman and

Rubin 1992). Models all converged within 20,000 iterations, which was designated as our burn-

in period. We then ran 200,000 iterations thinned by a factor of 31 to reduce MCMC

autocorrelation to obtain the log-likelihoods for each model.

Due to the time-intensive nature of these models, we performed a two-step modeling

procedure. First, we divided our 17 predictor variables into five groups characterized by scale

and variable type. These groups were land cover, land use, landscape, local, and chemical (Table

2-1). Within each of these categories, we identified the best fitting model (see model

evaluation), which was then combined with best fitting models from other groups to identify

additive effects among variable categories. To avoid multicollinearity, we evaluated Pearson's

product-moment correlations for combinations of all variables. If variables were correlated ($R \geq$

0.6), they were not included in the same model to prevent inferential uncertainties of the

influence of correlated variables (Burnham and Anderson 2002, Appendix 2-1), but multiple

models were then run containing all possible permutations of that model without including

correlated variables. We elected this approach rather than developing principle components to

develop predictors based on correlated variables because this approach allows for direct

inference between the predictor variable and the response variable (Burnham and Anderson

2002). Likewise, principle components would not allow us to determine if one of the correlated

variables was more important than another in predicting salamander patch occupancy.

To determine the relative plausibility of each model given our data, we used Akaike's

Information Criteria (AIC: Akaike 1973) and adjusted this value for small sample sizes using the

small-sample bias adjustment (AIC_c; Hurvich and Tsai 1989). We calculated AIC_c weights and

assessed the fit of each model by ranking these models from highest to lowest weight (Burnham and Anderson 2002). Lastly, importance weights were calculated for each variable included within the confidence set or top ten models for each species and stage combination (Burnham and Anderson 2002, Royall 1997). Model selection uncertainty was incorporated by calculating model averaged parameter estimates using the $\hat{\bar{\beta}}$ method (Burnham and Anderson 2002). This process allowed us to incorporate uncertainty due to model selection as well as the uncertainty associated with each parameter estimate to develop the unconditional error for each parameter estimate (Burnham and Anderson 2002).

RESULTS:

We captured 2,008 larval and adult salamanders of nine different streamside salamander species. Of these captures, 554 captures were *D. quadramaculatus* larvae, 190 captures were *D. quadramaculatus* adults, and 833 captures were larval *E. wilderae*. Study sites varied considerably with respect to our predictor variables. Comparable to other streams in this region, our sites varied in elevation from 619 – 1,058 m with drainage areas between 18 and 1,670 hectares (Table 2-2). Overall, the catchments of our study sites remained largely forested with the most developed catchment retaining 29.7% forest, but when we examined the point buffer, our sites ranged from having a 100% forested buffer to a buffer with 0% forest (Table 2-2). Catchments with anthropogenic activity have been disturbed for a maximum of 161 years and a minimum of 41 years (Table 2-2). Patch occupancy estimates of larval and adult *D. quadramaculatus* varied at relatively well forested sites (> 80% forest cover) between 0.05 and 1.00 whereas their patch occupancy varied between 0 and 0.17 at sites with little forest cover (< 30%). The lowest patch occupancy probability for *E. wilderae* larvae was 0.033, but *E. wilderae* tended to have higher occupancy estimates than *D. quadramaculatus* (Table 2-2).

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Model selection results varied widely among species and stages. Generally, global models including variables from multiple groupings (i.e. land cover, land use, landscape, local, and chemical) were selected over models containing predictors from a single grouping with the exception of land cover (Table 2-3). The effect of our random effect to incorporate spatial autocorrelation and inherent differences among watersheds was moderate, but varied between species and stage in strength and direction of the relationship (Appendix 2-2).

For larval *D. quadramaculatus,* the best predictive model included forest within the 100 m network buffer and stream substrate. This model was 2.7 times more likely than the next best model which included forest in the 100m network buffer and elevation, and 3.7 times more likely than models containing either the 100m network buffer or stream substrate alone (Table 2-3). Absent from the candidate set for larval *D. quadramaculatus* are any land-use variables or most of the local predictors, although stream substrate was indicated to have a positive relationship with patch occupancy(Table 2-4). Conversely, adult *D. quadramaculatus* had far less resolution among models than larvae (Table 2-3). The top model of forest within a 100m network buffer was 1.4 times more likely than the next best predictive model of canopy cover for adult *D. quadramaculatus* (Table 2-3). The majority of models within the candidate set for *D. quadramaculatus* were global models containing a land-cover and local predictor although each variable category was represented in the candidate set (Table 2-3). Consistent with larval *D. quadramaculatus,* the forest within a 100m-network buffer was the most important variable for predicting *D. quadramaculatus* patch occupancy (Table 2-4). Larval and adult *D. quadramaculatus* share several important predictors such as forest within a 100m network buffer, but larvae were influenced more by in-stream characteristics such as stream substrate and water chemistry whereas adults were more influenced by landscape level factors such as land

cover and elevation in addition to local out-of-stream conditions such as canopy cover (Table 2-4). Collectively, patch occupancy of larval _and_ adult _D. quadramaculatus_ was positively associated with forest within a 100m network buffer, more complete canopy cover, smaller stream particle sizes, and higher elevations (Figure 2-2, Figure 2-3).

Occupancy predictors for larval _E. wilderae_ differed considerably from those of larval and adult _D. quadramaculatus._ The best fitting model contained forest within the watershed, stream substrate and canopy cover and was 5.7 times more likely than the next best model containing stream substrate and canopy cover (Table 2-3). Local variables were more important in predicting _E. wilderae_ larval patch occupancy than for _D. quadramaculatus._ The forest located within a 100m network buffer was not represented in the candidate model set for larval _E. wilderae_ with whole catchment forest cover being a better land-cover predictor (Table 2-4). Larval _E. wilderae_ patch occupancy was negatively associated with large particle sizes and forested land use, but positively associated with increased canopy cover (Figure 2-4).

DISCUSSION:

Stream studies in the upper Little Tennessee River have documented high variability in biological, chemical, and physical condition of streams in the upper Little Tennessee River as a result of long-term human influences in stream valleys and recent upslope development (Long 2011, Kirsch 2011, Webster et al. 2012). Generally, stream salamanders were predicted to occupy more disturbed sites with lower probabilities, but the strength and direction of the relationships were species and stage specific. Combinations of landscape and local features were generally better at predicting salamander patch occupancy than models containing local or landscape features alone. Because local variables were also important in predicting salamander occupancy and are often related to forest cover loss, connections drawn between the most

important landscape and local features may imply mechanisms by which losses in forest cover may influence salamander patch occupancy (Burcher et al. 2007, Rastetter et al. 2003).

Forest cover was one of the best predictor variables for each life-stage and species groups in our study, but the scale of the influence of forest cover on salamander patch occupancy varied by species with *D. quadramaculatus* patch occupancy best predicted by forest cover within a 100m stream network buffer whereas larval *E. wilderae* patch occupancy was best predicted by whole catchment forest cover. Not only did the scale of the influence of forest cover vary between the species, the direction and strength of these relationships differed with *D. quadramaculatus* being positively influenced by forest cover, but *E. wilderae* were negatively associated with increasing forest cover. Similarly, forest cover within a 100m stream network buffer was 1.7 and 2.3 times more important in predicting larval and adult *D. quadramaculatus* patch occupancy probability than the influence of watershed forest cover on *E. wilderae* patch occupancy. The positive association between *D. quadramaculatus* patch occupancy and high riparian forest cover is likely indicative of the affinity of *D. quadramaculatus* to streams and stream banks (Peterman and Semlitsch 2008, Petranka 1998). Although *D. quadramaculatus* do leave the stream for foraging, the distances of their movements are limited and unlikely to be greater than 100 m from the stream (Petranka 1998). Conversely, *E. wilderae* adults often move greater distances than *D. quadramaculatus* adults despite their smaller sizes due to *E. wilderae*'s use of upslope habitats during the non-breeding season (Petranka 1998). Relative to *D. quadramaculatus*, *Eurycea wilderae* also appear to show increased tolerance and preference for features associated with smaller or absent riparian zones such as increased water temperature variation and increased sedimentation associated with altered stream geomorphology (Crawford and Semlitsch 2008b, Miller et al. 2007). These tolerances may explain why *E. wilderae* patch

occupancy was best-predicted using watershed scale forest cover rather than just riparian forest cover. These relationships between species' movements, preferences, and the spatial scale of predictor variables to which they are sensitive, indicate that the life history traits of an animal are critical for understanding which spatial scale is most appropriate for management.

Overall, the effect of forest cover is unlikely to provide a clear hypothesis for mechanisms contributing to the observed patch occupancy patterns. Because local variables of canopy cover and substrate were also important for predicting salamander occupancy, the effects of forest cover may influence salamander abundance via the effects of local scale variables (e.g. Burcher et al. 2007). For example, riparian forest cover is highly correlated with canopy cover preventing their co-occurrence in models because of the difficulty in disentangling their effects ($R = 0.787$), and this relationship may indicate one mechanism responsible for declines in *D. quadramaculatus* patch occupancy following riparian forest removal. Proximate cues altering salamander distributions involve the abiotic cues associated with canopy cover losses such as increases the duration and intensity of light that reaches the streambed, increases in stream temperature, and reductions in streamside soil humidity (Poole and Berman 2001, Wilkerson et al. 2006). Salamanders tend to avoid moving in areas of high temperatures and low humidity due to the risk of desiccation via their highly permeable skin therefore negatively affecting their activity and performance (Feder 1983, Marvin 2003a,b, Spotila 1972). Although Desmognathines in this region are potentially limited by their thermal tolerances, occupancy patterns of *D. quadramaculatus* suggest that they are more associated with canopy cover rather than maximum daily water temperature variation (Bernardo and Spotila 2006). Similarly, behavioral avoidance of low canopy cover regions may also decrease the risk of predation by

visual predators (Chalfoun et al. 2002). Therefore, low patch occupancy in regions of low-canopy cover may be due to behavioral avoidance of light cues.

The association between salamander patch occupancy and riparian forest cover indicate significant variability in salamander patch occupancy even under natural conditions. Recent studies have highlighted the inherent value of understanding the historic range and variability in ecological conditions especially as researchers seek to understand how populations have changed and should be managed (Benedetti-Cecchi 2003, Fraterrigo and Rusak 2008, Landres et al. 1999). As riparian forest declines in this region, the range of patch occupancy probabilities contracts where sites with high occupancy probabilities are lost (Figure 2-2, 2-4). As forest cover in this area is projected to decrease with increasing exurban development, we may expect to find fewer locations with high salamander patch occupancy in the upper Little Tennessee River basin (Figure 2-2). Salamander patch occupancy may vary simply due to stochastic variability in demographic rates (Engen et al. 1998), but streams are also naturally heterogeneous environments where the morphology can change at small scales creating natural variability in microhabitats, resource availability, and predation risk driving variability in stream salamander abundances (Schlosser 1991). Because this region still remains largely forested, we were also unable to sample a sufficient number of deforested streams with a variety of other conditions. For example, we sampled few locations with little forest cover at high elevations limiting our abilities to disentangle the effects of related predictors. Had our study been conducted in a fully forested landscape, predictor variables not highly weighted in our study may better predict salamander patch occupancy in natural environments to explain why we observed such high variability in undisturbed catchments and why variables found to be important in other studies such as elevation were not found to be important in this region (Grant et al. 2005, Ward et al.

2008). Therefore, these variables should not be excluded from future studies despite weak

support for their effects in our study. Lastly, the influence of stream predators such as fish may

explain our observations of large variability. Although fish were not present in each of our sites,

native, cold-water fishes generally demonstrated similar relationships with forest cover loss in

this region (Kirsch 2011). Likewise, at fine spatial scales such as within our sites, fish are

known to alter the occupancy and distribution of larval salamanders, but at broader spatial scales,

stream fish also tend to exhibit similar occupancy patterns with respect to forest loss (Barr and

Babbitt 2002).

Although aspects of our study indicate clear predictive relationships of salamander

landscape occupancy patterns, we are aware of the limitations of our study. First, we were able

to obtain variable patch occupancy probabilities with clear relationships to predictors, but we

recognize that the relationship between our estimates of patch occupancy probability as a

surrogate for abundance remains uncalibrated due to logistical constraints of our study (Conroy

et al. 2008). Although we assume that most of the variability in patch occupancy probabilities

was due to variations in abundance, we acknowledge that this variability may also be due to

differences in our abilities to detect a species among sites (MacKenzie et al. 2005). Following

calibration, this method would be an effective rapid assessment technique to survey cryptic

species across large spatial scales. Secondly, comparisons of our results with those from

previous literature indicate that environmental processes may affect species and life stages

differently, and the direction of these responses can vary depending on the context (e.g. Barrett et

al. 2010, Peterman and Semlitsch 2008, Price et al. 2011). For example, sedimentation has often

been cited as a primary driver of stream amphibian declines (e.g. Barr and Babbitt 2002, Lowe et

al. 2004, Orser and Shure 1972, Miller et al. 2007, Welsh and Olliver 1998), but increasing

evidence from our study and others have found non-negative or even positive relationships between sedimentation and salamander occupancy (Sepulveda and Lowe 2009, Keitzer and Goforth 2012). These results suggest that sedimentation is only one of many local variables that influence salamander patch occupancy in this region. Because our study landscape included various human land uses, the overwhelming influence of forest cover loss may have prevented us from detecting the influence of other factors such as drainage area or elevation that may prove to be more important predictors of stream amphibian occupancy in other areas. Likewise, our study occurred at the southern range limit for many of the southern Appalachian species suggesting that they may be more sensitive to environmental degradation than individuals found closer to the center of their distribution (Bernardo and Spotila 2006). Our study corroborates others in finding that forest loss is a major driver of stream amphibian declines suggesting that forest cover loss has the greatest potential to allow researchers to describe stream amphibian declines on a broad scale (e.g. Barrett et al. 2010, Price et al. 2006, Welsh and Olliver 1998, Welsh and Lind 2002), but we strongly encourage researchers to consider the effects of anthropogenic change on multiple amphibian species and life stages to fully understand the dynamics of environmental change.

Management Implications

Because of the unique hierarchical organization of streams, the scale of anthropogenic development is often different than the scale at which stream organisms operate and respond to their environments. Consequently, distant changes within a stream catchment can negatively influence downstream populations. Our study highlights the need to consider whole network riparian buffers to manage stream salamander populations at a regional scale. Although prior studies have identified local riparian buffers as critical to maintaining core habitat for stream

salamanders, our study suggests that these local buffers will be insufficient to prevent stream

salamander declines without absolute retention of riparian buffers along the entire upstream

length of the stream (Crawford and Semlitsch 2007). Similarly, several studies have identified

local stream substrate as a key driver of stream amphibian distributions (e.g. Barr and Babbitt

2002, Welsh and Olliver 1998). Similarly, our results suggests that focus on a single local scale

variable will fail to adequately prevent degradation of all stream conditions necessary for stream

amphibian persistence. Riparian zone retention is known to mitigate the negative influences of

anthropogenic land-use change such as sedimentation (Naiman et al. 2005). By applying a

watershed scale perspective to stream amphibian conservation, regional managers should be able

to effectively manage stream amphibian populations while simultaneously preventing stream

degradation.

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Table 2-1. Hypotheses associated with each predictor variable and supporting literature.

Group	Predictor Variable	Hypothesis	Direction of Relationship	Support
Landscape, Land Cover				
	Catchment Forest	Streams integrate and process changes occurring throughout the watershed due to land-cover change known to affect salamander populations.	Positive	Price et al. 2011
	100m Network Buffer	Network buffers can filter runoff from the catchment to reduce sedimentation and inputs of other nutrients and chemicals known to influence salamander populations.	Positive	Willson and Dorcas 2003
	100m Point Buffer	Local conditions influence survival and dispersal of salamanders.	Positive	Lowe et al. 2005, Price et al. 2011
Landscape, Land Use				
	Catchment Commercial	Commercial land use is associated with increased impervious surface which greatly affects flood frequency and magnitude that may flush salamanders from downstream study reaches.	Negative	Barrett et al. 2010
	Catchment Agriculture	Agricultural land use is associated with increased sedimentation, which embeds large sediments and reduces refuge availability. Furthermore, fertilizer applications from agricultural land use may alter food webs.	Negative	Webster et al. 2012
	Maximum Building Age	The temporal scale of catchment disturbance will increase the effects of altered conditions on salamander populations through iterations of demographic processes.	Negative	Harding et al. 1998
Landscape, Physical				
	Elevation	Elevation is negatively correlated with stream order and stream temperatures that positively influence salamander occupancy.	Positive	Grant et al. 2005, Petranka 1998, Ward et al. 2008
	Drainage Area	Small drainage areas are correlated with stream order. Low-order streams have low discharge and often an absence of fish known to prey on salamanders.	Negative	Lowe 2005, Petranka 1998, Sepulveda and Lowe 2009
	Network	Confluences are hypothesized to increase stream populations' connectivity increasing the probability of long-term persistence by stream salamanders.	Positive	Grant et al. 2009

Group	Predictor Variable	Hypothesis	Direction of Relationship	Support
Local, Physical				
	Stream Substrate (ϕ)	Finer substrates reduce the availability of refuge and increase the probability of salamanders being flushed from a stream reach.	Positive	Barrett et al. 2010
	Riparian Canopy Cover	Salamanders are adapted to heavily canopied streams that regulate temperature and stream bank soil moisture to allow for successful terrestrial foraging by adults and juveniles.	Positive	Ash 1997, Peterman et al. in press, Rieman et al. 1998, Ward et al. 2008,
	Mean Daily Stream Water Temperature Range	Salamander movement is influenced by stream temperatures. Salamanders may be unable to tolerate large ranges in stream water temperature.	Negative	Bernardo and Spotila 2006, Feder 1983, Marvin 2003a,b
	Large Woody Debris	Large woody debris is one type of refuge typically found in forested streams. They increase habitat heterogeneity.	Positive	Kluber et al. 2009
	Percent Riffle	Riffles increase water oxygenation that is important for vertebrates that respire through the skin and are areas of hyporheic water exchange where salamanders may occur when they move out of the mainstream channel.	Positive	Lowe et al. 2004, Stoddard and Hayes 2005, Welsh and Olliver 1998
Local, Chemical				
	Total Dissolved Phosphorus	Southern Appalachian streams show evidence of having phosphorus limitation. Increases in phosphorus should stimulate the food web providing increased salamander prey biomass and growth rates.	Positive	Rosemond et al. 2008, Johnson et al. 2006
	Sodium	Sodium from road salt contributions can be toxic to amphibians.	Negative	Karraker et al. 2008
	Calcium	Desmognathine salamanders have heavily ossified skulls that require calcium for development.	Positive	Petranka 1998

Table 2-2. Summary statistics for predictor variables and species patch occupancy estimates quantified from surveys of 37 sites within the upper Little Tennessee River basin.

Parameter	Code	Mean (Standard Error)	Range	Unit
Watershed Forested Land Cover	Watershed	0.846 (0.031)	0.30 - 1.00	Proportion
100m Stream Network Buffer Forested Land Cover	100m Network Buffer	0.732 (0.041)	0.13 - 1.00	Proportion
100m Point Buffer Forested Land Cover	100m Point Buffer	0.450 (0.062)	0.00 - 1.00	Proportion
Elevation	Elevation	693 (14)	617 - 1058	Meters
Drainage Area	Drainage Area	421 (66)	18 - 1670	Hectares
Shreve Stream Order	Network	2.78 (0.40)	0 - 9	Confluences
Age of Human Disturbance	Maximum Age	118 (9)	41 - 161	Years
Catchment Area in Agricultural Land Use	Agriculture	0.091 (0.015)	0.00 - 0.27	Proportion
Catchment Area in Commercial Land Use	Commercial	0.009 (0.004)	0.00 - 0.11	Proportion
Substrate (Φ Scale)	Substrate	-4.96 (0.15)	-6.43 – (-3.32)	Log (mm)
Canopy Cover		0.736 (0.046)	0.00 - 0.982	Proportion
Maximum Daily Temperature Variation	Temperature Change	7.61 (0.77)	1.66 - 21.83	° C
Large Woody Debris		8.5 (2.3)	0 - 63	Logs
Riffle and Fast Flowing Water	Percent Riffle	0.609 (0.059)	0.053 - 0.994	Proportion
Total Dissolved Phosphorus		6.94 (0.54)	2.50 - 13.20	µg P/L
Sodium		2.06 (0.14)	0.76 - 4.74	mg Na/L
Calcium		1.50 (0.15)	0.26 - 3.15	mg Ca/L
Desmognathus quadramaculatus Larvae		0.36 (0.05)	0.00 - 1.00	Probability
Desmognathus quadramaculatus Adults		0.28 (0.04)	0.00 - 0.86	Probability
Eurycea wilderae Larvae		0.72 (0.05)	0.04 - 1.00	Probability

Table 2-3. Patch occupancy model rankings in the candidate model sets of our study organisms. Group indicates whether the model came from a single group of variable types or if the model includes predictors from multiple variable groups (Global). Models are ranked according to AIC$_c$ model weights.

Group	Model	Parameters	AIC$_c$	Δ AIC$_c$	AIC$_c$ Weight
Desmognathus quadramaculatus Larvae					
Global	100m Network Buffer + Stream Substrate	3	1509.73	0.00	0.379
Global	100m Network Buffer + Elevation	3	1511.73	2.00	0.139
Local - Physical	Stream Substrate	2	1512.35	2.63	0.102
Land Cover	100m Network Buffer	2	1512.35	2.63	0.102
Global	100m Network Buffer + Total Dissolved Phosphorus + Sodium	5	1512.94	3.21	0.076
Landscape - Physical	Network	2	1513.35	3.63	0.062
Landscape - Physical	Drainage Area	2	1513.35	3.63	0.062
Global	100m Network Buffer + Elevation + Stream Substrate	4	1514.25	4.52	0.039
Desmognathus quadramaculatus Adults					
Land Cover	100m Network Buffer	2	725.45	0.00	0.182
Global	100m Network Buffer + Total Dissolved Phosphorus	3	725.93	0.48	0.143
Local - Physical	Canopy Cover	2	726.25	0.80	0.122
Global	Canopy Cover + Total Dissolved Phosphorus	3	726.43	0.98	0.111
Land Cover	Watershed	2	727.05	1.60	0.082
Global	100m Network Buffer + Commercial	3	727.43	1.98	0.068
Global	100m Network Buffer + Elevation	3	727.93	2.48	0.053
Global	Elevation + Canopy Cover	3	728.03	2.58	0.050

Group	Model	Parameters	AIC$_c$	Δ AIC$_c$	AIC$_c$ Weight
Desmognathus quadramaculatus Adults					
Global	100m Network Buffer + Commercial + Total Dissolved Phosphorus	4	728.05	2.60	0.050
Global	Commercial + Canopy Cover	3	728.13	2.68	0.048
Global	100m Network Buffer + Elevation + Total Dissolved Phosphorus	4	728.25	2.80	0.045
Local - Physical	Canopy Cover + Percent Riffle	3	729.23	3.78	0.028
Local - Physical	Canopy Cover + Large Woody Debris	3	730.13	4.68	0.018
Eurycea wilderae Larvae					
Global	Watershed + Stream Substrate + Canopy Cover	4	1909.25	0.00	0.658
Local - Physical	Stream Substrate + Canopy Cover	3	1912.73	3.48	0.116
Local - Physical	Stream Substrate + Canopy Cover + Percent Riffle	4	1913.25	4.00	0.089
Global	Maximum Age + Stream Substrate + Canopy Cover	4	1915.25	6.00	0.033
Global	Maximum Age + Sodium	4	1916.25	7.00	0.020
Global	Watershed + Sodium	4	1916.25	7.00	0.020
Local - Chemistry	Sodium	3	1916.73	7.48	0.016
Global	Watershed + Stream Substrate + Canopy Cover + Sodium	6	1916.80	7.55	0.015
Local - Chemistry	Total Dissolved Phosphorus + Sodium	4	1917.25	8.00	0.012
Global	Network + Stream Substrate + Canopy Cover	4	1919.25	10.00	0.004

Table 2-4. Model averaged parameter estimates, 95% credible intervals, and importance weights for variables in the confidence set of each species and age combinations.

Parameter	Estimate	2.5% Credible Interval	97.5% Credible Interval	Importance Weights
Desmognathus quadramaculatus Larvae				
100m Network Buffer	3.114	1.298	5.013	0.747
Stream Substrate	0.684	0.172	1.226	0.539
Elevation	0.002	-0.002	0.006	0.190
Total Dissolved Phosphorus	-0.011	-3.227	3.194	0.087
Sodium	0.542	-0.458	1.508	0.087
Network	-0.058	-0.083	-0.037	0.066
Drainage Area	-0.347	-0.516	-0.215	0.066
Desmognathus quadramaculatus Adults				
100m Network Buffer	2.580	0.835	3.488	0.541
Canopy Cover	0.023	0.006	0.041	0.377
Total Dissolved Phosphorus	0.054	-3.163	3.280	0.350
Commercial	0.002	-0.002	0.007	0.165
Elevation	1.52×10^{-4}	-0.002	0.005	0.148
Watershed	2.732	0.7373	4.618	0.086
Percent Riffle	0.007	-0.007	0.021	0.028
Large Woody Debris	0.018	-0.008	0.052	0.018
Eurycea wilderae Larvae				
Stream Substrate	0.306	-0.114	0.734	0.916
Canopy Cover	0.018	-0.009	0.046	0.916
Watershed	-1.383	-3.744	1.026	0.693
Percent Riffle	-0.008	-0.027	0.010	0.089
Sodium	1.471	0.579	2.470	0.083
Maximum Age	-0.004	-0.046	0.014	0.053
Total Dissolved Phosphorus	-0.008	-3.242	3.212	0.012
Network	-0.011	-0.028	0.014	0.004
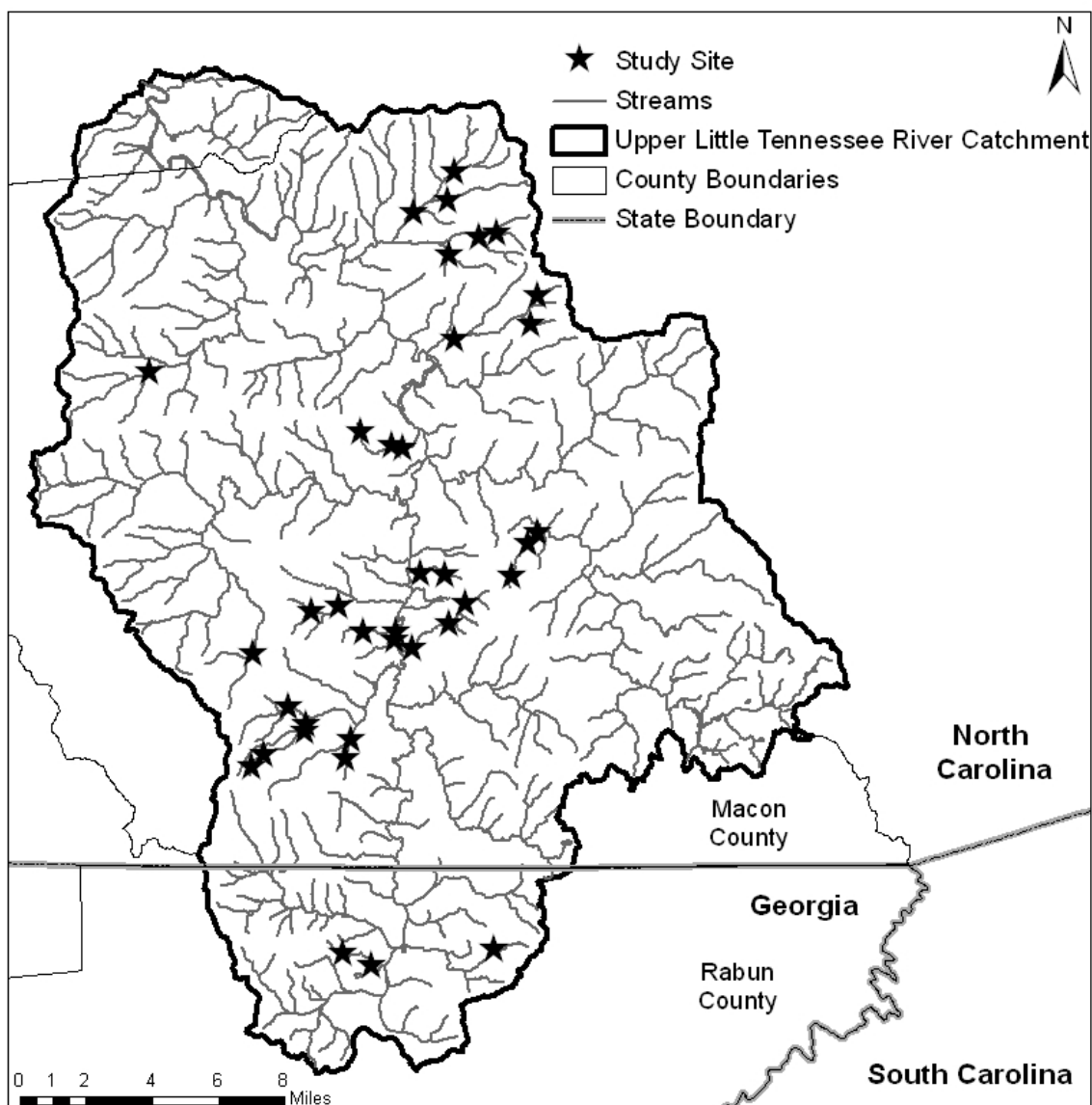
Figure 2-1. Location of study sites (N = 37) throughout the upper Little Tennessee River basin. These sites were a subset of 58 sites surveyed by Webster et al. (2012). Note that multiple sites may occur within a single watershed. We accounted for this spatial autocorrelation by including a random effect for each watershed in our modeling.
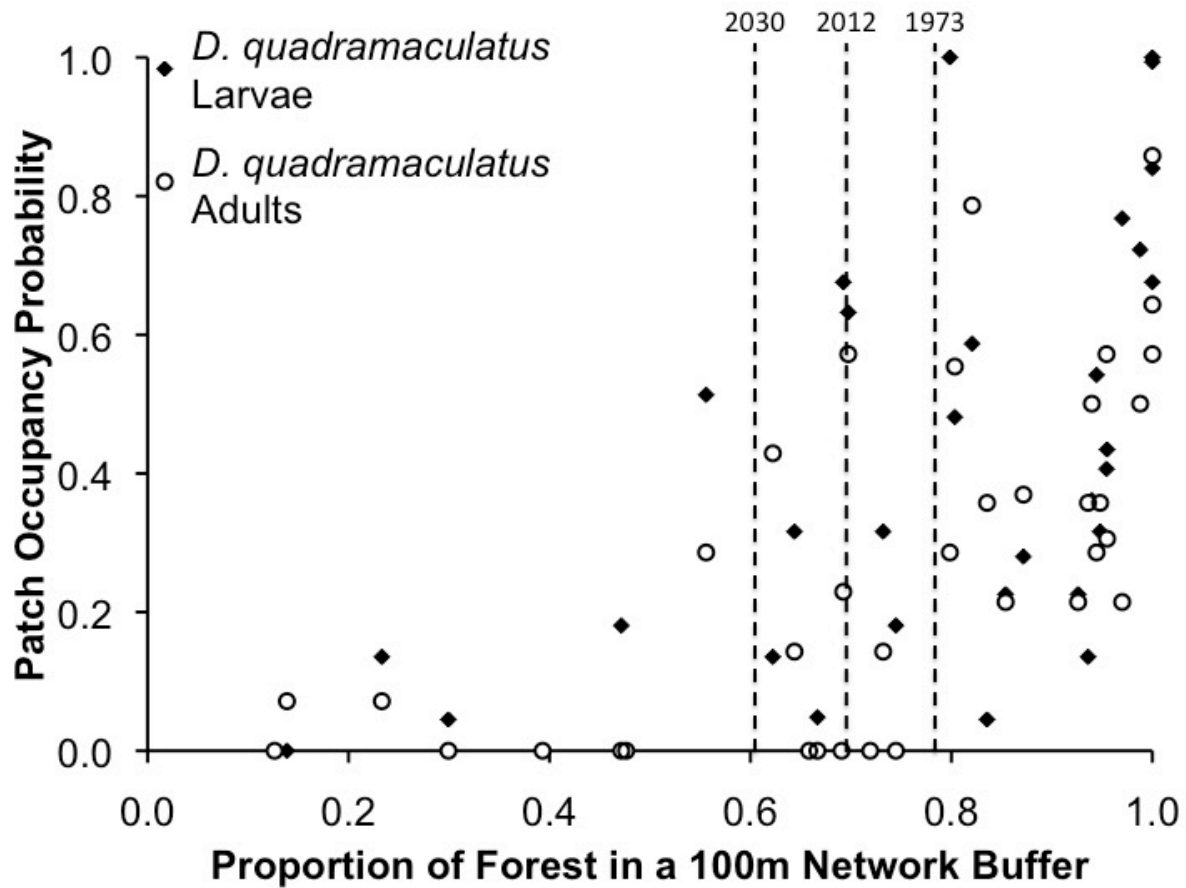
Figure 2-2. The effect of forest cover within a 100m buffer upstream of our sampling location on patch occupancy of larval and adult *D. quadramaculatus*. The vertical dashed lines indicate proportion of forest cover for Macon County at different time intervals. In this region, most of the development has occurred along the riparian areas in low elevation indicating that these values may be conservative estimates of riparian forest within a 100m-stream buffer. Estimates of forest cover for 1973 and 2012 were obtained from Griffith et al. (2003) and Kirk et al. (2012), but the forest cover estimate for 2030 was projected from mean annual forest cover changes experienced between 1973 and 2012 assuming that this rate would remain constant.
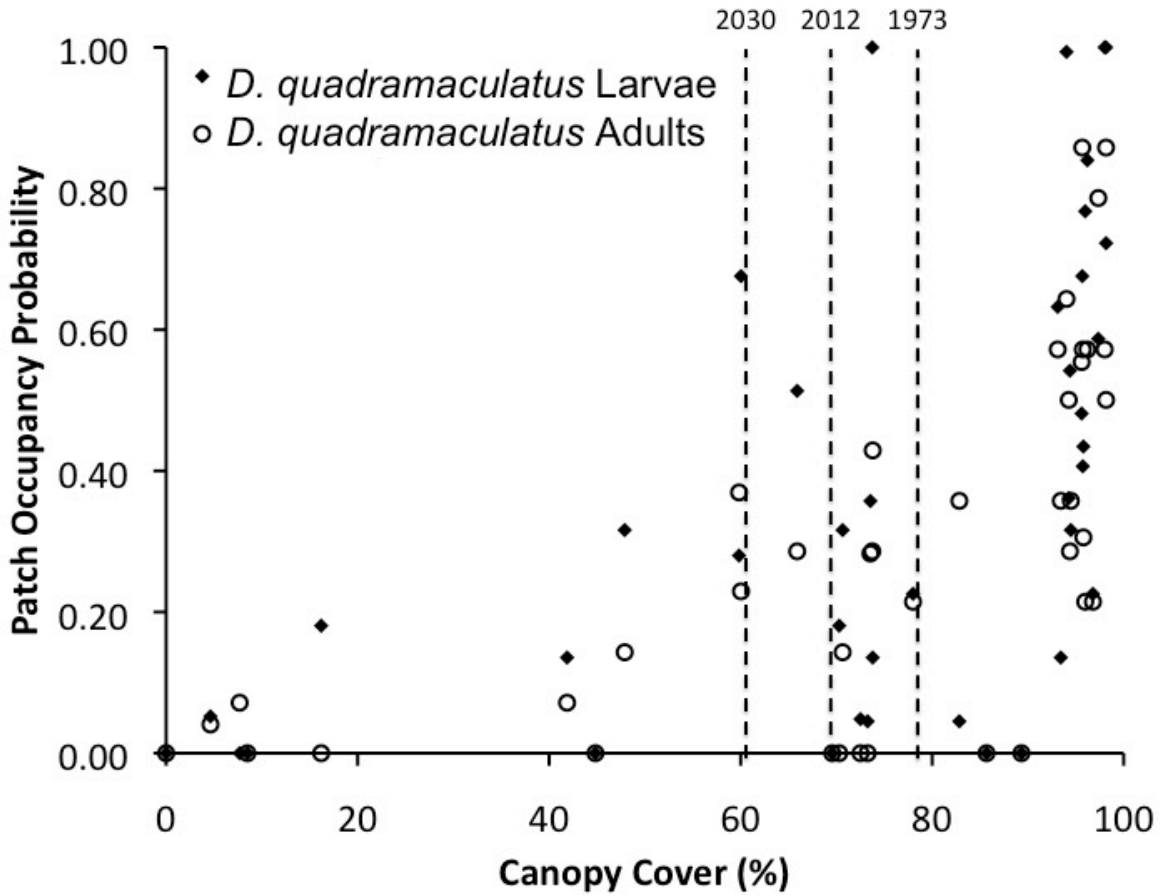
Figure 2-3. The effect of canopy cover on larval and adult *D. quadramaculatus*. Dark circles located on the x-axis indicate sites where the patch occupancy probabilities for larval and adult D. quadramaculatus were both approximately zero. Estimates of forest cover for 1973 and 2012 were obtained from Griffith et al. (2003) and Kirk et al. (2012), but the forest cover estimate for 2030 was projected from mean annual forest cover changes experienced between 1973 and 2012 assuming that this rate would remain constant.
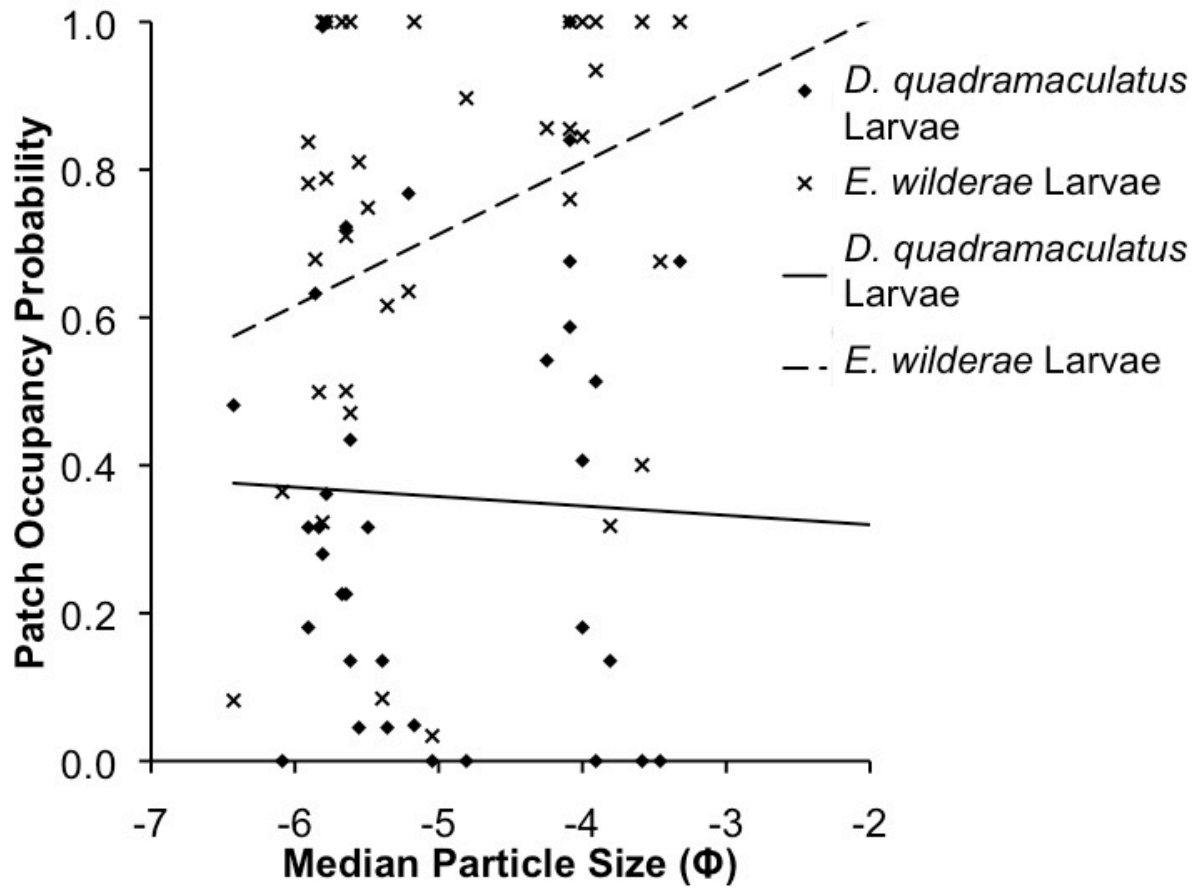
Figure 2-4. The effect of median substrate size on patch occupancy of larval *Desmognathus quadramaculatus* and *Eurycea wilderae.* On the Φ scale, larger values indicate small sediment sizes such as pebble and sand in this system whereas smaller values indicate larger particles including boulder and bedrock.

Appendix 2-1. Pearson product moment correlations for all variables included in our models. Variables with evidence of correlation (R > 0.6) were not used together within the same model. If parameters were correlated within the global models, all permutations of that model excluding the correlated parameter pair were performed.

	100m Network Buffer	100m Point Buffer	Elevation	Drainage Area	Network	Maximum Age	Agriculture	Commercial
Watershed	0.884*	0.623*	0.417	0.045	0.055	0.055	0.118	0.173
100m Network Buffer	-	0.732*	0.512	0.000	0.000	0.110	0.063	0.247
100m Point Buffer		-	0.683*	0.170	0.141	0.170	0.164	0.224
Elevation			-	0.235	0.249	0.219	0.212	0.228
Drainage Area				-	0.942*	0.089	0.249	0.187
Network					-	0.055	0.310	0.224
Maximum Age						-	0.265	0.369
Agriculture							-	0.864*
Commercial								-

	Substrate	Canopy Cover	Temperature Change	Large Woody Debris	Percent Riffle	Total Dissolved Phosphorus	Sodium	Calcium
Watershed	0.446	*0.769**	*0.642**	0.390	0.569	0.401	0.210	0.255
100m Network Buffer	0.305	*0.787**	*0.678**	0.501	0.498	0.358	0.257	0.219
100m Point Buffer	0.110	*0.620**	0.596	*0.654**	0.425	0.327	0.219	0.202
Elevation	0.237	0.427	0.444	*0.850**	0.401	0.268	0.192	0.219
Drainage Area	0.428	0.095	0.100	0.255	0.126	0.130	0.095	0.130
Network	0.425	0.095	0.122	0.261	0.095	0.145	0.071	0.089
Maximum Age	0.138	0.148	0.055	0.385	0.084	0.361	0.415	0.342
Agriculture	0.298	0.000	0.214	0.145	0.141	0.100	0.045	0.045
Commercial	0.055	0.114	0.292	0.126	0.077	0.000	0.077	0.045

	Canopy Cover	Temperature Change	Large Woody Debris	Percent Riffle	Total Dissolved Phosphorus	Sodium	Calcium
Substrate	0.411	0.084	0.126	0.365	0.205	0.167	0.251
Canopy Cover	-	*0.676**	0.431	*0.610**	0.345	0.077	0.134
Temperature Change		-	0.412	0.452	0.134	0.214	0.298
Large Woody Debris			-	0.363	0.387	0.356	0.324
Percent Riffle				-	0.210	0.277	0.176
Total Dissolved Phosphorus					-	0.377	0.348
Sodium						-	*0.847**
Calcium							-

Appendix 2-2. Model averaged estimates of the random effects for each species-stage pair. Each

estimate of a random effect indicates the effect that each watershed had upon the patch

occupancy probabilities.

Desmognathus quadramaculatus Larvae	*Eurycea wilderae* Larvae	*Desmognathus quadramaculatus* Adults
0.76	0.97	-3.66
2.38	2.51	-3.50
-0.42	0.32	-4.31
-1.60	0.20	-3.92
0.35	-2.09	-3.55
0.84	1.84	-3.56
0.36	1.56	-3.67
-3.03	-3.29	-4.44
-1.03	-0.03	-3.79
-0.16	1.45	-3.32
-0.31	-1.13	-3.45
1.23	-1.93	-3.43
-0.29	0.00	-3.61
-2.35	3.14	-4.60
-1.24	0.55	-3.72
-4.00	2.22	-4.50
-4.89	-1.59	-5.39
-1.56	1.26	-4.79
-1.74	0.38	-4.59
-0.67	1.54	-4.04
1.44	3.69	-4.02
0.65	1.34	-4.39

CHAPTER 3

EFFECTS OF LANDSCAPE DISTURBANCE ON FINE-SCALE PHOTOTAXIC BHAVIORS

BY LARVAL STREAM SALAMANDERS[1]

ABSTRACT:

The ecological responses of species to environmental change may often be regulated proximately by behavior. Integrating behavioral responses into ecological inferences can be difficult without considering the context-dependent nature of behaviors. Animals evolve to select habitats based on cues that were historically reliable indicators of habitat quality; however, responses to those cues may be modified by experience. In human altered environments, behavioral responses to cues may dictate how species respond to land-use change. Blackbelly salamanders (*Desmognathus quadramaculatus*) naturally occupy high elevation, low-order, forested streams with dense tree and shrub canopies that produce a low-light environment that is often disturbed following land-use change. We tested the effects of prior experience and environmental context (substrate availability) on the phototaxic behaviors of larval *D. quadramaculatus*) in a laboratory and field setting. We expected *D. quadramaculatus* to exhibit consistent negative phototaxis despite the environmental context or individual experience. Individuals from natural low-light environments exhibited stronger negative phototaxis relative to individuals from a high-light environment (forest clearing); however, these responses were conditional on substrate availability. When tested with different substrates, larvae from both environments showed a greater tendency to remain in high-light portions of the enclosures when presented with cobble refuge; however, when tested on leaf substrates, only larvae from low-light environments avoided the high-light areas. In field enclosures, naïve larvae exhibited negative phototaxis, but experienced individuals exhibited positive phototaxis to sunlight. These results suggest that local adaptation, via experience or local evolution, will interact with substrate modification to determine how larval *D. quadramaculatus* respond to human altered light environments. Ultimately, as human activities in the landscape that reduce canopy cover and

cobble and leaf availability due to siltation, consistent negative phototaxis could create behavioral barriers to movement that can fragment populations.

INTRODUCTION:

Habitats vary in quality based on a number of factors that influence survival, growth, and reproduction (Werner and Anholt 1993), and it is widely accepted that habitat selection behaviors have evolved to maximize an organism's fitness. Animals may accomplish this goal by responding to direct or indirect cues that maximize their performance due to physiological limits or by avoiding habitats based on cues associated with predation risk (Brown et al. 1996, Gilliam and Fraser 1987, Lima and Dill 1990, Roberts and Liebgold 2008, Werner et al. 1983). Although animals may often have instinctive behaviors that guide their responses to certain cues, these behaviors are only advantageous when the cue reliably indicates environmental conditions over large temporal scales (measured in generations). In the absence of temporally stable cues, adaptive modification of behavior through experience (i.e. learning) is favored to allow individuals to maximize their fitness in dynamic environments (Borenstein et al. 2008). Associative learning of the adaptive response to cues can only be successful when the cost of learning is low and the cue remains a consistent predictor of habitat quality on short temporal scales (Borenstein et al. 2008).

Often cues associated with high fitness exist in conflict requiring that animals make trade-offs among patches. For example, the use of high resource habitats with variable predation risk will select for context dependent responses to environmental cues to maintain a balance between resource needs and predation risk (e.g. Dingemanse et al. 2010, Madison et al 1999, Maerz et al. 2001, Pike et al. 2010, Roberts and Liebgold 2008, Werner et al. 1983). Contextual changes in the environment are "all of the external stimuli that impinge on an individual when it

expresses a behavior" (Stamps and Groothuis 2010). Therefore, evaluating and predicting how species respond to a change in one environmental cue may require examining how these responses interact with other physical or biological changes in the environment.

In the context of anthropogenic global change, it is also important to know whether evolved responses to habitat cues are easily modified by experience or local adaptation. An increasing number of studies demonstrate that instinctive responses to environmental cues create evolutionary traps for species in human modified landscapes (summarized in Schlaepfer et al. 2002). For example, aquatic insects will oviposit on roads because polarized light reflected from asphalt is similar to the polarized light reflected by water bodies (Horváth et al. 2009). An instinctive response to this once reliable cue is now maladaptive in a heavily modified landscape (Schlaepfer et al. 2002). However, behaviors associated with dispersal and habitat selection are also influenced by local adaptation or experience (summarized in Davis and Stamps 2004, Bernard and McCauley 2008, Immelmann 1975). In particular, experience in early life stages during a natal habitat preference induction period can shape future responses to habitat cues (Davis and Stamps 2004). It is hypothesized that by forming responses to habitat cues early in life, older animals can use familiar cues to disperse efficiently into suitable habitats (Davis and Stamps 2004, Stamps 2001, Stamps 2009). When individual differences in experience interact with contextual responses to environmental cues in heterogeneous environments, drawing ecological inferences about species or population preferences can be difficult (Gordon 2011, Lima and Zollner 1996).

The objective of this study was to examine the interactions between experience and context (stream substrate condition) on the response of larval blackbelly salamanders (*Desmognathus quadramaculatus*) to light. *Desmognathus quadramaculatus* are members of a

diverse guild of streamside salamanders within the family Plethodontidae that are widely distributed throughout streams of the eastern United States. Many streamside salamanders are physiologically limited by high temperatures, and therefore generally associated with cool, forested streams; however, species show varied tolerance to disturbances such as the removal of riparian forest cover (Bernardo and Spotila 2006, Petranka 1998, Price et al. 2011, Willson and Dorcas 2003, Chapter 2). The loss of forest cover is known to affect behaviors of many organisms including dispersal behaviors by forest interior species (Rittenhouse and Semlitsch 2006, Schreiber and Graves 1977, Vistnes et al. 2004).

Removal of riparian forest is commonly associated with urban and suburban development. In addition to increasing light penetration to the stream and warming stream temperatures (Paul and Meyer 2001, Walsh et al. 2005), riparian forest removal is associated with a suite of changes to stream environments including increased primary productivity, reduced inputs and retention of allochthonous leaf litter, and siltation of cobble substrates (Allen 2004, Paul and Meyer 2001, Runyon et al. 1994). The creation of canopy gaps and edge habitat can also increase the presence of predatory mesomammals and birds (Chalfoun et al. 2002, Crooks and Soulé 1999). Overall, the removal of forest canopy is generally associated with reduced salamander diversity and abundance (Ash 1988, 1997, Ford et al. 2002, Peterman et al. in press).

In urban and exurban landscapes of the eastern United States, stream salamanders exist in streams of highly variant canopy cover and refuge availability creating variability in their natal experiences with high-light environments and the availability of refuge from high-light conditions. We used a controlled laboratory study to examine habitat selection by a larval blackbelly salamander (*Desmognathus quadramaculatus*) to determine if their experience with

high-light environments or the environmental context of stream substrate availability and type interacted to influence their behavior. Salamanders are generally reclusive and use substrate objects such as cobble and leaves as refuge. Salamander behaviors were quantified by measuring the distance that individuals were found from a light source. We hypothesized that 1) salamanders would exhibit negative phototaxis being found further from a light source than predicted by random chance, 2) salamander distance from a light source would increase in the absence of refuges, and 3) individuals naïve to high-light environments would be found further from a light source than experienced individuals. To determine if any directional movements or observed behavioral differences among naïve and experienced larvae were due to the artificial laboratory environment, we also tested the location of naïve and experienced larval *D. quadramaculatus* relative to sunlight and shade in a field enclosure.

METHODS:

Study Organism

Larval *D. quadramaculatus* were chosen as our focal organism because larvae of this species are highly abundant in the southern Appalachian Mountains. This species metamorphoses after 2 – 4 years spent in stream environments where they can exceed 54 mm in snout-vent length and form the majority of larval salamander biomass in headwater streams (Petranka 1998, Milanovich 2010). Previous research demonstrated that local larval occupancy of this species is positively associated with canopy cover, but larvae are also found in streams with little to no canopy cover (Chapter 2). This species belongs to the most diverse stream salamander genus, and observations of their behaviors could be used to predict behaviors of other species.

Capture Methods

Desmognathus quadramaculatus larvae were captured from 3 fishless streams in the
upper Little Tennessee River basin. Naïve individuals with respect to high-light environments
were collected within the fully forested Ball Creek watershed at the Coweeta Hydrological
Laboratory in Macon County, North Carolina. This watershed is a control basin that has been
undisturbed since 1927. Individuals with experience in high-light environments, defined as
experienced individuals, were collected from first-order streams with less than 10% canopy
cover. Landowners have maintained this canopy cover for at least the past 50 years.
Experienced individuals for the laboratory experiment (see below) were collected from a single
stream located in Rabun County, Georgia, but experienced individuals for our field experiment
were collected from a different stream located in Macon County, North Carolina. Because each
of these collection locations were part of a larger study, these sites were selected because they
had similar physical attributes with the exception of canopy cover (Chapter 2). Landowners
have maintained this canopy cover for at least the past 50 years. Salamanders were captured
opportunistically using dipnets and cover object searches. Upon capture, salamanders were held
individually in a cooler during transport where they were placed in containers with a paper towel
cover object, water from their source stream, and ultimately, kept in a temperature controlled
room (15.5 °C) with a natural photoperiod. Individual behaviors were tested within 48 hours of
capture, and individuals were released at their capture location within one week.

Laboratory Behavioral Testing

We designed a full factorial experiment to determine the effects of light presence, natal
experience, and local context on salamander distance from a light source. This study was
performed in a temperature and light controlled room. Animals were studied individually in 150

X 25 cm enclosures filled with aged tap water to a depth of 2 cm. Each enclosure had a sand substrate soaked in a 1% bleach solution for 24 hours. At one end of each enclosure, a light source was placed with a low-heat emitting lamp (compact fluorescent lamp) with wavelength peaks similar to those experienced by salamanders that was either turned on for our light presence trials or turned off for completely dark, light absent, trials (Makino and Dodd 1996). This light source provided a gradient from high-light conditions close to the light source and low-light conditions at the far end of the enclosure. To examine the effects of context on behavior, we tested salamanders in response to the absence of refuge (sand) and in the presence of two types of commonly used refuge, cobble and leaves. We refer to this set of treatments as the substrate treatment. Fifteen different objects of equal size were placed uniformly along the long, center axis of the enclosure. Leaves were craft leaves allowed to soak for 48 hours to remove any excess dye, and cobble pieces less than 20 cm^2 were collected from local stream and soaked in a 2% bleach solutions for 24 hours prior to use.

Each salamander was used only once within the study and was randomly assigned to a treatment. Thirty individuals were tested for each combination of treatment conditions. Animals were initially placed halfway between the high-light and low-light regions, and their distance from the light source was measured every hour for 12 hours.

Field Behavior Testing

Salamander behavioral responses to sunlight rather than a lamp were tested using a field enclosure. In-stream enclosures for this study were designed to allow stream water to pass through the enclosure and were placed in a stream lacking canopy cover to use natural sunlight cues. We used a 0.8 mm mesh to form the enclosure boundaries and added no additional substrate to the enclosure. Each of these enclosures was 150 X 25 cm and was set with a water

depth less than 10 cm. To create shade, we used 4 layers of shade cloth to shade half the enclosure to light levels similar to those found above a forested stream. Shade was randomly assigned to either the upstream or downstream half of the enclosure. We tested the responses of 20 naïve and 20 experienced individuals. *Desmognathus quadramaculatus* larvae were placed in the center of the enclosure, and their distance from the treatment edge of the enclosure was recorded every hour for 12 hours. Individuals were only studied once, and trials began by 7:00 AM to ensure daylight for the length of the trial.

Data Analysis

We performed a repeated-measures ANOVA and performed a Mauchly's sphericity test to examine if our data violated assumptions of sphericity (Scheiner and Gurevich 2001, SAS Institute Inc, Cary, NC). If our data departed from assumptions of sphericity, we used the multivariate ANOVA (MANOVA) output that is robust to violation of this assumption and included time as an additional variable in the model. Roy's Greatest Root test was used to assess the significance of independent variables, and an α of 0.05 was used to determine significance for this analysis. A Tukey's honestly significant difference post-hoc test was used to determine differences among the means of the substrate predictor. Lastly, we calculated effect sizes of all the different treatments to evaluate the relative performance of each predictor. For our field experiment, we tested for an effect of time on the habitat selection of larval *D. quadramaculatus*. If this effect was not significant, we performed a t-test to determine if taxis by naïve individuals was different than experienced individuals.

RESULTS:

We recorded observations of 402 larval *D. quadramaculatus*. Mauchly's sphericity test on the orthogonal components revealed that our laboratory data did not meet the repeated

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measures ANOVA assumptions (χ^2_{65}= 1133.89, p < 0.001). Therefore, we used the MANOVA results to evaluate the effects of our treatments on *D. quadramaculatus* distance from a light source.

Time was likely a source of variability in the distance of *D. quadramaculatus* from the light (Table 3-1; F=1.51, p = 0.13). Each of our factors of light, substrate, and experience demonstrated evidence that they influenced *D. quadramaculatus* distance from a light source (Table 3-1). The presence of light appears to have the largest effect on salamander distance from the light source, followed by the absence of refuge (sand substrate) and naivety to high-light environments (Table 3-2). Individuals tested in the absence of light showed non-directional responses, indicating the absence of taxis (Figure 3-1). Similarly, experienced individuals provided with refuge of any type (leaves or cobble) also demonstrated non-directional responses to light (Figure 3-1). Naïve individuals were found further from the light source than experienced individuals, but this response was weaker when provided with refuge (Figure 3-1). Unlike experienced individuals, naïve individuals were found further from the light source in the presence of leaf refuge, but not cobble refuge (Figure 3-1).   Interactions between substrate and experience were significant at the α = 0.05 level (F = 1.89, p = 0.007; Table 3-1), but model results indicated some support for the interactions of light and substrate (F = 1.36, p = 0.053) and light and experience (F = 1.61, p = 0.095, Table 3-1). Tukey HSD post-hoc tests were non-conclusive in indicating significant differences among substrates. Among the comparisons at each observation, sand treatments did not significantly differ from leaves, but sand and leaf treatments differed significantly from cobble treatments in 5 and 4 of our 12 observations respectively indicating an interaction between time and substrate type (Appendix 3-1).

Field observations of individual responses to sunlight indicated that time did not influence salamander responses (Roy's greatest root = 0.230, p = 0.396). Naïve individuals were found under shade and closer to the shaded treatment edge than experienced individuals that were found further from the treatment edge in the sunlit region of the enclosure ($t_{df=405}$ = -15.4, p < 0.001; Figure 3-2).

DISCUSSION:

Although studies have repeatedly demonstrated negative responses of salamanders to canopy disturbance, larval responses to the same cues have largely been overlooked (e.g. Ash 1988, 1997, Ford et al. 2002, Peterman et al. in press). Larval salamanders in this study generally demonstrated negative phototaxis consistent with responses reported for adults within this genus and other salamander groups (e.g. Placyk and Graves 2001, Sugalski and Claussen 1997, Wilder 1913). Several studies suggest that negative phototaxis in salamanders may be a behavior to avoid desiccation (Placyk and Graves 2001, Sugalski and Claussen 1997). Plethodontid salamanders may be particularly sensitive to desiccation in the presence of high temperatures and low humidity due to their highly permeable skin necessary for respiration. Despite larval skin being thinner than adult skin, larval salamanders escape these threats because they inhabit aquatic habitats (Vitt and Caldwell 2008). Therefore, alternate explanations are necessary to explain trends observed in this study.

Due to the conservation of negative phototaxic behaviors by many salamander groups, these behaviors may be genetically coded to maximize adult fitness (Angilletta et al. 2002, Plomin et al. 2000). Therefore, these preferences and behaviors may carry over to larvae despite their abilities to avoid desiccation risk. Alternatively, salamanders may use light as an indirect cue for temperature. In the southern Appalachian Mountains, adult Desmognathine salamanders

exhibit metabolic depression at high temperatures that may be experienced in well-lit streams (Bernardo and Spotila 2006). Therefore, negative phototaxis may allow individuals to avoid warm conditions that could have negative effects on their metabolism. Researchers have also reported that closed canopy wetlands tend to produce higher biomass of metamorphosing salamanders than open canopy wetlands suggesting that higher food resources in closed canopy systems may increase larval growth rates (Earl et al. *In press*). Likewise, *D. quadramaculatus* diets are largely composed of collectors, scrapers, and predators often found within leaf litter packs (Trice 2011). Therefore, larvae may use shade as a cue to guide them towards high food resources. Lastly, negative phototaxis may be an effective anti-predator behavior against visual predators. Despite reports that most salamander predators are other aquatic organisms, any number of terrestrial predators may preferentially forage within canopy gaps such as snakes or raccoons (Chalfoun et al. 2002, Crooks and Soulé 1999, King 1939).

Although negative phototaxis appears to be consistent within salamanders, experience with high-light environments reduced individual reactions to light environments. The simplest explanations for our observations are that repeated experience with high-light environments habituated salamanders to these environments, or inherent differences exist among the populations surveyed in this study. Population-level differences are unlikely to explain our results because experienced individuals, regardless of collection location, demonstrated a greater tolerance for high-light environments and did not exhibit greater variability surrounding the mean distance found from the light source than naïve individuals. Secondly, individuals may use associative learning to preferentially use high-light environments if they are associated with novel resources or fewer competitors. High-light habitats will have increased autotrophic production that could also increase the biomass of aquatic invertebrates frequently consumed by

aquatic salamanders (Bolnick et al. 2003, Hagen et al. 2010, Trice 2011). Studies in other aquatic organisms have demonstrated that bold individuals are often willing to enter risky environments to gain resources and improve their fitness (Davis and Stamps 2004, Fraser and Gilliam 1987, Garcia and Sih 2003). Lastly, the observed larval behavioral differences may result from inherited adult preferences. Larval salamanders display habitat selection, yet their initial starting position is dependent upon oviposition site selection by adults. Given that individuals often select habitat based on their natal position (Davis and Stamps 2004), hatching in a region with low canopy cover may result in those individuals habitually selecting high-light environments relative to their counterparts hatched in areas of low light. Each of these mechanisms could explain why individuals captured in regions of high-light intensity demonstrated weaker responses to light.

Larval phototaxis in this study was altered by the presence of refuge. In lighted environments with refuge, individuals showed reduced phototaxic behavior that may result from their ability to avoid light by moving underneath these objects. Despite the ability of individuals to select the nearest available shaded environment provided by the refuge, naïve individuals still selected cover objects further from the light source than experienced individuals and differentiated between leaf and cobble cover objects. Because local stream salamander abundance is influenced by substrate (Barr and Babbitt 2002, Chapter 2), our results imply that larval salamanders may persist in high-light environments provided that these habitats continue to offer refuge. Unfortunately, streams with canopy gaps and cobble refuge are largely unavailable because riparian deforestation is generally highly correlated with increased sedimentation and loss of cobble refuge (Burcher et al. 2007).

Generally, larvae avoided high-light environments, but experienced individuals exhibited a weaker response to light. These results were robust in that similar preferences were observed in the presence of lamplight and natural sunlight. The presence of refuge can dampen responses regardless of experience. Therefore, canopy gaps created by agricultural, urban, industrial, and residential land use could result in barriers to movement for naïve and experienced individuals given that these land-use practices are also associated with siltation and a reduction in refuge availability (Paul and Meyer 2001, Walsh et al. 2005). Lastly, these conditions may result in an ecological trap if responses to light override their decision-making process regarding predator presence by co-occupying a refuge and increasing their mortality risk (Schlaepfer et al. 2002). Implications of this research for conservation warrant further investigation in field experiments and highlight the importance of considering individual experiences when studying the ecological implications of fluctuating environmental conditions.

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Table 3-1. Multivariate ANOVA results using Roy's Greatest Root values. Time indicates the repeated observation of larval *D. quadramaculatus* distance from the light source. Light indicates the presence and absence of a light source. Substrate indicates the presence of no refuge, leaf refuge, or cobble refuge, and experience indicates the experience of the individuals with high-light environments.

Model	Roy's Greatest Root Value	F-Value	Num DF	Den DF	p-value
Time	0.953	1.51	11	340	0.126
Time + Light	0.922	2.61	11	340	0.003
Time + Substrate	0.861	2.41	22	680	<0.001
Time + Experience	0.895	3.63	11	340	<0.001
Time + Light + Substrate	0.917	1.36	22	680	0.053
Time + Light + Experience	0.951	1.61	11	340	0.095
Time + Substrate + Experience	0.888	1.89	22	680	0.007
Time + Light + Substrate + Experience	0.945	0.88	22	680	0.316

Table 3-2. Effect sizes of treatments on larval *D. quadramaculatus* locations. Positive values indicate positive phototaxis, but negative values indicate negative phototaxis. Larger absolute values indicate a larger effect of the treatment on salamander behavior. Experience indicates the state of the individual with respect to high-light environments. CI indicates the confidence interval for the estimate.

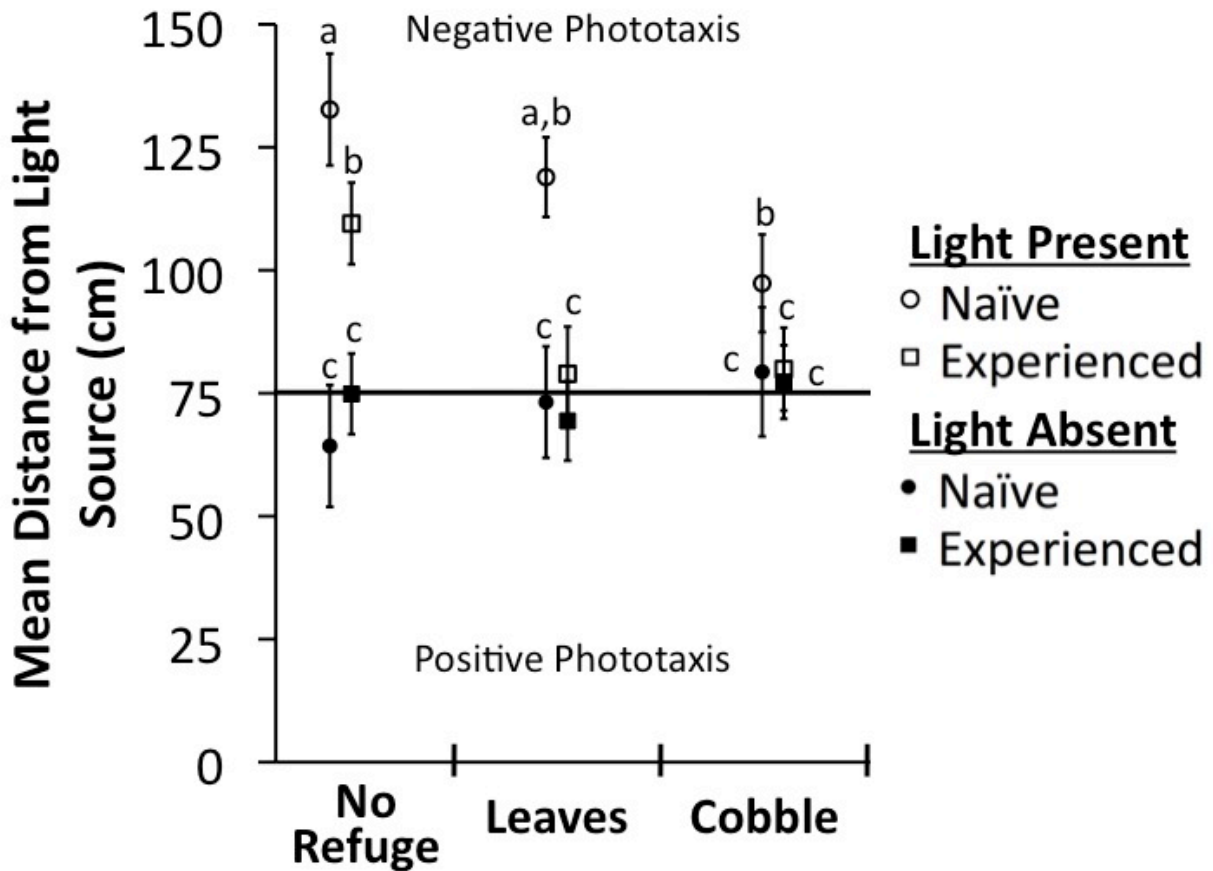|	Effect Size	Standard Error	Lower 95% CI	Upper 95% CI
Light				
Light present	-28	4	-60	4
Light absent	-1	3	-16	15
Context				
No refuge	-23	5	-72	16
Leaf refuge	-10	5	-57	14
Cobble refuge	-8	4	-47	9
Experience				
Naïve	-21	4	-57	15
Experienced	-7	4	-25	11

Figure 3-1. Mean location selected by larval blackbelly salamanders with different experience with light in different environmental contexts. Salamanders either had little experience with high-light environment – those collected from fully forested sites (naïve) - or they had extensive experience with high-light environments - from sites with little to no canopy cover (experienced). Environmental context was manipulated by altering the presence and type of refuge. No refuge treatments had only sand substrate whereas leaves and cobble were two different types of refuge typically used by salamanders in their natal environments. The solid horizontal line indicates the location where salamanders were initially placed. Any data point that includes this line within the error bars representing ± 1 SE indicates a non-directional response with respect to the location of the light source regardless of whether it was on or off.

Means with statistically significant differences at the $\alpha = 0.05$ level are denoted with different

letters.
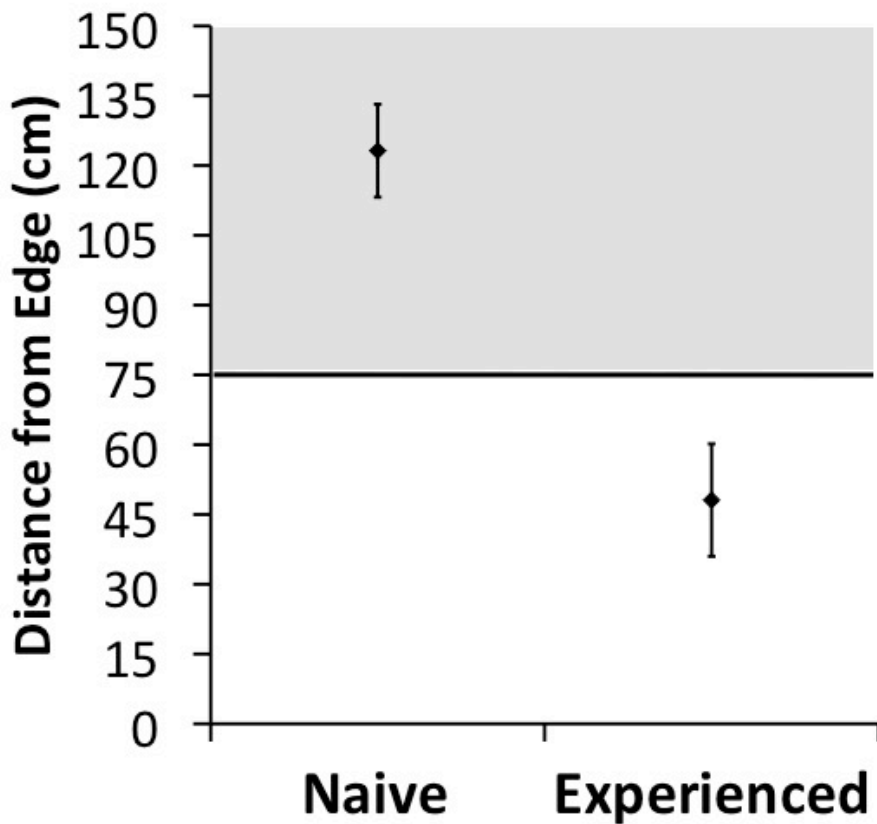
Figure 3-2. Mean location selected by larval *D. quadramaculatus* with different experience with light in response to sunlight in a field enclosure. Salamanders were either naïve (collected from a forested stream) or experienced with high-light environments (collected from a canopy gap). The solid horizontal line indicates the location where salamanders were initially placed and the shaded area below represents the shaded region of the enclosure.

Appendix 3-1. Tukey honestly significant difference post-hoc test results among the substrate treatments. Because 12 observations were conducted, a post-hoc test was required for each time step. P-values for each comparison at each observation are reported.

Comparison	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12
No refuge - Leaves	0.740	0.441	0.292	0.928	0.992	0.992	0.684	0.996	0.548	0.825	0.994	0.804
No refuge - Cobble	*0.011*	0.680	0.380	0.643	0.945	0.446	0.125	0.138	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Leaves- Cobble	0.082	0.920	0.983	0.860	0.979	0.518	*0.015*	0.115	*0.016*	*<0.001*	*<0.001*	*<0.001*

CHAPTER 4

SMALL RIPARIAN DISTURBANCE RESTRICTS CONNECTIVITY OF APPALACHIAN

STREAM SALAMANDER POPULATIONS[1]

ABSTRACT:

Movement and dispersal among populations can be critical for long-term population persistence, particularly in the context of environmental change. For organisms with movements restricted to streams, barriers to movement can be particularly effective at fragmenting and isolating stream reaches. Although research has identified several types of in-stream barriers to connectivity of stream populations, the influence of out-of-stream conditions on in-stream dispersal is less understood. We investigated the potential for canopy gaps to fragment stream-salamander populations by examining the willingness of individuals to move across canopy gaps. We used capture-mark-recapture of displaced larval and adult *Desmognathus quadramaculatus* individuals to estimate return rates across canopy gaps of varying widths. We found that *D. quadramaculatus* individuals were 7.0 times more likely to return to their capture location along a fully forested stream than they were to return if it required crossing a forest gap as short as 13 m in length. Because small gaps can dramatically reduce the movement of both adult and larval salamanders, even local streamside activities such as roads and power lines could create barriers to significantly fragment stream populations in otherwise fully forested areas. Although streams are often considered to have high permeability to aquatic movement, our study demonstrates that out-of-network riparian disturbance can greatly reduce this permeability. Because small streams are bisected frequently by human-created canopy gaps and often have lax regulatory protection and enforcement, the accumulation of these small land-use changes and their effects have the potential to profoundly reduce connectivity among populations even in the absence of additional habitat alteration.

INTRODUCTION:

Animal responses to environmental change can be conditional upon the effects of change on the demographic processes that regulate animal populations. Among the processes important for population persistence is immigration, which buffers populations against extinction and increases recolonization rates. Although barriers to immigration are known to negatively influence resiliency and long-term persistence of populations (Brown and Kodric-Brown 1977, Frankham 2005, Holland and Hasting 2008, Pulliam 1988), identifying the mechanisms and scales limiting dispersal can be difficult (Ims and Hjermann 2001, Nathan 2001, Wiens 2001). Dispersal can be affected by relatively minor environmental changes and may affect dispersal behaviors differently for different ages or classes of individuals (Haughland and Larson 2004, McPeek and Holt 1992, Stamps 2001).

In dendritic ecological networks such as streams, animals may select to move within the network or via out-of-network pathways (Fagan 2002, Grant et al. 2007). Dispersal in dendritic ecological networks is most often conducted via within-network pathways due to the low habitat resistance offered by this pathway (reviewed in Grant et al. 2007). Consequently, movement in dendritic networks is often linear, making movement barriers particularly effective in limiting connectivity among habitat patches (Fagan 2002). Barriers to movement within streams can be physical obstacles (such as waterfalls, culverts, and dams; Blakely et al. 2006, Carlsson and Nilsson 2001, Neraas and Spruell 2001, Novinger and Rahel 2003), biological (predators, fish stocking invasive predators; Fraser et al. 1995, Ruzycki et al. 2003), or abiotic conditions (including high-temperature or high-light conditions; Bozinovic et al. 2011), but these conditions often interact with the behaviors of animals to create movement barriers (Blakely 2005, Wofford et al. 2005). If species have evolved to avoid conditions associated with these barriers, barriers

may operate by causing animals to avoid crossing these areas within the landscape (e.g. deMaynadier and Hunter 1999, Todd and Rothermel 2006).

For forest-adapted species, canopy gaps created by human land uses could potentially act as barriers to movement. Although several studies have shown that large-scale deforestation for agriculture, residential, and commercial land uses can impede movement (Eikass et al. 2005), effects of small - yet pervasive - gaps associated with road crossings and utility right-of-ways are poorly understood. These effects may be prevalent in the southern Appalachian Mountains where land-use conversion generally occurs along stream corridors (Wear and Bolstad 1998). Although this area remains largely forested, the southern Appalachians are undergoing extensive residential development including expansion of roads and installation of right-of-ways for a growing population (Kirk et al. 2012). This region also includes a high diversity of stream-associated species such as stream salamanders with aquatic larvae and streamside dwelling adults (Stein et al. 2000).

Stream salamanders have evolved in streams with limited light penetration due to well-developed over- and mid-story canopies (Kozak and Weins 2010). Within these shaded streams, salamanders are known to disperse most frequently along aquatic pathways. This movement may be important for the long-term persistence of salamander populations (Grant et al. 2010), but little information is available to understand how movement along these pathways may be altered due to human land-uses. In exurban landscapes, salamander occupancy is highest in streams with connectivity to other streams and well-forested riparian zones (Chapter 2, Grant et al. 2009). Likewise, increased light associated with reduced riparian canopy cover has been demonstrated to negative influence salamander occupancy and fine-scale habitat selection behaviors of salamanders (Chapter 2, 3). Because salamanders behaviorally avoid moving into

light gaps, canopy gaps may result in fragmentation due to behavioral avoidance (Chapter 3).

Our objective was to determine whether maintained canopy gaps could alter natural landscape

movement patterns of stream salamanders.

Specifically, we sought to estimate the probability of a salamander to cross a canopy gap

as a function of its width. Rather than relying on natural dispersal, we capitalized on the

tendency of Plethodontid salamanders to home when displaced (Marsh et al. 2004, Madison

1964). Specifically, we investigated blackbelly salamander (*Desmognathus quadramaculatus*)

homing across a range of small and moderate canopy gaps. We hypothesized that animals

displaced across a canopy gap would have a lower probability of returning than those displaced

inside an intact forest corridor. Furthermore, we hypothesized that movement probabilities

would be negatively correlated with gap size.

METHODS:

Study Organism

We selected to focus our study on *D. quadramaculatus* as a model species because

several of their life history traits make them ideal to study while remaining representative of the

range of species present in the streamside-salamander community of the southern Appalachian

Mountains. First, *D. quadramaculatus* is one of the most abundant and widely distributed

species within this region providing a higher probability of detecting successful movement in a

larger sample size. Contributing to their streamside abundance is their long larval period lasting

2 – 3 years. Likewise, this species is known to be philopatric and found most frequently in

streams or immediately adjacent stream banks (Petranka 1998). To allow for reliable detection

of difficult to detect and capture adults, the large size of *D. quadramaculatus* adults allowed us

to mark them using passive integrated transponders to improve our ability to detect adult movement (Connette and Semlitsch 2012, Cucherousset et al. 2008, Hamed et al. 2008).

Experimental Methods

In May of 2010, we established six experimental sites with canopy gaps ranging from 13 – 85 m of stream length and two control sites with full canopy cover over the stream for greater than the length of our study area. Canopy gaps were all created by transmission power line right-of-ways. During this study, there was no active management of the power lines such as mowing or herbicide application. We surveyed each site between 40 and 49 times during May – September 2010 and May – October 2011. Generally, sites were surveyed biweekly depending on accessibility. In 2010, control sites were surveyed by establishing a 10m downstream plot with 5m plots located 10, 20, 40, and 80 m upstream from the upstream edge of the downstream plot (Figure 4-1a). Our design shifted in 2011 to improve our sample size with eight 10m plots established with pairs of plots located 10, 20, 40, and 80 m apart (Figure 4-1b). At each experimental site, we identified the boundaries of the canopy gap and designated two 20 m stream reaches upstream and downstream of the canopy gap (Figure 4-1c). We also established two additional 10 m forested stream reaches to estimate demographic rates in the absence of translocation. Each of these transects included the stream and surrounding stream bank.

At experimental sites, individuals collected from the 20 m transect downstream of the canopy gap were captured, marked, and translocated to the upstream transect and vice versa. At control sites in 2010, individuals collected in the 10 m downstream transect were captured, marked, and translocated to randomly assigned upstream plots. Individuals captured in the upstream plots were captured, marked, and translocated to the larger downstream plot designated at meter zero. At control sites in 2011, individuals were captured within the 10 m plots and

translocated predetermined distances upstream or downstream depending on whether the individual was captured in the upstream or downstream plot.

Salamanders were captured at each transect by setting 25 X 40 cm leaf litter bags at a density of one leaf litter bag per stream meter and by conducting active stream and bank surveys (Marsh 2009). Leaf-litter bags were checked at each visit by removing the bag from the stream, placing it in a bin filled with water before gently agitating the trap to remove any organisms that were inhabiting the bag. Water, debris, and organisms removed from the leaf-litter bag during agitation were then poured through a net to detect larval, juvenile, and adult *D. quadramaculatus*. After larval and juvenile salamanders were captured, they were batch marked by site, plot, and date using visual implant elastomer (Northwest Marine Technology, Bailey 2004). Upon recapture, individuals received a second mark allowing us to develop individual capture strings. We recorded snout-vent length, life stage, and capture location for all recaptured animals. Most new individuals were identified by life stage, but early in the 2010 season, this information was not collected for some individuals marked and never recaptured. Thus, to prevent a positive bias in estimates of return probabilities, we needed to include these individuals. We used the ratio of larvae to juvenile captures to randomly assign these capture strings to larval or juvenile groups.

Adult *D. quadramaculatus* were also detected by performing nighttime surveys of streamside burrows. Following capture, *D. quadramaculatus* adults were housed separately in Tupperware containers with stream water and leaves from their capture location and brought back to the laboratory for marking. Individuals were anesthetized with a buffered 500 mg L^{-1} solution of MS-222 before being injected with a passive integrated transponder (PIT tags; 8.5 mm long and 2.1 mm diameter, TX148511B, BioMark, Boise, ID, Connette and Semlitsch 2012,

Hamed et al. 2008, Peterman and Semlitsch 2006). Individuals were allowed to recover for 24 hours to ensure full recovery from anesthesia and to prevent loss of the PIT tag before being translocated and released. Resighting of adult *D. quadramaculatus* was conducted by detection of the PIT tag via an RFID detection system (BioMark FS-2001F-ISO Reader and portable antenna, Connette and Semlitsch 2012). Because these tags have an estimated detection range of < 20 cm underground, these surveys were conducted in the morning to allow for detection of the PIT tab before salamanders moved too far underground to be detected by the antenna (Connette and Semlitsch 2012, Kevin Hamed Personal Comment).

Statistical Analysis

To test if return rates were different for individuals returning across a canopy gap than those moving through the forest, we designed Cormack-Jolly-Seber multi-state models implemented in Program MARK to test various hypotheses about influences on transition probabilities (Brownie et al. 1993, Cormack 1964, Hestbeck et al. 1991, Jolly 1965, Seber 1965, Table 4-1). We used an information theoretic approach to determine the relative support for each of our hypotheses given our data (see below, Burnham and Anderson 2002). To evaluate the plausibility of each model, we used Akaike's Information Criteria (AIC, Akaike 1973) corrected for small sample sizes using the small-sample bias adjustment in Program MARK (White and Burnham 1999). We calculated AIC_c weights for each candidate model and ranked these models from highest weight to lowest weight to allow us to draw inferences on which models held the most support given our data. Goodness of fit was tested on the global, time-dependent model in program UCARE (Choquet et al. 2009).

Because many of our sampling events resulted in few or no captures, particularly during nighttime surveys for adults, we collapsed our sampling events into 14 sampling occasions

including the 2010 and 2011 seasons (Grant et al. 2010). Most of our sampling occurred in the months of June and July, requiring us to form two sampling occasions for these months, but we adjusted the intervals among sampling occasions in Program MARK to reflect this variation. To avoid overparameterization of our models and improve confidence in our parameter estimates due to low observed return rates, we assumed that all monthly parameter estimates were constant temporally. To address each of our hypotheses regarding the influence of canopy gap presence, translocation distance and direction, and life stage (see below), we had to divide our data into twelve different groups for each state in our model that limited the quantity of data available to estimate parameter values. By including a temporal component, this data would have then be split into 324 different categories to estimate each parameter estimate for a fully parameterized model. For this reason, we would have been unable to reliably detect differences in monthly return probabilities.

Generally, we used a sequential modeling approach to determine the best fitting model for our data. First, we wanted to best represent the survival and capture probabilities by testing for differences among life stages, among individuals translocated, the direction of that translocation, and whether individuals were translocated in our control sites or across canopy gaps in our experimental sites. After identifying the models with the greatest support for survival and capture probability, we used those models to test our specific hypotheses about the influences on salamander return probabilities.

We designed subsequent models that would allow us to evaluate evidence that return rates were either similar or different between our control and experimental sites containing a canopy gap between the capture and translocated transects. Because this was our primary objective, we first examined whether model selection results indicated support for models

considering each site individually or support for grouping these models when modeling the transition probabilities. Because models indicated little support for considering each site separately, we grouped sites into control or experimental groups. To model the return probabilities, we had three potential states for each individual: captured-marked but not translocated (detection transects), captured upstream, and captured downstream. New individuals to be translocated were assigned to the state where they were released. Therefore, individuals captured and marked from the downstream transect, but released in the upstream transect were assigned to the captured upstream state and vice versa. The transition probabilities reflect the probability that an individual returns to their capture location while accounting for whether and which direction they were displaced. Because no individuals were found to move among the translocation transects and the detection transects (no translocation), we fixed the transition probabilities to and from the detection transect to zero.

Because the probability of successful movement is known to vary among salamander life stages (Grant et al. 2010), we explicitly tested whether life stages had different return rates by examining support for models grouping all life stages together or for models including each life stage separately (Table 4-1). However, because the majority of recaptured individuals did not progress to the next life stage during our study, we did not allow for individuals to transfer between life stages in our model (Petranka 1998). Stream salamanders also have upstream movement tendencies that may make them more likely to return upstream than downstream (Cecala et al. 2009, Grant et al. 2010, Lowe 2003, Table 4-1). Therefore, we examined if model selection results indicated support for models allowing the transition probabilities to vary among the captured-upstream and captured-downstream states or for models considering these two groups together. We also included a normalized individual covariate representing the

displacement distance for each individual corresponding to the canopy gap width for experimental sites or the predetermined translocation distance for control sites because successful return is more likely for shorter distances than for longer distances (Madison 1969, Marsh et al. 2004; Table 4-1). For individuals captured and released within the detection transects, we set the translocation distance to zero. Before including the influence of translocation distance on return probabilities, we first examined support for models using all permutations of our hypotheses regarding the presence or absence of a canopy gap, life stages, and translocation direction. From the top two models only, we designed two additional models to include the influence of translocation distance on return probabilities and evaluate support for this final hypothesis (Table 4-1).

RESULTS:

We captured, and marked 1,398 larval, juvenile, and adult *D. quadramaculatus*. Of these, 1,148 individuals were translocated with 814 of those translocated across a canopy gap. The time intervals necessary for homing of recaptured animals were shorter for adults (1.79 ± 0.54 months; mean ± 1 standard error [SE]) than for larvae or juveniles (3.5 ± 0.45 months, 4.38 ± 1.10 months respectively), and neither the direction nor distance of translocation appeared to influence the return interval. Although our data showed some evidence of being too sparse, the global, time-dependent model demonstrated fit.

The most parsimonious model for survival allowed this parameter to vary among life stages, control versus canopy gap sites, and whether individuals were translocated (Appendix 4-1). The most parsimonious model for capture probability included variation among life stages, control versus canopy gap sites, translocated or non-translocated individuals, and translocation direction (Appendix 4-1). Survival and capture probability varied by these factors, but 95%

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confidence intervals were broadly overlapping preventing us from drawing robust conclusions about the influence of life stage and canopy gaps on survival and capture probability (Appendix 4-2). The presence of canopy gaps was the most important variable influencing return probabilities (Table 4-2). The model including canopy gap presence was 2.4 times better than the next best model at predicting return probabilities. The second best model included the influence of translocation distance on return probabilities (Table 4-2). All other models had ΔAIC_c values much larger than two, indicating that they had little support given our data (Table 4-2).

Return rates were 7.03 times larger along forested streams (0.146 ± 0.023, forested stream, probability of return ± 1SE) than along streams that required crossing a canopy gap (0.021 ± 0.004, experimental stream). Return probabilities across a canopy gap declined with increasing gap width. However, within fully forested streams there was no measurable negative relationship between displacement distance and homing probability. In streams with a canopy gap, return probabilities were greater than 0.1 with canopy gaps of less than 8 m but declined to a return probability less than 0.01 when canopy gaps were greater than 80 m (Figure 4-2). Though models that allowed return probability to vary by life stage received little support, graphical interpretations suggested that larval return probabilities across gaps may be lower than juveniles and adults (Figure 4-3).

DISCUSSION:

Our results demonstrate that even relatively small canopy gaps act as barriers to the movement of larval and adult salamanders, and the effectiveness of this barrier increases with the width of the gap. These results are consistent with studies on terrestrial and wetland breeding amphibians that show similar behavioral resistance to moving into canopy gaps (reviewed in

Cushman 2006, Semlitsch et al. 2009). As these amphibians disperse, they orient towards forest and often move slower within deforested regions (deMaynadier and Hunter 1999, Rittenhouse and Semlitsch 2009, Rothermel 2004, Rothermel and Semlitsch 2002). A key difference between these studies and the present study is that for wetland and terrestrial species dispersing through a terrestrial landscape, the proposed mechanism is desiccation risk as these regions tend to be hotter and drier environments (Rittenhouse and Semlitsch 2006, Todd et al. 2009), but this mechanism does not explain resistance to cross canopy gaps in species using aquatic habitats to disperse. Therefore, additional mechanisms are necessary to explain resistance to moving into canopy gaps by stream salamanders. Prior behavioral studies indicate that this species selects habitat with lower light intensities suggesting that resistance to crossing canopy gaps may be due to negative phototaxis (see discussion in Chapters 2 and 3).

For organisms that rely on stream habitats, undisturbed aquatic stream habitats have high permeabilities to movement despite the potential for out-of-network movement. Our results suggest that canopy gaps are significant barriers to movement, but we speculate that in-stream movement pathways through canopy gaps may be less resistant to movement than overland movement through canopy gaps due to the risk of desiccation demonstrated for other amphibian species moving terrestrially (Rothermel and Semlitsch 2006, Todd et al. 2009). Consequently, management of riparian zones is critical to maintain population connectivity in human-influenced regions. Despite common perceptions that streams are relatively continuous and homogenous with respect to movement (see discussion in Roberts and Angermeier 2007), even small canopy gaps with little influence on the physical structure of the stream can dramatically reduce habitat permeability. For example, a two-lane road in this area requires a 20 m right-of-way devoid of all trees, which would reduce the return probability of salamanders in this study

by 56%. These barriers are particularly troubling to consider because although dispersal capabilities often vary among life stages, all life stages of this species were negatively influenced by the presence of a canopy gap indicating that even small gaps are effective barriers to movement.

Although our study quantified return probabilities rather than natural dispersal rates to improve the likelihood of detecting movers (Nathan 2001), we suggest that these results provide insight into the dispersal patterns of highly aquatic stream salamanders in disturbed and fragmented regions. Plethodontid salamanders have been repeatedly demonstrated to home when displaced (Madison 1964, Marsh et al. 2004). Because salamanders expend energy defending and maintaining a territory, they are highly philopatric, and the motivation of individuals with established territories to return to their capture location through a canopy gap may be higher than for dispersing individuals (Camp and Lee 1996). Therefore, the effects of canopy gaps on dispersal of *D. quadramaculatus* may be larger if individuals have less motivation to cross canopy gaps while dispersing, and our observed return rates within our control streams were equivalent to upstream dispersal rates observed for other Desmognathines in undisturbed habitats (Grant et al. 2010). Simulation modeling on those stream salamander metapopulations indicates that declines in stream dispersal rates may decrease long-term persistence of stream salamander metapopulations (Grant et al. 2010).

Evidence from around the globe has demonstrated that humans are altering the commonness and occurrence of organisms across large landscapes (Foley et al. 2005). Increasing evidence suggests that these effects can also take place in otherwise heavily forested landscapes as a result of moderate forest cover loss (e.g. Bender et al. 1998, Sutherland et al. 2002, Welsh and Lind 2002). In our study, we demonstrated that relatively benign land-use

changes in the form of small canopy gaps can greatly impact natural behaviors of forest-dwelling organisms by creating barriers to movement. The density of road networks in the eastern United States and often-lax regulation regarding development around headwater streams suggests that streams may be bisected frequently by canopy gaps for a variety of purposes (Fahrig and Rytwinski 2009). The accumulation of these small land-use changes and their effects have the potential to profoundly alter connectivity among populations even in the absence of additional habitat alteration.

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Table 4-1. Hypotheses associated with each variable included in our candidate models. Intervening habitat type, life stage, and translocation direction were tested using all possible permutations. Translocation distance was only included in the top two candidate models following evaluation of model fit for the previous models.

Variable	Abbreviation	Hypothesis	Support
Intervening Habitat Type	Habitat	Salamanders are less likely to return to their capture location when they need to move through a canopy gap because of their behavioral avoidance of high light habitats.	Rothermel and Semlitsch 2006, Todd et al. 2009
Life Stage	Stage	Stream salamander life stages have different dispersal probabilities with juveniles more likely to disperse than larvae or adults.	Grant et al. 2010
Translocation Direction	Direction	Stream salamanders move upstream more frequently than downstream.	Cecala et al. 2009, Lowe 2003, Grant et al. 2010
Translocation Distance	Distance	Salamanders are more likely to return when displaced shorter distances.	Madison 1969

Table 4-2. Results of model ranking procedures describing our hypotheses about the factors that may influence return probabilities of *D. quadramaculatus.* The most parsimonious model for survival and detection probability was used for each of the models tested below. Survival probabilities varied among life stages (Stage), experimental and control sites (Habitat), and individuals translocated and those released at their capture location (State). Capture probability varied among life stages (Stage), experimental and control sites (Habitat), translocation direction (Direction), and individuals translocated and those released at their capture location (State).

| Model	K	AIC_c	ΔAIC_c	AIC_c Weight	Hypothesis
Habitat	23	2718	0.00	0.705	Return probabilities vary depending on the presence or absence of a canopy gap.
Habitat*Distance	26	2720	1.74	0.295	Return probabilities vary depending on the presence or absence of a canopy gap and return distance.
Habitat*Stage*Distance*Direction	31	4010	1291.82	<0.001	Return probabilities vary depending on the presence or absence of a canopy gap, life stage, and return distance and direction.
Habitat*Stage*Direction	29	4019	1301.28	<0.001	Return probabilities vary depending on the presence or absence of a canopy gap, life stage, and return direction
Habitat*Stage	27	4030	1311.72	<0.001	Return probabilities vary depending on the presence or absence of a canopy gap and life stage.
Stage*Direction	27	4042	1323.67	<0.001	Return probabilities vary depending on the life stage and return direction.
Stage	24	4044	1325.83	<0.001	Return probabilities vary depending on the life stage.
Habitat*Direction	24	4050	1332.48	<0.001	Return probabilities vary depending on the presence or absence of a canopy gap and return direction.
Direction	23	4074	1356.04	<0.001	Return probabilities vary depending on the return direction.
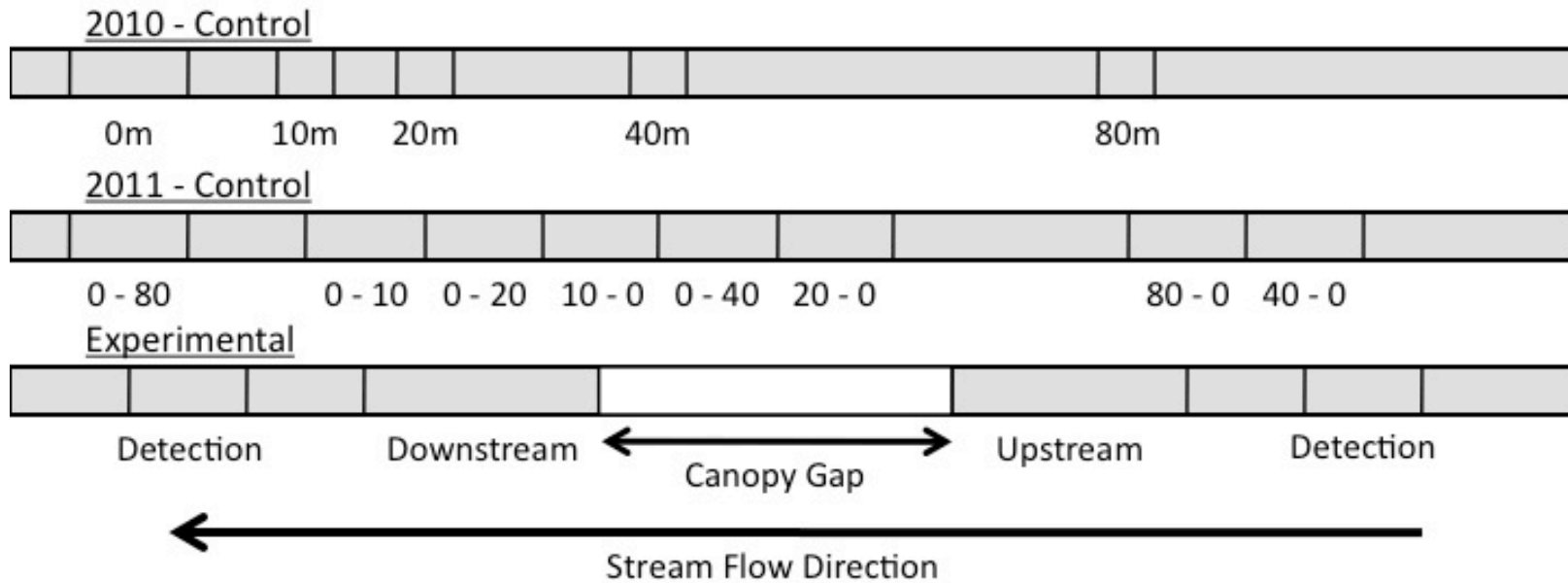
Figure 4-1. Study design of experimental and control plots. The shift between 2010 and 2011 control designs did not necessarily overlap as suggested in this diagram. The shaded transects indicate that they were forested reaches. Non-shaded regions indicate canopy gaps located above the stream. Canopy gaps were formed by cleared right-of-ways that bisected our study streams and ranged in width from 13 – 85 m.
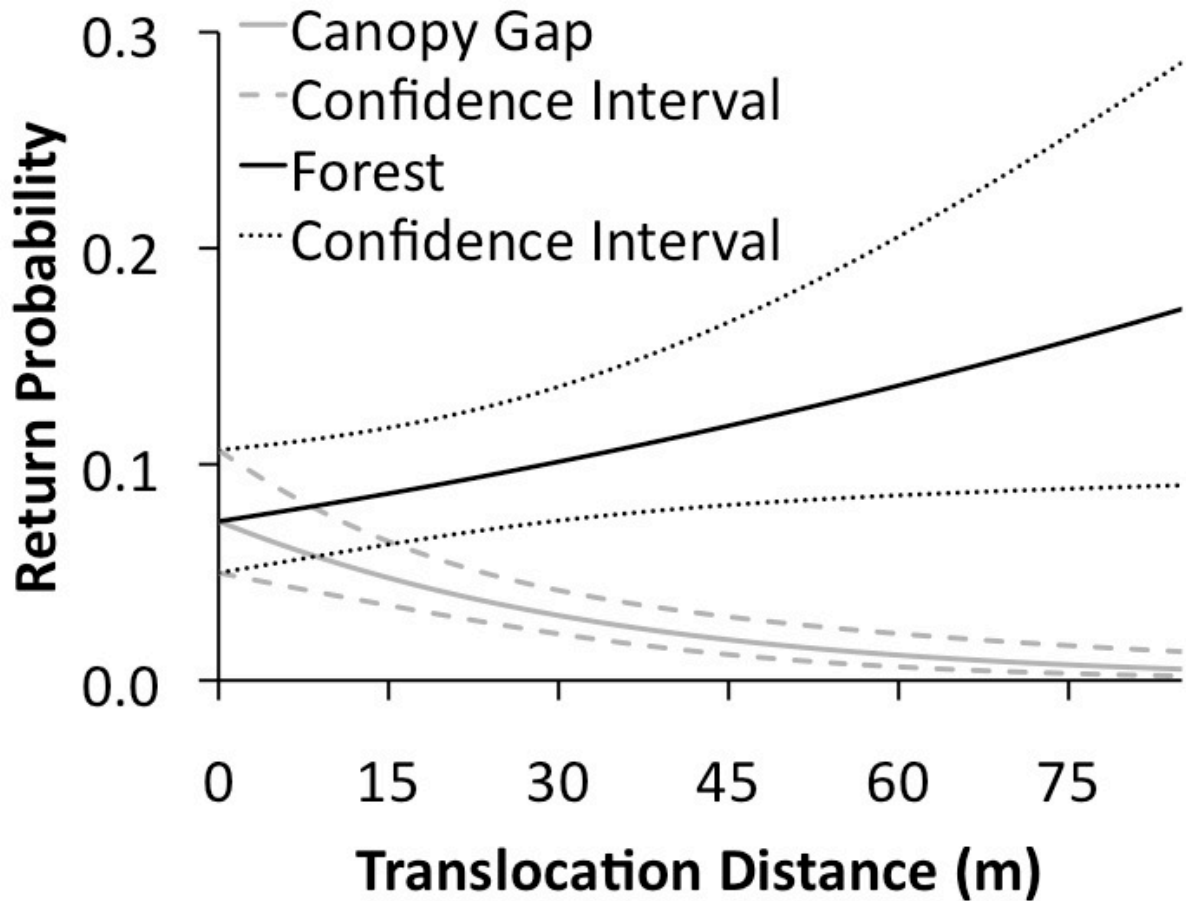
Figure 4-2. Joint survival-return probabilities are reduced if homing individuals are forced to move through a canopy gap to return to their capture location, and this probability in altered habitats declined as the return distance increased. These results indicate collective results of all life stages and movement directions. Typical 2-lane roads have right-of-ways width ranging between 8 – 20 m with power line transmission lines often requiring right-of-ways greater than 60 m. Both relationships demonstrated here use the detection transects located at each experimental site to inform the model about the demographic rates of individuals not translocated (or translocated zero meters).
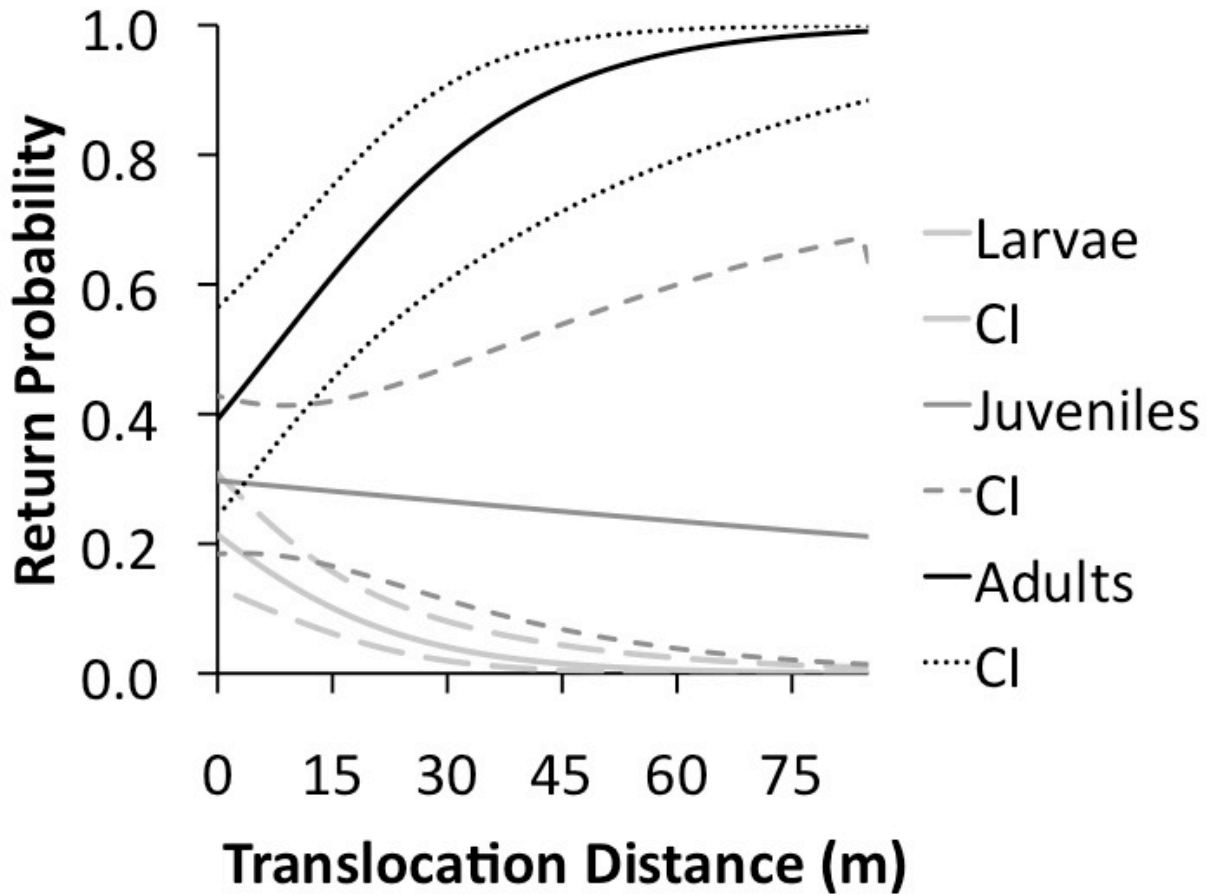
Figure 4-3. Joint survival-return probabilities across a canopy gap for each life stage. Larvae were least likely to return across a canopy gap, and this relationship declined with increasing translocation distance. Alternatively, juvenile and adult return probabilities remained relatively constant in relation to distance, but juvenile return probabilities were higher than larvae and lower than adults with much greater variability. CI indicates the 95% confidence interval surrounding the estimates.

Appendix 4-1. Model selection results for survival and capture probability to determine the most

parsimonious model to describe the salamander population surveyed in this study.

Model	K	AIC$_c$	Δ AIC$_c$	AIC$_c$ Weights
Survival				
Habitat*Stage*State	23	2717.92	0.00	1.00
Habitat*Stage*State*Direction	29	4019.20	1301.28	0.000
Stage*State*Direction	28	4031.01	1313.08	0.000
Habitat*State*Direction	26	4031.64	1313.71	0.000
State*Direction	24	4037.49	1319.57	0.000
Habitat*Stage	28	4050.57	1332.65	0.000
Habitat	27	4072.74	1354.82	0.000
Stage	26	4074.49	1356.56	0.000
Constant	24	4080.05	1362.13	0.000
Capture Probability				
Habitat*Stage*State*Direction	23	2717.92	0.00	1.00
Habitat*Stage*State	26	4026.89	1308.97	0.000
Habitat*State*Direction	22	4029.87	1311.95	0.000
Stage*State*Direction	25	4036.21	1318.29	0.000
State*Direction	22	4049.08	1331.16	0.000
Habitat	21	4056.44	1338.52	0.000
Stage	22	4067.73	1349.81	0.000
Constant	20	4067.96	1350.03	0.000

Appendix 4-2. Parameter estimates for survival and capture probability from the most parsimonious model.

Survival

	Translocated			Not Translocated	
	Larvae	Juveniles	Adults	Larvae	Juveniles
Control	0.714 ± 0.080	0.537 ± 0.216	0.455 ± 0.233	0.314 ± 0.068	0.484 ± 0.144
Experimental	0.545 ± 0.028	0.759 ± 0.036	1.000 ± 0.000	-	-

Capture Probability

	Upstream Return			Downstream Return			Not Translocated	
	Larvae	Juveniles	Adults	Larvae	Juveniles	Adults	Larvae	Juveniles
Control	0.100 ± 0.033	0.121 ± 0.098	1.000 ± 0.000	0.116 ± 0.037	0.105 ± 0.090	0.786 ± 0.829	0.253 ± 0.083	0.135 ± 0.074
Experimental	0.228 ± 0.035	0.087 ± 0.021	0.040 ± 0.017	0.189 ± 0.028	0.119 ± 0.028	0.064 ± 0.021	-	-

CHAPTER 5

GENERAL CONCLUSIONS

Freshwater biodiversity is threatened globally by human activities, but we lack

mechanistic understandings for most of these declines (Dudgeon et al. 2006). Although animal

distributions are ultimately limited by evolutionary constraints, occupancy within these regions is

determined by more proximate ecological and physiological mechanisms (Bernardo and Spotila

2006, Brown et al. 1996, Cunningham et al. 2009, Guisan and Thuiller 2005). Mechanistic

descriptions of the influence of ecological interactions and physiological limits require attention

to the animal behaviors that allow individuals to make adaptive habitat selection decisions (Frid

and Dill 2002, Gordon 2011, Lima and Zollner 1996). Although the role of behavior in

conservation biology has been questioned in recent years (Butcholtz 2007, Caro 2007), this

dissertation provides critical support for the consideration of behavior in conservation biology as

I describe one proximate behavioral driver consistent with regional occupancy trends in an

anthropogenically influenced area.

Although regional surveys of stream-associated amphibians are not new, chapter two

reflects the first regional survey of the most diverse stream salamander guild located in the

southern Appalachian Mountains. Previous regional surveys have described stream amphibian

distributions in fully forested landscapes, those deforested for wood products, and heavily

urbanized landscapes while investigating the roles of landscape or local features on their

distribution (e.g. Peterman and Semlitsch 2008, Price et al. 2011, Stoddard and Hayes 2005,

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Welsh and Lind 2002). Chapter two is a regional survey that incorporated a comprehensive set of multiscalar influences on stream salamander distributions in a heavily forested area increasingly influenced by human activities. Unique to chapter two is the inclusion of local and landscape scale factors that are common consequences of any type of land-use change as my study area includes most common human influences on this landscape. Although riparian zones are known to be relevant to protect stream processes and stream amphibian populations, our survey suggests that absolute retention of all upstream riparian zones is critical for preventing stream amphibian declines. These results are contrary to studies in other geographical regions emphasizing the importance of more fine-scale conditions such as sedimentation and indicate that regional managers need to take a more whole watershed approach to conservation and management of stream amphibians (e.g. Barr and Babbitt 2002).

Chapter two indicated that species may respond differently to forest cover loss, but both surveyed species and life stages were positively associated with more complete riparian canopies. Results of chapter three indicate that fine-scale negative phototaxis by larval blackbelly salamanders was consistent with these regional patterns. Likewise, regional surveys demonstrated that despite general behavioral avoidance of high-light environments, salamanders continued to occupy sites with low canopy cover albeit often at lower patch occupancy rates. Concurrent with these observations, chapter three results demonstrated that salamanders with experience in high-light environments had weaker behavioral avoidance of light in the lab and positive phototaxis in response to sunlight cues. Despite differences in experience, individual phototaxic responses were conditional on the environmental context. In human influenced streams, loss of riparian canopy cover is generally accompanied by increased inputs of fine sediments that bury cobble and leaves typically used as refuge (Allan 2004, Paul and Meyer

2001, Walsh et al. 2005). Negative phototaxis was most extreme in the absence of refuge consistent with conditions in highly disturbed streams. Conversely, retention of cobble in canopy gaps may allow for persistence of stream salamanders in canopy gaps. Similar to fish unwilling to move through pool habitats, the presence of cobble for salamanders may promote movement through habitats that they would otherwise avoid (Roberts and Angermeier 2007). The positive influence of refuge availability could also increase if individuals adjacent to high-light habitats can adapt to express weaker negative phototaxis in the presence of multiple types of refuge.

Chapter four extrapolated on behavioral observations in chapter three to determine if fine-scale habitat selection behaviors could have consequences for movement patterns in natural environments bisected by canopy gaps. Although several studies have hypothesized or inferred that deforested areas are barriers to movement by stream organisms (e.g. Eikass et al. 2005), none have directly examined how stream movement is altered by changes in riparian forest cover. Likewise, most surveys of potential barriers to aquatic movement consider in-stream conditions without examining how out-of-network conditions influence movement. Our study demonstrated that even small canopy gaps dramatically reduced connectivity among upstream and downstream stream reaches, and this effect was consistent for all life stages. This research contributes to our understanding of how disturbance influences movements by stream associated species recognized as a gap in our knowledge particularly for stream amphibians (Grant et al. 2007, Grant et al. 2010). Unwillingness to enter canopy gaps lends support that our fine-scale observations of negative phototaxis is an important mechanism influencing occupancy patterns observed in chapter two.

These studies collectively suggest that riparian forest loss influences stream salamander regional occupancy because individuals behaviorally avoid entering these areas and that the influences of riparian deforestation may extend beyond its footprint by increasing the isolation of stream populations. Because the southern Appalachians harbor a high diversity of stream amphibians and remain largely forested, the challenge to protecting the diversity and abundance of stream salamanders is to develop management and planning recommendations for new development, particularly as it moves upslope. Although the valleys of main tributaries in this region are already highly disturbed, high-elevation headwaters remain largely undisturbed. Results of this dissertation suggest that whole network protection of riparian zones may increase the probability of high salamander occupancy within these networks. Secondly, efforts should be made to mitigate the effects of road and utility right-of-way crossings. Management of these zones typically requires periodic removal of limbs and elimination of tree growth in the area via herbicide application. By allowing shrub growth over and around streams, light penetration to streams can be reduced. In particular, *Rhododendron* spp. is capable of persisting in canopy gaps and provides almost complete canopy cover while reducing tree seedling survival, decreasing temperatures, and increasing soil moisture (Clinton and Boring 1993, Clinton and Vose 1996).

This dissertation surveyed the effects of small-scale disturbance on stream salamanders and observed significant effects on natural behaviors of stream salamanders. These results indicate that large-scale disturbance such as that observed along main valley roads in this region may act as an insurmountable dispersal barrier isolating populations within small drainage basins. Lastly, this dissertation contributes to the general understanding of the effects of disturbance on southern Appalachian streams at the Coweeta Long Term Ecological Research site (Coweeta LTER). Although the Coweeta LTER site has a rich history of salamander

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research, long term monitoring of stream salamander populations has not been conducted (e.g. Bruce and Hairston 1990, Hairston 1949, Hairston 1980, Tilley and Harrison 1969). This study has outlined an effective protocol for monitoring and has contributed to developing a baseline understanding of regional stream salamander populations in a region subject to environmental change (Burkett et al. 2001, Kirk et al. 2012).

Limitations and Remaining Questions

As with most studies, mine was also limited by logistical constraints that restrict my ability to draw inferences from my data. I was limited to collecting data of a snapshot in time in a small geographical region in the southern Appalachian Mountains. Regional surveys of stream salamander patch occupancy were conducted in only one sub-basin of the southern Appalachian Mountains. This basin is also one of the southernmost drainages of the Appalachian Mountains close to the southern range limits of the species surveyed in this dissertation indicating that they may be experiencing other sub-lethal stresses in addition to land-use change (Bernardo and Spotila 2006). Because amphibian populations are known to vary temporally, snapshots of populations may not always be the best indication of the current status or trajectory of a population (Pechmann et al. 1991, Blaustein et al. 1994). Lastly, behavioral observations were conducted on a single species within the stream salamander community of the southern Appalachian Mountains. Blackbelly salamanders (*Desmognathus quadramaculatus*) are larger, often more abundant, and more sensitive to land-use change than other species within this group, which is why they were chosen for this study. Other species within this group demonstrated abilities to occupy highly degraded environments suggesting that conclusions drawn about the influence of canopy gaps on stream salamander populations may not be universal to all species.

This dissertation also raised many questions about how stream salamanders respond to their environments. First, I examined only one potential mechanism driving stream-salamander responses to canopy losses. High-light environments also have the potential to create an ecological trap if responses to light override responses to other cues in the environment such as predator cues. High-light environments are also related to high temperatures and increased primary production that may both alter an individual's decision to enter a high-light stream patch. Likewise, several of these chapters yield additional questions for study. Lastly, land-use change is only one stressor influencing stream-amphibian populations in the southern Appalachian Mountains, and these stressors may combine in different ways for different species or geographical areas. Because few streams in this area experienced total extirpation of the stream salamander community, the variability in how amphibians respond to environmental change raises the question of whether amphibians are good environmental indicators.

Potential Alternate Mechanisms

As animals move throughout a landscape, they respond to a variety of cues about a habitat patch's quality to make habitat selection decisions that maximize their fitness. Often these decisions involve weighting the risk against the benefit of moving into a patch, but these decisions are conditional upon the context in which the decision occurs (McNamara and Houston 1992, Stamps and Groothuis 2010). For example, starved black widow spiders will prioritize access to food resources above reclusive behaviors relative to well-fed individuals (Pruitt et al. 2011). My research has identified light as one important cue influencing movement of salamanders, but individuals are responding to a multitude of cues simultaneously. The concept of evolutionary and ecological traps has been highlighted in recent years to understand the ways humans have altered animal behavior and population persistence as a result of altered cues or the

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conditions that cues indicate (Battin 2004, Robertson and Hutto 2006, Schlaepfer et al. 2002). Although I have demonstrated that larval *D. quadramaculatus* exhibit negative phototaxis, their reclusiveness and orientation towards refuge in the presence of high-light conditions may also indicate an ecological trap if light causes salamanders to prioritize finding refuge over avoiding predators. Because larval stream salamanders are most often prey for other stream organisms that also tend towards refuge use such as other salamanders, crayfish, or benthic feeding fish, a prioritization for refuge may cause individuals to ignore or override cues indicating predator presence within their refuge increasing their risk for mortality. Behavioral observations of individuals tested with shade and predators cues presented in conflict suggest that larval salamanders can appropriately respond to predator cues despite their preference for shaded environments (Figure 5-1). Consequently, lower salamander patch occupancy in canopy gaps may not be due to lowered survival in an ecological trap.

Salamanders may behaviorally avoid canopy gaps if these patches harbor lower biomass of prey resources. Headwater streams in the southern Appalachian Mountains are naturally heavily forested with little light penetration to stream surfaces. Consequently, autotrophic production is limited, and headwater food webs are reliant on allochthonous carbon (Wallace et al. 1997). Because leaf litter is generally the majority of allochthonous inputs, canopy gaps yield reductions in detrital inputs while simultaneously allowing greater light penetration to increase primary production (Benfield 1997, Delong and Brusven 1994, Wallace et al. 1995). Although a recent survey of stream metabolism in this area suggests that autotrophic production can compensate for losses in allochthonous carbon in agricultural areas, these stream reaches may have increased autotrophic production due to nutrient inputs from streamside fertilization of crops or livestock waste absent from canopy gaps surveyed in chapter four (Bernot et al. 2006,

Hagen et al. 2010, Young and Huryn 1996). Given that basal biomass is necessary to support higher trophic levels, declines in basal carbon possible within canopy gaps could result in lowered consumer and predator biomass that serve as prey for aquatic salamanders (Trice 2011). With the exception of heavily impacted streams, trends in carbon supply suggest that autochthonous production generally compensates for losses in allochthonous carbon, which could yield similar prey biomass in canopy gaps as in forested reaches (Hagen et al. 2010), but the composition of this prey community could change and have unpredictable effects on salamander growth and production (e.g. Davis et al. 2010).

Plethodontids demonstrate risk sensitive foraging indicating that they can detect and avoid predator cues in their environments (Maerz et al. 2001, Roberts and Liebgold 2008). Forest edge habitats have been debated to harbor larger densities or activities of nest predators such as raccoons or snakes than forest interiors, but these predators also consume amphibians (Chalfoun et al. 2002, Crooks and Soulé 1999). In a test of adult behavior in terrestrial raceways located at forest ecotones and within the forest, I failed to detect approximately 90% of the individuals released in the ecotone enclosures, but detected all individuals released within the forest. Although multiple explanations exist for the disappearance of adults within the ecotone enclosures, subsequent surveys of the region similarly failed to detect adults suggesting that they could have been consumed by edge dwelling predators. During surveys at this location, I have noted the presence of feral pigs, raccoons, opossums, and snakes that may all serve as occasional salamander predators.

Canopy gaps not only increase light penetration to streams, but also influence thermal dynamics of streams (Caissie 2006). Well-lit streams often experience higher temperatures during the day because of increased solar radiation, but because canopy cover also serves to

insulate streams from changes in air temperature, streams in canopy gaps can also experience lower nighttime temperatures (Beschta 1997, Johnson 2004, Poole and Berman 2001). Consequently, streams passing through canopy gaps experience a greater range of water temperatures than forested streams. Because salamanders are hypothesized to be physiologically restricted by high temperatures, light may serve as cue for areas that experience high temperatures despite chapter two results suggesting that canopy cover is a more important predictor of salamander patch occupancy than stream temperature ranges (Bernardo and Spotila 2006). Negative phototaxis would help salamanders remain in climatically suitable areas. Researchers have also suggested that behaviors that help individuals remain within their physiological limits should be under strong selection, which would yield consistent behavioral tendencies as observed for naïve individuals in chapter three (Angilletta et al. 2002). To test this hypothesis that light is a cue for temperature, I would need to observe habitat selection of salamanders in response to conflicting temperature and light gradients where negative phototaxis would require moving into warmer temperatures. Lending support for light as a proximate cue for other environmental conditions are the nocturnal tendencies of salamanders. In the absence of sunlight cues, salamanders may be responding to moonlight or the range of altered conditions in canopy gaps including temperatures. Moonrise and progression towards the full moon reduce road crossing of other nocturnal herpetofauna presumably because of increased predation risk (Kevin Messenger, Personal Comment). Alternatively, salamanders may avoid moving into canopy gaps for any number of other reasons that coincidentally align with hypotheses resulting from my observations of negative phototaxis.

Relationship between Phosphorus and Stream Salamanders

In chapter two, one unexpected pattern was the positive and negative influence of total dissolved phosphorus on adult blackbelly salamander patch occupancy although this pattern is not without precedent (Table 2-4). In Italy, watershed land use negatively impacted the stream salamander, *Salamandra salamandra,* primarily via the effects of land use on phosphate concentrations (Ficetola et al. 2011). Several explanations for the negative effects of increased total dissolved phosphorus concentrations on stream-salamander patch occupancy include the positive effects of phosphorus and atrazine, a common agricultural chemical, on parasite density (Rohr et al. 2008), the potential for lowered benthic dissolved oxygen and acidity in low turbulence streams with high phosphorus concentrations (Corell 1998, Green and Peloquin 2008), or the general relationship of high phosphorus concentrations in areas with significant non-point source pollution and poor overall water quality (Paul and Meyer 2001, Carpenter et al. 1998). Alternatively, increased phosphorus concentrations in nutrient-limited watersheds of the southern Appalachian Mountains may increase biomass and productivity of heterotrophic and autotrophic communities yielding increased prey resources, and salamander growth rates (Johnson et al. 2006, Rosemond et al. 2001, 2002, but see Davis et al. 2010).

Adaptation to Novel Environments and Personalities

Chapter three indicated consistent differences in behavior between individuals naïve to high-light environments and those with prior experience with these environments, but the mechanism behind these differences is unclear without further testing. Experienced individuals may learn to respond differently to environmental cues or local evolution may have a larger concentration of individuals with bolder personalities or a lack of instinctive negative phototaxic behaviors. Individuals hatched in and around canopy gaps may find themselves exposed to high-

light environments at a greater frequency than individuals hatched in fully forested streams.

Therefore, if experienced individuals do not have negative interactions in high-light

environments, they may learn by habituation to stop responding to light cues (Davis and Stamps

2004). Alternatively, if experienced individuals find positive conditions within high-light

environments such as increased prey resources or refuge from predators, they may be attracted to

light cues as a result of associative learning. If high-light environments are riskier than low-light

environments because of the risk of predation or lethal temperature changes but provide

advantages to individuals willing to enter those areas such as increased access to prey, the fitness

of individuals entering canopy gaps may increase (Fraser et al. 2001, 2006). Because behaviors

exist on a continuum with some individuals having bolder or shyer personalities or strong versus

weak instinctual responses to light cues, increased fitness of bolder personalities or individuals

with weak, instinctual phototaxis will produce a higher frequency of these traits over time

(Fraser et al. 2001). Resolving the mechanism behind behavioral differences between

experienced and naïve individuals requires additional behavioral experiments designed to test

each of these hypotheses. Salamanders inhabiting gaps may have other adaptations that maintain

their weaker negative phototaxis relative to naïve individuals. For example, I noted that

individuals from open canopy streams were often lighter than their counterparts in forested

streams, but this condition may be temporary and was not quantified. Lighter skin colors may

prevent overheating when exposed to direct solar radiation or my assist in predator avoidance in

canopy gaps (Garcia and Sih 2003).

Extrapolating to Out-of-Network Movement

Chapter four surveyed the effects of disturbance on linear in-stream movements, but in

reality, stream networks are dendritic and composed of connected linear transects where nodes

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act as within-network connectors between branches (Grant et al. 2007). Thus, to move between branches, salamanders must either move terrestrially (out-of-network), or aquatically (within-network). Little research has focused on determining the behavioral mechanism that dictates whether a dispersing individual uses within- or out-of-network pathways or whether disturbance could affect these decisions. In fragmented areas where matrix habitat may increase desiccation risk such as canopy gaps, aquatic habitats may be more permeable to movement than terrestrial, out-of-network movement despite the importance of this movement pathway for long-term persistence of stream salamander metapopulations (Fagan 2002, Grant et al. 2010). Likewise, the spatial arrangement of forest gaps could serve to further influence an individual's decision to move terrestrially or aquatically (Grant et al. 2009). For example, canopy gaps located over stream nodes would likely decrease the probability of within-network movement, and canopy gaps located over intervening terrestrial habitat may decrease the probability of out-of-network movement (Figure 5-2). Further study is necessary to elucidate the influence of canopy gaps on all movement pathways of semi-aquatic species to determine the full impact of canopy gaps on stream salamander movement.

<center><i>Stream Amphibians as Environmental Indicators</i></center>

Collectively, amphibian decline research has identified a series of causes, but determining their impact is difficult because they often act in concert (Collins and Storfer 2003, Hamer and McDonnell 2008, Stuart 2004). Although disease is perhaps the most well known cause of amphibian declines, the effects of disease are not universal for all species or geographic regions similar to results found for the effects of land-use change in the stream salamander decline literature (Chapter 2, Lips et al. 2006). Habitat loss and degradation surveyed in this dissertation is one stressor influencing amphibian populations, but disease, climate change, UV

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radiation, and over-exploitation have been identified as other important stressors (Collins and Storfer 2003, Stuart 2004). Consequently, individuals or populations experiencing stress from land-use change may be more susceptible to other stressors. In the southern Appalachian Mountains where species ranges may be limited by thermal regimes, individuals may be more susceptible to forest loss or other habitat changes than individuals found in more northern populations where they may experience lower thermal maxima (Bernardo and Spotila 2006, Bernardo et al. 2007).

Amphibians are often promoted as indicators of environmental quality because of their observed sensitivity to losses in forest cover, but the role of stream-associated amphibians as indicators has been challenged in a recent debate (Kroll et al. 2008, Kroll et al. 2009, Welsh and Hodgson 2008, Welsh and Hodgson 2009). Several of their life history traits and physiological requirements suggest that they should be sensitive to environmental change including permeable skin and biphasic life histories. Recently, researchers have questioned the sensitivity of amphibians to declines in water quality due to their permeable skin and found that amphibians were often not the most sensitive vertebrate species (Kerby et al. 2009). Likewise, their biphasic life histories while requiring two high quality habitats for successful completion of their life cycle also provide a buffer to change in either of these habitats (Price et al. in press). By having long-lived terrestrial adults with low metabolic requirements, populations may persist despite limited recruitment from poor quality larval habitat (Price et al. in press). Lastly, one role of indicators is to have consistent, detectable responses to environmental changes. As demonstrated in the stream salamander decline literature, the effects of environmental change vary geographically within a species and among species in the same geographic region (e.g. Chapter 2, Price et al. 2011, Barrett et al. 2010, Kroll et al. 2009). Because of this variability, stream

amphibians may make poor indicators despite their general sensitivity to environmental change. Likewise, because of high variability in year-to-year breeding adult return rates, long-term trends in abundance can be difficult to assess when breeding amphibian adults are surveyed to assess population trends (Pechmann et al. 1991, Blaustein et al. 1994). Following study of the sensitivities of individual species within amphibian communities to environmental change, single species variability could indicate changes in environmental quality, but these protocols should not be applied over wide geographic regions without further study to confirm stable relationships between population status and environmental conditions.

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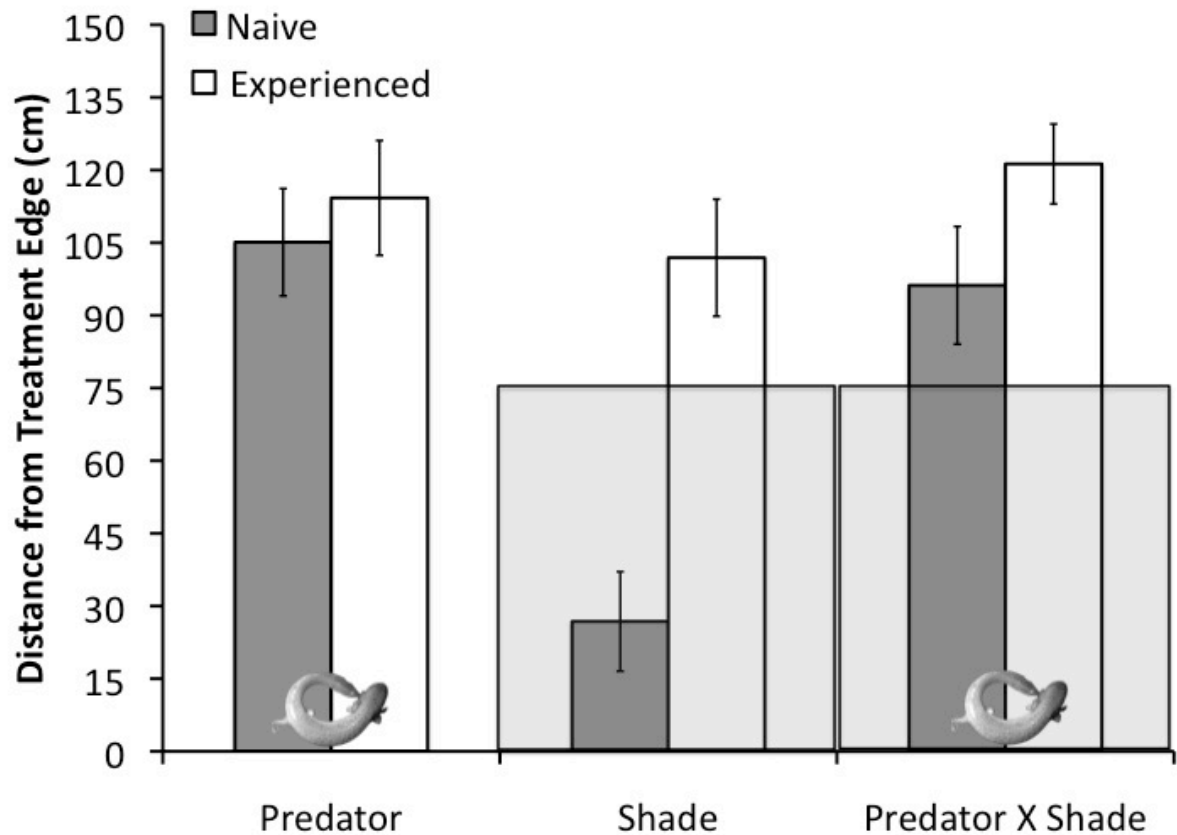
Figure 5-1. Habitat selection results from a test of conflicting cues of predators and shade for naïve and experienced individuals to determine if canopy gaps could serve as ecological traps if individual responses to light overrode their abilities to detect and avoid predators. Results of this study indicated that individuals were capable of making adaptive predator avoidance decisions despite a high-light environment, but naïve individuals remained closer to shade than experienced individuals despite the risk of predation. Salamanders indicate the presence and position of predators while the grey boxes indicate where shade was present within the test enclosures subject to sunlight. In-stream enclosures for this study were designed to allow stream water to pass through the enclosure and were placed in a stream lacking canopy cover to use natural sunlight cues. Each of these enclosures was 150 X 25 cm and was set with a water depth less than 10 cm. To create our shaded treatment, we used 4 layers of shade cloth to shade half the

enclosure to light levels similar to those found above a forested stream. Predator treatments were created by placing a single larval *G. porphyriticus* in a small mesh enclosure measuring 25 X 5 cm. We tested the responses of 20 naïve and 20 habituated individuals to shade only, predator only, and shade and predator treatments. Individual *D. quadramaculatus* larvae were placed in the center of the enclosure, and their position relative the treatment edge of the enclosure was recorded every subsequent hour for 12 hours.
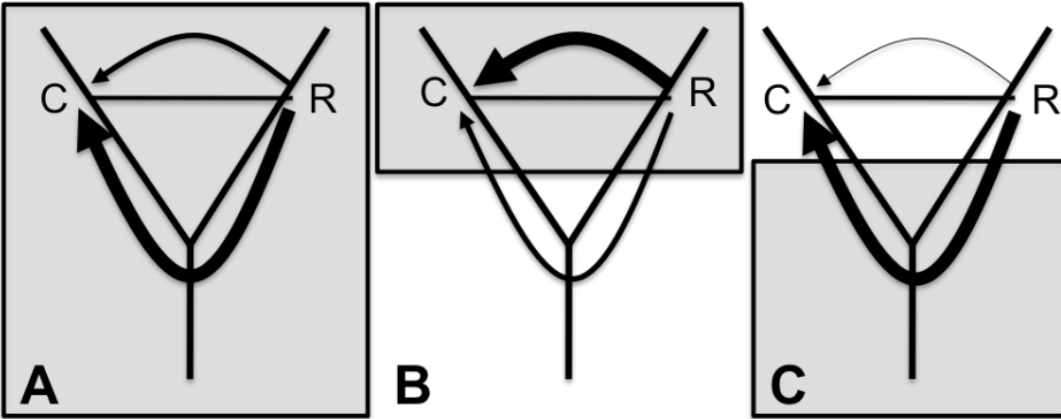
Figure 5-2. Predicted movement probabilities in three different spatial arrangements of canopy cover relative to the stream network. Grey areas represent forested regions. Arrows represent potential movement pathways with the weight of the line corresponding to the hypothesized probability of moving in that pathway. "C" represents the capture location with "R" representing the release location. Fencing will be constructed on the interior edge of each stream. The horizontal line between "R" and "C" represents the fenced pathway that will be open to the stream at the release location, but closed to the stream at the capture location to detect individuals using the terrestrial pathway. A) Fully forested streams where dispersers move along both pathways but are slightly more likely to move aquatically. B) Canopy gaps over the node may cause avoidance of aquatic movement. Terrestrial movement may increase or remain stable decreasing the connectivity between stream branches. C) A canopy gap located over intervening terrestrial habitat is likely to greatly decrease movement probabilities. Therefore, aquatic pathways may be used more frequently by dispersing individuals.