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MOVEMENT BEHAVIOR AND METAPOPULATION CONNECTIVITY OF STREAM SALAMANDERS IN RESPONSE TO DISTURBANCE EVENTS

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MOVEMENT BEHAVIOR AND METAPOPULATION CONNECTIVITY OF STREAM SALAMANDERS IN RESPONSE TO DISTURBANCE EVENTS

DISSERTATION

A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in the
College of Arts and Sciences
at the University of Kentucky

By

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2024

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ABSTRACT OF DISSERTATION

MOVEMENT BEHAVIOR AND METAPOPULATION CONNECTIVITY OF STREAM SALAMANDERS IN RESPONSE TO DISTURBANCE EVENTS

Metapopulations are shaped by the dispersal between populations in a landscape. Disturbance events can disrupt this connectivity resulting in local population extinction. For my dissertation, I used a combination of empirical and theoretical techniques to examine dispersal in response to disturbance and assessed it's population-level consequences. My research used capture-mark-recapture sampling techniques to evaluate stream salamander movement in response to (1) a supraseasonal drought and (2) mountaintop-removal-mining (MTR) and valley-filling (VF) and (3) agent-based simulation modeling to evaluate population extinction risk in response to varying dispersal and mortality rates.

First, I evaluated the effects of a supraseasonal drought, a severe drought that occurs outside of predictable seasonal dry periods for an extended period of time, on the movement frequency distribution, survival, and growth rates of adult *Desmognathus fuscus*. I found that salamanders were more likely to move immediately after the supraseasonal drought compared to before or during the drought. Salamanders who moved experienced slightly higher growth rates post-drought. Although movement frequency was low during the drought, survival was higher for individuals who moved in comparison to individuals who remained in their original capture location. My results suggest that adult salamanders were potentially displaying an adaptive movement strategy to resist drought conditions by moving away from affected (i.e., dry) areas within the study stream during the drought and moving towards replenished resources in other areas after the drought ended.

Next, I evaluated movement pathways (e.g. within-stream, overland), movement frequency distribution curves, individual body condition, and dispersal rates for two common stream salamander species (*D. fuscus* and *D. monticola*) within a reclaimed MTR and VF landscape and compared these populations with populations from an undisturbed, reference landscape. I found that stream salamanders utilized within-stream dispersal pathways in the reference and MTR and VF landscape. However, overland movement was only detected in the reference landscape, not in the MTR and VF landscape. Body condition was a potential driver for individuals engaging in dispersal and was overall lower for individuals in the MTR and VF landscape compared to the reference landscape. My results indicated that overland connectivity between salamander populations in the MTR and VF landscape was disrupted compared to the undisturbed landscape and resulted in population isolation, which, if left unchanged, could result in local population extirpation.

Finally, I constructed two agent-based models with different metapopulation structures and investigated how differences in extinction risk was affected by differences in dispersal and mortality probabilities between populations and between areas. I found that differences in dispersal and mortality did influence population extinction risk. My models demonstrated that increased dispersal into a population decreased it's extinction risk but only when population differences in mortality was low. In addition, when mortality was higher for an area, populations located on the fringe of the metapopulation network had a higher extinction risk compared to the populations that bordered other populations. My results indicated that maintaining connectivity between populations lowers population extinction risk, especially in areas of lower habitat quality resulting from a disturbance event.

This research demonstrates that long-distance movement allows populations to resist the negative effects of environmental and anthropogenic disturbance. Therefore, maintaining and, when applicable, restoring both aquatic and terrestrial habitat is likely vital for stream salamander population persistence.

KEYWORDS: Dispersal, Movement, Metapopulation, Population Connectivity, Stream Salamanders, *Desmognathus*

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04/24/2024

Date

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DEDICATION

I would like to dedicate my work to my fiancée, Colin Pilkington. Colin, thank you for providing on-going emotional and mental support throughout this time-consuming process. I truly could not have completed this dissertation without your love and guidance. Thank you love, for your never-faltering love and inspiration.

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The following dissertation, while an individual work, benefited from the insights and direction of several people. First, I want to thank my Dissertation Chairs, Dr. Jeremy Van Cleve and Dr. Steven Price for providing timely and instructive comments that allowed me to complete this project on schedule. I also wish to thank the complete Dissertation Committee, and outside reader, respectively: Dr. Catherine Linen, Dr. David Weisrock, Dr. Christopher Barton, and Dr. Nathan Haan. I would also like to thank Andrew Ibach, Sarah Tomke, Stacey Gade, Kristin Stiermann, and Colin Pilkington for their assistance in the field.

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1 INTRODUCTION

1.1 History of the metapopulation concept

The concept of metapopulations has evolved drastically since its conception in 1935. Although the term 'metapopulation' was not defined until 1969 by Levins, Nicholson & Bailey (1935) described a phenomenon in which populations are broken up into numerous separate groups "which wax and wane and then disappear, to be replaced by new groups in previously occupied situations" (pg. 551). Richard Levins coined the term metapopulation to describe a population of populations in single-species dynamics in pest control policies (Levins 1969), group selection (Levins 1970), and interspecific competition (Levins and Culver, 1971). After Levin's (1969) classical metapopulation was developed, many complex variants of the metapopulation concept were developed that incorporated additional concepts and environmental variables (Harrison and Taylor 1997; Hanski 1999). About two decades following its conception, metapopulation ecology was recognized as a key component of ecology (Hanski and Gilpin 1991).

Levin's (1969) model captured local population dynamics within a metapopulation by tracking $p(t)$, which represents the fraction of habitat patches (p) occupied by the species at time t. The fraction of occupied patches is affected by the rates of local extinction (e) and colonization (m) of empty patches (Levins 1969) as given by the following equation:

$$dp/dt = mp\,(1-p) - ep$$

The equilibrium value of p from the above equation is:

$$p = 1-e/m$$

Using an elaboration of this model, Levins (1969) was able to determine that the equilibrium habitat patch occupancy fraction (p) was reduced by increasing temporal variance in the extinction rate (e). Later adaptations of the model considered other factors such as the local population dynamics, unequal probabilities of moving to different patches, and the spatial arrangement of patches. For instance, dispersal to a nearby patch is typically more likely than dispersal to a far-away patch (Vance 1984; Gurney and Nisbet 1978). In addition, some have found that the assumption that all local populations have equal extinction probabilities was not always met since the extinction probability tends to decrease as p increases as a result of increase in population size N (Brown 1984). The general positive relationship between average population size N and the fraction of occupied patches p, and the feedback relationship between fraction of occupied patches and local extinction (aka the 'rescue effect'; Brown and Kodric-Brown 1977) has also been applied to single species dynamics (Brown 1984).

Quantifying a metapopulation empirically poses some challenges due to the many observed and predicted factors that can affect metapopulation dynamics. For instance, other metapopulation models have incorporated the effects of patch area, shape, isolation, and the effect of non-habitat between patches (e.g. matrix habitat) on extinction and colonization probabilities (Smith and Green 2005; Hanski 1999). The delimitation of local populations may be subjective if the habitat patches are more continuous rather than discrete (Hanski and Gilpin 1991). Hanski (et al. 1999; 1995) proposed 4 conditions that many have agreed are sufficient for identifying the presence of a simple metapopulation (Smith and Green 2005; Alford and Richards 1999; Harrison 1991): 1) habitat patches support local breeding populations, 2) no single population is large enough to ensure long-term survival, 3) patches are not too isolated to prevent survival, and 4) local dynamics are sufficiently asynchronous to make simultaneous extinction of all local populations unlikely.

One must also consider the structure of a metapopulation, which refers to how the system of habitat patches occupied by the metapopulation is distributed amongst different patch sizes and interpatch distances (Hanski and Gilpin 1991). One influential classification (Pannell and Charlesworth 2000; Harrison and Taylor 1997; Stith et al. 1996;

Boorman and Levitt 1973) yields four different metapopulation structures based on the relationship between patch size and patch isolation (Figure 1.1); 1) classical metapopulations based on Levin's original model in which there is moderate genetic differentiation between small patches because of moderate levels of connectivity that leads to recolonization of unoccupied patches; 2) mainland-island structures as described by Boorman & Levitt (1973) where a central population that contributes colonizers and sustains the surrounding smaller populations and produces low to moderate overall genetic differentiation between patches; 3) patchy metapopulations, which results from low genetic differentiation between subpopulations where there is high connectivity between small to large patches; and 4) nonequilibrium metapopulations where there is high genetic differentiation between subpopulations that occupy small, isolated patches (Figure 1.1).

1.2 Role of landscape arrangements and fragmentation

Most of the metapopulation models described above refer to 2-dimensional spaces where dispersers can move between pairs of patches via several possible dispersal routes (Sjorgen 1991; Harrison 1991; Figure 1.2A) or linear landscapes (also known as 'stepping stone' dispersal) where dispersers cannot move between distant patches without passing through the same series of intervening patches (Figure 1.2B). However, a 2-dimensional or linear framework is not appropriate for evaluating metapopulations in hierarchical, dendritic landscapes (Fagan 2002; Figure 1.2C). For example, although most amphibians can disperse overland, dispersal within a dendritic stream network is likely the primary dispersal pathway (Grant et al. 2010; Lowe et al. 2006). Fagan (2002) developed a model to demonstrate the considerations one must make when evaluating a metapopulation in a dendritic landscape. For instance, the branches of the dendritic landscape may strongly govern the direction of the colonization and therefore extinction patterns of local populations (Fagan 2002). When colonization occurs in both directions, dendritic landscapes are known to have enhanced connectivity and more persistent metapopulations compared to linear landscapes. However, dendritic systems are subject to the riverine "drift paradox" (Muller 1954) that causes colonization to occur in one direction, which may inhibit connectivity and persistence. The resulting fragmentation may compound the negative effect of smaller patch size in dendritic landscapes in comparison to linear and 2-dimensional systems.

Connectivity between neighboring populations via dispersal is a vital process that promotes population resilience via the ability of populations to resist perturbations and to recover from them (Reed 2004; Hakoyama et al. 2000; Iwasa et al. 2000; Purvis et al. 2000; Hakoyama and Iwasa 1998). Dispersal is a type of long-distance movement in which an individual leaves its natal area to enter a new population or colonize a new habitat. According to the movement ecology framework proposed by Nathan et al. (2008), animal movement has been described as an interplay between the individual's internal state (i.e. motivation for moving), motion capacity (i.e. ability to move), navigation capacity (i.e, deciding when and where to move), and external factors (abiotic and biotic conditions). Individuals may be motivated to move to find food, avoid predation, and/or search for a mate, which could ultimately result in gaining energy, safety, and/or reproducing (Nathan et al. 2008). On a population-scale, dispersal maintains population connectivity and stability by increasing gene flow and genetic diversity within local populations and supporting local abundance via source-sink dynamics. Consequently, population connectivity via dispersal can increase both local resilience to habitat degradation and regional resistance to species extinction (Reed 2004; Hanski and Ovaskainen 2003; Lowe and Bolger 2002; Purvis et al. 2000; Mills & Allendorf 1996; Kareiva & Wennergren 1995; Hanksi 1994). However, disturbance events, which can be described as temporary changes in the environment that affect the ecosystem dramatically but not severely enough to cause immediate population extinction, can hinder dispersal through habitat fragmentation (e.g. logging, mining) or physical barriers (e.g. roads, dams, fences), which could hinder population resilience and increase population extinction risk.

Understanding the role of dispersal in fragmented landscapes is complicated because past studies have observed both increases and decreases in dispersal rates as a result of the interaction between fragmentation and multiple individual/species factors (Cote et al. 2017; Baguette et al. 2013; Clobert et al. 2009). This knowledge gap could pose a problem because habitat fragmentation caused by disturbance events can instigate the local extirpation of populations through the introduction of one or multiple stressors (Hakoyama et al. 2000; Iwasa et al. 2000; Diamond 1984). For example, habitat fragmentation/reduction could lead to the accumulation of negative factors within a population such as decreased abundance, low genetic diversity, low resource availability, high competition, and inbreeding depression. If one local population is susceptible to extinction, the extinction risk for the entire metapopulation may increase, especially if populations develop synchronous population dynamics (Kahilainen et al. 2018; Hanski et al. 1995, 1999). Fragmentation can also influence metapopulation dynamics by disrupting the pattern of movement by reducing the patch area, increasing patch isolation and/or increasing the proportion of habitat edge (Haddad et al. 2017; Haila 2002). To prevent local and total extinction, metapopulation models need to be incorporated in conservation biology to understand the dynamics of these fragmented populations (Hanski and Gilpin 1991). Overall, there is a need to adopt multi-scale approaches (e.g. mechanisms at the population-level and large-scale landscape level) to understand disturbance events effects and their mechanisms (Haddad et al. 2017).

1.3 Overview of dissertation chapters

The goal of this dissertation is to assess how disturbance events affect dispersal and thus how they may affect metapopulation persistence. Previous studies have indicated that amphibians typically exhibit a metapopulation structure (Smith and Green 2005; Marsh and Trenham 2001; Alford and Richards 1999; Harrison 1991) because they predominately inhabit and breed in spatially disjunct habitat (e.g. first order streams, ponds; Grant et al. 2007, 2010; Duellman and Trueb 1986) and are characterized as poor dispersers with high site fidelity (Berry 2001; Beebee 1996; Blaustein et al. 1994; Sinsch 1990; Duellman and Trueb 1986). With stream salamander populations as my study system, I used a combination of empirical and theoretical techniques to examine the role of dispersal in response to disturbance and assessed the population-level consequences of such movement behavior.

In the first study (i.e. Chapter 2), I used five years of capture-mark-recapture data to evaluate movement trends in response to a supraseasonal drought. I specifically evaluated and compared the movement frequency distribution, survival, and growth rates of adult *Desmognathus* fuscus between the pre-drought, drought, and post-drought time periods. This study was previously published in the Journal of *Ichthyology and Herpetology.*

In the second study (i.e. Chapter 3), I evaluated and compared the movement trends and dispersal rates of stream salamander populations of a reclaimed mountaintop-removal-mining and valley filling landscape with populations from an undisturbed, reference landscape. Specifically, between the disturbed and undisturbed landscapes, I assessed the use of movement pathways (e.g. within-stream, overland), movement frequency distribution curves, individual body condition, and dispersal rates for two stream salamander species (*D. fuscus* and *D. monticola*).

In the final study (i.e. Chapter 4), I used agent-based simulation modeling to evaluate population extinction risk in response to varying dispersal and mortality rates. Specifically, I constructed two metapopulation models with different metapopulation structures (a two-population model and four-population dendritic model) to investigate how differences in extinction risk was affected by differences in dispersal and mortality probabilities between populations and between areas.

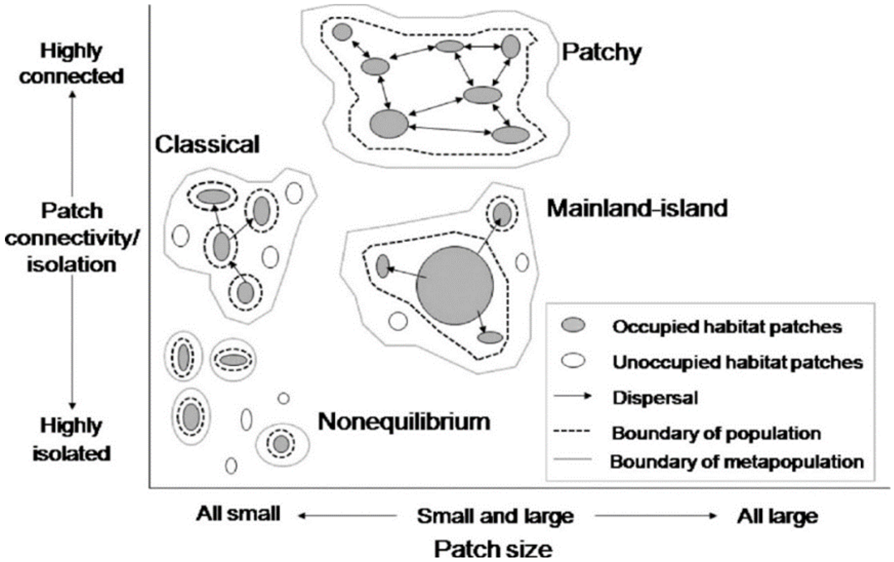

Figure 1.1 Diagram depicting the four metapopulation structure types. Figure from Acrigg and Garton 2014. Based on Harrison and Taylor 1997; Stith et al. 1996

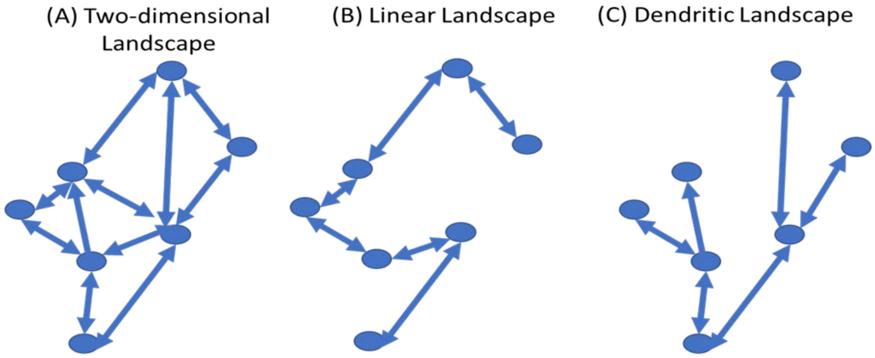

Figure 1.2 Metapopulation landscape structures. Each diagram depicts the connectivity of patches in a (A) two-dimensional landscape, (B) linear landscape, and (C) dendritic landscape.

2 SALAMANDER MOVEMENT PROPENSITY IN RESPONSE TO SUPRASEASONAL DROUGHT

This chapter has been previously published as:

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2.1 ABSTRACT

Movement can act as an effective strategy to avoid detrimental environmental conditions, particularly drought. However, due to the unpredictable nature of droughts, evaluating the patterns and consequences of movement has rarely been investigated. In 2007-2008, the southeastern United States experienced a supraseasonal drought that resulted in 110-yr low flow levels amongst first-order streams. In this study, 61 months of mark–recapture data collected from one first-order stream were used to examine the effects of drought on the movement frequency distribution, survival, and growth rates of adult *Desmognathus fuscus* (Northern Dusky Salamander). I hypothesized that salamanders would demonstrate a higher propensity to move during supraseasonal drought conditions and that moving salamanders would experience higher survival and growth rates. I found that salamanders were more likely to move immediately after the drought compared to the pre-drought and drought conditions. Although movement frequency was low during the drought, survival was higher for individuals who moved during drought conditions in comparison to individuals who remained in their original capture location. Although my model did not detect a significant trend, salamanders that moved experienced slightly higher growth in the post-drought conditions compared to salamanders who remained in their original location. My results suggest that adult salamanders were potentially displaying an adaptive movement strategy to resist drought

conditions by moving away from affected (i.e., dry) areas within the study stream. In addition, movement was likely utilized to access replenished resources in other areas after the severe effects of the drought ended. Therefore, both in-stream and riparian barriers that impede movement may inhibit resilience of streams amphibians during severe droughts.

2.2 INTRODUCTION

Movement that occurs outside the home range can determine the fate of individuals and ultimately have profound implications for population dynamics and persistence. The outcome of movements has been evaluated thoroughly in past studies (Pittman et al., 2014; Holyoak et al., 2008; Nathan et al., 2008; Wiegand, 2008), but the drivers of movement and associated population consequences of movement are less often identified. Although difficult to evaluate and often infrequent, determining why an individual moves outside their home range, as well as what proximate and ultimate goals moving serves, is vital because these movements strongly influence population dynamics (Cecala et al., 2014; Pittman et al., 2014; Harper et al., 2008; Nathan et al., 2008; Church et al., 2007; Taylor et al., 2005). Examples of proximate drivers of movement include prey acquisition, escaping predation, or searching for a mate, which contribute to ultimate goals such as gaining energy, seeking safety, and reproducing (Nathan et al. 2008). Variability in the environmental conditions can also be a driver of movement, often leading to more or less movement depending on the species, individual, and/or environment (Mandel et al., 2008; Nathan et al., 2008; Wittemyer et al., 2008; Wright et al., 2008). Yet, a clear relationship between environmental drivers of movement and the population-level consequences has rarely been established.

Amphibians have been the subject of many movement-related investigations, but most studies have focused on movement in relation to lentic or ephemeral wetland systems (Pittman et al., 2014; Pittman et al., 2013; Rittenhouse and Semlitsch. 2006; Malmgren 2002) and with aquatic larval and terrestrial juvenile stages (Cecala et al., 2014; Pittman et al., 2014; Lowe and McPeek, 2012). Studies have found that adult amphibians direct their movement either towards higher quality habitat or a known location with low net displacement from their home range or natal site (Pittman et al., 2014). Observations of adults exhibiting a high net displacement occur when individuals seasonally migrate to and from their known breeding or overwintering site (Semlitsch, 2008). The targeted movement of individuals toward known locations is a fundamental difference between adult migration and juvenile dispersal. Although studies have extensively documented adult movements to breeding and overwintering sites (Semlitsch, 2008), few have documented movement trends outside these seasonal movement events.

Freshwater animals are particularly vulnerable to extreme environmental events such as drought because they are dependent on a sufficient hydroperiod (i.e., the length of time that there is standing water at a location) to persist (Lamb et al., 2017; Aldous et al. 2011; Snodgrass et al. 1999). For example, drought-related habitat deterioration has been observed to affect the survivorship and recruitment of wetland-breeding salamanders (Lennox et al., 2019; Kinney et al., 2014; Love et al., 2008; Church et al., 2007; Hakala and Hartman, 2004). Some stream salamander species (e.g. *Desmognathus quadramaculatus, Eurycea wilderae, D. ocoee*) have exhibited decreases in body condition and abundance during drought (Currinder et al. 2014). In contrast, some animals occupying freshwater systems adapt to periodic (seasonal) droughts and exhibit high resistance and resilience to its effects (Aldous et al., 2011; Gasith and Resh, 1999). Droughts can also occur outside of predictable seasonal dry periods for extended periods of time and are referred to as supraseasonal droughts (Humphries and Baldwin, 2003). Supraseasonal droughts are known to reduce population densities (Church et al., 2007; Hakala and Hartman, 2004), change species composition (Love et al., 2008), and alter life-history scheduling (i.e., reproduction and recruitment; Lennox et al., 2019; Cowx et al., 1984). The response of stream-inhabiting amphibians to supraseasonal droughts has rarely been investigated. Yet, Price et al. (2012) found that adult *Desmognathus fuscus* maintained high survivorship during supraseasonal droughts due to increased rates of temporary emigration. Price et al. (2012) hypothesized that other factors, such as increased surface movements within the stream or riparian area, might be responsible for the high survival.

The aim of this study was to investigate the role of movement propensity on survival and growth of *D. fuscus* within a first-order stream that experienced varying drought conditions. Specifically, I evaluated: 1) the movement frequency distribution of *D. fuscus* across pre-drought, supraseasonal drought, and post-drought conditions as well as across the entire sampling period, 2) the survivorship of individuals who moved in pre-drought, drought, and post-drought conditions compared to individuals who remained in the area, and 3) growth rate across varying drought conditions and between individuals who moved versus individuals who remained in the area. My spatial scale was focused primarily on short and long-distance movements outside individual home ranges and within a single first-order stream. My study focused on adults over a five-year period, which potentially included multiple generations. I hypothesized that (1) salamanders would demonstrate a higher propensity to move during supraseasonal drought conditions, (2) individuals who have moved would experience higher survival, and (3) individuals who moved would also experience higher growth.

2.3 METHODS

2.3.1 Focal Species

The focal species of this study was *D. fuscus*, a semi-aquatic lungless salamander (Family *Plethodontidae*) that often resides under rocks, logs and other debris along margins of low-order streams. Unlike many pond-breeding species, *D. fuscus* are not known to undertake long-distance migrations to breeding or overwintering sites (Barthalmus and Bellis, 1972; Bishop 1941). Typically, *D. fuscus* adults remain within their home range located a few meters near a stream or spring (Barthalmus and Bellis, 1972; Bishop 1941). Females brood their clutch of around 21-33 eggs during the summer until the eggs hatch in late summer (Petranka, 1998). The fully aquatic larvae remain confined to the stream until they undergo metamorphosis 9-12 months after hatching (Danstedt, 1975). This species can exhibit high population densities (e.g. 1.42 post-metamorphic individuals/m^2; Spight, 1967) within streams and stream margins. Although home range size likely varies between localities, previous studies indicated that *D. fuscus* exhibits a high site fidelity (Berry 2001; Beebee 1996; Blaustein et al. 1994; Sinsch 1990; Duellman and Trueb 1986), typically occupying a small home range ranging from 0.1 to 3.6 m^2 (Ashton, 1975; Barthalmus and Bellis, 1972). Adults typically move very little within their home range, with estimates ranging from 0.3 m – 10.2 m (Ashton, 1975; Barthalmus and Bellis, 1972).

2.3.2 Study Area

My study site was a first-order headwater stream with a 100 m reach located in Stephen's Road Nature Preserve in Mecklenberg County, North Carolina (Universal Transverse Mercator coordinates E0504913, N3917456, Zone 17; datum = NAD83). The stream consisted of an upstream seep that was dammed to form a small pond at the headwaters, and a secondary seep that feeds the stream approximately 200 m upstream from the sampling location. The total length of the first-order stream was 929 m and connects to a second-order stream that flows into the Catawba River. Surface water flowed continuously throughout the 100 m reach throughout the sampling period, with the exception of July 2007 to October 2007 and May 2008 to July 2008 (i.e. during the peak of the supraseasonal drought). From July 2007 to October 2007, only the first 10 m and the final 10 m of the 100-m sampling section contained pools of surface water, and from May 2008 to July 2008, only the first 20 m and final 10 m contained water. The 100 m reach consisted predominately of coarse substrate (boulders and cobbles), sand, silt, and detritus. The catchment size of the stream was 35 ha, most of which was covered in forest (92% forested). Dominant tree species in the catchment included *Fagus grandifolia*, *Carpinius caroliniana*, *Quercus alba*, and *Acer rubrum*.

2.3.3 Drought data collection

Drought conditions were assessed by using the drought index data that was collected by the North Carolina Department of Environment and Natural Resources, Division of Water Resources for Mecklenburg County, NC (www.ncdrought.org, accessed March 2011). Drought categories were defined by the North Carolina

Department of Environment and Natural Resources as: normal, abnormally dry (D0), moderate drought (D1), severe drought (D2), extreme drought (D3), and exceptional drought (D4). The categories were simplified by creating three categories that assumed normal, typical drought (D0-D1), and supraseasonal drought (D2-D4) conditions. The categories were used to accurately identify when the supraseasonal drought occurred throughout the sampling. I conducted my analyses in respect to the time period of the supraseasonal drought rather than drought categories. Based on the drought categories (D2-D4), supraseasonal drought conditions occurred from August 2007 through August 2008, when stream levels were at 110-yr lows. Therefore, sampling that occurred before August 2007 were classified as the pre-drought period, August 2007 to August 2008 identified as the supraseasonal drought period (hereafter referred to as "drought"), and after August 2008 as the post-drought period.

2.3.4 Data collection for estimating movement distributions

To characterize movement distributions of adult *D. fuscus*, a capture-mark-recapture study was conducted along the 100 m reach of the SRNP stream twice per month from November 2005 to November 2010. Each survey involved turning over cover objects (e.g. rocks and logs) and searching leaf litter within the stream and riparian area up to 1 m from the stream bank (Price et al., 2012). Coverboards (73 cm x 73 cm, 1.1 cm thick) were also placed and checked at 5 m intervals along the stream bank to increase the number of individual captures. Within each month, both samples were separated by a maximum of 3 days during which population closure was assumed. All surveys were conducted during daylight hours.

After an individual was captured, the longitudinal position of capture was recorded in respect to the 10 m section of the 100 m transect. Individuals were taken to the lab to measure snout-to-vent length, total length, and mass. The analysis was restricted to adult salamanders with a minimum snout-to-vent length of 35 mm (Jones, 1986; Orser and Shure, 1975). Each individual was anesthetized in 1 g of maximum strength Orajel per 1 L of tap water (Del Pharmaceuticals, Uniondale, NY; Cecala et al., 2007), and then uniquely marked by the subcutaneous injection of visible implant elastomer (Northwest Marine Technologies, Shaw Island, WA). Individuals who moved ≥11 m throughout the sampling period were identified as a 'mover' while individuals who moved <11 m of original location were identified as a 'stayer'. My mover classification was based on previous findings that showed movements <11 m were more likely associated with daily movement within the home range (Ashton 1975; Bathalmus and Bellis 1972). Individuals were released at exact point of capture 1-2 days after processing. The handling and processing of these live animals followed the ASIH ''Guideline for Live Amphibians and Reptiles in Field and Laboratory Research.''

2.3.5 Movement distribution analysis

To evaluate the movement patterns of salamanders, the skew (g_3) and kurtosis (g_4) of the distribution of *D. fuscus* movement were calculated across the entire sampling period and across each drought period (i.e. pre-drought, drought, post-drought) in the program R Studio (R Core Team, 2020). Throughout the sampling period, I encountered individuals that moved multiple times and, in some instances, in different time periods (n=8). To account for multiple individual movement events, I evaluated the movement distribution in respect to frequency of movement events rather than frequency of individuals. The Jarque-Bera test (Jarque and Bera, 1980) is a goodness-of-fit test from the package, *moments*, (v0.14; Komsta and Novomestky, 2015) and was used to test whether the skewness and kurtosis of the movement distribution matched a normal distribution. If the result of the Jarque-Bera tests for skew and kurtosis were significant (alpha = 0.05), the movement distribution deviated from what was expected under a normal distribution. Specifically for skew, a significant result would indicate that *D. fuscus* adults exhibited a high net displacement either upstream (skew > 1) or downstream (skew < -1). A significant result for kurtosis would suggest that *D. fuscus* adults had a higher probability of moving short distances (kurtosis > 3) or long distances (kurtosis < -3) than would be expected by a normal distribution of random movements (e.g., Zhang et al., 2007; Fraser et al., 2001).

2.3.6 Movement propensity effects on survival

The Cormack Jolly Seber model (CJS; Cormack, 1964) was constructed in the program MARK (v. 6.0; White and Burnham, 1999) to evaluate the effects of varying drought conditions on salamander survivorship. The CJS model has 4 assumptions: (1) every marked animal present in the population at time (i) has the same probability of recapture (p_i), (2) every marked animal in the population immediately after time (i) has the same probability of surviving to time (i+1), (3) marks are not lost or missed, (4) all samples are instantaneous, relative to the interval between occasion (i) and (i+1), and each release is made immediately after the sample. The CJS model is composed of the following parameters: capture probability (p) and apparent survival rate (S). A step-down approach utilizing Akaike's information criterion (AIC) was used to evaluate each of the parameters (Lebreton et al., 1992; Akaike, 1973). Because population closure was assumed between first and second samples, the secondary sessions were collapsed within each primary session to increase the accuracy and precision of the evaluated parameters (e.g., Addis and Lowe, 2020; Grant et al., 2010).

First, I evaluated models for salamander capture probability (*p*) while assuming that *S* was constant between movers and stayers. The capture probability evaluated the probability of detecting an individual within the 100 m reach while assuming it was present in the sampled population at *i.* The following five candidate models were evaluated: constant capture probability (*p*), drought-specific capture probability (*p*[drought]), drought-period-specific capture probability (*p*[drought period]), month-specific capture probability (*p*[month]), and time-specific capture probability (*p*[time]). Probabilities that incorporated time-specific parameterization included variation in both month and year. Five additional candidate models were evaluated with the same parameterization as the previous models, but assumed differences between movers and stayers (i.e., mover status) in capture probability (Table 2.1). The most parsimonious model for *p* was selected using the AIC*c* weights (*w*) which indicates which model was the best in an information theoretic sense among the candidate models.

After selecting the top model for *p*, three models were evaluated for *S*: apparent survival constant over time for movers and stayers (*S*[mover status]), survival dependent on the drought conditions for movers and stayers (*S*[drought*mover status]), and survival dependent on when the drought occurred for movers and stayers (*S*[drought period*mover status]). Apparent survival probability is the probability that the individual at a monthly sample *i* survives to the next month's sample *i* +1 and remains in the study system (i.e. does not die or permanently emigrate). As before, the best fit model was identified by comparing the fit of the candidate models using AIC (Akaike, 1973).

2.3.7 Growth analysis

Growth for each individual encounter was calculated by taking the difference in snout-to-vent length between each consecutive encounter and dividing by the number of days between those encounters. I used a mixed effects model (fitted by the restricted maximum likelihood method, REML) from package *lme4* (Bates et al. 2015) to determine whether mover status (i.e., mover, stayer) and drought period (i.e., pre-drought, drought, post-drought) influenced individual growth (R Core Team, 2020). Individuals were identified as a random effect while mover status and drought period were fixed effects.

2.4 RESULTS

2.4.1 Data collection and movement overview

From November 2005 to November 2010, 653 adult *D. fuscus* were captured with 1539 total encounters recorded. Most individuals were recaptured at least once (n = 490) and were found at the original point of capture (74.49%, n = 365). Other recaptured individuals moved at least 11 m during the sampling period (25.51%, n = 125). Among individuals who moved, some moved more than once within the sampling period (27.88%, n = 46): 17.39% (n = 8) moved only downstream, 13.04% (n = 6) moved only upstream, and 69.57% (n = 32) moved both upstream and downstream from their original capture location. Some individuals (n=9) were sampled at least once in each drought period and most of these individuals (n=8) moved multiple times across the different drought periods. Of the 151 individuals whose sex was identified, there was no notable difference in the frequency (df = 1, F = 0.19, p = 0.67) or distance (df = 60.31, t = 0.07, p=0.95) of movement between females (N=108) and males (N=43).

2.4.2 Movement distribution analysis

Across all time periods, adults exhibited directionally biased movement downstream (Figure 2.1A; N = 371, mean distance traveled ± SE = 23.02 m ± 0.95, skew = -0.20, p = 0.007). The distribution was leptokurtic, suggesting that most individuals remained close to location of capture while only some individuals moved long distances (Figure 2.1A; kurtosis = 3.69, p = 0.007). Similar to the overall movement distribution, adults during the pre-drought period exhibited downstream-biased movement (Figure 2.1B; N = 59, mean distance traveled ± SE = 14.75 ± 1.52, skew = -0.72, p = 0.001) that was leptokurtic (kurtosis = 6.65, p = 0.001). During the drought period, adults exhibited a slight upstream-biased movement (Figure 2.1C; N = 60, mean distance traveled ± SE = 20.67 ± 2.20, skew = 0.54, p = 0.04) that was less leptokurtic in comparison to the pre-drought period (kurtosis = 4.18, p = 0.04). During the post-drought period, adults exhibited a normal distribution (Figure 2.1D; N = 252, mean distance traveled ± SE = 25.52 ± 1.21, skew = -0.28, p = 0.14) that was mesokurtic, suggesting that there is an equal distribution of individuals moving long and short distances in either direction (kurtosis = 3.24, p = 0.14).

More individuals moved during the post-drought period (67.92%; August 2008-November 2010; Figure 2) while some of individuals moved during the pre-drought (15.90%) and drought period (16.17%; Figure 2.1, 2.2). The maximum distance moved between encounters was approximately 90 m upstream by two individuals that moved during the post-drought period. Drought period did not influence the number of males and females that moved (paired t-test, p > 0.18).

2.4.3 Movement effects on survival

The top model for *p* indicated time-specific capture probabilities (Akaike weight = 1.00; Table 2.1) while the top model for *S* indicated that survivorship varied according to mover status and drought time period (*S*[drought period*mover status] *p*[time]; Akaike weight = 0.99; Table 2.2). For the top model, parameter estimates of *p* for adult *D. fuscus* ranged from 0.01 (SE = 0.01, 95% confidence interval [CI] = 0.002-0.08) in June 2009 to 0.30 (SE = 0.10, 95% CI = 0.14-0.53) in December 2005. Prior to the drought, estimates of *S* were similar between movers and stayers with an estimate of 0.99 (SE = 0.01, 95% CI = 0.83-0.99) and 0.97 (SE = 0.01, 95% CI = 0.95-0.98) respectively (Figure 2.3). During the drought, survival estimates were higher for movers with an estimate of 0.96 (SE = 0.01, 95% CI = 0.94-0.98) in comparison with stayers, 0.91 (SE = 0.01, 95% CI = 0.89-0.93; Figure 2.3). Following the drought, survival estimates were similar between movers and stayers with an estimate of 0.94 (SE = 0.01, 95% CI = 0.91-0.95) and 0.93 (SE = 0.01, 95% CI = 0.91-0.95) respectively (Figure 2.3).

2.4.4 Movement effects on growth rates

Salamander growth was similar across all time periods (N= 875 encounters, 490 individuals, df = 700.42, t = 1.619, p=0.11; Figure 2.4; Table 2.3), and mover status (N= 875 encounters, 490 individuals, df = 689.96, t = -1.34, p=0.18; Figure 2.4; Table 2.3). I did not find any interaction between mover status and time period (N= 875 encounters, 490 individuals, df = 729.16, t = 0.82, p=0.87; Figure 2.4; Table 2.3). However, I found average growth rate was slightly higher in the post-drought period (mean±SE: 0.06±0.00 mm per day) compared to pre-drought (mean ± SE: 0.04 ± 0.01) and drought (mean±SE: 0.03±0.01 mm per day; Table 2.3; Figure 2.4). Growth was also slightly greater for movers (mean±SE: 0.07±0.01 mm per day) compared to stayers (mean±SE: 0.05±0.00 mm per day) in the post-drought period (Table 2.3; Figure 2.4).

2.5 DISCUSSION

I hypothesized that salamanders would demonstrate a higher propensity to move during supraseasonal drought conditions compared to non-drought conditions. However, I found that movement primarily occurred during the post-drought period (67.92%) while only a small subset moved at least once during the drought (16.17%). During the post-drought period, the movement distribution matched a normal distribution, indicating that more individuals were engaging in random movement over varying distances, with no significant directional bias. Although only a small percent of the population moved during the supraseasonal drought, I found that individuals that moved experienced higher survivorship during the drought.

These findings suggest that *D. fuscus* adults may employ movement as a strategy to recover from extreme drought. Typically, adult salamanders have been observed to engage in directed/biased movement (Nowakowski et al., 2013; Pittman et al., 2013; Rittenhouse and Semlitsch, 2006) towards known locations such as breeding or overwintering sites. Individuals exhibiting directed movement are more likely to respond to habitat features at large spatial scales and more likely to avoid poor-quality habitat (Pittman et al., 2014). However, adult *D. fuscus* are not known to undergo extensive migrations outside their home range, especially for breeding or overwintering purposes

(Barthalmus and Bellis, 1972; Bishop 1941). Another movement type, known as the away mode, describes movement that is less responsive to external cues such as climatic conditions or habitat composition (Pittman et al., 2014). Individuals engaged in this type of movement are more likely to enter inhospitable areas and travel longer distances. Based on the movement distribution curves after the drought, adult *D. fuscus* in my study may have exhibited 'away' movement to increase the likelihood of finding new resources post-drought.

Although few animals moved during the drought, I found that individuals who engaged in movement experienced a higher survivorship during the supraseasonal drought. Previous research at this site (i.e., Price et al 2012) found adult temporary emigration probabilities were twice as high during supraseasonal drought conditions than during non-drought or typical drought conditions, which ultimately equated to high survival across environmental conditions. Thus, it appears the *D. fuscus* exhibited a variability in strategies to maintain high survival during drought conditions: some individuals emigrated to refuges whereas others moved away from their typical home range. Indeed, many freshwater animals have developed multiple strategies to circumvent the negative effects of drought (i.e., Riddell et al., 2018; Willson et al. 2006). Among amphibians, *Plethodon metcalfi* (Southern gray-cheeked salamander) has the capacity to exhibit physiological acclimatization and behavioral avoidance in increasing drought conditions (Riddell et al., 2018).

Although my model did not identify a relationship between growth and drought period, I did observe slightly higher growth in the post-drought period compared to before and during the drought (Table 2.3; Figure 2.4). Previous studies have also observed increases in growth following a drought event (Bendik and Glusenkamp, 2012) and have attributed the positive growth to the increased availability of resources following a drought. In addition, movers experienced higher average growth compared to stayers during the post-drought period in contrast to movers and stayers in the pre-drought and drought period (Table 2.3; Figure 2.4). During the drought, individuals from my study could have utilized strategies to reduce desiccation risk and food deprivation such as decreasing activity and lower resting metabolic rates (Riddell et al. 2018; Wells, 2007; Snodgrass, et al. 1999; Rose, 1966). For example, in response to an extreme drought, the *Eurycea tonkawae* (Jollyville Plateau Salamander) exhibited reversible body length shrinkage to reduce energy stores during the drought and underwent positive growth when stream flow returned (Bendik and Glusenkamp, 2012). These energy-saving strategies would allow individuals to persist during the drought until conditions were optimal post-drought to access replenished resources. Individuals that engaged in movement would have an advantage of accessing more resources outside their home range, thus increasing survivorship. Although I did not measure the amount of resources in my sample area, an increased growth rate combined with my movement distribution curves suggests that movers were likely accessing more resources to grow faster compared to stayers after the drought.

Many also have theorized that long-distance movement can increase the persistence and potentially the resilience of species in a disrupted landscape (Riddell at al. 2018; Grant 2011; Lowe, 2010; Dytham, 2009; Trakhtenbrot et al., 2005). A previous study found that survival and growth rates increased as dispersal distance increased in *Gyrinophilus porphyriticus* (Spring Salamander; Lowe, 2010). Researchers have speculated that, as the number of potential settlement sites increases, so should the range of overall site quality, assuming that the determinants of site quality exhibit only fine-scale spatial autocorrelation within the stream and are otherwise randomly distributed (Grant 2011; Lowe et al. 2006; Koenig et al.,1996). Based on that conclusion, as dispersal distance increases, the likelihood of discovering high quality sites for settlement should likewise increase (Lowe, 2010; Stamps et al., 2005; Futuyma and Moreno, 1988). In my study, more individuals engaged in long-distance movement during the post-drought period compared to the pre-drought period (Figure 2.1). Assuming the number of high-quality sites decreased during a supraseasonal drought, individuals that engaged in long-distance dispersal were more likely to find a high-quality site and survive as drought conditions shifted to normal.

Stream animals are known to implement movement strategies to utilize surrounding refuges such as moving to hyporheic zone (Griffith and Perry, 1993), permanent pools within dry streams (Labbe and Fausch, 2000), headwater seeps (Davey et al., 2006), and/or into substratum or interstitial spaces (Morrison, 1990). Given that I found most individuals moved more than once and the movement during the post-drought did not have a significant directional bias, individuals may be surveying for surrounding refuges rather than engaging in directed movement to a specific known location. There are multiple within-generation refugium-use strategies an individual may employ such as entering a stage of dormancy (Bradford, 1983), moving to subterranean refuges (Clinton et al., 1996), or surviving in microhabitats with high humidity (Boulton, 1989). For stream animals to utilize surrounding refuges, they must decide to move to discover and temporarily settle in these refuges to persist through the drought.

Further research may reveal additional factors that contribute to the increased movement following the supraseasonal drought. Conspecific density has been known to drive dispersal (Matthysen, 2005; Travis et al., 1999) because areas with high conspecific density and limited resources can result in elevated competition. If the supraseasonal drought decreased resources in a high-density site, then individuals may be more likely to move because the cost of staying outweighed the movement costs. Individuals that did not engage in long-distance movement may have a lower ability to withstand costs of movement and decided to remain in the area (Stamps et al., 2005; Johnson and Gaines, 1990). I was unable to evaluate these factors because I did not measure habitat quality; however, my observations demonstrate that supraseasonal droughts appear to have an impact on amphibian survival and movement. To further understand the potential impacts, the relationship between movement and habitat quality across changing environmental conditions must be further evaluated.

Climate adaptation strategies are essential to increase or sustain resilience of a species (Riddell et al., 2018; Holling, 1973). This investigation illustrates a strong need for adult-focused movement investigations across varying environmental conditions. Fine-scale movement assessments would yield more information about the different movement modes individuals may engage in to navigate varying habitat qualities that change over time. Understanding how populations implement behavioral strategies in unfavorable environmental conditions would also contribute to future predictions of extinction risk, especially in the wake of climate change (Riddell et al., 2018). Barriers that impede movement could prevent population recovery whenever drought events occur. Thus, reducing in stream barriers to movement (i.e., Kirchberg et al. 2016) and preserving the riparian habitat (Cecala et al. 2014) that supports high-quality microhabitats and refuges is necessary to promote movement and resilience of amphibians during severe droughts.

Table 2.1. Model rankings for estimating capture probability (*p)*. Survivorship was held constant between movers and stayers.

Model	Number of Parameters	AIC_c	ΔAIC_c	AIC_cw t
p[time]	62	5145.41	0.00	1.00
p[month]	14	5177.20	31.79	0.00
p[month*mover status]	26	5178.85	33.44	0.00
p[drought period*mover status]	8	5209.69	64.28	0.00
p[time*mover status]	122	5215.32	69.91	0.00
p[drought*mover status]	8	5218.29	72.88	0.00
p[drought period]	5	5219.40	73.99	0.00
p[drought]	5	5220.19	74.78	0.00
p[mover status]	4	5225.66	80.25	0.00
p	3	5230.86	85.45	0.00

Table 2.2. Model rankings for estimating survival (S). Capture probability was time specific.

Model	Number of Parameters	AIC_c	ΔAIC_c	AIC_cwt
S[drought period*mover status]	66	5119.04	0.00	0.99
S[drought*mover status]	66	5137.51	18.47	0.00
S[mover status]	62	5145.41	26.37	0.00

Table 2.3. Summary of growth and average size. Average size values were snout-to-vent length, mean ± standard error. Pre-drought was November 2005 to July 2007, drought was August 2007 to August 2008, and post-drought was September 2008 to November 2010.

Period	N (encounters)	Average Size (mm)	Growth (mm per day)	Growth Range (mm)
Pre-Drought				
Stayer	240	48.30 ± 0.47	0.05 ± 0.01	(-0.74, 1.83)
Mover	25	45.72 ± 1.10	0.03 ± 0.01	(0.00, 0.14)
Overall	265	47.98 ± 0.44	0.04 ± 0.01	(-0.74, 1.83)
Drought				
Stayer	128	52.41 ± 0.77	0.03 ± 0.01	(0.00, 0.84)
Mover	37	47.77 ± 1.10	0.02 ± 0.00	(-0.02, 0.15)
Overall	145	51.06 ± 0.65	0.03 ± 0.01	(-0.02, 0.84)
Post-Drought				
Stayer	288	47.85 ± 0.41	0.05 ± 0.00	(-0.23, 0.59)
Mover	177	48.60 ± 0.50	0.07 ± 0.01	(-0.01, 1.11)
Overall	465	48.12 ± 0.32	0.06 ± 0.00	(-0.23, 1.11)

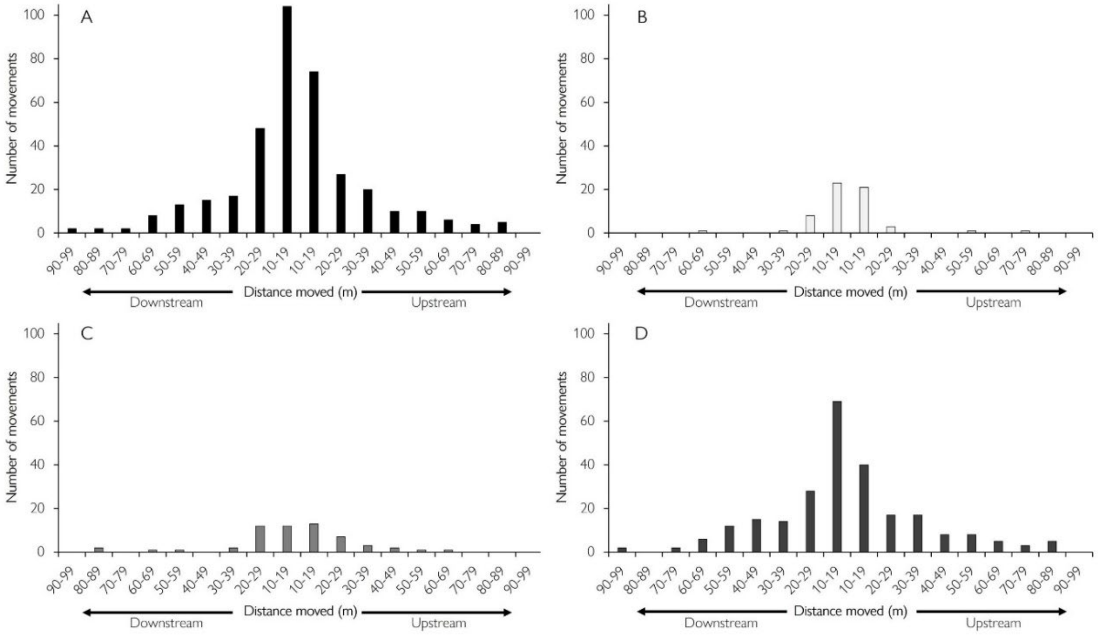

Figure 2.1 Movement frequency distribution of the distance traveled. (A) Entire sampling period (i.e., November 2005 to November 2010), (B) pre-drought period (i.e., November 2005 to July 2007), (C) Drought period (i.e., August 2007 to August 2008), and (D) post-drought period (i.e., September 2008 to November 2010).

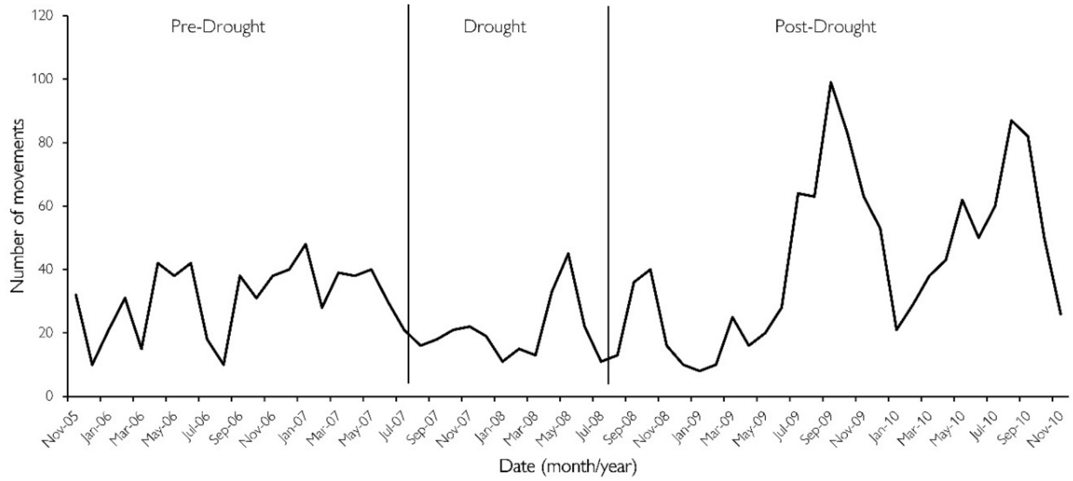

Figure 2.2 Movement propensity across sampling period. The vertical lines represent the beginning and end of the supraseasonal drought that occurred from August 2007 to August 2008.

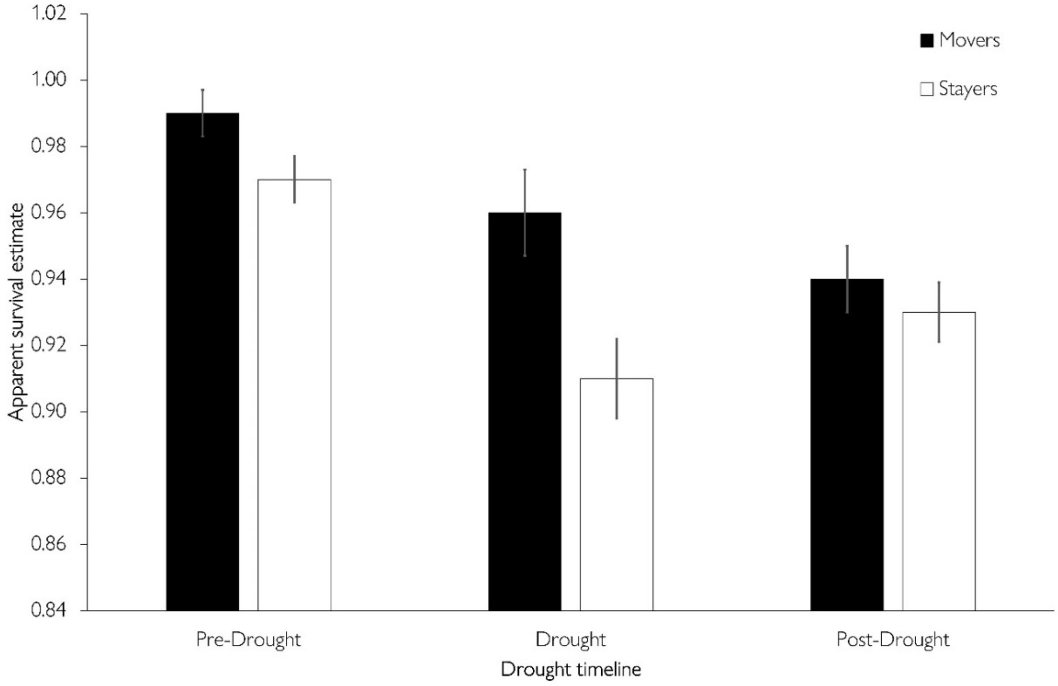

Figure 2.3. Survival estimates of ‘movers’ and ‘stayers’ across drought conditions. Pre-drought conditions included samples from November 2005 to July 2007, drought conditions occurred from August 2007 to August 2008, while post-drought occurred from September 2008 to November 2010. Error bars are ±1 SE.

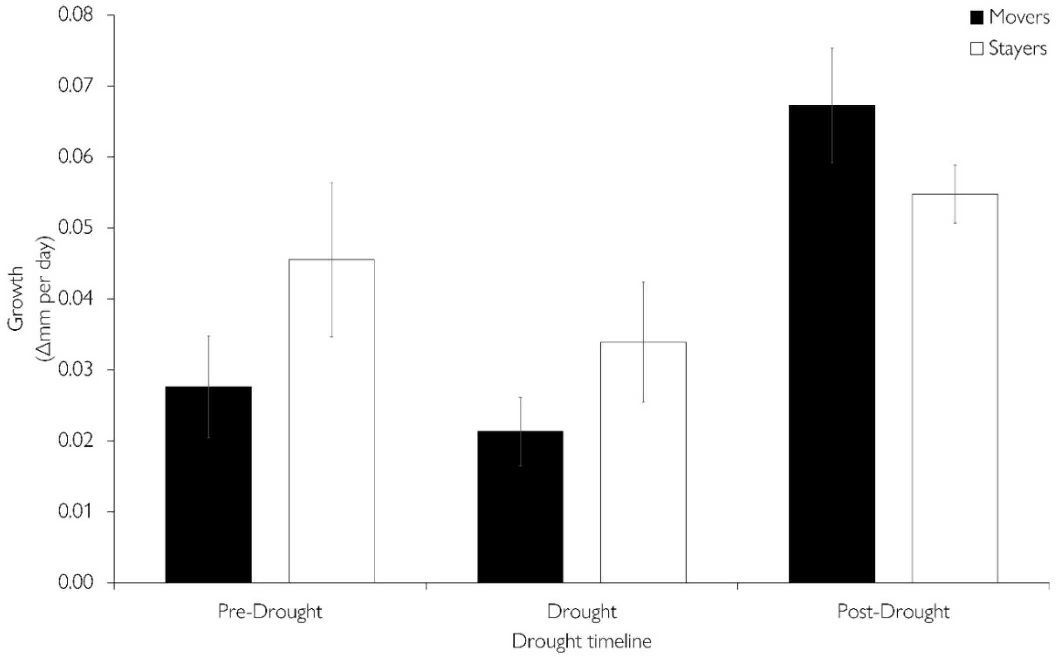

Figure 2.4 Growth estimates across drought conditions. Pre-drought conditions included samples from November 2005 to July 2007, drought conditions occurred from August 2007 to August 2008, while post-drought occurred from September 2008 to November 2010. Error bars are ±1 SE.

3 MOVEMENT TRENDS AND DISPERSAL RATES OF STREAM SALAMANDERS IN AN ALTERED AND UNALTERED LANDSCAPE

3.1 ABSTRACT

Dispersal is a process that shapes the connectivity of populations across the landscapes. Human-induced land-use change can disrupt dispersal, which can reduce the connectivity and resilience of populations in a metapopulation. The Central Appalachians represents a global hotspot for salamander diversity; however, mountaintop removal mining (MTR) and valley filling (VF) is increasingly pervasive in the region. Terrestrial and microhabitat conditions are drastically altered by MTR while VF physically and chemically alters stream conditions. Previous research has shown that salamander occupancy, abundance, colonization rates, persistence rates, and species richness are reduced in streams affected by MTR and VF. Specifically, reduced colonization and persistence in a fragmented landscape strongly implicates inhibited dispersal. Through capture mark recapture techniques, I directly evaluated 1) the use of movement pathways (e.g. within-stream, overland), 2) movement frequency distribution curves, 3) individual body condition, and 4) dispersal rates for two stream salamander species (*Desmognathus fuscus* and *D. monticola*) within a MTR and VF reclaimed landscape and compared with populations from an undisturbed, reference landscape. I found that stream salamanders, especially recent metamorphs, utilized within-stream dispersal pathways in the reference and MTR and VF landscape. Overland movement was detected in the reference landscape, but not in the MTR and VF landscape. Some age classes (e.g. *D. fuscus* juveniles, all *D. monticola* age classes) exhibited a normal movement frequency distribution in the MTR and VF landscape while adult *D. fuscus* exhibited a strong

upstream bias in the MTR and VF landscape. Body condition was a potential driver for individuals engaging in dispersal and was overall lower for individuals in the MTR and VF landscape compared to the reference landscape. My results indicated that overland connectivity between salamander populations in the MTR and VF landscape was disrupted and resulted in population isolation, which, if left unchanged, could result in local population extirpation.

3.2 INTRODUCTION

Dispersal, the long-distance movement of an individual leaving their natal area to either join another population or colonize a new area, strongly influences the stability, persistence, and structure of populations across a landscape (Miller et al. 2015; Grant et al. 2010; Clobert et al. 2009; Smith and Green 2005). Dispersal promotes the colonization of unoccupied habitat (Fagan 2002), maintains gene flow across existing populations (Miller et al. 2015; Labonne et al. 2008), and maintains metapopulation connectivity (Smith and Green 2005). The probability of successfully dispersing is often determined by the quality of the habitat patches across the landscape matrix (Ray et al. 2002; Turner et al. 1995). Determining the mechanisms and consequences of movement between populations is imperative as human-induced land-use change often results in barriers to dispersal, and can ultimately result in the decline of populations (Kuipers et al. 2019; Pimm and Brooks 2001).

A prominent type of land-use change that may create barriers to dispersal or movement is coal surface mining. Mountaintop removal mining (MTR) is a form of surface mining that involves the removal of mountaintops to extract coal from shallow seams. The Surface Mining Control and Reclamation Act of 1977 regulates the environmental effects of coal mining and requires coal mining companies to reclaim mined land via restoring the original contour and revegetating the landscape post-mining (Lambert et al. 2021; Green Forests Work 2020; Bulluck and Buehler 2006). Reclamation practices often involve soil compaction by heavy equipment and the planting of aggressive, non-native grasses (Angel et al. 2015). Collectively, surface mine reclamation frequently results in poor hydrological function, the loss of topographic complexity and arrested succession that inhibits the successful establishment of native forests (Angel et al., 2015; Wickham et al., 2013; Zipper et al., 2011; Bulluck & Buehler, 2006). Consequently, temperate deciduous forests were often transformed into a grassland/shrubland post reclamation in the Central Appalachian region (Wickham et al. 2013; Bernhardt and Palmer 2011; Zipper et al. 2011). Overall, more than 1.1million ha of forest land has been altered by MTR in Central Appalachia (Bernhardt and Palmer, 2011).

Mountaintop removal mining also results in the complete or partial burial of low-order streams via valley filling (VF), the process by which rock (i.e., overburden) is discarded from the mine site into adjacent valleys (Bernhardt and Palmer, 2011). Leaching and surface run-off from the unweathered, overburden materials changes water chemistry such that streams partially buried by VF have increased specific conductance, elevated levels of total dissolved solids and altered pH compared to reference streams (Palmer et al. 2010; Griffith et al. 2012). Physically, the VF completely or partially buries the streams, creating larger storm run-off, higher baseflow volumes, and increasing stream sedimentation (Ferrari et al. 2009; Simmons et al. 2008; Negley and Eshleman 2006). The US Environmental Protection Agency (USEPA 2011) estimated that Surface

Mining Control and Reclamation Act of 1977 permits from 1992 and 2002 authorized the destruction of ~1900 km of headwater streams in Central Appalachia. The modifications arising from MTR and VF resulted in local population declines of fauna in terrestrial and aquatic ecosystems throughout the Central Appalachian region (Price et al. 2016; Hitt and Chambers 2014; Wickham et al. 2013; Bernhardt and Palmer 2011, Pond 2010; Ferrari et al. 2009) and may have a profound effect on connectivity between populations in this region.

First-order streams in the Central Appalachian region serve as vital habitat for stream salamanders. The spatial arrangement and hierarchical organization of streams represent a dendritic network and are known to influence stream salamander species' movement behavior and population dynamics (Grant et al. 2007; Fagan 2002). Most stream salamander species use movement pathways both within and outside of the stream network (Miller et al. 2015; Grant et al. 2010). Dispersal through either pathway poses severe mortality risks: 1) Within the stream, individuals moving through higher-order streams to reach low-order streams have an increased chance of encountering aquatic predators (e.g. fish; Sepulveda and Lowe 2011; Storfer and Sith 1998; Petranka 1983) whereas 2) Outside the stream, individuals would have increased desiccation (Rothermel and Luhrig 2005; Feder and Londos 1984; Keen 1984), and terrestrial predation risk (e.g. mammals, birds, reptiles, etc; Rohr and Madison 2003). Despite the mortality risk, dispersal outside the network may be preferable if other low-order streams were closer with respect to Euclidean space, but farther with respect to distance along network branches (Rissler et al. 2004; Fagan 2002). Some have suggested that headwater specialists like salamanders adopt overland dispersal as a strategy to increase persistence in the spatially restricted stream networks (Grant et al. 2010; Grant et al. 2007). Even a small amount of overland movement has been shown to increase population stability in stream networks (Grant et al. 2010; Holland and Hastings 2008; Hill et al. 2002). Preference for a specific movement pathway can shape the population connectivity (Fagan 2002) and genetic relatedness of populations (Rissler et al. 2004). Consequently, any alteration to the surrounding terrestrial matrix and/or stream network could impact the movement behavior and population dynamics of stream salamanders.

The demographic stability and persistence of stream salamander metapopulations is dependent on dispersal among populations (Miller et al. 2015; Grant et al. 2010). However, few studies have compared movement trends and dispersal rates from unaltered landscapes with altered landscapes where land-use change affected both terrestrial and aquatic conditions (O'Donnell et al. 2016; Cecala et al. 2014; Grant et al. 2010; Smith and Green 2005). Streams impacted by MTR and VF provide a model system for such an investigation. Previous research has shown that stream salamander occupancy, abundance, colonization rates, and species richness were lower in streams affected by MTR and VF compared to reference streams (Hutton et al. 2021; Price et al. 2016, 2018; Muncy et al. 2014). In addition, persistence rates, which is the annual probability of a previously occupied area remaining occupied the following year, were notably lower at MTR and VF streams for adult Northern Dusky salamanders (*Desmognathus fuscus*) and Seal salamanders (*D. monticola*) compared to undisturbed, reference streams (Price et al. 2018). The reduced colonization and persistence rates observed in the MTR and VF landscape strongly implicate disruptions in dispersal and metapopulation connectivity

(Gamble et al. 2007; Harrison 1991). However, detailed studies on individual dispersal behavior and rates are needed to fully elucidate patterns found in the previous studies.

My objective was to compare the dispersal behavior and rates of two stream salamander species, *D. fuscus* and *D. monticola*, from a reclaimed MTR and VF landscape to an undisturbed, reference landscape. Specifically, for each landscape, species, and age class (larval, juvenile, adult), my objectives were to 1) determine which movement pathways (i.e. within-stream, overland) were being utilized in each landscape, 2) assess differences in movement skew and kurtosis using movement frequency distribution curves, 3) assess the differences in body condition between each landscape and evaluate the relationship between body condition and dispersal, and 4) calculate movement, survival, and transition probabilities. For the first and fourth objectives I predicted that within-stream and overland transition probabilities (i.e. dispersal rates) may be lower or absent in MTR and VF streams compared to reference streams, possibly because the survival for individuals who dispersed overland may be lower in MTR and VF streams compared to reference streams. Juveniles are widely regarded as the primary dispersers of salamander populations (Grant et al. 2010; Griffiths et al., 2010; Gamble et al., 2007; Gill, 1978), so I also predicted that dispersal rates were higher for this age class. For the second objective, I predicted that some age classes may exhibit upstream bias in the MTR and VF landscape to increase the likelihood of finding higher quality headwater habitat. For the third objective, I predicted that individuals in the MTR and VF landscape had lower body condition and were more likely to initiate in long-distance dispersal to improve fitness. If my predictions were met, dispersal may be disrupted in the MTR and VF landscape, because individuals were either dispersing but were dying in transit or deciding not to disperse because the inherent risks of moving in the MTR and VF riparian and terrestrial habitat were too high. My study would also support previous findings that the lower persistence and colonization rates were a result of inhibited dispersal/connectivity between populations (Price et al. 2018).

3.3 METHODS

3.3.1 Study area

I conducted capture-mark-recapture sampling at two pairs of reference first-order streams and two pairs of MTR and VF first-order streams (i.e. a total of eight stream transects). From May 2019-August 2019, I conducted a preliminary survey at each of the proposed streams to ensure that each species was present. Each stream was also used in previous count surveys (Hutton et al. 2021; Price et al. 2018; Muncy et al. 2014). All headwater streams were located in the interior of the Cumberland Plateau in Breathitt and Knott Counties, Kentucky, USA. The average catchment sizes were similar between landscape types (reference stream = 24.70 ha; MTR and VF stream = 24.51 ha; Muncy et al. 2014).

Reference streams were located in University of Kentucky's Robinson Forest, an approximately 100-year-old second growth forest. Reference streams include Field Branch B and C (node: 37.47064 N, -83.15401 W) and Little Millseat B and C (node: 37.47805 N, -83.16625 W). Reference streams had surface water flow throughout most of sampling period, except for late summer-early fall. Reference streams were dominated by second growth, mixed, mesophytic forests, consisting of white oak (*Quercus alba*), tulip tree (*Liriodendron tulipifera*), hickories, eastern hemlock (*Tsuga canadensis*). The streams are bordered by ridge-tops consisting of oak-hickory (*Quercus-Carya)* and oak-pine (*Quercus-Pinus*) communities (Overstreet 1984). Average forest cover within reference stream catchments exceeded 99% (Muncy et al. 2014).

The MTR and VF streams were located within the reclaimed Laurel Fork Surface Mine (4144091.438 N 307635.435 E Zone 17) directly southwest of Robinson Forest. Streams in MTR and VF include Turkey (37.42431 N, -83.18331 W), Spice (37.42444 N, -83.18521 W), Wharton (37.42519 N, -83.17512 W), and Hickory Log (37.4238 N, -83.17381 W). In contrast to the reference streams, surface water flow was present in the MTR and VF landscape year-round. Mining operations were active from the late 1990's to early 2000's and reclamation was completed in November 2007. Each of the MTR and VF streams were partially buried by overburden. Prior to surface mining, Laurel Fork was part of Robinson Forest until the early 1990s when mineral rights of the property were sold. Therefore, the MTR and VF streams shared many attributes with the reference streams prior to the surface mining (i.e. similar vegetation composition and age, elevation, subsurface geology; Wiken et al. 2011). The dominant vegetation within-stream catchments consisted of nitrogen-fixing herb sericea lespedeza (*Lespedeza cuneata)*, tall fescue (*Schedonorus arundinaceus)*, autumn olive (*Elaeagnus umbellate)*, Virginia pine (*Pinus virginiana)*, white oak (*Quercus alba)*, and black locust *(Robinia pseudoacacia)*. The average percentage of forest cover at within-stream catchments was low (mean (95% CI) = 0.25 (0.12-0.38)) in the Laurel Fork surface mine (Muncy et al. 2014).

3.3.2 Sampling design

Each stream included a 50 m transect partitioned into 2m segments that started at the stream's node, which refers to the location in which a stream connects to another stream. For MTR and VF streams, the transect was placed downstream of the VF. Each stream was paired with another stream located a maximum of 350 m across terrestrial habitat and each paired stream was paired with another set of streams located 500-800 m across terrestrial habitat, so overland movement could be assessed between paired streams and between watersheds (Figure 3.1). There were notable differences in the dendritic structure of first-order streams between the reference and MTR and VF landscapes (Figure 3.1). Unlike the reference landscape (Figure 3.1A), the paired first-order streams in the MTR and VF did not merge into a communal node (i.e. branched stream), rather they connected directly to a second-order stream (i.e. unbranched; Figure 3.1B). Despite the difference in stream structure, the streams were close enough in terms of Euclidean distance that overland movement was probable between streams (Miller et al. 2015; Grant et al. 2010; Smith and Green 2005).

3.3.3 Capture-mark-recapture

I conducted capture-mark-recapture sampling monthly at each stream from April 2020 to December 2021. Active searches for *D. fuscus* and *D. monticola* of all age classes (e.g. larval, juvenile, adult) were conducted within the 50 m stream reach during daylight hours. Active searches began downstream and were sampled upstream, typically with 1-2 people dip netting under cover objects (i.e. logs, rocks) and leaf litter within the stream, as well as manually searching under cover objects and leaf litter within 1 m of the stream bank. Captured salamanders were anesthetized in 1 g of maximum strength Orajel per 1 L of tap water (Del Pharmaceuticals, Uniondale, NY; Cecala et al., 2007) and individually marked with visual implant elastomers (Grant 2010; Heemeyer et al. 2007; Davis and Ovaska 2001). Morphometric measurements were also taken including snout-to-vent length, total length, and mass to track body condition and to aid with reidentification of individuals. I identified individuals as larvae if external gills were present, as juveniles if snout-to-vent lengths snout-to-vent length ≤ 35 mm and ≤ 45mm for *D. fuscus* and *D. monticola,* respectively, and as adults if they had greater snout-to-vent length (*D. fuscus:* snout-to-vent length ≥ 35 mm; *D. monticola:* snout-to-vent length ≥ 45mm) and/or prominent sexual characteristics (e.g. presence of teeth for males, gravid females; Orser and Shure 1975; Jones 1986). All marked individuals were released at the point of capture either the day of or day following capture. The handling and processing of animals was approved by the University of Kentucky Animal Care and Use Committee protocol (2021-3831).

3.3.4 Identifying dispersal movement

To exclude daily home-range movement (approximately 0.1 to 3.6m^2; Ashton, 1975; Barthalmus and Bellis, 1972), I only considered recaptured individuals found 6 m or more from their prior location as individuals who dispersed. If the recaptured individual was found in a new location located within the same 50 m stream reach, the type of movement was identified as ‘within-stream movement’ (Figure 3.1, blue lines). If the individual was found in the paired stream or another stream in the adjacent watershed, I assumed they moved over land to enter the different stream. I identified this type of movement as ‘overland movement’ (Figure 3.1, green lines) and distinguished between ‘paired stream’ and ‘different watershed’ movement for the multi-state analysis outlined below. To ensure that overland movement between the paired streams in the reference landscape did not include individuals who possibly moved downstream and then upstream into the paired stream, I did not include ‘overland’ movements that occurred within the first 6 m of the node.

3.3.5 Movement distribution analysis

3.3.5.1 Skew and kurtosis

The skew (g^3) and kurtosis (g^4) of the distribution of *D. fuscus* and *D. monticola* movement frequencies within the stream (excluding overland and no movement encounters) were calculated for each landscape type and age class in the program R (v. 4.3.2). The Shapiro Wilk test (Shapiro and Wilk, 1965) is a goodness-of-fit test from the package, *moments* (v0.14; Komsta and Novemestky 2015) and was used to test whether the movement distribution matched a normal distribution. If the result was significant (type I error rate $\alpha = 0.05$), the movement distribution deviated from what was expected under a normal distribution. Specifically for skew, a significant result would indicate that individuals exhibited a high net displacement either upstream (skew > 1) or downstream (skew < -1) whereas a non-significant result indicated no directional bias in movements (-1< skew < 1). For kurtosis, a significant result would suggest that individuals exhibited a higher probability of moving short distances (kurtosis > 3; leptokurtic) or long distances (kurtosis < -3; platykurtic) than would be expected by a normal distribution of random movements (mesokurtic; Fraser et al., 2001).

3.3.5.2 Body condition

Individual body condition has been identified as a potential driver for individuals to engage in long-distance dispersal (Lowe 2009), and because I suspect individual body condition was lower for individuals in the MTR and VF landscape (Hutton et al. 2021), I constructed two-way ANOVAs and used Tukey HSD in R (v. 4.3.2) to determine if body condition differed across landscape type and if prior body condition influenced whether individuals dispersed. I also constructed a linear regression to investigate whether prior body condition influenced the individual's movement distance. I also conducted a paired t-test to compare the body condition of individuals in the encounter before and after movement to assess whether an individual's decision to move affected their body condition. Body condition was calculated by taking the log of snout-to-vent length divided by log of mass for each individual encounter. The relationship between log snout-to-vent length and log mass was linear for *D. fuscus* and *D. monticola* ($R^2 = 0.90$, $p < 0.001$). I did not distinguish between age class or species for these analyses.

3.3.6 Multi-state modeling of individual capture histories

To evaluate the effects of MTR and VF on individual dispersal and survival, I constructed multi-state models (Brownie et al. 1993; Schwarz et al. 1993; Arnason 1972, 1973) with a Bayesian framework, using the program OpenBugs (v3.2.3, rev1012) through R (v. 4.3.2) with the package *R2OpenBugs* (Sturtz et al. 2005). Multi-state models include a variable known as a 'state', which describes a categorical factor of an individual that may change over time. For example, common 'states' identified in multi-state models include different locations, alive or dead, infection status, or breeding status. Typically, multi-state models evaluate two different states, *r* and *s*. The encounter history of recaptured individuals in each state are used to calculate three main parameters, the capture (p), survival (S), and movement probability (Ψ). The capture probability (p_i) represents the probability that a marked individual alive at time i is recaptured or resighted at time $i + 1$ (Table 3.1). The survival probability (S_i) represents the probability of survival from time i to $i + 1$ (Table 3.1). The movement probability ($\Psi^{rs}{}_i$) is the probability that an individual in state r at time i, changed to state s at time i+1. The survival and movement probabilities are used to calculate the transition probability, $\Phi^{rs}{}_i$ which is the conditional probability that an individual found alive in state r at time i, is found alive in state s at time i+1. In other words, the transition probability assumes that an individual must survive from time $i \rightarrow i + 1$ ($S^r{}_i$) to successfully change states from time $i \rightarrow i + 1$ ($\Psi^{rs}{}_i$; Table 3.1; Figure 3.2).

In my study, I classified two states: (1) ‘state A’ (i.e. no movement) in which an individual was encountered alive less than 6 m from the same location it was in during the prior encounter (i.e. did not ‘disperse’) and (2) ‘state B’ (i.e., moved within-stream, moved overland (between paired streams or between different watersheds)) in which an individual was encountered alive at a different location, more than 4 m away from its prior location (i.e. ‘dispersed’; Table 3.1; Figure 3.2). For each state, I aimed to evaluate the individual probabilities of two species (*D. fuscus, D. monticola*), found in each landscape type (reference, MTR and VF) and for each age class (larval, juvenile, adult). However, between encounters throughout the sampling period, the age class may change for *D. fuscus* and *D. monticola*, so I also included ‘transitional’ age classes (e.g. larval to juvenile, juvenile to adult). To calculate probabilities for each factor of interest (e.g. species, landscape type, age class), I constructed multiple ‘two-state’ models. The number of two-state models I constructed was constrained by the low detection of movement across some of the evaluated factors (Table 3.2, 3.3). For instance, I did not detect within-stream or overland movement for *D. monticola* in reference streams during the larval to juvenile stage. Overland movement occurrence was low between paired streams for post-metamorphic *D. monticola* juveniles and adults in the reference landscape. Overland movement of either type (paired stream and different watershed) was not detected in the MTR and VF landscape for either species. For each model, I ran 3 Monte Carlo Markov chains for 50,000 iterations and 5,000 burnin, and each starting parameter assumed a uniform distribution from 0 to 1 inclusive. I checked models for convergence by evaluating the parameter trace plots and ensuring the Gelman-Rubin statistic was at or below 1.01 (Gelman and Rubin 1992). Each model calculated five parameter estimates: $S^A{}_i$, $S^B{}_i$, $\Psi^{AB}{}_i$, $\Psi^{BA}{}_i$, and p_i (Table 3.1; Figure 3.2). The transition probabilities were calculated by multiplying the movement probability ($\Psi^{rs}{}_i$) with the corresponding survival probability ($S^r{}_i$; Table 3.1).

I compared the mean movement ($\Psi^{AB}{}_i$), survival ($S^A{}_i$ and $S^B{}_i$), and transition ($\Phi^{AB}{}_i$) probabilities with their corresponding 95% credible intervals across each age class, landscape type, and species. Bayesian 95% credible intervals indicate that there is a 95% probability that the estimate would lie between the lower (2.5% percentile) and upper limit (97.5% percentile) of the posterior distribution given the observed data (Hespanhol et al. 2019). Therefore, if the credible intervals between a set of probabilities did not overlap, I noted which mean probability was higher/lower for that set of factors.

3.4 RESULTS

3.4.1 Data collection and movement overview

Across the sampling period 1,709 *D. fuscus* were captured and marked across 2,530 total encounters while 504 *D. monticola* individuals were captured across 673 encounters (Table 3.2, 3.3). Many individuals were recaptured at least once (*D. fuscus*, n = 504, 29% recap; *D. monticola*, n = 133, 26%). Most recaptures did not 'disperse' (i.e. found less than 6 m from the original point of capture; *D. fuscus*, n = 317, 63%; *D. monticola*, n = 98, 74%) while 37% of *D. fuscus* (n = 187) and 37% of *D. monticola* (n = 35) 'dispersed' (i.e. moved either 6 m or more within-stream and/or moved overland during the sampling period; Table 3.2, 3.3). Among individuals who dispersed, 13% of *D. fuscus* (n = 25) and 8% of *D. monticola* (n = 3) moved more than once within the sampling period (Table 3.3, 3.4).

Of the 1,709 *D. fuscus* and 504 *D. monticola* captured individuals, 88% of *D. fuscus* (n = 1501) and 55% of *D. monticola* (n = 276) individuals were found in the reference landscape while 12% of *D. fuscus* (n = 208) and 45% of *D. monticola* (n = 228) were found in the MTR and VF landscape. In the reference landscape, 28% of *D. fuscus* (n = 127) and 27% of *D. monticola* (n = 19) recaptured individuals dispersed within the stream at least once in the sampling period while in the MTR and VF landscape, 24% of *D. fuscus* (n = 14) and 17% of *D. monticola* (n = 11) recaptures dispersed within the stream at least once (Table 3.3, 3.4). In the reference landscape, 10% of *D. fuscus* (n = 46) and 6% of *D. monticola* (n = 4) recaptures moved overland at least once in the sampling period (Table 3.3, 3.4). Except for one encounter involving a post-metamorphic (e.g. juvenile to adult) *D. monticola* who dispersed overland between one of the paired streams, overland movement was not detected for either species in the MTR and VF landscape (Table 3.3, 3.4).

3.4.2 Movement distribution analysis

3.4.2.1 Skew and kurtosis

Most *D. fuscus* age classes in both landscapes did not exhibit a normal distribution (Shapiro Wilk test <0.05; Table 3.5, Figure 3.3), with the exception of juveniles in the MTR and VF landscape who exhibited a normal distribution that was mesockurtic, suggesting that there was a random distribution of individuals moving long and short distances in either direction (skew = 0.11, kurtosis = 2.74, p = 0.63). Adult *D. fuscus* exhibited a strong upstream bias in the MTR and VF landscape (skew = 2.07; p = 0.0003 Table 3.5; Figure 3.3), and a slight upstream bias in the reference landscape (skew=0.25, p = $2x10^{-3}$). For most *D. fuscus* age classes in both landscapes, the distributions were leptokurtic, suggesting that most individuals remained close to original location while only some moved long distances (kurtosis: reference: juveniles = 7.55, p = $2x10^{-7;}$ adult = 7.21, P = $2x10^{-13}$; MTR and VF: adults = 9.32; p = $2x10^{-4}$; Table 3.5; Figure 3.3). However, within-stream movements did not exhibit a strong directional bias (-1< skew < 1; Table 3.5; Figure 3.3).

With the exception of *D. monticola* adults in the reference landscape who exhibited a leptokurtic distribution (skew = -0.8; kurtosis = 4.65, p = 0.03, Table 3.5), most *D. monticola* age classes exhibited a normal distribution (Shapiro-Wilk Test: P>0.05; Table 3.5; Figure 3.4). Specifically, *D. monticola* within-stream movements exhibited neither an upstream or downstream bias ($-1 < \text{skew} < 1$, $p > 0.05$) and the distributions were mesokurtic ($3.22 < \text{kurtosis} < 4.65$; $p > 0.05$; Table 3.5; Figure 3.4).

3.4.2.2 Body condition

The body condition of individuals before they moved within-stream (mean diff= -0.06, p = 0.05) or overland (mean diff = -0.10, p = 0.03) was lower compared to individuals who did not move in the next encounter (df = 2, F = 5.37, p = 0.005). Individuals overall had a lower body condition in the MTR and VF landscape (df = 1, F = 12.46, p = 0.0004). Individuals with lower body condition moved longer distances in the next encounter (p = 0.005) but not to a huge degree (R^2=0.009, slope = -3.24). I also found that body condition was higher after individuals moved compared to before movement (*Before* mean = 0.009, *After* mean = 0.11, mean-difference = 0.10, t = -6.53, df =133, p = 1.29×10^{-6}).

3.4.3 Multi-state modeling of individual capture histories

3.4.3.1 Capture probabilities

The capture probabilities were similar across all the multi-state models, except for *D. monticola* juveniles in the reference landscape who exhibited a higher capture probability compared to most other age classes [mean (95%CI) = 0.36 (0.24-0.49); Table 3.4].

3.4.3.2 Movement probabilities

In the reference landscape, within-stream movement probabilities varied slightly across age class and species. Post-metamorphic *D. fuscus* juveniles (i.e. juvenile to adult) exhibited higher within-stream movement probabilities [mean (95% CI) = 0.30 (0.14-0.47)] compared to adults [0.09 (0.07-0.13)] while other age classes exhibited similar movement probabilities [larvae to juvenile: 0.37 (0.11-0.74); juvenile: 0.17 (0.10-0.27); Figure 6]. In contrast, all *D. monticola* age classes exhibited similar within-stream movement probabilities [juvenile: 0.13 (0.04-0.27); juvenile to adult: 0.16 (0.03-0.40); adult: 0.12 (0.03-0.28); Figure 3.5].

In the MTR and VF landscape, within-stream movement probabilities were similar across most age classes for both species with some exceptions (Figure 3.5). All *D. fuscus* age classes exhibited similar within-stream movement [larval to juvenile: 0.44 (0.22-0.85); juvenile: 0.11 (0.04-0.20); juvenile to adult: 0.13 (0.04-0.27); adult: 0.08 (0.02-0.19); Figure 6]. In contrast, recently metamorphosed *D. monticola* [larval to juvenile: 0.77 (0.38-0.99)] exhibited higher movement probabilities compared to the other age classes [juvenile: 0.10 (0.03-0.23); adult: 0.06 (0.01-0.17)] apart from post-metamorphic juveniles [juvenile to adult: 0.13 (0.01-0.50); Figure 3.5]. Within-stream probabilities in the MTR and VF landscape were similar to the within-stream probabilities in the reference landscape across age class and species.

Between paired streams, overland movement probabilities in the reference landscape was similar across all age classes for both species [*D. fuscus*: larval to juvenile: 0.08 (0.01-0.25); juvenile: 0.05 (0.02-0.10); juvenile to adult: 0.08 (0.03-0.14); adult: 0.03 (0.01-0.05); *D. monticola*: juvenile: 0.03 (0.01-0.10); Figure 3.6]. Between different watersheds, overland movement probabilities in the reference landscape was similar across all age classes for both species [*D. fuscus*: juvenile: 0.03 (0.006-0.07); juvenile to adult: 0.02 (0.003-0.04); adult: 0.003 (0.0005-0.006); *D. monticola*: juvenile: 0.03

(0.0007-0.09); juvenile to adult: 0.05 (0.001-0.18); adult: 0.03 (0.0008-0.10); Figure 3.6]. As stated in the previous section, overland movement, for the most part, was not detected for either species in the MTR and VF landscape. Consequently, the estimated movement, survival, and transition probabilities in the MTR and VF landscape only reflected occurrences of within-stream movement.

3.4.3.3 Survival probabilities

Survival for individuals who did not move was similar across species, age class, and landscape type. In the reference landscape, monthly survival was similar across species and age class [*D. fuscus*: larval to juvenile: 0.98 (0.92-0.99); juvenile: 0.89 (0.80-0.98); juvenile to adult: 0.99 (0.98-0.99); adult: 0.99 (0.98-0.99); *D. monticola*: juvenile: 0.74 (0.63-0.86); juvenile to adult: 0.95 (0.85-0.99); adult: 0.96 (0.89-0.99); Figure 3.7]. Likewise in the MTR and VF landscape, survival was similar across species and age class [*D. fuscus*: larval to juvenile: 0.90 (0.70-0.99); juvenile: 0.96 (0.90-0.99); juvenile to adult: 0.96 (0.89-0.99); adult: 0.95 (0.89-0.99); *D. monticola*: larval to juvenile: 0.89 (0.64-0.99); juvenile: 0.93 (0.84-0.99); juvenile to adult: 0.95 (0.85-0.99); adult: 0.98 (0.93-0.99); Figure 3.7].

In the reference landscape, survival for individuals who moved within-stream was similar across some *D. fuscus* and *D. monticola* age classes [*D. fuscus*: larval to juvenile: 0.85 (0.52-0.99); *D. monticola*: juvenile: 0.52 (0.20-0.90); juvenile to adult: 0.78 (0.39-0.99); adult: 0.61 (0.15-0.97)] with the exception of *D. fuscus* juveniles and adults who exhibited lower survival [juvenile: 0.59 (0.29-0.91); adult: 0.73 (0.61-0.85)] compared to post-metamorphic juveniles [0.98 (0.93-0.99); Figure 3.8]. The survival probabilities of *D. fuscus* adults who moved within-stream were lower compared to the survival of *D.*

fuscus adults who did not move [within-stream movement: 0.73 (0.61-0.85); no movement: 0.95(0.89-0.99)].

In the MTR and VF landscape, survival for individuals who moved within-stream was similar across *D. fuscus* and *D. monticola* age classes, although some credible intervals exhibited a larger range compared to others [*D. fuscus*: larval to juvenile: 0.82 (0.45-0.99); juvenile: 0.67 (0.25-0.97); juvenile to adult: 0.70 (0.28-0.98); adult: mean (95%CI) = 0.91 (0.67-0.99); *D. monticola*: larval to juvenile: 0.76 (0.45-0.96); juvenile: 0.38 (0.02-0.89); juvenile to adult: 0.57 (0.04-0.98); adult: 0.39 (0.02-0.90); Figure 3.8]. The survival probabilities for *D. monticola* adults who moved within-stream were lower compared to the survival probabilities of *D. monticola* adults who did not move [within-stream: 0.39 (0.02-0.90); no movement: 0.98 (0.93-0.99)].

Survival for individuals who moved overland between paired streams in the reference landscape was similar across all *D. fuscus* and *D. monticola* age classes although the credible intervals for some age classes had a larger range compared to others [*D. fuscus*: larval to juvenile: 0.55 (0.04-0.97); juvenile: 0.26 (0.01-0.74); juvenile to adult: 0.97 (0.90-0.99); adult: 0.92 (0.76-0.97); *D. monticola*: juvenile: 0.66 (0.15-0.99); Figure 3.9]. Survival for individuals who moved overland between different watersheds in the reference landscape was similar across all *D. fuscus* and *D. monticola* age classes, although the credible intervals for some age classes had a larger range compared to others [*D. fuscus*: juvenile: 0.85 (0.50-0.99); juvenile to adult: 0.82 (0.36-0.95); adult: 0.65 (0.15-0.99); *D. monticola*: juvenile: 0.39 (0.02-0.93); juvenile to adult: 0.66 (0.21-0.83); adult: 0.41 (0.02-0.94); Figure 3.9]. The survival probabilities for *D. fuscus* juveniles who moved between paired streams were lower compared to the survival probabilities of individuals who did not move [paired stream: 0.26 (0.01-0.74); no movement: 0.89 (0.80-0.98)]. The survival probabilities of post-metamorphic *D. fuscus* juveniles and post-metamorphic *D. monticola* juveniles that moved between different watersheds were also lower compared to the survival of individuals who did not move [*D. fuscus*: different watershed: 0.82 (0.36-0.95); no movement: 0.99 (0.98-0.99); *D. monticola*: different watershed: 0.66 (0.21-0.83); no movement: 0.95 (0.85-0.99)].

3.4.3.4 Transition probabilities

The transition probabilities for within-stream movement (Figure 3.10) were similar to the estimated movement probabilities across each species, landscape type, and age class (Figure 3.5). In the reference streams, post-metamorphic *D. fuscus* juveniles (i.e. juvenile to adult) exhibited higher within-stream transition probabilities [0.29 (0.13-0.47)] compared to adults [0.07 (0.04-0.11)] while the other age classes exhibited similar transition probabilities [larval to juvenile: 0.32 (0.06-0.73); juvenile: 0.10 (0.03-0.25); Figure 3.10]. The *D. monticola* age classes exhibited similar within-stream transition probabilities [juvenile: 0.07 (0.01-0.24); juvenile to adult: 0.12 (0.01-0.39); adult: 0.07 (0.01-0.27); Figure 3.10].

Likewise for the MTR and VF streams, the within-stream transition probabilities (Figure 3.10) were similar to the estimated movement probabilities (Figure 3.5). Within-stream transition probabilities for *D. fuscus* was similar across all age classes [*D. fuscus*: larval to juvenile: 0.36 (0.10-0.84); juvenile: 0.07 (0.01-0.22); juvenile to adult: 0.09 (0.01-0.27); adult: 0.08 (0.02-0.19); Figure 3.10]. Recently metamorphosed *D. monticola* [larval to juvenile: 0.59 (0.17-0.96)] exhibited higher transition probabilities compared to the other age classes [juvenile: 0.04 (0.01-0.16); adult: 0.02 (0.01-0.15))] except for post-metamorphic juveniles [juvenile to adult: 0.08 (0.01-0.49); Figure 3.10]. Compared to the reference landscape, within-stream transition probabilities in the MTR and VF landscape were similar across age class and species.

The overland transition probabilities between paired streams and different watersheds (3.12) in the reference landscape were also similar to the estimated movement probabilities (Figure 3.6). Between paired streams, overland transition probabilities in the reference landscape were similar across all age classes for both species [*D. fuscus:* larval to juvenile: 0.07 (0.008-0.25); juvenile: 0.04 (0.01-0.10); juvenile to adult: 0.07 (0.03-0.14); adult: 0.03 (0.01-0.05); *D. monticola*: juvenile: 0.02 (0.0004-0.08) Figure 3.11]. Between different watersheds, the overland transition probabilities in the reference landscape was similar across all age classes for both species [*D. fuscus:* juvenile: 0.03 (0.005-0.07); juvenile to adult: 0.02 (0.003-0.04); adult: 0.004 (0.0005-0.01); *D. monticola*: juvenile: 0.02(0.0004-0.08); juvenile to adult: 0.04 (0.0009-0.18); adult: 0.03 (0.0007-0.10); Figure 3.11].

3.5 DISCUSSION

My analysis confirmed that mining-related alterations disrupted terrestrial dispersal, which could explain the reduced persistence and colonization rates that was reported by Price et al. (2018). I detected 1) differences in which movement pathways were utilized in each landscape, 2) normal distribution of movement frequency across most *D. monticola* age classes and directional bias in *D. fuscus* adults in the MTR and VF landscape 3) lowered individual body condition in MTR and VF landscape and 4) differences in movement, survival and transition rates across species, age class, and landscape type.

Overland dispersal between paired streams and different watersheds was not detected in the MTR and VF landscape. I originally speculated that if dispersal was detected in the MTR and VF landscape, individuals were either dispersing but were dying in transit, or deciding not to disperse because of the inherent risks of moving in the suboptimal MTR and VF habitat. Unfortunately, my capture-mark-recapture relied on successful dispersal outcomes, therefore I could not account for individuals that dispersed but did not survive. When juvenile salamanders disperse into the terrestrial landscape, they are susceptible to several mortality risks including desiccation (Rothermel and Luhrig 2005; Feder and Londos 1984; Keen 1984) and predation (Rohr and Madison 2003), especially if the terrestrial habitat lacks the necessary resources for survival, such as refuges (Grant et al. 2010; Rothermel and Luhrig 2005). In addition, I suspected that salamander populations in two MTR and VF streams declined into local extirpation: fewer than five individuals were detected at each stream in the first year of sampling, and I failed to detect any individuals the following years. Unlike the reference landscape that consisted of closed canopy temperate deciduous forest with branched first-order streams, the MTR and VF landscape was composed of partial open canopy shrubland/grassland with unbranched first-order streams as well as compacted sediment that is not as suitable for maintaining cooler, humid conditions. However, similar rates of within-stream dispersal were detected for each age class and species between each landscape suggesting the riparian habitat may be suitable for within-stream dispersers. Overall, I pinpointed that the lowered colonization and persistence rates were more likely a result of unsuccessful overland dispersal in the MTR and VF landscape.

In the MTR and VF landscape, most *D. monticola* age classes and *D. fuscus* juveniles exhibited a normal distribution in movement frequency, indicating that more individuals were engaging in random movement over varying distances, with no significant directional bias. Undirected movement is indicative of dispersal or 'away' movement and generally increases the likelihood of individuals entering inhospitable areas, traveling longer distances, and potentially finding more resources (Chapter 2; Pittman et al. 2014). Typically, salamanders exhibit high site fidelity and have been observed to infrequently engage in short, directed movement towards known locations such as foraging, breeding, or overwintering sites (Nowakowski et al., 2013; Pittman et al., 2013; Rittenhouse and Semlitsch, 2006), similar to what I observed with *D. fuscus* age classes that exhibited a leptokurtic distribution. In the MTR and VF landscape, *D. fuscus* adults exhibited a strong upstream bias which, based on previous research, suggests that these headwater specialists were trying to locate suitable headwater habitat within the stream (Cecala et al. 2014; Macneale et al. 2005; Lowe 2003). In the MTR and VF landscape, baseflow volumes and storm discharge are higher compared to streams in the reference landscape (Bernhardt and Palmer 2011; Ferrari et al. 2009; Negley & Eshleman 2006), which may be preventing smaller *D. fuscus* age classes from moving upstream until they mature into adults. Overall, the dispersal behavior of adult *Desmognathus* differed considerably in the MTR and VF landscape compared to the reference landscape.

I found support that individuals of lower body condition were more likely to engage in long-distance dispersal. Temporal variation in habitat quality is critical to initiating dispersal and typically dispersal distance increases when an individual must move farther to encounter higher-quality habitat (Lowe 2009). I found that individuals with lower body condition were more likely to disperse within-stream or overland, and if they successfully dispersed, individuals experienced an increase in body condition. Individuals in the MTR and VF landscape had lower body condition compared to individuals from the reference landscape. Although I failed to detect overland movement in the MTR and VF landscape, the body condition results from the reference landscape infer that individuals may be engaging in long-distance movement in the MTR and VF landscape, but unsuccessfully. The lower body condition in MTR and VF landscape may have also contributed to the potential dispersal mortality. Salamanders can spend limited time outside of moist habitats before desiccating but this time limit is reduced for active salamanders who lose water quicker (Feder and Londos 1984) or have less access to refuges (Grant et al. 2010; Rothermel and Luhrig 2005). The lowered body condition is most likely attributed to lower availability of aquatic prey in streams impacted by MTR and VF (Hutton et al. 2021).

Dispersal within the stream network and outside the stream network were, for the most part, similar between species, age class, and landscape. My results confirm evidence within the literature that juvenile salamanders were more likely to disperse shortly after metamorphosis (Grant et al. 2010; Griffiths et al., 2010; Gamble et al., 2007; Gill, 1978). Unlike other studies (Grant et al. 2010), I also detected within-stream and overland dispersal in the later age classes (e.g. juvenile to adult, adult) suggesting that salamanders may move more frequently than documented previously (Chapter 2). Although the lack of overland dispersal detection in the MTR and VF landscape hindered my ability to calculate movement and survival probabilities of overland dispersers, my results from the body condition analysis suggests that individuals in the MTR and VF landscape were likely dispersing overland, but unsuccessfully. My observations in comparison to the reference landscape strongly suggest that populations were isolated in the MTR and VF landscape. Overland dispersal is poorly characterized for most salamander species, mostly because it is difficult to observe empirically, and usually inferred genetically (Miller et al. 2015) or theoretically (Lowe 2009). My study provides much needed empirical data of *Desmognathus* dispersal rates between an undisturbed and altered landscape which can inform future simulation models and other research studies.

Dispersal via different pathways is driven by the ability of an organism to move between habitat patches across a landscape matrix characterized by suboptimal habitat (Miller et al. 2015; Lowe and Allendorf, 2010; Fagan, 2002; Turner et al. 1995). The lack of overland movement in the MTR and VF landscape could be increasing demographic and genetic isolation among populations (Grant et al. 2009). Restricted dispersal results in lower gene flow between populations, which in the long-term can cause inbreeding depression, genetic load, and extinction vortices to occur amongst populations. Promoting dispersal via multiple pathways can help circumvent the negative effects of disturbance on local abundances (Robinson et al. 1995). My results suggest that with respect to stream salamander populations, traditional reclamation practices were insufficient in restoring the original ecosystem function of the terrestrial habitat surrounding first-order streams. The application of the modified Forestry Reclamation Approach (Burger 2013; Zipper et al., 2011) could reverse the damage caused by the traditional reclamation practices because this approach focuses on promoting native forest growth by de-compacting the soil, removing non-native species, planting native trees and shrubs, loading woody debris, and creating wetlands (Burger et al., 2013).

Table 3.1 Parameters of interest that composed the multi-state models. Each parameter explanation includes a technical and broad description of what it represented for my study.

Parameter	Description
Φ_i	• $\underline{\Phi^{AB}_i = S^A_i \Psi^{AB}_{i;}}$ The probability of an individual that was found alive and in same location (state A) at time *i*, is alive and dispersed to a new location (state B) at time *i*+1. Represents the likelihood of individuals surviving and dispersing away from their assumed home range.
S_i	• $\underline{S^A_i}$;The probability of survival from time *i* to *i + 1*, given that the individual did not change locations (state A) at time $\underline{i}$. Represents the likelihood of individuals surviving when not dispersing • $\underline{S^B_i}$;The probability of survival from time *i* to *i + 1*, given that the individual changed locations (state B) at time $\underline{i}$. Represents the likelihood of individuals surviving when dispersing
Ψ_i	• $\underline{\Psi^{AB}}_i$; The probability that an individual in the same location (state A) at time *i,* changed locations (state B) at time *i*+1. Represents the likelihood of individuals moving away from their assumed home range. • $\underline{\Psi^{BA}}_i$; The probability that an individual in a different location (state B) at time *i,* remained in the same location (state A) at time *i*+1. Represents the likelihood of individuals settling in a location after dispersal.
p_i	• The probability that a marked individual alive at time *i* is recaptured or resighted at time *i.*

Table 3.2 Summary of the number of marked individuals for each species, age class, and dispersal state. Across the sampling period, multiple individuals were in different dispersal states and age classes across multiple samples. Therefore, the sum of these counts does not reflect the number of unique individuals sampled (*D. fuscus*: n = 1709, *D. monticola*: n = 504). Bold numbers refer to the totals of all the age classes for that species, landscape, and dispersal type.

Dispersal type	**No dispersal**		**Within stream**		**Paired stream**		**Different watershed**	
Site Type	**Reference**	**MTR and VF**	**Reference**	**MTR and VF**	**Reference**	**MTR and VF**	**Reference**	**MTR and VF**
D. fuscus	**1580**	**207**	**127**	**14**	**37**	**0**	**12**	**0**
Larval	210	38	2	0	0	0	0	0
Juvenile	606	81	29	5	9	0	6	0
Adult	764	88	96	9	28	0	6	0
D. monticola	**296**	**237**	**19**	**11**	**1**	**1**	**4**	**0**
Larval	60	54	2	0	0	0	0	0
Juvenile	144	118	7	7	1	0	2	0
Adult	92	65	10	4	0	1	2	0

Table 3.3 Summary of the number of encounters for each species, age class, and dispersal state. Across the sampling period, multiple individuals were in different dispersal states and age classes across multiple samples. Bold numbers refer to the totals of all the age classes for that species, landscape, and movement type.

Dispersal type	**No dispersal**		**Within stream**		**Paired stream**		**Different watershed**	
Landscape Type	**Reference**	**MTR and VF**	**Reference**	**MTR and VF**	**Reference**	**MTR and VF**	**Reference**	**MTR and VF**
D. fuscus	**2054**	**258**	**128**	**15**	**43**	**0**	**12**	**0**
Larval	214	40	2	0	0	0	0	0
Juvenile	684	99	29	5	9	0	6	0
Adult	1156	119	97	10	34	0	6	0
D. monticola	**353**	**286**	**20**	**11**	**1**	**1**	**4**	**0**
Larval	60	57	2	0	0	0	0	0
Juvenile	176	141	8	7	1	0	2	0
Adult	117	88	10	4	0	1	2	0

Table 3.4 Capture probabilities estimated from the multi-state models. Compared State A: 'no dispersal' vs. State B: 'dispersed', for each species, age class, and landscape type. Values represent the mean capture probability estimate with lower and upper 95% credible intervals.

D. fuscus	**Reference**	**MTR and VF**
Larval to Juvenile	0.13 (0.09-0.19)	0.13 (0.05-0.25)
Juvenile	0.15 (0.11-0.19)	0.17 (0.12-0.23)
Juvenile to Adult	0.11 (0.09-0.13)	0.16 (0.11-0.23)
Adult	0.14 (0.13-0.16)	0.14 (0.09-0.20)
D. monticola	**Reference**	**MTR and VF**
Larval to Juvenile	NA	0.31 (0.13-0.53)
Juvenile	0.36 (0.24-0.49)	0.15 (0.09-0.22)
Juvenile to Adult	0.17 (0.09-0.27)	0.16 (0.07-0.28)
Adult	0.13 (0.08-0.19)	0.14 (0.09-0.20)

Table 3.5 Skew, kurtosis, and Shapiro-Wilk p values of movement frequency distribution curves evaluated for each species, landscape type, and age class.

	Reference			**MTR and VF**		
	Skew	Kurtosis	P value	Skew	Kurtosis	P value
D.fuscus						
Larvae	NA	NA	NA	NA	NA	NA
Juveniles	-0.3	7.55	$2\text{x}10^{-7*}$	0.11	2.74	0.63
Adults	0.25	7.21	$2\text{x}10^{-3*}$	2.07	9.32	$2\text{x}10^{-4*}$
D. monticola						

Larvae	NA	NA	NA	NA	NA	NA
Juveniles	0.93	4.01	0.23	-0.03	3.22	0.67
Adults	-0.8	4.65	0.03*	-0.33	4.26	0.09

**** Shapiro-Wilk test P<0.05***

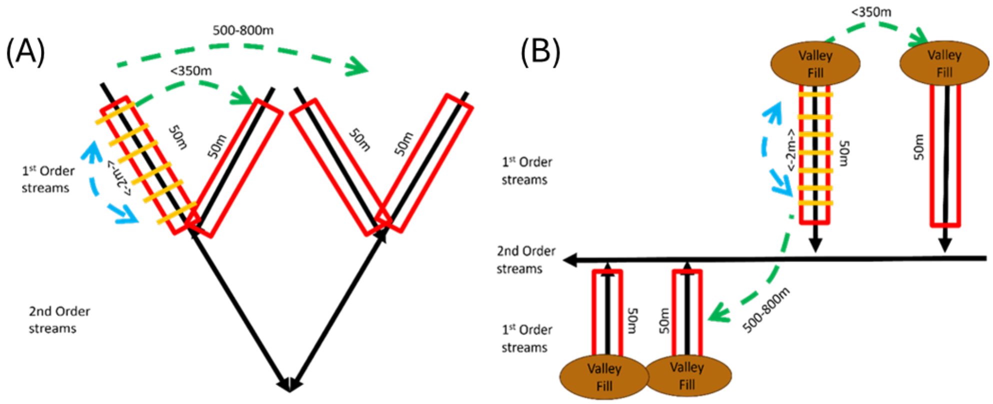

Figure 3.1 Diagram of dispersal pathways and sampling design. The dispersal pathways were across two pairs of streams in the (A) reference and (B) MTR and VF landscape. Black lines represent the streams and red boxes represent 50 m transects partitioned into 2 m segments (yellow lines) that were actively searched within each stream. Blue and green arrows represent potential individual dispersal within-stream and overland respectively.

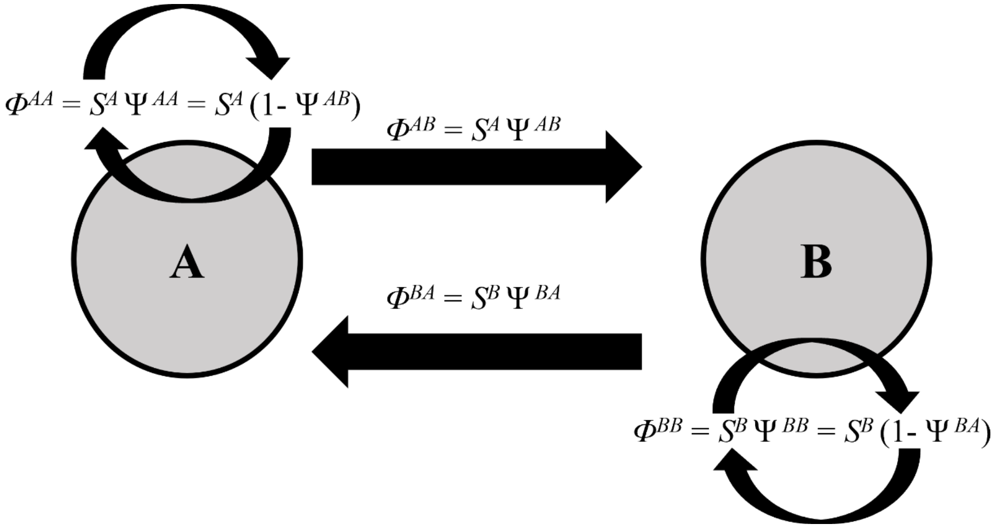

Figure 3.2 Schematic representing a 'two-state' multi-state model. Circles represent individuals in either of two states: state A, dispersal movement did not occur between encounters and state B, dispersal movement occurred between encounters. The probability of moving, conditional on survival, between state A and B is determined by parameter ϕ^{AB} which is also partitioned as the product of survival (S) and movement (ψ). Some movement probabilities such as ψ^{AA}, are calculated by taking the complement of ψ^{AB}.

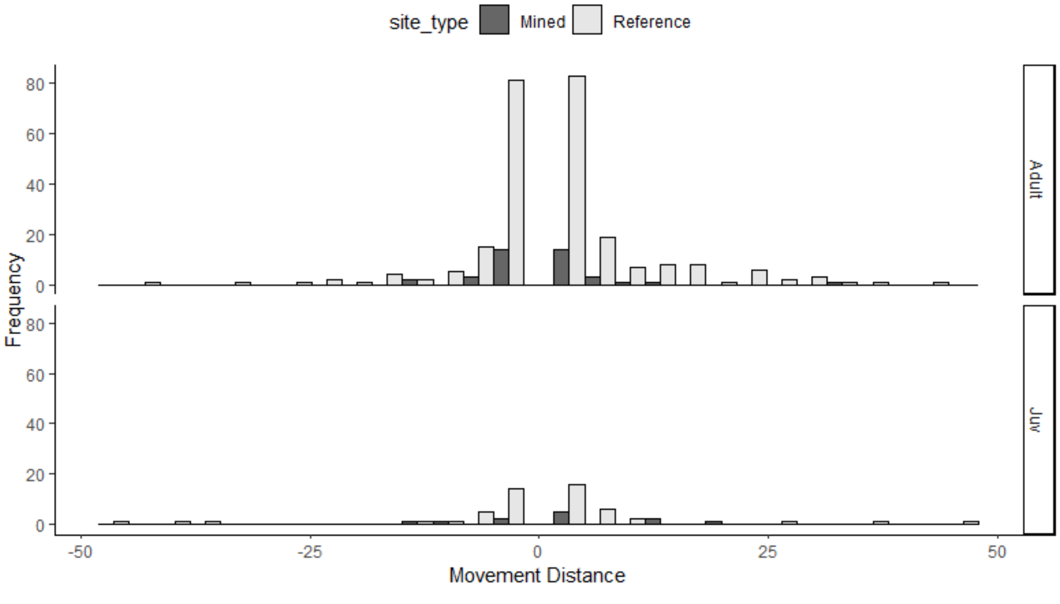

Figure 3.3 Movement frequency distribution of *D. fuscus* within-stream movements across age class and landscape type.

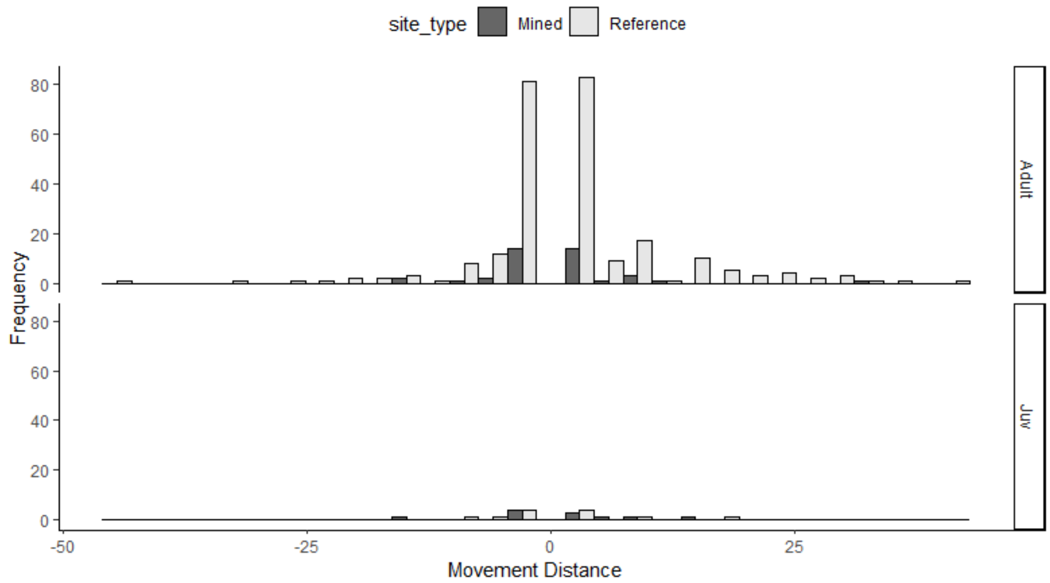

Figure 3.4 Movement frequency distribution *of D. monticola* within-stream movements across age class and landscape type.

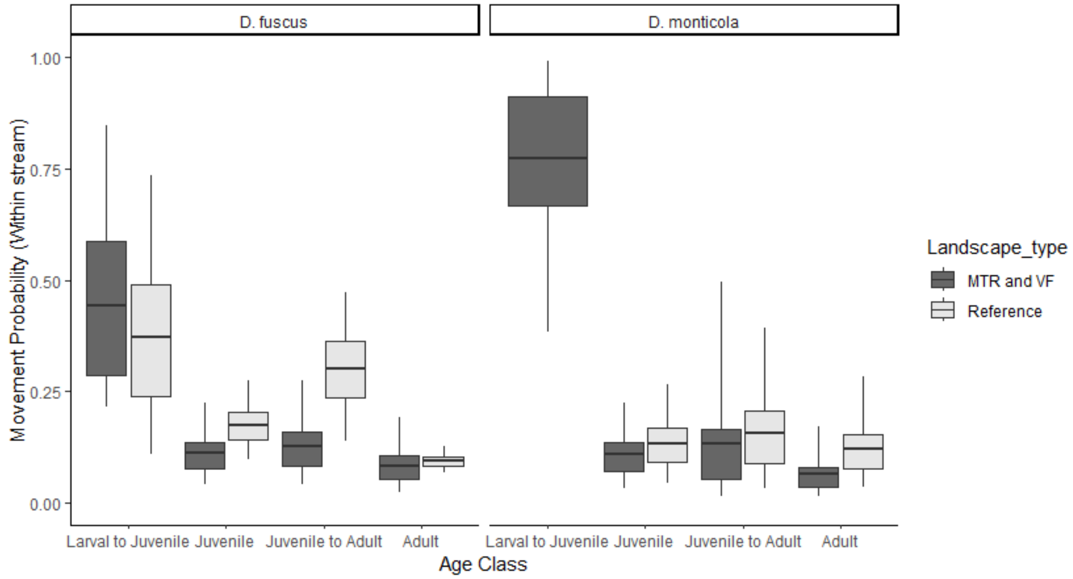

Figure 3.5 Monthly within-stream movement probabilities of *D. fuscus* and *D. monticola* across different age classes and landscape types (dark grey = MTR and VF, light grey = Reference). The movement probability describes the likelihood of individuals dispersing in the next encounter to a different location (≥6m) within the same stream, given that they did not disperse within the stream in the previous encounter. The bars represent 95% credible intervals.

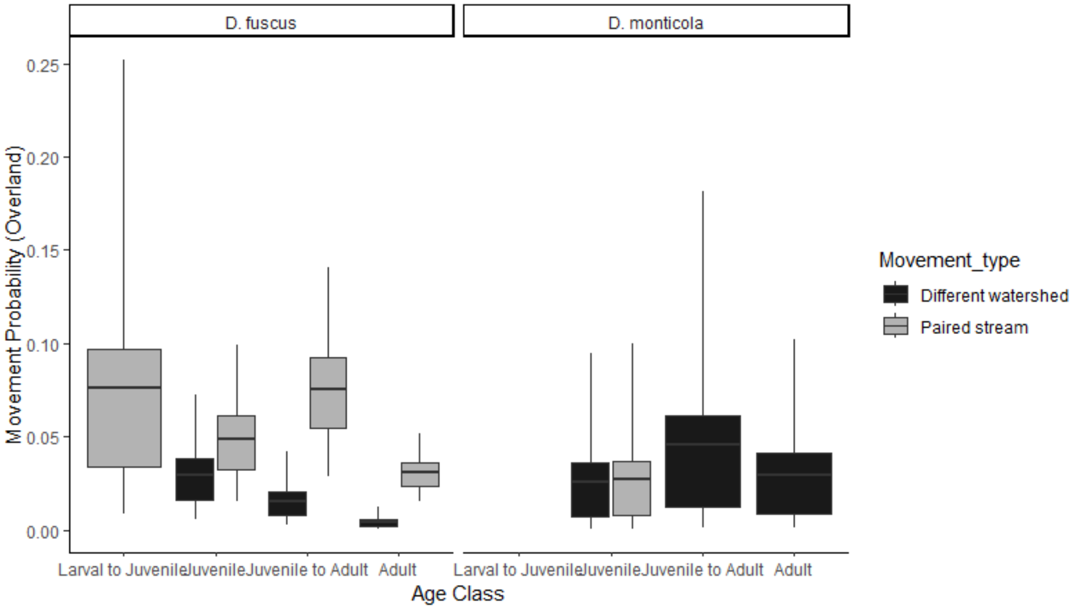

Figure 3.6 Monthly overland movement probabilities of *D. fuscus* and *D. monticola* (dark grey = dispersed to different watershed, light grey = dispersed between paired streams) across different age classes in the reference landscape. The movement probability describes the likelihood of individuals dispersing in the next encounter to a different location (≥6m) in a different stream or different watershed, given that they did not disperse overland in the previous encounter. The bars represent 95% credible intervals.

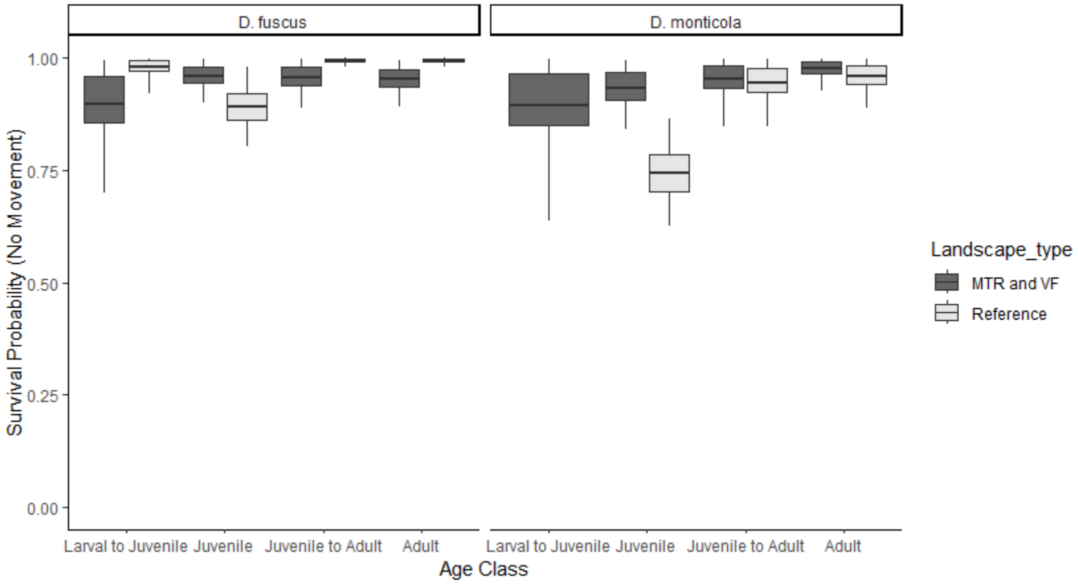

Figure 3.7 Monthly survival probabilities of *D. fuscus* and *D. monticola* individuals who did not disperse between encounters (dark grey = MTR and VF, light grey = Reference). The survival probability describes the likelihood of individuals surviving between encounters, given that they did not disperse in the previous encounter. The bars represent 95% credible intervals.

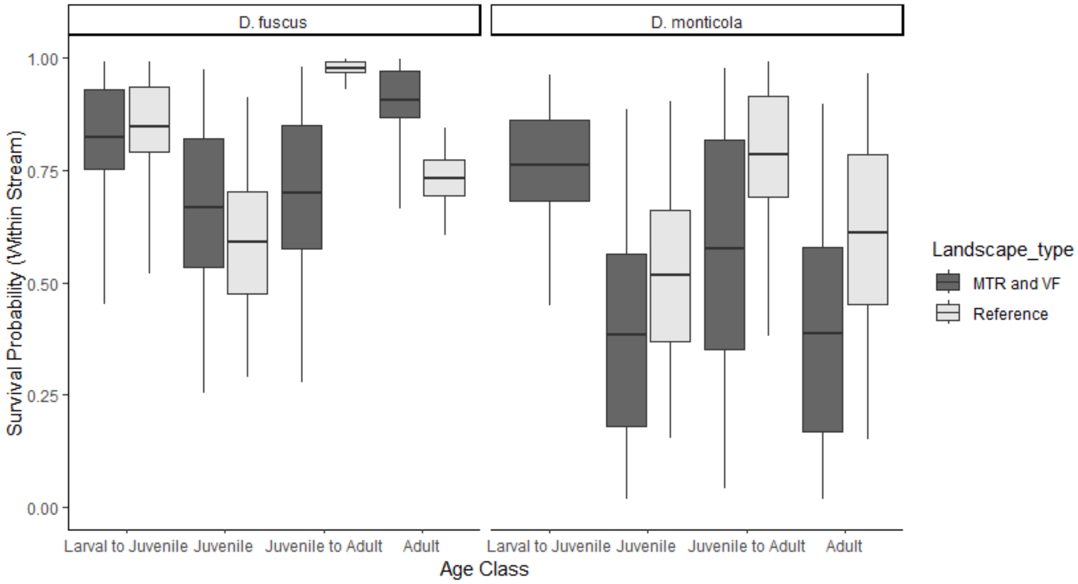

Figure 3.8 Monthly survival probabilities of *D. fuscus* and *D. monticola* individuals who dispersed within the stream (dark grey = MTR and VF, light grey = Reference). The survival probability describes the likelihood of individuals surviving between encounters, given that they dispersed within the stream in the previous encounter. The bars represent 95% credible intervals.

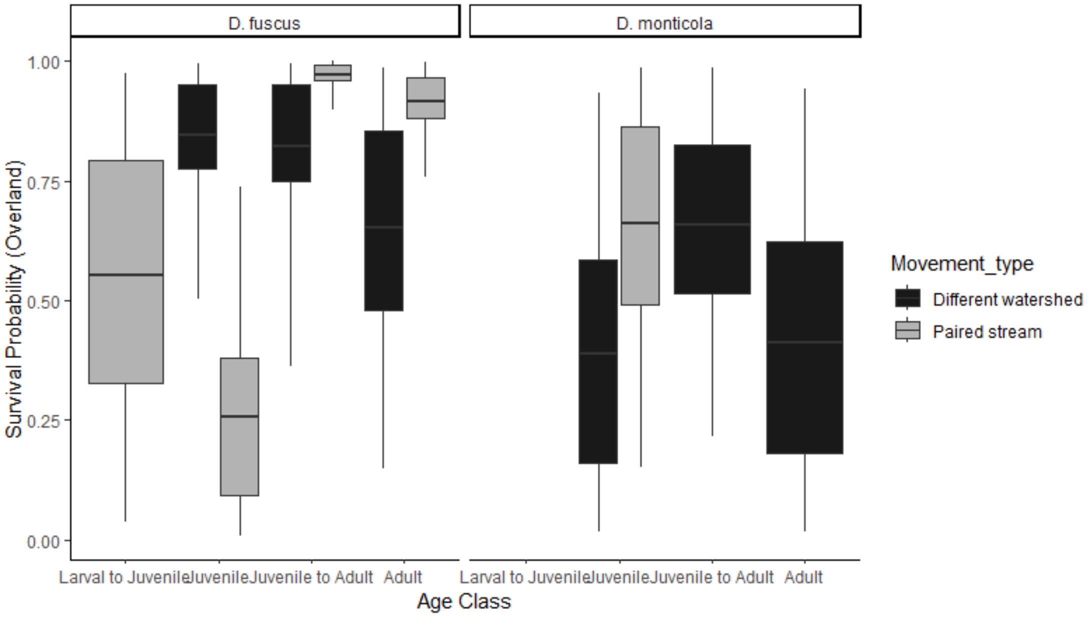

Figure 3.9. Monthly survival probabilities of *D. fuscus* and *D. monticola* individuals who dispersed overland (dark grey = dispersed to different watershed, light grey = dispersed between paired streams) across different age classes in the reference landscape. The survival probability describes the likelihood of individuals surviving between encounters, given that they dispersed overland in the previous encounter. The bars represent 95% credible intervals.

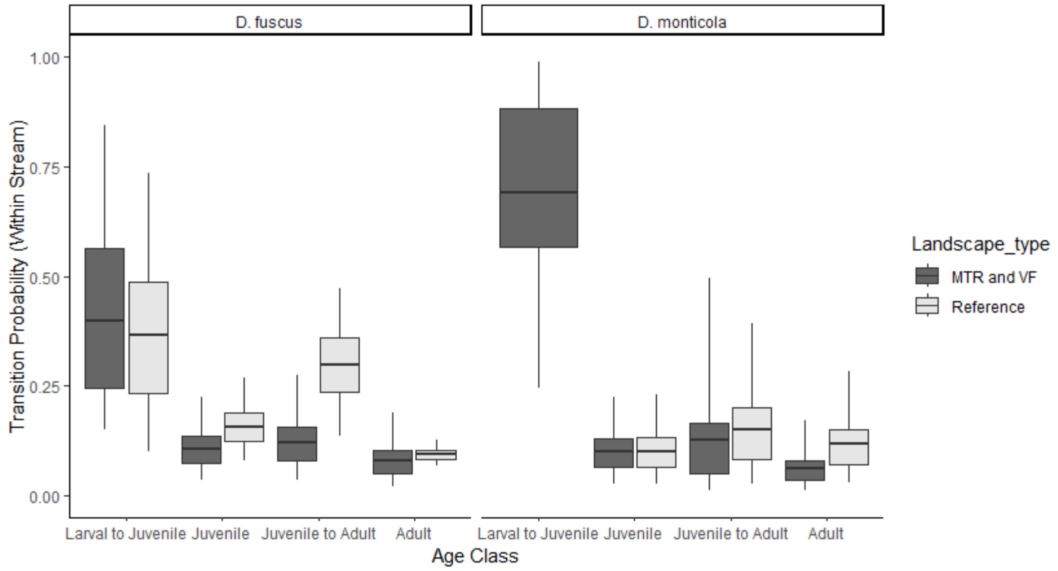

Figure 3.10 Monthly within-stream transition probabilities of *D. fuscus* and *D. monticola* across all age classes and landscape type (dark grey = MTR and VF, light grey = Reference). The transition probability describes the likelihood of individuals dispersing in the next encounter to a different location (≥6m) within the same stream and surviving, given that they did not disperse within the stream and were alive in the previous encounter. The bars represent 95% credible intervals.

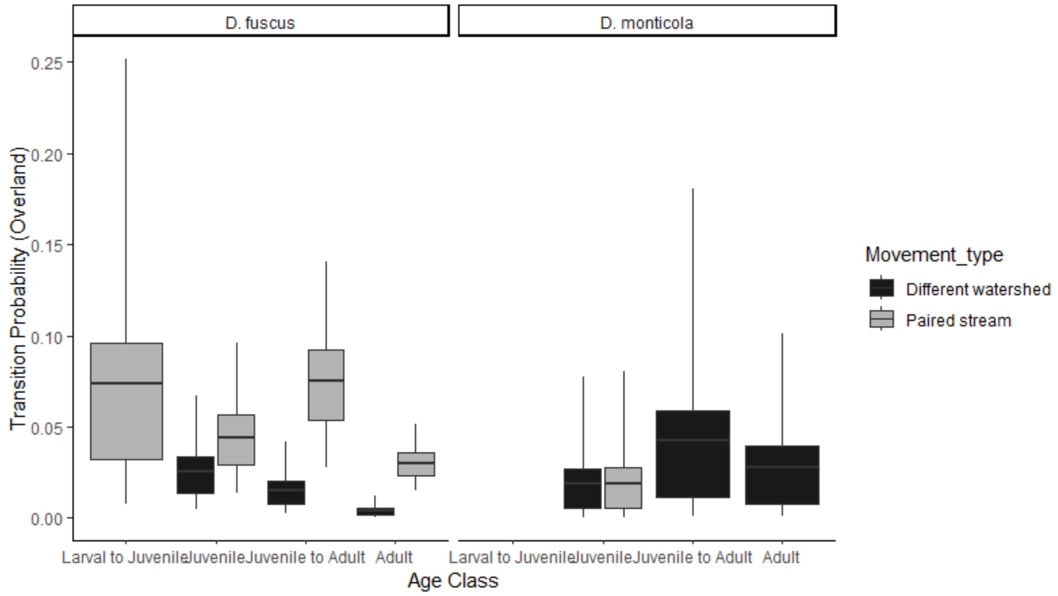

Figure 3.11. Monthly overland transition probabilities of *D. fuscus* and *D. monticola* (dark grey = dispersed to different watershed, light grey = dispersed between paired streams) across different age classes in the reference landscape. The transition probability describes the likelihood of individuals dispersing in the next encounter to a different location (≥6m) in a different stream or watershed and surviving, given that they did not disperse overland and were alive in the previous encounter. The bars represent 95% credible intervals.

4 THE ROLE OF DISPERSAL AND MORTALITY ON METAPOPULATION EXTINCTION RISK

4.1 ABSTRACT

Understanding how population connectivity decreases local population extinction risk is vital for conservation ecology, but evaluating the extinction risk is difficult to accomplish practically and ethically in an empirical setting. I constructed two agent-based models with different metapopulation structures (a two-population model and a four-population dendritic model) and conducted a simulation study to investigate how differences in extinction risk were affected by differences in movement and mortality probabilities between populations and areas. I found that movement and mortality rates did influence population extinction risk. In the two-population model, increased movement to a population decreased its extinction risk but had a stronger effect when the differences in mortality rate between populations were low. From the four-population model, increased movement similarly decreased extinction risk up to a certain threshold depending on differences in mortality. However, between paired populations, increased movement into a population consistently decreased its extinction risk regardless of the mortality rate of the area. In addition, when mortality was higher for an area, populations located on the fringe of the metapopulation network had a higher extinction risk compared to the populations that bordered other populations. In conclusion, decreasing differences in mortality between populations and improving the habitat quality of potential movement corridors is needed to promote rescue effects via dispersal.

4.2 INTRODUCTION

The extinction time of a population is dependent on the population's resilience, or the ability of the population to resist change and recover (Reed 2004; Purvis et al. 2000; Iwasa et al. 2000; Hakoyama et al. 2000; Hakoyama and Iwasa 1998). One process that promotes population resilience is connectivity with neighboring populations via dispersal (Reed 2004; Hanski and Ovaskainen 2003; Lowe and Bolger 2002; Purvis et al. 2000; Mills & Allendorf 1996; Kareiva & Wennergren 1995; Hanksi 1994). However, populations with high mortality rates could hinder population resilience and increase population extinction risk despite the metapopulation connectivity. For instance, disturbance events can increase population mortality rates while simultaneously hindering population connectivity by fragmenting habitat, decreasing resource availability, increasing competition, and/or instigating inbreeding depression (Iwasa et al. 2000; Hakoyama et al. 2000; Diamond 1984). Understanding how population connectivity decreases local population extinction risk is vital for conservation ecology, but isolating and evaluating the process can be difficult to accomplish empirically.

Agent-based models are a valuable tool that has been used to evaluate wildlife habitat selection behavior and predict how it affects individual, population, metapopulation or community dynamics (McLane et al. 2011; Revillia et al. 2004; Grimm 1999). Agent-based models are computational simulation tools that simulate autonomous individuals (i.e. "agents") that move and interact with each other and the environment. When using agent-based models, the goal is to understand how certain properties or patterns emerge from the interactions among components of the system (Grimm et al., 2005; Grimm, 1999). For instance, in ecological agent-based models, dynamics on the individual, population, metapopulation or community level can emerge and be quantified based on interactions between individual agents and the environment (Grimm et al., 2005; Grimm, 1999). Agent-based models can be used to simulate adaptive animal-movement in response to a changing landscape (McLane et al. 2011; Nonaka and Holme 2007; Revilla et al. 2004). For instance, the movement ecology of organisms which includes their internal state, movement capacity, and decision-making ability of the individual (Nathan et al. 2008), provides insight into how they are affected by matrix heterogeneity and can generate emergent properties that improve our understanding of the demography of stochastic, spatially structured populations (McLane et al. 2011; Revilla and Wiegand 2008).

Salamanders are an excellent organism for metapopulation models because they form extensive metapopulation structures across different landscape structures (Griffiths et al 2010; Grant et al. 2007, 2010; Fagan 2002; Gill 1978). Stream salamanders tend to form discrete populations in first-order streams (Grant et al. 2009; Peterman et al. 2008; Snodgrass et al., 2007), because headwater habitat typically provides an abundance of natural refuge and prey, optimum microhabitat conditions, and lack notable aquatic predators such as fish (Petranka 2010; Grant et al. 2009; Peterman et al., 2008; Snodgrass et al., 2007). First-order streams are a part of a dendritic network whose arrangement is known to enhance or reduce metapopulation connectivity depending on the species' dispersal behavior (Grant et al. 2007, 2009; Fagan 2002). For instance, potentially due to the occurrence of within-stream and overland dispersal, stream salamander populations were more likely to occupy first-order streams that have adjacent, connected branches than in streams that connect directly into lower order streams (Grant et al. 2009; Strahler 1957). Salamanders exhibit high site fidelity (Berry 2001; Beebee 1996; Blaustein et al.

1994; Sinsch 1990; Duellman and Trueb 1986), but, typically in the juvenile stage, they can disperse long distances either within the stream network or outside the stream network to neighboring populations or to colonize new habitat (Figure 3.11, Grant et al. 2010). Although the within-stream network movement is likely the primary dispersal pathway (Grant et al. 2010; Lowe et al. 2006; Chapter 3), overland (out-of-network) movements are shown to increase population stability (Grant et al. 2010; Holland and Hastings 2008) and reduce metapopulation extinction risk (Grant et al. 2010; Fagan et al. 2010; Lowe and Bolger 2002). However, the negative effects of habitat fragmentation tend to be more severe in dendritic landscapes compared to linear landscapes (Fagan 2002). In streams impacted by mountaintop-removal mining (MTR) and valley filling (VF), a previous study found that persistence and colonization rates were lower compared to populations from an undisturbed, reference landscape (Price et al. 2018). Upon further investigation, I found that within-stream dispersal rates were similar across landscape types, but I did not detect overland movement between populations in the MTR and VF landscape (Chapter 3). I suspect that stream salamander populations in the MTR and VF landscape are isolated and vulnerable to extinction (Chapter 3).

To investigate the consequences of disrupted dispersal on metapopulation persistence in a dendritic landscape, I conducted a simulation study to investigate the drivers of local population extinction. Based on findings from the previous study (Chapter 3), I suspect that local population extinction in metapopulations is primarily driven by the relationship between overland dispersal and mortality rates between neighboring populations. I used mortality probabilities compatible with estimated survival probabilities (Price et al. 2018) associated with a high quality (e.g. undisturbed forest) and low quality (e.g. reclaimed mountaintop-removal mining site) habitat. I also used dispersal probabilities compatible with estimated transition probabilities of *Desmognathus fuscus* who moved overland between stream populations and different watersheds in a branched network from the undisturbed landscape (Figure 3.11; Chapter 3). I constructed two metapopulation models with different metapopulation structures (a two-population model and a four-population dendritic model) to investigate how differences in extinction risk were affected by differences in movement and mortality probabilities between populations and between areas. I predicted that increased dispersal rates would decrease extinction risk for populations regardless of the mortality rates.

4.3 METHODS

4.3.1 Study organism

The behaviors and parameters used in the metapopulation model was modeled around the focal species from my empirical study, *D. fuscus*. This prevalent, semi-aquatic lungless salamander (Family *Plethodontidae*) often resides under rocks, logs and other debris along margins of low-order streams. Females brood their clutch of around 21-33 eggs during the summer until the eggs hatch in late summer (Petranka, 1998). The fully aquatic larvae remain confined to the stream until they undergo metamorphosis 7-12 months after hatching (Danstedt, 1975) and juveniles mature into adults around 2-3 years of age. This species can exhibit high population densities (e.g. 1.42 post-metamorphic individuals/m^2; Spight, 1967) within streams and stream margins. Previously estimated mean *D. fuscus* abundances from the undisturbed reference landscape informed the initial population size and age distribution of individuals for the models (Price et al. 2018).

4.3.2 Model design

I constructed two metapopulation models in R (v. 4.3.2). First, I built a two-population model to investigate how differences in movement and mortality probabilities between two populations on neighboring branches (i.e. paired streams) affected differences in the population's extinction risk (Figure 4.1A, Table 4.1). Second, I built a four-population model that replicated a dendritic metapopulation structure in which two populations are located on neighboring branches (i.e. 'paired streams') and these paired streams are neighboring another set of paired streams (i.e. 'different watershed', Figure 3.1A; Figure 4.1B). Specifically for the four-population model, I investigated whether differences in movement and mortality influenced extinction risk on a broader scale, between areas of paired populations (Figure 4.1B, Table 4.1). Additionally, I assessed whether extinction risk differed between the pair of populations in the same area (Figure 4.1B, Table 4.1). In both models, the movement probability represented the monthly probability of individuals moving overland into the population from another population while mortality represented the monthly probability of individuals dying in each population/area (Table 4.1). To minimize the number of parameters in the model, there were no births in the model; additionally, adding births that were identical in rates in the different populations would not have substantially changed the results qualitatively.

4.3.3 Model setup

4.3.3.1 Two-population model

At the start of each simulation, two populations (A and B) were established, each with the same population size and distribution of larval, juvenile, or adult age classes informed from mean abundance values from a previous study (Price et al. 2018). Each population was assigned a movement and mortality probability. I investigated five movement probabilities (0.001, 0.01, 0.05, 0.1, 0.2; Table 4.1) and five mortality probabilities (0.01, 0.05, 0.1, 0.3, 0.5; Table 4.1) which were informed from empirical values obtained from the previous chapter (Figure 3.11) and from a previous study conducted in the same study area (Price et al. 2018). I performed a parameter sweep that incorporated all combinations of movement and mortality probabilities between two populations, which resulted in 626 parameter combinations. The simulation was replicated 1000 times for each parameter combination.

4.3.3.2 Four-population model

At the start of each simulation, four populations (A, B, C, and D) were established, each with the same population size and distribution of individuals that identified as either larvae, juvenile, or adults (Price et al. 2018). Each population was paired with another population (A with B, C with D) and was designated to its own area (Area AB, Area CD; Figure 4.1). The model assumed that populations B and C bordered each other between the areas, therefore all movement that occurs between the areas occurred between populations B and C (Figure 4.1). To replicate the population structure that was observed empirically (Figure 3.1), different sets of movement probabilities were assigned 1) between ‘paired’ populations located on neighboring dendritic branches, and 2) between populations on different branches in a different watershed (Figure 4.1). In other words, each population was assigned a movement probability while each area was assigned a different movement probability. I investigated three population movement probabilities (0.01, 0.05, 0.1; Table 4.1) and three area movement probabilities (0.005, 0.01, 0.05; Table 4.1) which were informed from empirical values obtained from the previous chapter (Figure 3.11). Each area was assigned a mortality probability and I investigated two mortality probabilities (0.05 and 0.3; Table 4.1) informed by empirical values estimated from a previous study (Price et al. 2018). I performed a parameter sweep that incorporated all population-movement, area-movement and area-mortality probability combinations, which resulted in 2916 parameter combinations (Table 4.1). The simulation was replicated 1000 times for each parameter combination.

4.3.4 Model simulation

4.3.4.1 Two-population model

Each timestep of a model simulation represented a month in real time. At each timestep individuals in each population die, age, and disperse.

Death: the number of individuals of each age class that 'died' in each population was calculated with a binomial distribution utilizing the population mortality value (i.e. 0.01, 0.05, 0.1, 0.3, 0.5). The number of 'dead' individuals from each age class were removed from each corresponding population.

Aging: at the 7th timestep (month), larval individuals aged into juveniles in each population. At the 36th timestep (month), juvenile individuals aged into adults in each population. The aging timesteps were informed by *D. fuscus* lifecycle. Typically, larval *D. fuscus* metamorphosis into juveniles 7-11 months after hatching and juveniles mature into adults 2-3 years (i.e. 36 months) after metamorphosis (Danstedt, 1975).

Movement: the number of juvenile and adult individuals moving from population A to population B was calculated with a binomial distribution utilizing the movement probability set for population B (i.e. 0.001, 0.01, 0.05, 0.1, 0.2). The number of individuals dispersing to population A was likewise calculated.

After each population completed the death, age, and movement steps, if one of the populations contained zero individuals, that population was identified as ‘extinct’, and the simulation ended. After 1000 simulations were completed for a parameter combination, the extinction risk for each population for that combination was calculated by taking the proportion of simulations in which each population went extinct.

4.3.4.2 Four-population model

In the four-population model, each simulation/timestep was identical to the two-population model, except for notable differences in the death and movement steps:

Death: the number of individuals of each class that ‘died’ in each population was calculated with a binomial distribution function utilizing the area mortality value (i.e. 0.05, 0.30). The number of ‘dead’ individuals from each class were removed from each population in the corresponding area.

Movement: two types of movement occurred in this model: 1) First, individuals would move between the different areas (area AB with area CD; Figure 4.1), 2) then, individuals would move between their paired populations (A with B and C with D; Figure 4.1). Under the assumption that populations B and C were bordering each other, individuals moving from area AB to area CD would disperse from population B to population C and vice versa (Figure 4.1). The number of juvenile and adult individuals moving from population B to population C was calculated with a binomial distribution utilizing the movement probability set for area CD (i.e. 0.005, 0.01, 0.05). The number of individuals dispersing to population B was likewise calculated utilizing the probability set for area AB. Movement between paired populations (A with B, C with D), was similar to the process outlined in the two-population model but with a different range of movement probability parameters (i.e. 0.01, 0.05, 0.1).

4.3.5 Analysis

4.3.5.1 Two-population model

For each parameter combination, I took the difference in the assigned mortality and movement probabilities between each population to assess how these parameters influenced the calculated population differences in extinction risk. I fitted a linear regression across the 626 parameter combinations to evaluate whether population differences in mortality and movement probabilities influenced population differences in extinction risk.

4.3.5.2 Four-population model

For each parameter combination, I calculated the area differences in extinction risk by using the sum of the extinction risk of the two paired populations as the area extinction risk (Figure 4.1). I fitted a linear regression using the area differences in movement and mortality probabilities across the 2916 parameter combinations to evaluate whether differences in movement and mortality between areas influenced the extinction risk of those areas.

For each parameter combination, I also calculated the population differences in movement probability between paired populations in each area to assess how these parameters influenced the calculated population differences in extinction risk. I fitted a linear regression to evaluate whether differences in movement between paired populations and the mortality probability of the area influenced extinction risk. When calculating the parameter differences, I subtracted parameters from populations that 'border' the other area (B and C) from the parameters for populations that were on the 'fringe' (A and D) of the metapopulation (Figure 4.1B). Therefore, positive differences indicated higher values for the fringe populations (A and D) while negative differences indicated higher values for the border populations (B and C).

4.4 RESULTS

4.4.1 Two-population model

Population differences in mortality and movement probabilities influenced population differences in extinction risk ($R^2= 0.78$, $F(3,621) = 724.2$; $p<2.2x10^{-16}$). As the difference in mortality probability increased between populations, differences in extinction risk increased (regression slope = 2.29; $p<2x10^{-16}$). In contrast, as population differences in movement probability increased, differences in extinction risk decreased (regression slope = -4.06, $p<2x10^{-16}$). There was no interaction between mortality and movement probability (regression slope = 0.16, p = 0.79), however when mortality differences were lower (≤0.09; Figure 4.2), differences in movement probability had a stronger negative effect on extinction risk compared to when mortality differences were larger (>0.09; Figure 4.2).

4.4.2 Four-population model

Differences in mortality and movement between areas influenced differences in extinction risk between areas ($R^2 = 0.86$, $F(3, 2912) = 6222$, $p<2x10^{-16}$). As the area differences in mortality increased, area differences in extinction risk increased (regression slope=3.99, $p<2x10^{-16}$, Figure 4.3). In contrast, as area differences in movement probability increased, differences in extinction risk decreased (regression slope = -1.97, $p<2x10^{-16}$, Figure 3). There was no interaction between area differences in mortality and movement probability (regression slope = -0.08, p = 0.94), however when the difference in area mortality was zero (Figure 4.3), differences in movement probability had a stronger negative effect on area extinction risk compared to when mortality differences were larger (±0.25; Figure 4.3).

Differences in area mortality and movement between paired populations influenced differences in extinction risk between the paired populations ($R^2 = 0.46$, F(3,5828) = 1666, $p<2x10^{-16}$). As the mortality probability increased in the respective area, extinction risk for the fringe population (A or D) increased relative to the border population (regression slope = 0.93, $p<2x10^{-16}$, Figure 4.4). As the movement probability increased for a population, extinction risk decreased for that population (regression slope = -3.87, $p<2x10^{-16}$, Figure 4.4). There was an interaction between differences in area mortality and population movement probability (regression slope = -3.25, $p = 9x10^{-9}$).

4.5 DISCUSSION

According to my models, dispersal between populations and mortality probability did influence population extinction risk. From my two-population model, increased dispersal rate between populations decreased population extinction risk but dispersal had a stronger effect when the differences in mortality between populations was low. Similarly, from my four-population model, increased dispersal decreased extinction risk but only at a certain threshold depending on area differences in mortality. When comparing extinction risk between paired populations in the four-population model, when mortality was higher for the area, populations located on the fringe of the metapopulation network had a higher extinction risk compared to their paired, border populations. I found that increased dispersal did decrease extinction risk for paired populations regardless of area mortality rate. By evaluating the effects of dispersal on extinction risk across different population structures and scales, the results suggest that maintaining connectivity between populations was important for lowering population extinction risk.

In a two-population structure, the population receiving more individuals (i.e. higher movement probability) from the neighboring population had lower extinction risk. However, if the difference in mortality rate was high between the populations, the population with the higher mortality would have a higher extinction risk compared to the other population regardless of the movement rate. Although birth was not simulated, the differences in mortality probability potentially simulated source-sink dynamics in which the populations with lower quality/higher mortality compared to their neighboring population became a 'sink' and was more susceptible to extinction despite being connected via dispersal. When the populations had similar mortality rates, extinction risk was more influenced by the number of dispersers entering the population. Previous studies have also found that even when dispersal rates were low, dispersal between populations decreased population extinction risk (Grant et al. 2010; Holland and Hastings 2008; Hill et al. 2002). Hill et al. (2002) similarly found that dispersal rate had a threshold when minimizing extinction probabilities that depended on mortality probability. When mortality probability increased, dispersal had less of an effect on extinction time (Hill et al. 2002). Therefore, dispersal has a strong rescue effect on neighboring populations once the sources of mortality (e.g. disturbance events, habitat fragmentation, competition, etc.) have been removed.

When evaluating from a larger scale with my four-population model, I found that a more complex metapopulation structure yielded similar and different results in respect to the two-population model. When evaluating extinction risk trends between areas, increased movement between areas decreased extinction risk when mortality was equal between the areas of paired populations. However, when I evaluated the extinction risk between the paired populations in this four-population structure, I found that movement had a consistent negative effect on extinction risk for both mortality parameters. In contrast to the two-population model, I assumed that mortality was the same between the paired populations and differed between areas. Under this assumption, I found that fringe populations were more at risk of extinction if the area had higher mortality. Therefore, when the mortality probability is high on a landscape/area-level, populations with less neighbors inherently had higher extinction risk. In comparison, the border populations had lower extinction risk when mortality was high, because they had an additional source of dispersers from the neighboring area. However, when mortality probability was low, the border populations were at a higher risk compared to the fringe populations. In this scenario, border populations acted as a source of dispersers for two populations rather than one. If the neighboring area had higher mortality in comparison, then the resulting source-sink dynamics may make border populations more susceptible to extinction risk compared to the fringe populations.

At the landscape scale, the structure and complexity of dendritic stream networks may affect the dispersal of stream salamander individuals through the network, resulting in different extinction risks for the metapopulation (Fagan et al., 2010; Grant et al. 2009; Grant et al. 2007). My models were structured to represent a branched dendritic network which tends to have larger habitat areas and lower isolation than metapopulations in a two-dimensional landscape (Fagan 2002; Hanski, 1998; Figure 1.2A). However, my models did not account for unbranched stream networks, like the observed MTR and VF landscape (Figure 3.1B), which may have increased isolation between populations because individuals are less likely to disperse within the stream network and/or the streams may be further away overland (Grant et al. 2007). Additionally, the relationship between animal dispersal and the heterogeneity of the habitat surrounding populations (e.g. matrix) should be investigated because this relationship is known to affect metapopulation-level parameters (Revilla et al. 2004; Vandermeer and Carvajal 2001). In addition, evaluating how different dispersal pathways, such as within stream dispersal, affects metapopulation dynamics could also be insightful because, in relation to stream salamanders, the within-stream network is a common pathway that connects populations located near the nodes of the first-order streams or lower-order streams (Grant et al. 2007, 2010).

Metapopulations located in landscapes with varying levels of habitat quality are vulnerable to extinction risk. My mortality probabilities were informed from salamander survival estimates from a high quality (e.g. undisturbed forest) and low quality (e.g., mountain top removal) habitat, suggesting that the observed effects of mortality on extinction risk could be attributed to differences in habitat quality caused by a disturbance event (e.g. mountain top removal). Disturbance events rarely cause immediate population extinction, but through the introduction of one or multiple stressors that increase population mortality rates, disturbance can begin the process (Iwasa et al. 2000; Hakoyama et al. 2000; Diamond 1984). Dispersal can decrease local population extinction risk, but its effect can be complicated by source-sink dynamics that occur due to differences in mortality probability between populations. Organisms that form metapopulation structures tend to have low dispersal rates and high site fidelity (Smith and Green 2005; Hanski 1999; Levins 1969) so identifying the threshold in which dispersal is effective for population stability is vital for wildlife management and conservation practices (McLane et al. 2011; Hills et al. 2002). In light of my results, lowering the mortality rates of populations and improving the habitat quality of potential movement corridors is required so that rescue effects via dispersal could occur (Revilla et al. 2004). Maintaining the presence of stable, neighboring populations is also integral for the benefit of other populations. Decreasing the local population extinction rate would simultaneously decrease the extinction risk of the entire metapopulation. I also demonstrated how agent-based models can be an effective tool in investigating the drivers of population extinction risk in response to landscape changes that affect mortality (McLane et al. 2011). This study also shows how understanding the role of the interaction between movement behavior and habitat structure on population decline and persistence can be improved through theoretical investigations informed by empirical results.

Table 4.1 Movement and mortality probabilities assigned to each metapopulation model on the population and/or area-level.

	Population-Level		**Area-Level**	
Model	Movement Probabilities	Mortality Probabilities	Movement Probabilities	Mortality Probabilities
Two-Population	0.001, 0.01, 0.05, 0.1, 0.2	0.01, 0.05, 0.1, 0.3, 0.5	NA	NA
Four-Population	0.01, 0.05, 0.1	NA	0.005, 0.01, 0.05	0.05, 0.3

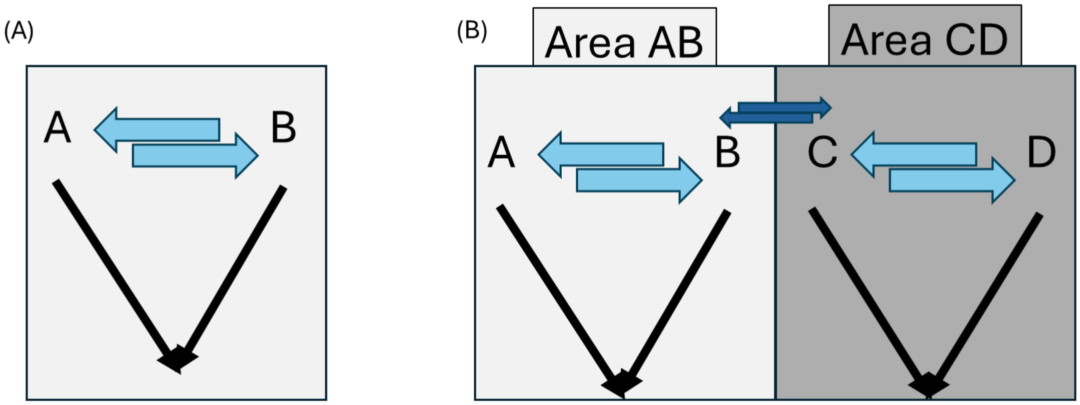

Figure 4.1 Metapopulation structure of the (A) two-population model and the (B) four-population model. The black arrows represent the first-order streams while the lighter blue, larger arrows represent movement between populations. In the (A) two-population model, movement probabilities ranged from 0.001, 0.01, 0.05, 0.1, and 0.2 between populations A and B and a mortality probability was assigned for each population ranging from 0.01, 0.05, 0.1, 0.3, and 0.5. In the (B) four-population model, movement probabilities ranged from 0.01, 0.05, and 0.1 between populations within an area, and a mortality probability was assigned for each area ranging from 0.05 and 0.3. In the (B) four population model, the darker blue, smaller arrows represent movement between populations B and C and thus represent movement between areas AB and CD (probabilities = 0.005, 0.01, 0.05).

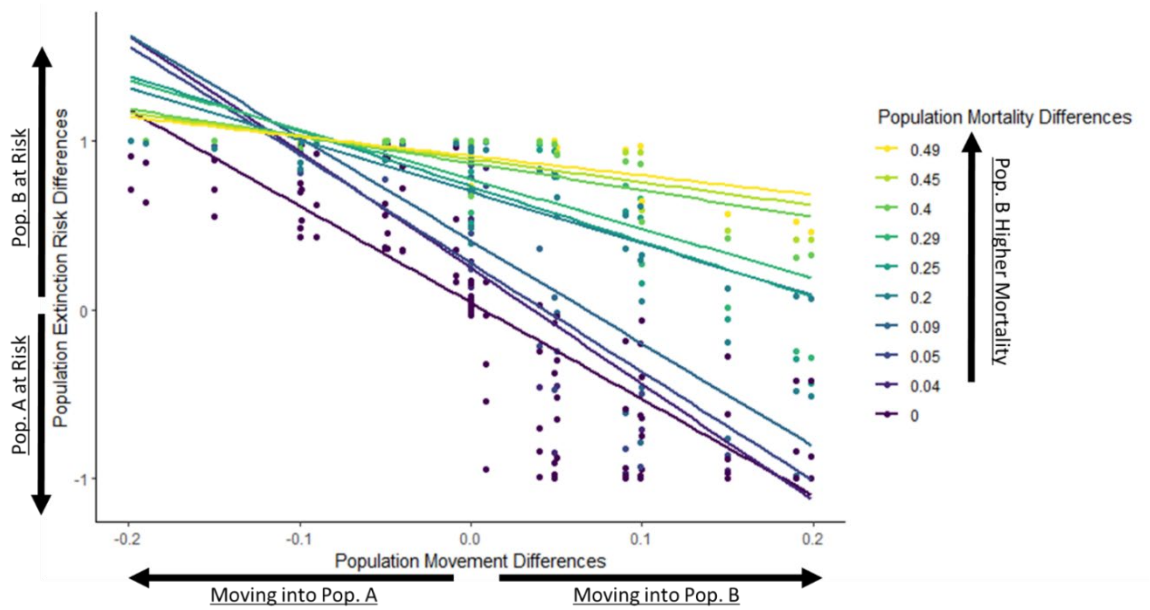

Figure 4.2 A subset of the simulation results from the two-population model (i.e. includes models in which mortality at Population A ≤ Population B). Positive values represent instances when extinction risk, movement probability, and/or mortality was higher for Population B whereas negative values represent instances when parameters were higher for population A.

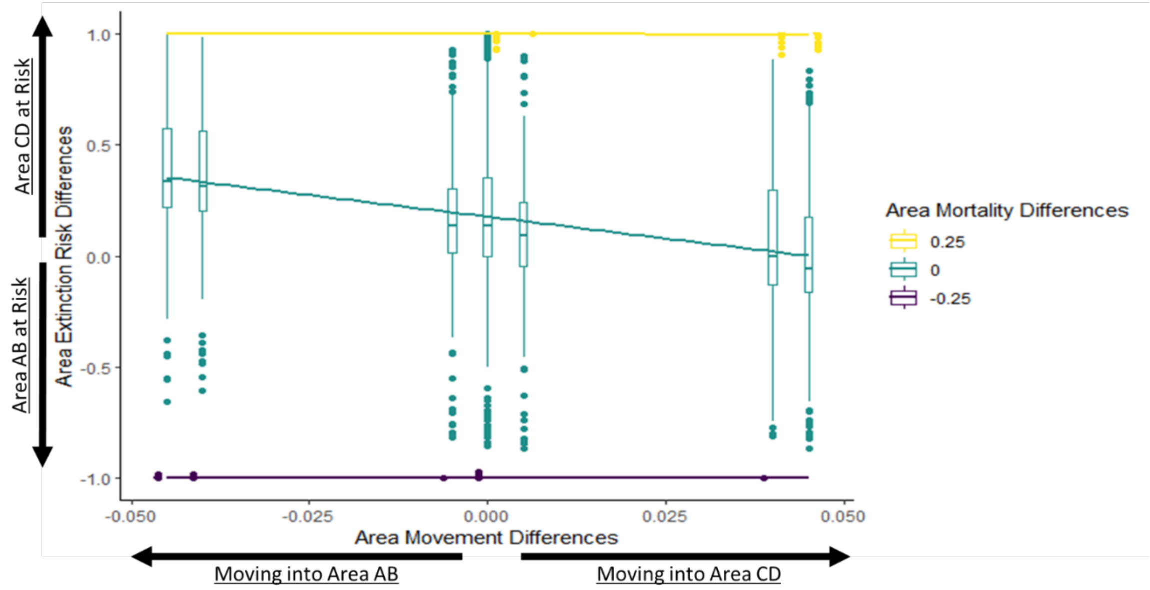

Figure 4.3 Simulation results from the four-population model. Positive values represent instances when extinction risk, movement probability, and/or mortality was higher for Area CD whereas negative values represent instances when parameters were higher for Area AB.

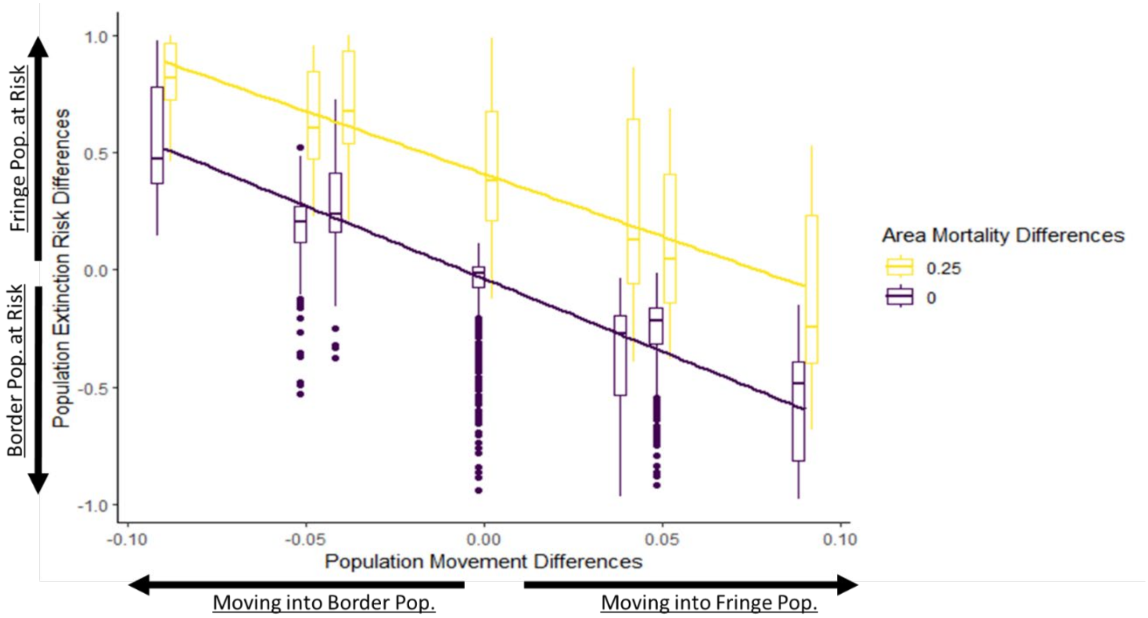

Figure 4.4. A subset of simulation results from the four-population model (i.e. includes models in which area mortality differences ≥ 0). When calculating the difference, the parameters for 'border' populations (B and C) were subtracted from the parameters from the 'fringe' populations (A and D). Therefore, positive differences indicated higher values for the fringe populations while negative differences indicated higher values for the border populations.

5 CONCLUSION

5.1 Overview of main takeaways

In Chapter 2, I observed movement being utilized as a strategy for adult D. fuscus to resist the negative effects of the supraseasonal drought. Individuals that moved during the drought experienced higher survivorship compared to individuals who did not move, suggesting that adult salamanders, who are usually sedentary (Barthalmus and Bellis, 1972; Bishop 1941), were potentially displaying an adaptive movement strategy to resist drought conditions by moving away from affected (i.e., dry) areas within the study stream. In addition, I found that movement occurred in high frequency during the post-drought and those that moved experienced a higher growth rate indicating that individuals moved to other areas to access replenished resources after the severe effects of the drought ended.

In Chapter 3, I compared movement trends and dispersal rates of salamander populations from an undisturbed, reference landscape to a reclaimed MTR and VF landscape. I found that stream salamanders, especially recent metamorphs, utilized within-stream dispersal pathways at similar rates in the reference and MTR and VF landscape. However, overland movement was not detected in the MTR and VF landscape, only in the reference landscape. I suspected that individuals were engaging in movement in the MTR and VF landscape but dying in transit and therefore undetectable. The lack of detection of salamanders throughout the latter half of the sampling period suggests that the two MTR and VF streams were most likely declining into local extirpation. My results indicated that overland connectivity between salamander populations in the MTR and VF landscape was disrupted and resulted in population isolation, which, if left unchanged, could result in local population extirpation.

In Chapter 4, I utilized the overland dispersal rates and population structure observed from the reference landscape in Chapter 3 to investigate the long-term consequences of varying dispersal and mortality probability on population extinction risk. I found that dispersal between populations and mortality rate did influence population extinction risk. When I evaluated trends between two populations, increased dispersal decreased population extinction risk, but dispersal had less of an impact when the differences in mortality between populations were high. When evaluating trends between four populations, I similarly observed that high dispersal decreased extinction risk up to a certain threshold depending on differences in mortality. When mortality was the same between paired populations, increased dispersal consistently decreased extinction risk. In addition, when mortality was high for an area, populations located on the fringe of the metapopulation network had a higher extinction risk compared to the populations that bordered other populations.

Multi-year monitoring of individuals' movement, growth, and survival has provided insight into the strategies stream salamanders use to remain resilient in the wake of disturbance events. My results indicated that salamanders utilize movement as a strategy to resist negative effects of disturbance and to decrease extinction risk.

5.2 Implications and Future directions

My findings from each empirical chapter consistently demonstrated that riparian and terrestrial habitat needs to be restored and maintained to increase population resilience. Chapter 2 demonstrated that promoting movement into surrounding riparian and terrestrial habitat would allow populations to resist severe supraseasonal droughts. As shown in Chapter 3 and 4, disrupted overland connectivity between salamander populations could result in local population extinction. Restoring the riparian habitat would help decrease population mortality rate differences between populations while restoring terrestrial habitat would help maintain connectivity between populations. In the future, combining my demographic measures with genetic and landscape measures through next generation sequencing and resistance surface techniques would help elucidate the patterns of genetic connectivity and identify dispersal corridors and landscape barriers to movement. Conduction of overland movement trials in the MTR and VF landscape could also elucidate whether individuals are unable to successfully move through the MTR and VF terrestrial landscape. Overall, the traditional reclamation practices applied to the MTR and VF landscape seemed to be insufficient in restoring pre-mining landscape conditions and is contributing to local extinction of stream salamander populations.

Several management options are available that could potentially restore the ecosystem function of the reclaimed MTR and VF landscape. In 2005, a new approach to reclamation, the Forestry Reclamation Approach was developed to restore ecosystem function and native forest vegetation to active and reclaimed mine lands (Burger 2013; Zipper et al., 2011). Compared to traditional reclamation practices, the Forestry Reclamation Approach has proven to be successful in accelerating the natural succession and maintaining ecological conditions inherent of the native Appalachian forests (Groninger et al., 2007). A modified version of the Forestry Reclamation Approach was developed for traditionally reclaimed mined lands with the aim to reverse the damage through soil decompaction, non-native species removal, the planting of native trees and shrubs, woody debris loading, and wetland creation (Burger et al., 2013). The MTR and VF landscape I evaluated would benefit from the Forestry Reclamation Approach since this practice aims to restore the ecological conditions and biotic communities reminiscent of the native Appalachian Forest ecosystem.

APPENDICES

APPENDIX A. CHAPTER 4 SUPPLEMENTARY INFORMATION

APPENDIX A1. Agent-based model code for ‘two-population model’

R version 4.3.2

```
#======================================================
#Loading Packages
#======================================================
library(R.utils)
library(dplyr)
library(tidyverse)
library(rlist)
#======================================================
#Death function, site-specific
#======================================================
death = function(current_pop){
 #Site A Mortality
 for (i in 1:3){
  num_dead=rbinom(1,current_pop[,i],SiteA_mortality)
  current_pop[,i] = current_pop[,i]-num_dead}
 #Site B Mortality
 for (i in 4:6){
  num_dead=rbinom(1,current_pop[,i],SiteB_mortality)
  current_pop[,i] = current_pop[,i]-num_dead}
 return(current_pop)}
#======================================================
#Aging function
#======================================================
```

```
age = function(current_pop){
  #------larval2juvenile aging------
  if (current_pop[,7]==7){
    #Site A
    current_pop[,2] = current_pop[,1] + current_pop[,2]#larvae join juvenile
    current_pop[,1] = 0 #no more larvae
    #Site B
    current_pop[,5] = current_pop[,4] + current_pop[,5]#larvae join juvenile
    current_pop[,4] = 0 #no more larvae
}
  #------juvenile2adult counter------
  if (current_pop[,7]==36){
    #Site A
    current_pop[,3] = current_pop[,2] + current_pop[,3]#juveniles join adults
    current_pop[,2] = 0 #no more juveniles
    #Site B
    current_pop[,6] = current_pop[,5] + current_pop[,6]#juveniles join adults
    current_pop[,5] = 0 #no more juveniles
  }
  return(current_pop)
}
#==================================================
#Dispersal function, only focusing on overland movement, site specific
#==================================================
dispersal = function(current_pop){
  #------Juveniles moving---------------
  #SiteB juveniles leaving SiteB to go to SiteA
  num_move2SiteA=rbinom(1,current_pop[,5],SiteA_move)
```

```
 #SiteA juveniles leaving SiteA to go to SiteB
 num_move2SiteB=rbinom(1,current_pop[,2],SiteB_move)
 #Changes applied to populations at same time
 current_pop[,2] = current_pop[,2]+num_move2SiteA-num_move2SiteB #changes to SiteA pop
 current_pop[,5] = current_pop[,5]-num_move2SiteA+num_move2SiteB #changes to SiteB pop
 #------Adults moving--------------
 #SiteB adults leaving SiteB to go to SiteA
 num_move2SiteA=rbinom(1,current_pop[,6],SiteA_move)
 #SiteA juveniles leaving SiteA to go to SiteB
 num_move2SiteB=rbinom(1,current_pop[,3],SiteB_move)
 #Changes applied to populations at same time
 current_pop[,3] = current_pop[,3]+num_move2SiteA-num_move2SiteB #changes to SiteA pop
 current_pop[,6] = current_pop[,6]-num_move2SiteA+num_move2SiteB #changes to SiteB pop
 return(current_pop)}
#==================================================
#Simulation function
#==================================================
runsim = function(SiteA_mortality, SiteB_mortality, SiteA_move, SiteB_move){
 full_df = data.frame(matrix(ncol=2,nrow=0))
 colnames(full_df) = c("simulation #",
            "extinct population?")
for (i in 1:1000) {
#==================================================
#Parameter intialization
#==================================================
extinction=FALSE
extinct_pop = ""
#==================================================
```

```
#Population intialization, based off real abundance values
#=================================================
pop          = array(data = 0, dim = c(1,7));
colnames(pop) = c("SiteA_lar", "SiteA_juv","SiteA_adu",
                "SiteB_lar","SiteB_juv","SiteB_adu",
                "timesteps");
#Based on SaraBeths abundance values from reference sites x 5 to reflect 50m reaches
pop[, 1] = 43 #SiteA larvae
pop[, 2] = 37#SiteA juveniles
pop[, 3] = 30 #SiteA adults
pop[, 4] = 43 #SiteB larvae
pop[, 5] = 37 #SiteB juveniles
pop[, 6] = 30 #SiteB adults
pop[, 7] = 1 #simulation number
pop=data.frame(pop)
#=================================================
#Simulation of generation
#=================================================
#if extinction occured in last timestep, stop simulation
while (extinction!=TRUE) {
  current_pop = pop %>% slice(n()) #Retrieve current pop #s from last time step
  current_pop = death(current_pop) #DIE
  current_pop = age(current_pop) #AGE
  current_pop = dispersal(current_pop) #MOVE
 #Checking to see if population went extinct after death or dispersal
 SiteA_pop_size = sum(current_pop[1:3])
 SiteB_pop_size = sum(current_pop[4:6])
 if (SiteA_pop_size<=0 | SiteB_pop_size <=0)
```

```
 {extinction = TRUE}
 #Which population went extinct?
 if (SiteA_pop_size <=0){extinct_pop = "SiteA"}
 if (SiteB_pop_size <=0){extinct_pop = "SiteB"}
  current_pop[,7]=current_pop[,7]+1 #add to timestep counter
  pop = rbind(pop,current_pop) #add current pop to pop_database
}
#=====================================================
#Storing simulation result
#=====================================================
#adding outcome of simulation to database w/simulation number
sim_num = i
full_df[sim_num,]=c(sim_num,extinct_pop)
}
#Calculating extinction risk
extinct_riskA = length(which(full_df$`extinct population?` =="SiteA"))/1000
extinct_riskB = length(which(full_df$`extinct population?` =="SiteB"))/1000
extinct_row = data.frame(SiteA_mortality,
                         SiteB_mortality,
                         SiteA_move,
                         SiteB_move,
                         extinct_riskA,
                         extinct_riskB)
#adding dataframe to csv file
write.table(extinct_row, file = 'extinction_results.csv', sep = ",",
          append = TRUE, quote = FALSE,
          col.names = FALSE, row.names = FALSE)
}
```

```
#==================================================

#Parameter Set

#==================================================

mortality_values = c(0.01,0.05,0.1,0.3,0.5)

move_values = c(0.001,0.01,0.05,0.1,0.2)

model_num = 1

#==================================================

#Running model with all parameter combinations

#==================================================

for (SiteA_mortality in mortality_values){

 for(SiteB_mortality in mortality_values){

  for (SiteA_move in move_values){

   for (SiteB_move in move_values){

    runsim(SiteA_mortality, SiteB_mortality, SiteA_move, SiteB_move)

    print(model_num)

    model_num = model_num + 1

   }

  }

 }

}
```

APPENDIX A2 . Agent-based model code for ‘four-population model’

R version 4.3.2

```
#==================================================

#Loading Packages

#==================================================

library(R.utils)

library(dplyr)

library(tidyverse)
```

```
library(rlist)
#==================================================
#Death function, currently assuming its only area-specific
#==================================================
death = function(current_pop){
  #AreaAB Mortality
  for (i in 1:6){
    num_dead=rbinom(1,current_pop[,i],AreaAB_mortality)
    current_pop[,i] = current_pop[,i]-num_dead}
  #AreaCD Mortality
  for (i in 7:12){
    num_dead=rbinom(1,current_pop[,i],AreaCD_mortality)
    current_pop[,i] = current_pop[,i]-num_dead}
  return(current_pop)
}
#==================================================
#Aging function
#==================================================
age = function(current_pop){
  #------larval2juvenile aging------
  if (current_pop[,13]==7){
    #pop A
    current_pop[,2] = current_pop[,1] + current_pop[,2]#larvae join juvenile pop
    current_pop[,1] = 0 #no more larvae
    #pop B
    current_pop[,5] = current_pop[,4] + current_pop[,5]#larvae join juvenile pop
    current_pop[,4] = 0 #no more larvae
    #pop C
```

```
    current_pop[,8] = current_pop[,7] + current_pop[,8]#larvae join juvenile pop
    current_pop[,7] = 0 #no more larvae
    #pop D
    current_pop[,11] = current_pop[,10] + current_pop[,11]#larvae join juvenile pop
    current_pop[,10] = 0 #no more larvae
  }
  #------juvenile2adult counter------
  if (current_pop[,13]==36){
    #pop A
    current_pop[,3] = current_pop[,2] + current_pop[,3]#juveniles join adults pop
    current_pop[,2] = 0 #no more juveniles
    #pop B
    current_pop[,6] = current_pop[,5] + current_pop[,6]#juveniles join adults pop
    current_pop[,5] = 0 #no more juveniles
    #pop C
    current_pop[,9] = current_pop[,8] + current_pop[,9]#juveniles join adults pop
    current_pop[,8] = 0 #no more juveniles
    #pop D
    current_pop[,12] = current_pop[,11] + current_pop[,12]#juveniles join adults pop
    current_pop[,11] = 0 #no more juveniles
  }
  return(current_pop)
}

#==================================================
#Dispersal function, only focusing on overland movement, pop and area specific
#==================================================
dispersal = function(current_pop){
```

```
#----------------------Different Watershed Movement--------------------------
#------Juveniles moving---------------
#popC juveniles leaving popC to go to popB
num_move2popB=rbinom(1,current_pop[,8],AreaAB_move)
#pop B juveniles leaving popB to go to popC
num_move2popC=rbinom(1,current_pop[,5],AreaCD_move)
#Changes applied to population at same time
current_pop[,5] = current_pop[,5]+num_move2popB-num_move2popC #changes to popB
current_pop[,8] = current_pop[,8]-num_move2popB+num_move2popC #changes to popC
#checking for negatives
if (current_pop[,5]<0)
{(current_pop[,8] = current_pop[,8] + current_pop[,5]) & (current_pop[,5]=0)}
if (current_pop[,8]<0)
{(current_pop[,5] = current_pop[,5] + current_pop[,8]) & (current_pop[,8]=0)}
#------Adults moving---------------
#popC adults leaving popC to go to popB
num_move2popA=rbinom(1,current_pop[,9],AreaAB_move)
#popB juveniles leaving popB to go to popC
num_move2popB=rbinom(1,current_pop[,6],AreaCD_move)
#Changes applied to populations at same time
current_pop[,6] = current_pop[,6]+num_move2popB-num_move2popC #changes to popB
current_pop[,9] = current_pop[,9]-num_move2popB+num_move2popC #changes to popC
#checking for negatives
if (current_pop[,6]<0) {(current_pop[,9] = current_pop[,9] + current_pop[,6]) &
(current_pop[,6]=0)}
if (current_pop[,9]<0) {(current_pop[,6] = current_pop[,6] + current_pop[,9]) &
(current_pop[,9]=0)}
#-------------------------Paired Stream Movement--------------------------
```

```
#------Juveniles moving---------------
#popB juveniles leaving popB to go to popA
num_move2popA=rbinom(1,current_pop[,5],popA_move)
#popA juveniles leaving popA to go to popB
num_move2popB=rbinom(1,current_pop[,2],popB_move)
#popD juveniles leaving popD to go to popC
num_move2popC=rbinom(1,current_pop[,11],popC_move)
#popC juveniles leaving popC to go to popD
num_move2popD=rbinom(1,current_pop[,8],popD_move)
#Changes applied to populations at same time
current_pop[,2] = current_pop[,2]+num_move2popA-num_move2popB #changes to popA
current_pop[,5] = current_pop[,5]-num_move2popA+num_move2popB #changes to popB
current_pop[,8] = current_pop[,8]+num_move2popC-num_move2popD #changes to popC
current_pop[,11] = current_pop[,11]-num_move2popC+num_move2popD #changes to popD
#Checking for negatives and correcting if necessary
if (current_pop[,2]<0) {(current_pop[,5] = current_pop[,5] + current_pop[,2]) &
(current_pop[,2]=0)}
if (current_pop[,5]<0) {(current_pop[,2] = current_pop[,2] + current_pop[,5]) &
(current_pop[,5]=0)}
if (current_pop[,8]<0) {(current_pop[,11] = current_pop[,11] + current_pop[,8]) &
(current_pop[,8]=0)}
if (current_pop[,11]<0)  {(current_pop[,8] = current_pop[,8] + current_pop[,11]) &
(current_pop[,11]=0)}
#------Adults moving---------------
#popB adults leaving popB to go to popA
num_move2popA=rbinom(1,current_pop[,6],popA_move)
#popA juveniles leaving popA to go to popB
num_move2popB=rbinom(1,current_pop[,3],popB_move)
```

```
         #popD adults leaving popD to go to popC
         num_move2popC=rbinom(1,current_pop[,12],popC_move)
         #popC juveniles leaving popC to go to popD
         num_move2popD=rbinom(1,current_pop[,9],popD_move
        #Changes applied to populations at same time
         current_pop[,3] = current_pop[,3]+num_move2popA-num_move2popB #changes to popA
         current_pop[,6] = current_pop[,6]-num_move2popA+num_move2popB #changes to popB
         current_pop[,9] = current_pop[,9]+num_move2popC-num_move2popD #changes to popC
         current_pop[,12] = current_pop[,12]-num_move2popC+num_move2popD #changes to popD
        #Checking for negatives and correcting if necessary
         if (current_pop[,3]<0) {(current_pop[,6] = current_pop[,6] + current_pop[,3]) &
(current_pop[,3]=0)}
         if (current_pop[,6]<0){(current_pop[,3] = current_pop[,3] + current_pop[,6]) &
(current_pop[,6]=0)}
         if (current_pop[,9]<0) {(current_pop[,12] = current_pop[,12] + current_pop[,9]) &
(current_pop[,9]=0)}
         if (current_pop[,12]<0) {(current_pop[,9] = current_pop[,9] + current_pop[,12]) &
(current_pop[,12]=0)}
         return(current_pop)}
        #==================================================
        #Simulation function
        #==================================================
        runsim = function(AreaAB_mortality,
                  AreaCD_mortality,
                  AreaAB_move,
                  AreaCD_move,
                  popA_move,
                  popB_move,
```

```
               popC_move,
               popD_move){
  full_df = data.frame(matrix(ncol=2,nrow=0))
  colnames(full_df) = c("simulation #",
                    "extinct population?")
for (i in 1:1000) {
#====================================================
#Parameter intialization
#====================================================
extinction=FALSE
extinct_pop = ""
#====================================================
#Population intialization, used real abundance values
#====================================================
pop          = array(data = 0, dim = c(1,13));
colnames(pop) = c("popA_lar","popA_juv","popA_adu",
               "popB_lar","popB_juv","popB_adu",
               "popC_lar","popC_juv","popC_adu",
               "popD_lar","popD_juv","popD_adu",
               "timesteps");
#Based on SaraBeths abundance values from reference sites x 5 to reflect 50m reaches
pop[, 1] = 43 #popA larvae
pop[, 2] = 37#popA juveniles
pop[, 3] = 30 #popA adults
pop[, 4] = 43 #popB larvae
pop[, 5] = 37 #popB juveniles
pop[, 6] = 30 #popB adults
pop[, 7] = 43 #popC larvae
```

```
pop[, 8] = 37#popC juveniles
pop[, 9] = 30 #popC adults
pop[, 10] = 43 #popD larvae
pop[, 11] = 37 #popD juveniles
pop[, 12] = 30 #popD adults
pop[, 13] = 1
pop=data.frame(pop)
#==================================================
#Simulation of generation
#==================================================
#if extinction occured in last timestep, stop simulation
# for (i in 1:100){
while (extinction!=TRUE) {
  current_pop = pop %>% slice(n()) #Retrieve current pop #s from last time step
  current_pop = death(current_pop) #DIE
  current_pop = age(current_pop) #AGE
  current_pop = dispersal(current_pop) #MOVE

  #Checking to see if population went extinct after death or dispersal
  popA_size = sum(current_pop[1:3])
  popB_size = sum(current_pop[4:6])
  popC_size = sum(current_pop[7:9])
  popD_size = sum(current_pop[10:12])
  pops=c(popA_size,popB_size,popC_size,popD_size)
  if (any(pops<=0)){extinction = TRUE}
  #Which population went extinct?
  if (popA_size <=0){extinct_pop = "popA"}
  if (popB_size <=0){extinct_pop = "popB"}
```

```
  if (popC_size <=0){extinct_pop = "popC"}
  if (popD_size <=0){extinct_pop = "popD"}
  current_pop[,13]=current_pop[,13]+1 #add to timestep counter
  pop = rbind(pop,current_pop) #add current pop to pop_database
}
#==================================================
#Storing simulation result
#==================================================
#adding outcome of simulation to database w/simulation number
sim_num = i
full_df[sim_num,]=c(sim_num,extinct_pop)}
extinct_riskA = length(which(full_df$`extinct population?` =="popA"))/1000
extinct_riskB = length(which(full_df$`extinct population?` =="popB"))/1000
extinct_riskC = length(which(full_df$`extinct population?` =="popC"))/1000
extinct_riskD = length(which(full_df$`extinct population?` =="popD"))/1000
extinct_row = data.frame(AreaAB_mortality,
                         AreaCD_mortality,
                         AreaAB_move,
                         AreaCD_move,
                        popA_move,
                        popB_move,
                        popC_move,
                         popD_move,
                         extinct_riskA,
                         extinct_riskB,
                        extinct_riskC,
                        extinct_riskD)
write.table(extinct_row, file = 'metapop_extinction_results.csv', sep = ",",
```

```
      append = TRUE, quote = FALSE,
      col.names = FALSE, row.names = FALSE)}
#=====================================================
#Parameter Set
#=====================================================
mortality_values = c(0.05,0.3)
pop_values = c(0.01,0.05,0.1)
area_values = c(0.005,0.01,0.05)
model_num = 1
#=====================================================
#Running model with all parameter combinations
#=====================================================
for (AreaAB_mortality in mortality_values){
 for(AreaCD_mortality in mortality_values){
  for (AreaAB_move in area_values){
   for (AreaCD_move in area_values){
    for(popA_move in pop_values){
     for (popB_move in pop_values){
      for (popC_move in pop_values){
       for (popD_move in pop_values){
        runsim(AreaAB_mortality,
            AreaCD_mortality,
            AreaAB_move,
            AreaCD_move,
            popA_move,
            popB_move,
            popC_move,
            popD_move)
```

```
print(model_num)

model_num = model_num + 1}}}}}}}}
```

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PUBLICATIONS

Greene, K.M., J. Van Cleve, and S.J. Price. 2023. Salamander movement propensity resist effects of supraseasonal drought**.** Ichthyology & Herpetology 111(1): 109-118.

Lovich, J.E., J.W. Gibbons, and **K.M. Greene**. 2018. Life history of the diamond-backed terrapin with emphasis on geographic variation. In, Roosenburg W.M. and V.S. Kennedy (eds.). Ecology and conservation of the diamond-backed terrapin Malaclemys terrapin. Johns Hopkins University Press, Baltimore.

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GRANTS AND AWARDS

2023. Association of Southeastern Biologists Student Research Award
2023. Southeastern Partners of Amphibian and Reptile Conservation Oral Presentation Award
2020. Kentucky Society of Natural History Research Grant
2019. National Science Foundation Graduate Research Fellowship Program
2019. Eller Billings Summer Research Mini-Grant, UK Appalachian Center Research Grant
2018. University of Kentucky's Biology summer Fellowship Summer Research Grant
2018. Gertrude Flora Ribble Research Fellowship
2016. Davidson Research Initiative Summer Research Grant
2016. Association of Southeastern Biologists Oral Presentation Award in Animal Biology