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Abstract approved:

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Investigation into how animals move within the landscape is important for both understanding of ecological processes and conservation management. Animal movement is important in shaping life history transitions, demographics, individual fitness, and species distributions. However, as landscapes become increasingly affected by human activities, movement becomes important as species navigate landscapes experiencing habitat fragmentation, isolation, and degradation. To address how human activities are changing animal movement, there is a need to understand the movement patterns and behaviors of an animal during early life stages. Amphibian species often have bi-phasic life histories with aquatic larval tadpoles and terrestrial juveniles and adults. All dispersal between populations and across the landscape occurs during these terrestrial stages. In particular, the juvenile life stage is thought to be an important dispersal stage, but has been understudied in amphibian biology. In this dissertation, I performed several projects investigating the factors that shape juvenile movement and how aquatic conditions before metamorphosis may express latent effects on these behaviors. I also examined how these observed behaviors may affect the population connectivity in future climates. The movement behavior of juveniles was strongly influenced by the identity of the species, environmental conditions, and individual size. Aquatic environments expressed latent effects on juvenile amphibian size, but not directly on movement behavior. Terrestrial environmental conditions were also important with dry terrain and low ambient humidity associated with increased movement distances. Using an individual-based simulation model, the observed effect of environmental conditions on movement behavior also reduced population connectivity in future climate conditions, when compared to current climates. Movement ecology is a growing field, and through the application of various tools and techniques that are being developed we can fill in the gap of knowledge around amphibian terrestrial movement.

Jumping in with Both Feet: Exploring Factors that Shape Juvenile Amphibian Movement

by
Evan M. Bredeweg

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Evan M. Bredeweg, Author

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DEDICATION

To my son for his energy, love, and future dreams

&

To my wife for her unwavering support and encouragement through my successes and times of poor humor.

JUMPING IN WITH BOTH FEET: EXPLORING FACTORS THAT SHAPE JUVENILE AMPHIBIAN MOVEMENT

CHAPTER 1 – INTRODUCTION

Movement is a central and integral aspect of animal biology. Animal behaviors such as foraging, predator avoidance, and reproduction all require some element of movement within and across habitats. Movement represents a complex behavior that is the expressed result of multiple needs of an organism combined with individual response to the environment (Semlitsch, 2008). In addition, movement is the product of an organism's history and experience (Benard and McCauley, 2008; Burgess et al., 2012). These individual scale movement behaviors across a species determine the spatial extent, pattern, and dynamics of a population and its role in the ecosystem (Lowe et al., 2008; Nams, 2005; Revilla et al., 2004; Stevens et al., 2006a).

Human modifications to the landscape have changed the underlying environment and ecology by altering the risks and benefits associated with wildlife movement (Baguette and Dyck, 2007). Anthropogenic changes in land cover interrupt the continuity of habitats with non-habitat areas (matrix) which can leave remnant habitat areas (patches) isolated in a landscape (Pope et al., 2000). The process of habitat fragmentation is a hallmark of human modified landscapes and has greatly increased habitat isolation for many species (Fischer and Indenmayer, 2007). In order to understand the impacts of human modifications to the landscape, a central focus of wildlife research has been to understand how animal species change their movement patterns in response to stress. With the loss and isolation of wildlife habitat, a major concern is the preservation of individuals moving between distinct populations (connectivity) in order to maintain gene flow (Safner et al., 2010; Stevens et al., 2006b). Both population genetics and metapopulation theory have established the importance of connectivity to wildlife persistence within landscapes (Greenwald, 2010; Purrenhage et al., 2009). Extrapolating this population centric view to the landscape level, landscape ecology research has focused on the response of species' movement to changes in arrangement, composition, and shape of landscape elements (Fahrig, 2003; Fahrig et al., 2011; Wiens, 1976).

This landscape-scale research allows the for the quantification of population connectivity based on habitat structure and other emergent properties of the landscape (e.g. diffusion models and landscape resistance surfaces; McRae, 2006). Yet, such simplification ignores the behavior shaping this pattern: population connectivity is the result of animal movement behavior. Landscape-scale movements of wildlife are the amassed result of animal movement choices in response to their environment (Revilla et al., 2004). In order to understand movements on the population scale, we must understand smaller scale movement behaviors, and factors and stressors that serve as mechanisms of movement decisions (Nathan, 2008). Therefore, preservation and conservation of wildlife species requires our understanding all integrated aspects of their biology, including movement behavior in response to human land use.

The identification of scale is critically important in landscape ecology, as well as movement behavior (Table 1.1). To date, landscape ecology has primarily focused on dispersal and migration movements, whereas movement ecology has focused on the factors that drive and shape all movement types (Nathan et al., 2008). This more generalized, and integrated animal-centric approach allows researcher to evaluate factors that impact all aspects of a species' biology that involve movement. Integration at the landscape level is vital for effective conservation practices because, like the pressures that affect wildlife populations, implementation of conservation occurs across a variety of scales (Saab, 1999).

Available techniques and technologies to record movement across scales requires tailoring to specific species; and challenges exist with doing so for each individual species. For some species, capture-mark-recapture (CMR) methods have been a classic approach used to examine movement over several years (Baguette and Dyck, 2007). On an individual scale, technological advancements have improved tracking methods which include radio telemetry to new technologies such as Global Positioning System (GPS) tracking and genetic measures of connectivity (Schofield et al., 2013; Stevens et al., 2006b). Radio telemetry and GPS tracking are dependent on battery power and attachment methods which have primarily driven research on larger or easily collared animals (Bowyer et al., 1998). Genetic analyses are expensive and cannot examine small-scale or contemporary movements because of the scale of genetic structure and the inherent lag in genetic signals (Coster et al., 2015). CMR methods rely on the ability to permanently mark animals and require extensive investments of labor and time (Govindarajulu et al., 2005). Such challenges and limitations have left the movement behavior of a variety of wildlife, such as terrestrial amphibians, fossorial species, and biphasic stream insects, conspicuously understudied.

While challenges exist in field-based studies of movement for all species, , experimental manipulations provide an alternative opportunity (Stevens et al., 2006a). Instead of tracking natural movements to infer about behaviors, experimental manipulation allows for observation of behavioral responses during specific movement phases. These observation and experimental results then can be used in population modeling frameworks to extend findings to landscape scales (Chelgren et al., 2008; Gurarie, 2008; Stevens et al., 2006b). While experimental movement responses typically cannot exactly replicate a natural environment, careful selection of our experimental factors and design can provide insight on how specific factors about the landscape will change movement behavior.

Technical challenges with tracking and data limitations has left amphibian species movement ecology largely a mystery (Pittman et al., 2014). Yet, amphibians are a group of international conservation concern, with 32.4% of species listed as threatened or extinct as a result of stressors such as environmental contaminants, invasive species, disease, and of course habitat loss and modification (Blaustein et al., 2002; IUCN, 2014). Amphibian species are particularly vulnerable because of their reliance on wetland and pond habitats that are often situated in landscapes dominated by humans. In addition, historical removal of wetlands to create arable land and close proximity to other human land uses has made habitat modification and fragmentation a major concern for this group (Piha, 2006).

Pond-breeding amphibians have biphasic lifecycles whereby they have aquatic eggs and larvae (tadpoles) and terrestrial juveniles and adults. As a result, they rely on aquatic and terrestrial habitats for their complete lifecycle, making amphibians sensitive to the spatial arrangement, quality, and availability of both habitat types (Earl and Semlitsch, 2013; Johansson et al., 2005). To access aquatic and terrestrial habitats, amphibians regularly migrate between ponds and upland areas. Additionally, populations rely on movements in addition to individuals annual migration to maintain connectivity between isolated breeding ponds (Funk et al., 2005; Popescu and Hunter, 2011; Todd et al., 2009). The primary dispersal stage of many amphibian species is the emerging juvenile stage, or metamorphs (Osbourn et al., 2014; Semlitsch, 2008). The importance of the juvenile life-stages in the demographic trajectory of a population, in addition to their role in dispersal, mean that information on emerging metamorphs represent an important opportunity for conservation (Gibbons et al., 2006; Popescu and Hunter, 2011).

Given the need to navigate the terrestrial environment after emerging from a aquatic environment, amphibians illustrate remarkable developmental, morphological and behavioral plasticity to stressors. This plasticity can drastically alter the ecology of larvae and may have significant impacts on later life stages as well (Denver et al., 1998; Morey et al., 2004; Relyea, 2004; Shaffery, 2013). There is evidence that responses to larval stressors such as predator exposure and hydroperiod can have lasting effects on the size, behavior, and movement of terrestrial juveniles (Barbasch and Benard, 2011; Rohr and Palmer, 2005; Van Allen et al., 2010). The influence of latent effects of larval stressors on the movement behavior have potential ramifications for population dynamics at the landscape and population scale (Benard and McCauley, 2008; Pechenik, 2006).

This dissertation focuses on how aquatic stressors and terrestrial conditions interact to shape the physical traits and movement behaviors of amphibians. With the limited experience of newly emerged juveniles, stressors of the aquatic environment may change movement behaviors that can accumulate to influence long term displacement of an organism (Figure 1.1). I used experimental approaches to disentangle the relative importance of environmental conditions with latent effects including species identity (Chapter 2), aquatic hydroperiod (Chapter 3), and aquatic predator exposure (Chapter 4). Finally, I examined the implications of changing movement behavior for population connectivity when environmental-based landscape-level dispersal interacts with a changing climate (Chapter 5). Through these projects, I contributed to the growing study of amphibian movement research and work to place the effects of amphibian plasticity into a broader landscape-level context for the ecology of these species.

Table 1.1 – Descriptions of distinct amphibian movement types across various scales.

Movement	**Description**	**Scale**	**Examples**
Dispersal	One-way movement	Large Scale	Natal, Breeding
Migration	Round-trip movement	Medium to Large Scale	Seasonal, Daily
Phase	Movement to achieve some goal or need	Small to Medium Scale	Foraging, Resting, Predator Escape
Step	Smallest unit of movement	Small Scale	Moving, Stopped, Direction change

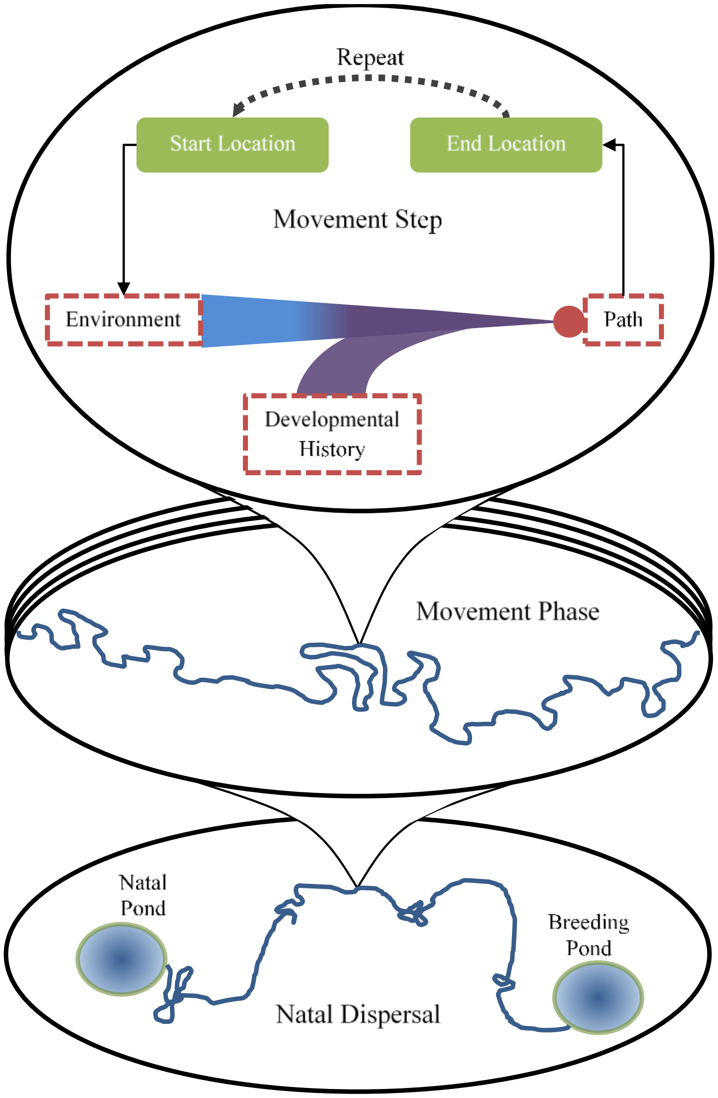

Figure 1.1 – Larval stressors that change the movement tendencies and decisions of amphibians on the step or phase scale will impact movement on larger scales. Figure was adapted from Nathan (2008). The first section illustrates how larval stressors and environment may influence movement steps. These movement steps are aggregated to create the expressed movement phases. Groups of movement phases then compile through time to create the long-distance movements, such as natal dispersal.

JUMPING IN WITH BOTH FEET: EXPLORING FACTORS THAT SHAPE JUVENILE AMPHIBIAN MOVEMENT

CHAPTER 2 – THE INTEGRATIVE EFFECTS OF BEHAVIOR AND MORPHOLOGY ON AMPHIBIAN MOVEMENT

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Abstract

Animal movement and dispersal are key factors in population dynamics and support complex ecosystem processes like cross-boundary subsidies. Juvenile dispersal is an important mechanism for many species and often involves navigation in unfamiliar habitats. For species that metamorphose, such as amphibians, this transition from aquatic to terrestrial environments involves the growth and use of new morphological traits (e.g. legs). These traits strongly impact the fundamental ability of an organism to move in novel landscapes, but innate behaviors can regulate choices that result in the realized movements expressed. By assessing the integrative role of morphology and behavior, we can improve our understanding of juvenile movement, particularly in understudied organisms like amphibians. We assessed the roles of morphological (snout-vent length and relative leg length) and performance (maximal jump distance) traits in shaping the free movement paths, measured through fluorescent powder tracking, in three anuran species, Pacific treefrog (*Hyliola regilla*), Western toad (*Anaxyrus boreas*), and Cascades frog (*Rana cascadae*). We standardized the measurement of these traits to compare the relative role of species' innate differences versus physical traits in shaping movement. Innate differences, captured by species identity, was the most significant factor influencing movement paths via total movement distance and path sinuosity. Relative leg length was an important contributor but significantly interacted with species identity. Maximal jump performance, which was significantly predicted by morphological traits, was not an important factor in movement behavior relative to species identity. The importance of species identity and associated behavioral differences in realized movement provide evidence for inherent species differences being central to the dispersal and movement of these species. This behavior may stem from niche partitioning of these sympatric species, yet it also calls into question assumptions generalizing anuran movement behavior. These species level effects are important in framing differences as past research is applied in management planning.

Introduction

Movement and dispersal of organisms across a landscape are key drivers of ecosystem function. This repositioning of individuals is central to processes such as nutrient cycling, population genetics, and cross-boundary subsidies (Baguette et al., 2013; Bohonak and Jenkins, 2003; Carlson et al., 2016; Massol et al., 2011). Animal dispersal, broadly defined by Bowler & Benton (2005) as "movement between habitat patches", is often characterized by resource or environmentally directed movements that are strongly influenced by organismal condition, and involves shifts in habitat during natural growth and development (e.g., green sea turtles: Arthur, Boyle, & Limpus, 2008; migrant passerines: Chernetsov, 2006; anadromous salmonids: Kahler, Roni, & Quinn, 2001). Therefore, the study of dispersal requires a life history framework to better understand the integrative effects of movement to a species' ecology across ontogenetic transitions (Benard and McCauley, 2008; Whitlatch et al., 1998).

Juvenile dispersal is a movement phase that is often a major life history transition, requiring individuals to navigate new and unfamiliar habitats (Clobert et al., 2012; Popescu et al., 2012a). For example, amphibian and macroinvertebrate metamorphosis, with subsequent transition from aquatic to terrestrial habitats, represents a distinct shift in habitat in which movement ability is dependent on newly acquired morphological traits, such as legs and wings (Bilton et al., 2001; Rowe and Ludwig, 1991; Smith and Green, 2005). While these morphological traits allow for simple quantification, the link between these emerging traits, behavior, and dispersal ability is not clearly established (Sekar, 2012). We posit that the ability to disperse into new and unfamiliar habitats may be more strongly regulated by behavior than morphology (Dyck and Baguette, 2005). Individual variation in the ability to move and the choice of how to move could have critical implications for survival and fitness (Bonte et al., 2012).

Behaviors, such as movement timing, directionality, and microhabitat preference, strongly regulate the potential movement ability of an organism (Rehage and Sih, 2004). For example, a highly mobile hummingbird (green hermit, *Phaethornis guy*) will increase movement distance and path sinuosity to remain in their preferred forested habitats while homing through a complex composition landscape (Hadley and Betts, 2009). Organisms experiencing unfamiliar habitats, such as newly-metamorphosed amphibians experiencing terrestrial habitats for the first time, must rely heavily on innate behaviors to guide their movements (Popescu et al., 2012a; Rothermel, 2004). Thus, the integration of morphological and behavioral trait response may be the guiding principle in shaping juvenile orientation and dispersal (Patrick et al., 2008).

Movement is not only important for the fulfillment of resource needs and life history transitions, but can be an important mechanism to allow for species coexistence (Jeltsch et al., 2013). Differences in movement behavior of ecologically similar spadefoot toad species provide a mechanism to reduce competition (Székely et al., 2017). High-eleveation pond-breeding amphibian communities rely on shared habitats during a narrow breeding window (Lannoo, 2005). This results in overlapping development and emergence creating a scenario with intense intra- and interspecific competition: variability in movement behaviors between species and within cohorts could reduce this competition pressure (Harper and Semlitsch, 2007).

In this study, we use a behavioral and morphological framework to understand amphibian movement ecology. Further, we apply this conceptual model to juvenile life stages, a critically under-studied life history stage that coincides with transitional movement from aquatic to terrestrial habitats (Cline and Hunter, 2016; Ramírez et al., 2017; Roe and Grayson, 2008). Laboratory-based quantification of individual performance measures, such as jumping ability, speed, and endurance, have been commonly used as proxies for individual dispersal and natural movement (Binning et al., 2017; Llewelyn et al., 2010; Louppe et al., 2016; Phillips et al., 2006). Body size and morphology have also been important determinants of individual performance and in some cases dispersal (John-Alder and Morin, 1990; Yagi and Green, 2017). Important measures have included leg length and body size to predict movement ability of juvenile amphibians (Gomes et al., 2009; Tejedo et al., 2000). We used an experimental approach to assess the roles of individual performance ability, morphological traits, and species-specific intrinsic behavior in shaping realized movement. Understanding how juvenile amphibians, with limited experience, adjust to both new morphological traits and habitats will provide insights into potential constraints on dispersal and movement in a taxon of conservation concern (Pittman et al., 2014).

Our objective was to compare the role of morphological and species-specific traits in shaping movement paths of amphibians in a transitional phase using three sympatric amphibian species, Pacific Treefrog (*Hyliola regilla*), Western Toad (*Anaxyrus boreas*), and Cascades Frog

(*Rana cascadae*). To do this, we quantified athletic performance and morphometrics by measuring maximal jump distance, snout-vent length, and leg morphology. We then used fluorescent powder tracking in a bare agricultural field to observe and quantify the free-movement behavior of these individuals. These three species comprise the anuran community of high elevation ponds in the Cascade Mountains of Oregon with similar reproductive and emergence phenologies. By representing three distinct anuran families, each with their unique adaptations, we can compare the relative contributions individual performance and morphology with species-level differences on movement. We hypothesized that during this transitional phase, variation in movements would be best explained by innate differences between species, whereas morphological and performance-based variation would play a minor role.

Methods

Collection and Rearing

Egg masses of each species were collected from five breeding sites in the central Oregon Cascades between 1800 - 2050 m elevation during the summer breeding season of 2014. Individuals were collected from at least six separate clutches per species per population to reduce clutch effects. Embryos were pooled by species and reared to hatching in a temperature-controlled environmental chamber set at 15 °C with a 12L:12D photoperiod at Oregon State University. Within 8 hours of hatching, individuals were grouped by species and raised in an outdoor mesocosm array.

The outdoor mesocosm array consisted of 30, 120-L HDPE plastic tubs filled with well-water and stocked at a constant density of 30 individuals of a species per mesocosm. Outdoor mesocosms were located in the Willamette Valley at Oregon State University’s Lewis-Brown Horticulture Farm. Given these species exist across a gradient of hydroperiod conditions, we randomly assigned individuals to mesocosms with either a permanent or ephemeral hydroperiod to simulate more natural conditions and determine if the larval environment had any latent effect on juveniles. Water volume in the permanent hydroperiod mesocosms (n=15 tubs) was maintained at 100 L throughout the course of development, resulting in a density of 0.3 individuals/L. Water volume in the ephemeral hydroperiod mesocosms (n=15 tubs) was reduced at a rate of 8 L every 5 days, beginning with 100 L water volume (0.3 individuals/L) and ending with 12 L water volume (2.5 individuals/L) over the course of 60 days. While part of the initial experimental design, larval mesocosm condition did not impact any quantified movement parameters and was instead included as a blocking variable in our analyses. Mesocosms were checked daily for juveniles emerging onto floating platforms starting at day 20 or at Gosner (1960) stage 42.

Upon emergence, animals were moved to a temperature-controlled environmental chamber set at 20 °C with a 12L:12D photoperiod at Oregon State University and maintained in 5-L HDPE plastic containers grouped by mesocosm and fed wingless fruit flies *ad libitum.* Individuals were held for at least 10 days to ensure they had survived metamorphosis and were accepting food as juveniles.

Experimental Design

We assessed maximal jump performance and movement behavior for each individual (total n=175) on the same day. The experiment was blocked across 7 trial days (September 24, 25, 27 – October 1, 2014). Twenty-four individuals were assessed on a single trial day except for Day 7 when 33 animals were sampled. Each trial day included an equally representative sample of all three species (n=8 per species). Logistical demands required all remaining individuals to be run on day 7 (*H. regilla*: n=14, *A. boreas*: n=12, and *R. cascadae*: n=7).

Maximal jump performance was measured as the longest observed jump across two trials of four jumps with a minimum of two hours of rest in between trials (John-Alder and Morin, 1990). Jump trials took place during the day between the hours of 10:00 and 17:00 on a cleaned, sterilized, and dry lab bench. Individuals jumped along the bench, stimulated with an approaching gloved hand, and gentle prods of the individual’s posterior were used when animals stopped jumping for more than 2 seconds (Mitchell and Bergmann, 2016). After four jumps were recorded, animals were held in individual perforated plastic 1-cup containers with moisten paper towels until their next measurement. After the conclusion of the jump trials, individuals were measured for snout-vent length and mass. After at least 2 hours of additional rest time, individuals were transported to Hyslop Field Lab where we measured free-movement behavior in a plowed and smoothed dirt field. This environment allowed for a standardized surface for all individuals and acted to limit the effect of microhabitat on movement. Movement measurements began after sunset at 20:00 (around nautical twilight) on nights free of precipitation to standardize abiotic conditions as much as possible. We used only dim red lights during the releases to minimize the effect of artificial lighting on behavior. We implemented a staggered release schedule over 60 minutes and provided each individual 60 minutes of free movement. Each individual was placed at least 10 m away from the nearest individual to limit interactions from influencing movements. Individuals were lightly dusted with fluorescent tracking powder (ECO Pigments, Day-Glo Color Corp.) and placed on a petri dish lid under a cover object for a 5-minute acclimation period. After acclimation, cover objects were gently removed, and individuals were given 60 minutes to freely move about the field. After 60 minutes, individuals were located using UV lights and their final position was marked. The first individual was recapture at 21:05, we recaptured in the same sequence with the last recaptured at 22:05. The movement path of each individual during the trial was then observable via tracking the powder residue on the ground under UV illumination. We measured total path length and net distance from start using measuring tapes.

Measures of abiotic conditions for each night were measured using the AgriMet Weather Station (CRVO) onsite for nightly temperature, relative humidity, wind speed and direction, and 24-hour precipitation history (Table 2.1). Upon completion of both jump and movement trails, all individuals were humanely euthanized using MS-222 and preserved in 70% ethanol. Preserved animals were then photographed on a gridded and scaled background for measurement of average rear leg lengths in ImageJ (Schneider et al., 2012).

Statistics

Morphology and Jumping Ability

To investigate the factors that influenced maximal jump performance, we fit a linear regression model to the data from all species and individuals (Table 2.2). Since there are inherent differences in jumping ability between species, the response variable of maximal jump performance was centered by subtracting the mean and scaled by dividing by the standard deviation for each species to account for this variation while making the general athletic ability of each individual comparable between species (Emerson, 1978). The predictor variables of this model were species, snout-vent length (SVL), relative leg length (RLL). Larval mesocosm conditions and trial day were included as blocking factors. Interactions of species with all morphometric measurements were included to allow for species-specific effects on predictor variables. Both the values for SVL and RLL were centered and scaled (subtracting the mean and dividing by the standard deviation) within each species to again account for species-specific morphological differences. Relative leg length was calculated as the ratio of average rear leg length (mm) to snout-vent length (mm). All effects discussed are back-transformed onto the original response-variable scale.

Morphology and Movement

Our analysis of movement path shape included response variables of total movement distance and straightness index (Nosek et al., 2012). We performed an analysis of movement paths using a multivariate linear regression model with both response variables fit simultaneously (Table 2.2). The variable of total movement distance was log-transformed to correct for non-normality. The path sinuosity measure was determined by the ratio of total distance moved to net distance from start to finish. This index measure of path straightness ranges from 0 to 1; movement paths closer to 1 approached straight lines and paths closer to zero exhibited increasing sinuosity. This model similarly used species, SVL, RLL, larval mesocosm condition, and trial day as predictor variables, with SVL and RLL centered and scaled (subtracting the mean and dividing by the standard deviation) for each species. We included interaction terms for species and all morphometric variables to allow for species-specific effects of predictor variables. Using this model, Pillai’s trace tested for significant effects of predictor variables on movement paths. In addition, we compared the relative proportion of total variance explained by predictor variables using a measure of η^2_{partial} (partial eta-squared).

Jumping Ability and Movement

Performance measures such as jumping ability have been useful proxies for individual fitness and dispersal ability (Mitchell and Bergmann, 2016; Pough, 1989). To avoid multicollinearity we did not include jump performance with the morphometric predictor variables in the analysis of movement path. Yet jump performance could have an important connection to the free movement of these amphibians. To explore the relevance of maximal jump performance, we built an additional multivariate linear regression model with the same movement path response variables and replaced morphometric measurements with jump performance (Table 2.2). Maximal jump distances were centered and scaled (subtracting the mean and dividing by the standard deviation) for each species to correct for inherent differences in ability. The predictor variables of this model included species and the interaction of species with jump performance. In addition to jump performance and species, we included larval mesocosm condition and experimental night as blocking variables. We again tested variables for significance using Pillai's trace and compared the relative proportion of total variance explained by predictor variables using a measure of η^2_{partial}.

All statistical tests were performed in R (version 3.4.0; R Core Team, 2017) using packages 'car' (Fox and Weisberg, 2011), 'heplots' (Fox et al., 2016), and 'ggplot2' (Wickham, 2009) for analysis and creation of graphs.

Results

The three species included in our study had distinct jumping abilities and movement behaviors (Figure 2.1). The average maximal jump distance for *A. boreas* was 5.06 cm (n = 60, SD = 0.97), which was shorter relative to *R. cascadae* and *H. regilla*, with average maximal jumps of 13.4 cm (n = 53, SD = 1.88) and 18.7 cm (n = 60, SD = 4.55), respectively. The movement paths for *A. boreas* were short and sinuous (total distance: $\bar{x}$ = 1.95m, SD = 1.7; straightness index: $\bar{x}$ = 0.57, SD = 0.26). *Rana cascadae* movement paths closely resembled those of *A. boreas* (total distance: $\bar{x}$ = 1.88m, SD = 2.3; straightness index $\bar{x}$ = 0.63, SD = 0.27). The movements of *H. regilla* were the longest and straightest of the three species tested (total distance: $\bar{x}$ = 5.29m, SD = 5.1; straightness index: $\bar{x}$ = 0.78, SD = 0.21).

Morphology and Jumping Ability

From a biomechanical perspective, there is evidence of a strong relationship between morphometric measures and jump performance (Emerson, 1978). Our results found that across all species, the snout-vent length was the most significant predictor of maximal jump performance ($F_{1,158} = 72.2$, $p < 0.0001$;Table 2.3). This effect of SVL on jumping performance indicated an increase in maximal jumping distance with increasing SVL (Figure 2.2). This was in addition to a significant interaction of species and SVL ($F_{2,158} = 3.36$, $p = 0.037$), where the strength of this effect of SVL and jumping performance was significantly smaller for *A. boreas*. An individual's relative leg length also had a significant direct effect on maximal jump performance ($F_{1,158} = 4.85$, $p = 0.029$) and significant interaction with species ($F_{2,158} = 3.12$, $p = 0.047$). Individuals with relatively longer legs for their body length showed increased maximal jump performance (Figure 2.2). The relationship of RLL and maximal jump performance was significantly stronger in *H. regilla*.

Morphology and Movement

Movement paths were significantly affected by species identity (Pillai's trace = 0.258, $F_{4,314} = 4.85$, $p < 0.0001$) and RLL (Pillai's trace = 0.085, $F_{2,156} = 4.85$, $p = 0.001$), as well as the interaction between these two variables (Pillai's trace = 0.030, $F_{4,314} = 4.85$, $p = 0.046$; Table 2.4). The specific effects on path sinuosity involved the interaction of species identity and RLL. Path shape became more sinuous for *A. boreas* as RLL increased, yet RLL had minimal impact on path shape for the other two species (Figure 2.3). While both species identity and the morphometric trait of RLL were significant predictors in our model, our analysis revealed that species identity explained a higher proportion of the relative proportion of total variance in movement paths (Species identity = 12.9%, RLL = 8.5%; Figure 2.4). Only species identity was a significant predictor of total movement distance. Total movement distance was only impacted by species identity with *H. regilla* increasing total distance by 210% (95% CI:135%-325%) compared to the other two species.

Jumping Ability and Movement

Our analysis of movement path variables with both species identity and maximal jump performance indicated that species identity was also the only significant predictor of movement path variables (Pillai's trace = 0.252, $F_{4,320} = 11.53$, $p > 0.0001$; Table 2.5). When effects of species identify on the univariate responses were examined, the differences were exhibited in the paths of *H. regilla* with 210% longer total movement distances than the other species (95% CI: 135% - 325%) and straighter paths than the other species with an increase of 0.22 in the straightness index (95% CI: 0.13 – 0.31). This importance of species identity is similarly apparent by explaining 12.6% of the relative proportion of total explained variance (η^2_{partial}, Figure 2.5).

Discussion

Our study found an important interaction between morphology and behavior on the movement and dispersal potential within three amphibian species. As predicted, morphology was a strong predictor of juvenile frog jump performance. Larger-bodied individuals were able to jump farther regardless of species. Species-level differences, however, emerged during our field trials as a key determinant of free-movement paths. Powder tracking allowed for parameterization of path straightness and total distance. Straightness was predicted by both morphology (RLL) and species identity. Total distance traveled, however, was not a function of morphology, but solely of species identity. These results indicate that a reliance on morphology alone to understand movement is overly simplistic. Broad generalizations of movement based on organismal measures exclude important species-specific behaviors (Hillman et al., 2014). Integration of morphology and species-specific differences are particularly important as independent factors influencing sinuosity or total distance moved together result in realized movements. Only through this integration is a holistic understanding of movement and dispersal potential possible.

To bridge existing research on performance measures with movement behavior, we first quantified a common amphibian performance metric: maximal jump performance. Our results found evidence that both individual body size and relative leg length are important predictors of maximal jump performance in these three species, which supports past work in anurans showing a strong morphological basis of jumping performance (Boes and Benard, 2013; Johansson et al., 2010; Tejedo et al., 2000). Individuals with longer bodies (SVL) increased their maximal jumping distance. Jump performance also improved with increasing leg length relative to body size (RLL). These two factors were significant variables in individual maximal jump performance, though their relative importance did vary between species.

When individuals were moved out of the lab environment to the field, RLL continued to demonstrate importance in our measurement of free-movement paths. However, species identity was an overwhelmingly important factor in determining movement. We found distinct species differences in movement behaviors such as path sinuosity and total distance traveled. Though it is important to note that the observed effects did not quantify population or clutch specific effects which could be an additional source of variation. Our hydroperiod treatment also did not control for density or water level independently as these are inherently linked in natural ephemeral ponds. Even with these added sources or variation, we observed distinct movement differences that we interpret as being ecologically relevant, with our most morphologically and behaviorally mobile species (*H. regilla*) occupying a generalist niche throughout their range relative to the other two species tested (*A. boreas* and *R. cascadae*) (Lannoo, 2005). Aspects of movement biology and niche breadth have actually been proposed as explaining differences in species ranges (Penner and Rödel, 2019).

Our results fit into a niche partitioning perspective nicely. These three amphibian species are sympatric in the Cascade Mountain Range during their aquatic life history stages. Differences in natal dispersal capacity and behavior could provide an important mechanism for reducing overlap during the transition of these species to terrestrial habitats. The importance of species identity in our analysis does encompass a variety of potential aspects of biology that contribute to these movement behaviors. For example, *A. boreas* may have less motivation to move in an effort to find moist micro-habitats, as toads are more tolerant of dry conditions (Gatten, 1987). Species-specific morphology and locomotion type can also impact movement ability (Petrović et al., 2016). Variation in juvenile and adult terrestrial habitat requirements may also impact these movement behaviors (Lannoo, 2005). Ranid species such as *R. cascadae* often rely on habitats in, or surrounding, lentic areas and may not commonly move large distances after metamorphosis (Semlitsch and Bodie, 2003). Other studies have found that land cover can also impact movement behavior (Cline and Hunter, 2014; Stevens et al., 2004; Youngquist and Boone, 2014) which could be differentially responded to by species. The synchrony and timing of metamorphosis, which varies between species, could influence movement behavior for species that rely on conspecific density to trigger mass emergence from pond margins. As individual size was also an important factor, species or individuals that emerge earlier could grow faster thereby providing additional potential for movement. Regardless, there is very little known about the juvenile dispersal and movement of these species outside of occasional observational notes.

The variation in habitat, life history, and ecology captured by species identity can be the result of many biological mechanisms. As such, the ability to generalize movement and dispersal across anuran species is potentially called into question. The diversity of species movement makes knowledge gaps extremely concerning; in a biological database of European amphibians, 26 species of anurans (52%) and 23 species or urodeles (63.8%) lacked movement data (Trochet et al., 2014). Conservation planning for any data deficient species would require managers to assume similar responses to amphibians more generally (Woltz et al., 2008). Our results indicate that species identity plays an overarching role in shaping the movement behavior of juvenile amphibians. More research should be directed at identifying the important mechanisms that drive movement behavior and management decisions should avoid the assumption that all anuran species exhibit the same morphological and/or behavioral capacity to move and disperse.

The limited predictive ability of maximal jump performance on movement potential also indicates that we need to move away from lab-based performance measures into realistic movement scenarios or *in situ* animal tracking (e.g., Cline & Hunter, 2014, 2016; Ramírez et al., 2017; Roe & Grayson, 2008; Zamora-Camacho, 2018). Performance measures have an important role as proxies for fitness in controlled studies on morphology and physiology (Pough, 1989). Our results confirm the strength of this relationship as we found a significant predictive power of morphology on maximal jump performance. Research has additionally extended these relationships by incorporating ecological diversification to account for species differences in performance (Gomes et al., 2009). The opportunity to generalize individual physiology and lab performance into movement seem to provide an option to address deficient field data (Hillman et al., 2014), yet the measures do not always relate to movement paths (Walton, 1988).

Performance ability is only expressed in movement paths and subsequent dispersal when combined with individual movement behavior (Yagi and Green, 2017). Further, some free-movement endpoints, such as total distance traveled, were not strongly tied to morphology or jump performance. We found that after 60 minutes of movement in the field, the point where a frog ended up was largely determined by species identity, or more succinctly, species-specific behavioral choices. Such information further supports our key finding that performance measures and morphology need to be used in combination with realized movement behavior to establish their relative importance for movement more generally in amphibians.

Juvenile amphibians are also an important and critically-understudied life stage to focus additional research efforts. For a taxonomic group that is of serious conservation concern, it is essential that we direct research towards a more holistic understanding of their ecology and behavior. For instance, we could potentially learn a great deal about how amphibians respond to novel environmental and/or climatic conditions from how they respond to novel habitats through ontogeny. Immediately after metamorphosis, juvenile amphibians have very limited experience with which to influence their movement behavior in the terrestrial environment. To survive in this novel environment, juveniles must appropriately respond to and learn from a suite of selective pressures through choices in behaviors like movement, refuge use, and foraging. Even beyond individual responses, differential mortality of dispersing juveniles could have strong selective pressures on the connectivity of populations (Delgado et al., 2011). Information on the innate behavior and learning processes that impact movement, dispersal, and subsequent survival of juveniles will be essential information for conservation analyses and planning.

Conclusion

Our results suggest that individual morphology and associated performance measures can impact aspects of organism movement, but species-specific behavioral traits were the driving factor of free-movement paths in these juvenile amphibians. Performance measures can be useful proxies for some aspects of an organism's biology, yet we must be critical of their predictive use as they may not always correspond to natural movements. To properly develop our understanding of the ecology of amphibian movement in their natural habitats, we must coalesce the associated physiological and performance information and expand it to include real-world movement and behavior. Our understanding of movement and its drivers, particularly during major life history transitions, offers an advancement in our understanding of species' interactions with their environment and identifying aspects of habitat that are important across life stages.

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Table 2.1 – The ambient conditions measured at AgriMet Weather Station (CRVO) during field measurements across trial days.

Variable	**Average**	**SD**
Temperature (°C)	15.5	1.6
Wind Speed (kph)	5.3	2.7
Humidity (%)	80.5	12.1
Daily Rain (mm)	0.25	0.25

Table 2.2 – The explicit statistical models used in the analysis of each section. Factor variables are denoted by an asterisk. Factor variables used as blocks in the analysis are denoted by a solid square. Interaction terms are listed as the two variables separated by a colon.

Section	**Response**	**Model**
Morphology and Jumping Ability	Maximal Jump	Spp* + RLL + SVL + Spp*:RLL + Spp*:SVL + trial_day■ + mesocosm■
Morphology and Movement	Total Distance, Path Shape	Spp* + RLL + SVL + Spp*:RLL + Spp*:SVL + trial_day■ + mesocosm■
Jumping Ability and Movement	Total Distance, Path Shape	Spp* + Max_Jump + Spp*:Max_Jump + trial_day■ + mesocosm■

Table 2.3 – ANOVA table with type III sums of squares for the analysis of maximal jump performance with morphological characteristics and species identity predictors. Mesocosm condition and trial day are included as blocking variables. P-values were considered significant at levels less than 0.05 and are marked with an asterisk.

Response	**Source**	***df***	***SS***	***F***	***p***
Maximal Jump Performance	(Intercept)	1	0.602	1.314	0.253
	Species	2	0.003	0.003	0.997
	Relative Leg Length	1	2.222	4.847	0.029 *
	Snout Vent Length	1	32.859	71.675	<0.001 *
	Mesocosm Condition	1	0.086	0.187	0.666
	Trial Day	6	3.435	1.249	0.284
	Spp:RLL	2	2.884	3.146	0.046 *
	Spp:SVL	2	3.008	3.281	0.040 *
	Residuals	157	71.975		

Table 2.4 – MANOVA table with Pillai's trace test statistic for the multivariate analysis of path with responses of total distance and path sinuosity. Predictor variables included morphological and species identity. Mesocosm condition and trial day are included as blocking variables. P-values were considered significant at levels less than 0.05 and are marked with an asterisk.

Response	**Source**	**df**	**V**	**approx. F**	**num df**	**den df**	**p**
Total Distance	(Intercept)	1	0.232	23.560	2	156	<0.001 *
Path Sinuosity	Species	2	0.258	11.634	4	314	<0.001 *
	Relative Leg Length	1	0.085	7.244	2	156	0.001 *
	Snout Vent Length	1	0.008	0.609	2	156	0.545
	Mesocosm Condition	1	0.002	0.158	2	156	0.854
	Trial Day	6	0.114	1.581	12	314	0.096
	Spp:RLL	2	0.060	2.448	4	314	0.046 *
	Spp:SVL	2	0.033	1.319	4	314	0.263

Table 2.5 – MANOVA table with Pillai's trace test statistic for the multivariate analysis of path with responses of total distance and path sinuosity. Predictor variables included maximal jump performance and species identity. Mesocosm condition and trial day are included as blocking variables. P-values were considered significant at levels less than 0.05 and are marked with an asterisk.

Response	**Source**	**df**	**V**	**approx. F**	**num df**	**den df**	**p**
Total Distance	Species	2	0.252	11.532	4	320	<0.001 *
Path Sinuosity	Maximal Jump	1	0.023	1.865	2	159	0.158
	Mesocosm Condition	1	0.004	0.327	2	159	0.721
	Trial Day	6	0.118	1.672	12	320	0.072
	Spp:Jump	2	0.040	1.629	4	320	0.167

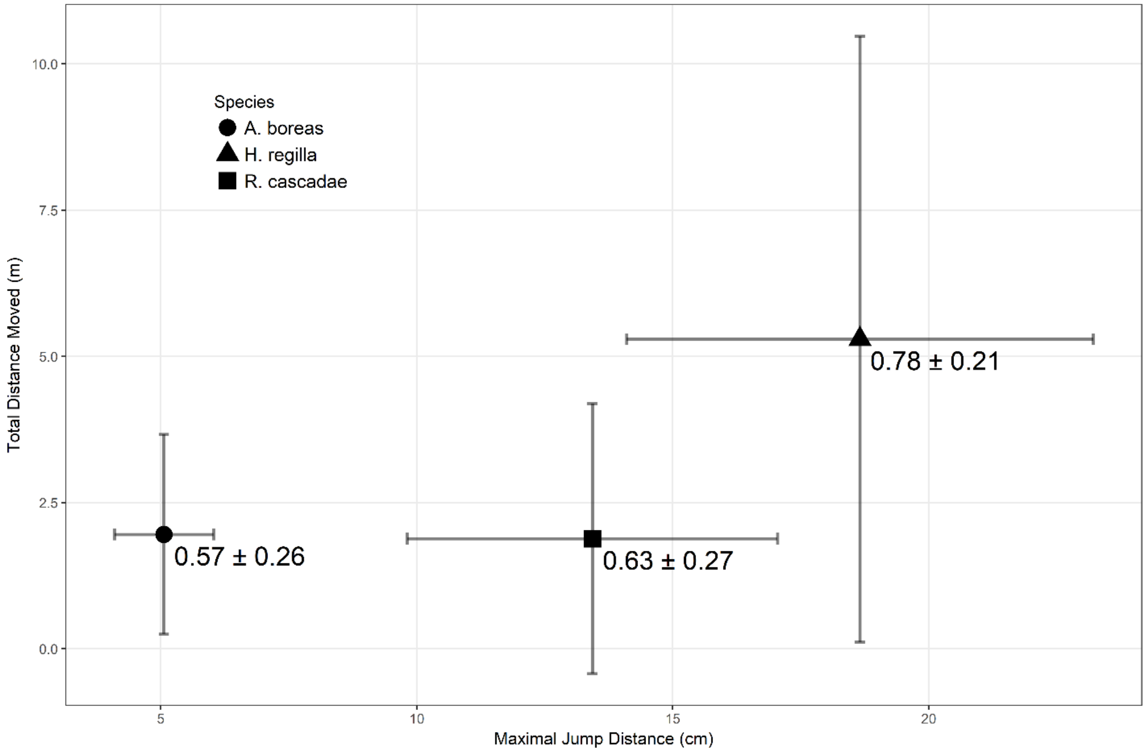

Figure 2.1 – The average maximal jump distance and total movement distance for *Anaxyrus boreas*, *Hyliola regilla*, and *Rana cascadae*. Error bars represent one standard deviation. Numerical values on the plot represent the average path straightness index with one standard deviation.

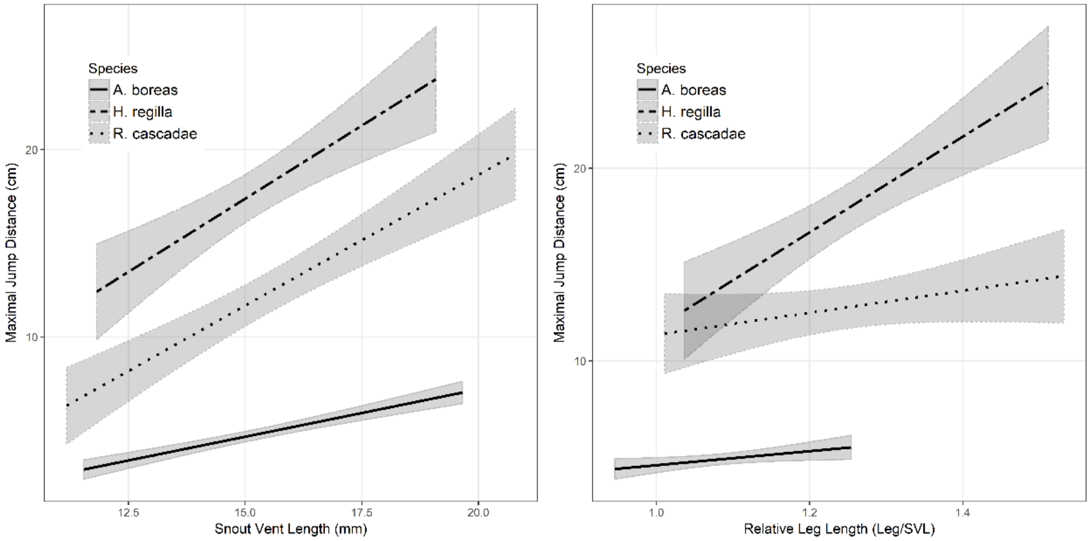

Figure 2.2 – Model predicted effects of snout-vent length (SVL) and relative leg length (RLL) on the maximal jump distance of three anuran species: *Anaxyrus boreas*, *Hyliola regilla*, and *Rana cascadae*. The left panel shows the species-specific impact of SVL on maximal jump performance. The right panel shows the species-specific impact of RLL on maximal jump performance. Values are back-transformed onto their original scale. Shaded regions indicate 95% confidence intervals.

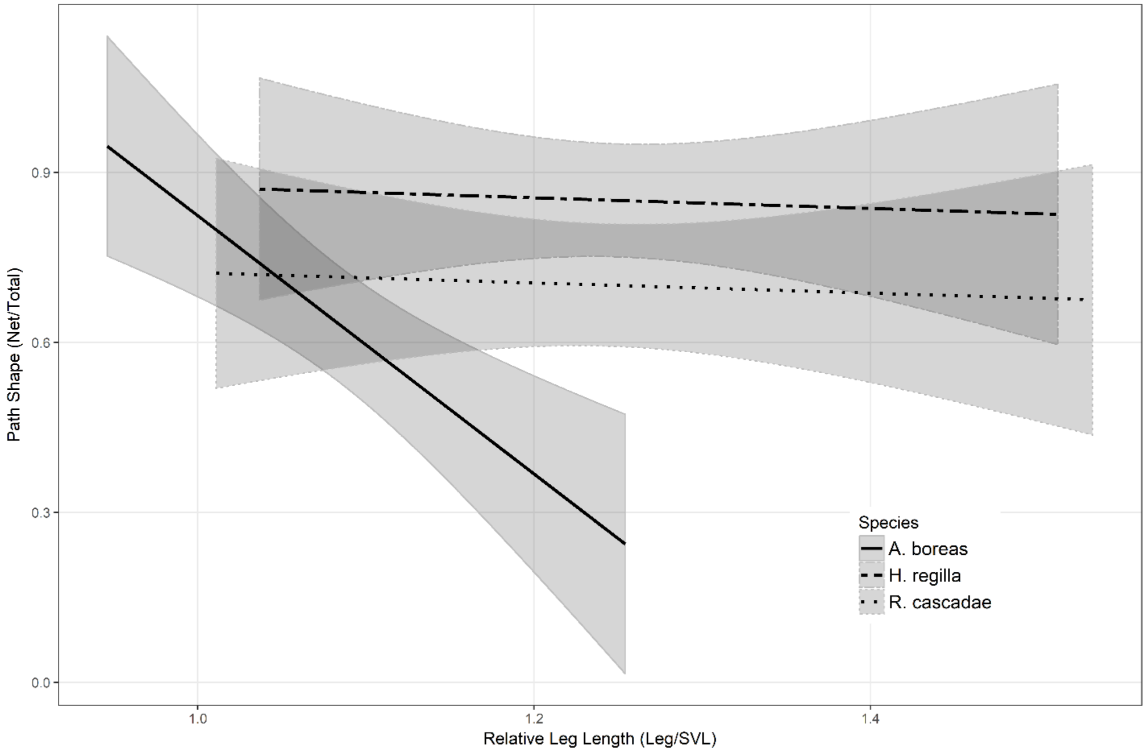

Figure 2.3 – Model predicted effects of Relative Leg Length (RLL) on path shape in *Anaxyrus boreas*, *Hyliola regilla*, and *Rana cascada*e. The index of path shape indicates straightness of movement with lower values representing more tortuous paths. Values are back-transformed onto their original scale. Shaded regions indicate 95% confidence intervals.

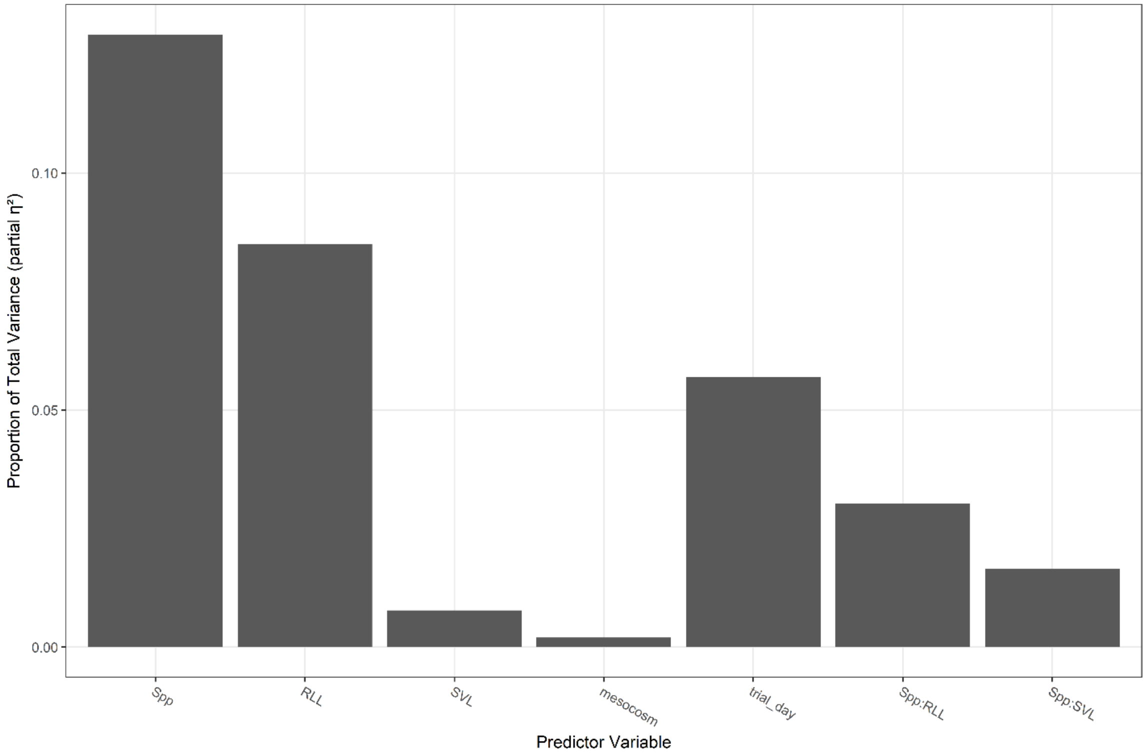

Figure 2.4 – The relative proportion of total variance (η^2_{partial}) explained by the modeled predictor variables on movement path variables of total movement distance and path shape using predictors of species identity and morphometric traits.

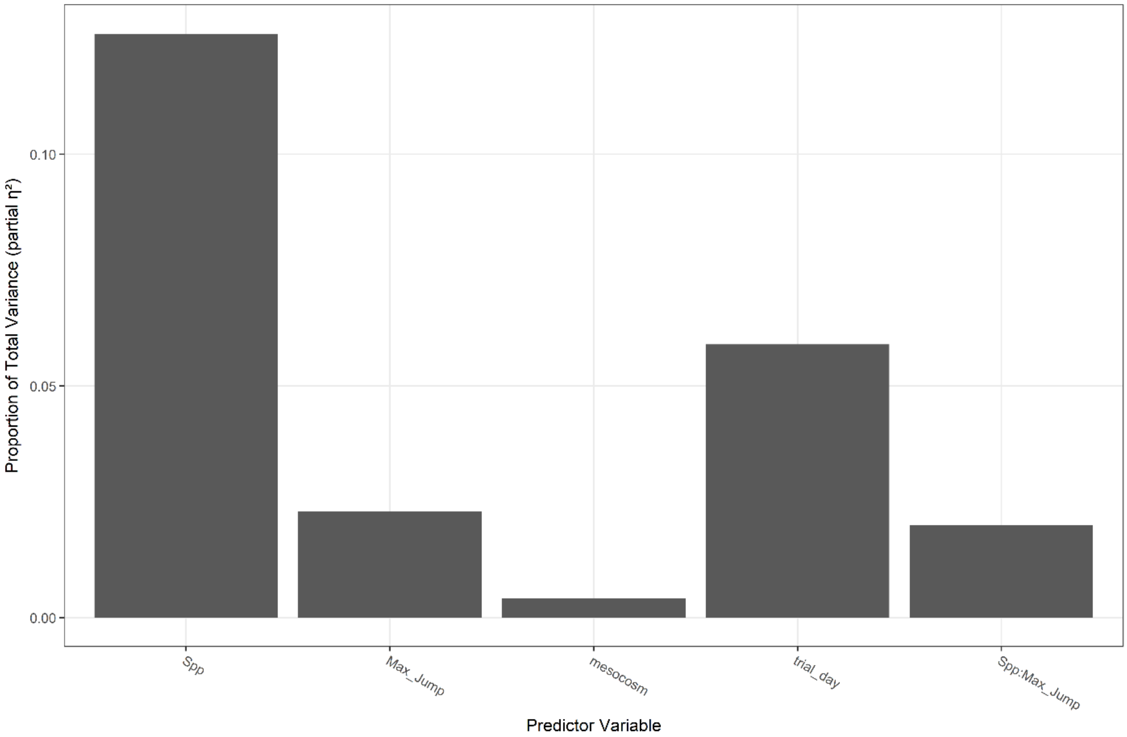

Figure 2.5 – The relative proportion of total variance (η^2_{partial}) explained by the modeled predictor variables on movement path variables of total movement distance and path shape using predictors of species identity and standardized maximal jump performance.

JUMPING IN WITH BOTH FEET: EXPLORING FACTORS THAT SHAPE JUVENILE AMPHIBIAN MOVEMENT

CHAPTER 3 – STARTING ON THE RIGHT FOOT: CARRYOVER EFFECTS OF LARVAL HYDROPERIOD AND TERRAIN MOISTURE ON POST-METAMORPHIC FROG MOVEMENT BEHAVIOR

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Abstract

Changing patterns of precipitation and drought will dramatically influence the distribution and persistence of lentic habitats. Pond-breeding amphibians can often respond to changes in habitat by plastically shifting behavioral and developmental trait response. However, fitness tradeoffs inherent in life history strategies can carry over to impact development, behavior, and fitness in later life stages. In this experiment, we investigated carryover effects of hydroperiod permanence on the movement behavior of newly-metamorphosed juvenile Northern Red-legged Frogs (*Rana aurora*). Frogs were raised through metamorphosis in mesocosms under either permanent or ephemeral hydroperiod conditions. After metamorphosis, individuals were removed from the mesocosms, measured, uniquely tagged with elastomer, and moved to holding terrariums. Movement behavior was quantified under two terrain conditions: a physiologically-taxing, dry runway treatment, or a control, moist runway treatment. Individuals were given 30 minutes to move down the 1x20m enclosed structure before distance was measured. We applied a hurdle model to examine two distinct components of movement behavior: 1) the probability of moving away from the start location, and 2) movement distance. We found that hydroperiod condition had an indirect carryover effect on movement via the relationship between individual size and the propensity to move. Individuals from ephemeral mesocosm conditions metamorphosed at a smaller size but showed increased growth rates as compared to individuals from permanent hydroperiod conditions. Individual snout-vent length and runway condition (moist or dry) were significant predictors of both aspects of movement behavior. Larger individuals were more likely to move down the runway and able to move a farther distance than smaller individuals. In addition to the influence of size, dry runway conditions reduced the probability of individuals moving from the start location, but increased the distance traveled relative to the moist runway. The demonstrated cumulative impact of stressors suggests the importance of addressing direct, indirect, and carryover effects of stressors throughout ontogeny.

Introduction

Climate change is projected to influence many aspects of the environment, including temperature and storm intensity (Hughes, 2000). Critical to lentic organisms, climate change also alters precipitation patterns, which are key in the predictability and variability of water cycling and storage (Smith et al., 2018; Williams et al., 2015). For animals such as aquatic insects and amphibians, with complex life histories that require movement between aquatic and terrestrial habitats, this variation can determine the success of individual development and survival (Cayuela et al., 2016a; Robson et al., 2011; Suislepp et al., 2011).

Life history theory suggests that a dynamic yet predictable environment would select for a flexible life history strategy, such as life-cycle staging or phenotypic plasticity (Meyers and Bull, 2002; Roff, 2002). Developmental plasticity has allowed some amphibian species with complex life histories to adjust trait response, such as development rate, antipredator behavior, and metamorphosis timing in response to a variety of aquatic environmental stressors (desiccation - Denver et al., 1998; competition and predation - Relyea, 2004; temperature - Thurman and Garcia, 2017; multiple predators - Vonesh and Warkentin, 2006). However, plasticity has physiological costs and trade-offs that can constrain the degree of response both immediately and across ontogeny (Relyea, 2002). The true price of plasticity may only be understood when considering the entire life cycle.

Carryover effects, also termed latent effects, have been increasingly apparent in biological systems (O'connor et al., 2014; Pechenik, 2006). Carryover effects of larval plasticity may be important in determining response to changing environmental conditions (Johansson et al., 2010). Early life stages can be more susceptible to shifting environmental conditions than adults, an effect that has been observed in diverse taxa from reptiles to butterflies (Levy et al., 2015; Radchuk et al., 2013). Several carryover effects to larval stress in anurans have been observed: for example, drying conditions experienced by developing Túngara frog tadpoles reduced leg length and jumping performance (Charbonnier and Vonesh, 2015), and high larval densities of Red-eyed treefrogs resulted in smaller juveniles with reduced livers and fat bodies (Bouchard et al., 2016).

To date, assessment of potential impacts of climate change on amphibians have focused on adult stages, with little attention to other sensitive life history stages or across ontogeny

(Lancaster et al., 2017; Levy et al., 2015). Dramatic shifts in environmental conditions that are stressors during early life stages may fundamentally change the ability of individuals to respond to stress later in development. The physiological changes and energy investment in larval trait response can represent an opportunity cost that limits the ability to respond to future stressors (Amburgey et al., 2016; Weinig and Delph, 2001). As such, investments in plastic responses at the larval, aquatic stage have the potential to carry over to influence the developmental trajectory and behavior of juvenile frogs, and limit capacity to manage stress in terrestrial life stages.

We studied the combined influence of aquatic and terrestrial environmental condition across a life history transition in the Northern Red-legged Frog (*Rana aurora*) to examine the interaction of direct and carryover effects on juvenile movement behavior. We chose movement behavior as our response variable because of its importance in a range of ecological aspects, such as foraging, predator avoidance, refuge discovery, and population connectivity (Osbourn et al., 2014; Schwalm et al., 2016; Székely et al., 2017). We selected pond permanence as a larval stressor because of the extensive documentation of amphibian plasticity in response to drying conditions (Charbonnier and Vonesh, 2015; Johansson et al., 2010; Thurman and Garcia, 2017). *Rana aurora* utilizes both ephemeral and permanent lentic waters for breeding habitat, with ephemeral ponds being important for larval success (Adams, 2000; Hayes et al., 2008). After metamorphosis, we tested for carryover effects on juvenile movement behavior under two physiologically distinct conditions: a moist, low-stress terrain or a dry, high-stress terrain. Based on past research (see above), we hypothesized that individuals who (plastically) responded to drying (ephemeral) hydroperiods would be less suited to movement under stressful conditions. A trade-off between structural growth and energy stores (Morey and Reznick, 2004) suggests that larval development has inherent resource limitations. The increased density and limitations of ephemeral conditions may tax this trade-off and change the physiology of juvenile frogs and their subsequent movement behavior.

Amphibians are species that are dependent on water throughout their life cycle. Yet, to our knowledge, impacts of two critical aspects of amphibian habitat affected by changing precipitation - drying ponds and dry terrain - have not been directly assessed for amphibian species across metamorphosis. As climate change influences precipitation patterns and the availability of moisture in the environment, the mechanisms by which amphibians modify their development, manage the physiological stress, and respond behaviorally to these changing conditions will be important for continued survival of those species (Mazerolle and Desrochers, 2005; Watling and Braga, 2015).

Methods

Animal collection and rearing

On 31 January 2015, we collected eight recently laid *R. aurora* egg masses from three separate populations in the Willamette Valley, Oregon. Egg masses were immediately transported to Oregon State University and placed in de-chlorinated water in individual 75 L glass aquaria. Individuals were reared in the laboratory through hatching until Gosner developmental stage 25 (Gosner, 1960) and fed a mixture of ground fish flakes and rabbit chow *ad libidum*. Water changes were performed every 10 days. On 3 March 2015, tadpoles were combined into a common pool and randomly assigned to a mesocosm tub. Each mesocosm was populated with 50 randomly selected larvae, with 10 replicates per hydroperiod treatment (permanent or ephemeral). Mesocosms were held outdoors at the Lewis Brown Horticultural Farm (44.551346, -123.215831) under a mixed oak canopy. Mesocosms (120 L HDPE stock tanks) were prepared with 100 grams of dried and autoclaved oak leaves and 5 grams of rabbit chow in 100 liters of well-water. Each mesocosm tub was then inoculated with algae and microorganism communities 2 weeks prior to the introduction of tadpoles using 4 L of water from an onsite source-mesocosm. Mesocosm tubs were then fitted with mesh screen lids to prevent predation or introduction of other species.

Two weeks after the introduction of *R. aurora* larvae, water levels in the ephemeral treatment mesocosms were drawn down by 4 liters every week until water levels reached a total 30 liters. At this point, water levels were maintained for the remainder of the experiment. Permanent hydroperiod treatments were maintained at 100-liter levels with additional well-water every week as needed. As individuals neared metamorphosis, two mesh floats were added to mesocosms to allow individuals to emerge. Individuals were removed from the mesocosms at Gosner developmental stage 45 (Gosner, 1960), measured (snout-vent length, total length, and mass), and marked with a unique color tag. Color tags consisted of 3 subcutaneous injections of visible implant elastomer (Northwest Marine Technology, Inc.) in the belly, right leg, and left leg (Govindarajulu et al., 2006; Swanson et al., 2013). Individuals were then transferred to outdoor terrariums adjacent to the mesocosm array. Treatment groupings were maintained throughout this process. Terrariums (120 L HDPE tubs) contained moistened coconut husk bedding, well-water pools, and dried grass and leaves for refuge. Individuals in terrariums were fed an excess of wingless fruit flies (*Drosophila melanogaster*) 3 times a week. Emerging individuals were collected starting on 25 June and continued until we collected at least 200 individuals which occurred on 14 September. Logistical seasonal weather constraints of our runway assays prevented the inclusion of individuals that metamorphosed after our collection window, which does limit our inference to those early emerging individuals. This is an important consideration as emergence date has shown to change the size and dispersal of individuals (Chelgren et al., 2006).

Behavioral Assay- Runway Dispersal

Four 1m x 20m runways were constructed at the Lewis Brown Horticultural Farm. Each runway was constructed from a single piece of 7-millimeter white plastic sheet draped across parallel wires suspended 75 centimeters above the perimeter of the runways. This plastic sheeting prevented individuals from escaping the runways and maintained moisture conditions within assays. The runway substrate consisted of smoothed and compacted topsoil to a depth of 7cm. The 4 runways were arranged in pairs and placed on level ground under the dappled shade of several surrounding trees on an angle from northeast to southwest. Runways were paired, with each pair containing a dry and wet treatment runway.

Immediately prior to each assay, all runways were prepared according to their assigned moisture treatment. Wet condition runways had the entire length of substrate moistened with well water to the point of near saturation to minimize standing pooled water. Dry condition runways had no added water except for the release point. In each runway, a release point was constructed by placing a 15cm disk of moist sphagnum moss in the northeast end of the runs. The immediate area around this release point was gently moistened in both the wet and dry conditions to provide a place of hydrologic refuge. Runways were cleaned of detritus prior to each assay and the release point moss was replaced each day.

Individuals from a single terrarium were ordered by age and alternately assigned to runway condition to provide equal representation across ages and terrariums. Each animal was measured (snout-vent length, mass, etc.) and then allowed to acclimate within the runway under a clay pot cover in the center of the release point. Individuals were anointed with a small application of high visibility fluorescent powder (ECO Aurora Pink® Pigment, DayGlow Color Corp.) on their back. After a 5-minute acclimation period, the clay pot was remotely removed, and the animal was given 30 minutes to freely move in the runway. Runway assays occurred during daylight-hours; average start time was at 13:25h (SD = 1:45 hours) and ranged from 08:25 to 15:40h. At the end of the assay, animals were located, recaptured, and returned to their terrarium. In between each assay, the moss disk at the release point was rinsed and immediate area remoistened. Wet runways were also remoistened as needed in between each assay. Each animal was run through the assay twice with at least 14 days between each run. Animals assigned to a runway condition were maintained in the same runway condition for their second assay. At the end of the second runway assay, individuals were humanely euthanized with a solution of Tricaine Methanesulfonate (Leary et al., 2013).

Statistical analysis

We examined the relationship between larval hydroperiod and frog body size using two models to assess the responses of individual length at two time points: once upon metamorphic emergence from the mesocosms, and once at the time of the runway assay (juvenile growth). To assess potential carryover effects of hydroperiod conditions on frog size, we fit a linear mixed-effects regression model of metamorphic emergence snout-vent length (SVL) based on mesocosm hydroperiod, day of emergence, and a random effect of mesocosm tub. To assess carry over on juvenile growth, we built a second linear mixed-effects model that examined SVL growth after metamorphic emergence and before the first the runway assay. For this model, we fit data from the first assays with predictor variables of mesocosm hydroperiod, day of emergence, days since emergence, and a random effect of enclosure. We also included the total number of animals per enclosure (container density) as a predictor variable. The measure of density provided a continuous classification of terrarium density outside of the random effect of enclosure but was not unique for each individual. Despite feeding an excess of fruit flies, the density of animals in a terrarium could have had other effects on growth (Altwegg, 2003; Harper and Semlitsch, 2007).

We tested two distinct movement aspects of each individual: the decision to attempt a movement, and how far to travel during a movement event. A hurdle regression model was used to assess these two aspects of an individual response (Falke et al., 2013). Individuals that were within 20 cm from the start location (a 15cm disk of moss) were not considered to have moved since they were near the moss refuge of the release point; this created a binomial response variable of a movement attempt. This analysis simultaneously fits a binomial model for the decision to leave or stay in the start location with a zero-truncated count regression model of distance for individuals that move down the runway. The models were fit using the “glmmTMB” library in R, which allowed for inclusion of random effects of experimental enclosure (Brooks et al., 2017). Only animals that completed both trials were included in the final analysis.

As this experiment ranged across a metamorphic life history transition, there were a suite of individual measurements that could be included as covariates in this modelling framework. To reduce the likelihood of an over fit model, predictor covariates were grouped into three sets: environmental conditions (day of assay, time of assay, ambient temperature), individual characteristics (SVL, body condition, days since emergence), and individual traits at metamorphic emergence (emergence SVL, emergence body condition, day of emergence). Humidity is likely an important aspect of the environmental conditions in shaping movement (Chan-McLeod, 2003), but is integrally determined by temperature which had a finer resolution measurement and was used in place of humidity. Correlation between covariates within each group were assessed to check for multicollinearity. In addition to our experimental treatments (hydroperiod, runway condition, run number, random effect of enclosure), these covariate groups were used to develop four candidate models (Table 3.1). Body condition was calculated using the scaled mass index proposed by Peig and Green (2009), which incorporates allometric scaling of body size to better represent an individual’s energy stores. Predictor covariates were standardized by subtracting the mean and dividing by their standard deviations to make them more directly comparable in the model and subsequently back transformed onto their original scales for interpretation. These four candidate models were then compared using AIC (Symonds and Moussalli, 2011). The best fit model (lowest AIC) was based on individual characteristics including SVL, body condition, and days since emergence. We assessed the presence of interaction with the best fitting model and adding interactions with and between all experimental factors and covariates. The AIC values from all interaction models showed no significant improvement (ΔAIC > 2) in model fit over the additive model. In the interest of parsimony, we used the additive individual characteristic model for interpretation (Aho et al., 2014). All statistical analyses were performed in R (version 3.5.0) using RStudio (version 1.1.447, RStudio Team, 2016).

Results

We tested 204 animals that emerged within our experimental window and successfully completed both runway assays. These animals emerged from 18 of our mesocosms (9 Ephemeral and 9 Permanent) with an average emergence of 11.3 (SD = 4.8) animals per mesocosm. Two of the mesocosms did not have any emergence within our experimental window (1 Ephemeral and 1 Permanent). The 82 individuals from Ephemeral mesocosms were subsequently divided evenly into Wet and Dry runway treatments. Permanent mesocosms had 122 individuals emerge, resulting in 63 and 59 respectively in Wet and Dry runway treatments.

Our analysis on size at emergence found that both day of emergence ($z = -5.16$, $p < 0.001$) and hydroperiod ($z = 2.98$, $p = 0.003$) had a significant effect on emergence SVL. Snout-vent length at emergence decreased by 0.12mm for each additional week (95% CI = 0.08 to 0.17), meaning that individuals emerging earlier were relatively larger than later-emerging individuals. Individuals from permanent hydroperiods had 0.66mm longer SVL (95% CI = 0.23 to 1.10) than individuals from ephemeral hydroperiods (Figure 3.1A). In addition to this effect of hydroperiod on size at emergence, we also detected a significant difference in juvenile growth rates based on larval hydroperiod. Juvenile SVL was significantly affected by day of emergence ($z = -5.09$, $p < 0.001$), days since emergence ($z = 2.65$, $p = 0.008$), and hydroperiod ($z = -2.84$, $p = 0.005$). Individuals from ephemeral hydroperiods emerged at a smaller size relative to their counterparts from permanent hydroperiods but had faster growth post-emergence. Enclosure density did not have a significant effect on SVL growth ($z = -0.78$, $p = 0.437$). Like the above analysis, day of emergence had a negative effect on SVL growth after emergence with 0.19mm less growth for each additional week (95% CI = 0.12 to 0.27). Increased time elapsed since emergence resulted in increased SVL growth, with an additional 0.14mm for each week post-emergence (95% CI = 0.04 to 0.24). Further, we found the effect of mesocosm hydroperiod was opposite of the previous analysis, with individuals from permanent hydroperiods increasing SVL 0.61mm less than ephemeral conditions (95% CI = 0.19 to 1.04) after emergence (Figure 3.1B).

In our analysis of individual movement behavior, the best fit model included individual characteristics at the time of the runway assay, including SVL, body condition, and days since emergence, as covariates with experimental factors of larval hydroperiod, runway condition, and runway assay number (Table 3.1). The hurdle model allows the movement of each treatment group to be separated into the decision to leave the release point and the subsequent decision of how far to move. These two aspects of the model were fit with identical predictors but have distinct results. In order to distinguish between these two aspects of the behavior, they are referred to as the movement hurdle (decision to move, zero-inflated model component) and the movement distance (distance undertaken after movement decision, conditional model component).

From our model, two variables were significant to both the movement hurdle and movement distance: runway condition and SVL. Runway condition was a significant predictor of a frog crossing the movement hurdle ($z = -4.16$, $p < 0.001$). An individual in dry runway conditions is 60% less likely to move than in wet runway conditions (95% CI = 38% to 74%). After controlling the other variables, the probability an average individual moves away from the start position was 0.24 (±0.05 SE) in a dry runway compared to 0.44 (±0.06 SE) in a wet runway. Snout-vent length significantly influenced an individual’s willingness to cross the movement hurdle ($z = -2.86$, $p = 0.004$). With each millimeter increase in SVL at the time of the assay, the odds of crossing the movement hurdle and leaving the start position increased by 16% (95% CI = 0.05% to 25%). The probability of crossing the movement hurdle increased in wet runway condition and as SVL increased (Figure 3.2). However, after crossing the movement hurdle, the impact of runway condition changed. Runway condition still significantly influenced the distance an individual moved down the runway ($z = -3.01$, $p = 0.003$), but now wet runway condition reduced the distance moved by 36% (95% CI = 14% to 52%) compared to the dry runway condition. As in the movement hurdle, SVL was a significant predictor of movement distance ($z = 2.94$, $p = 0.003$). An increase of 1mm SVL increased the movement distance by 12% (95% CI

= 4% to 21%). Movement distance was highest for large individuals in dry runway conditions (Figure 3.3).

Neither body condition nor time since emergence (age) were significant in our model for movement hurdle (body condition: z = 0.20, p = 0.840; age: z = -0.28, p = 0.773) and movement distance (body condition: z = 0.81, p = 0.416; age: z = 0.40, p = 0.688). Repeatability of behavior by an individual across assays was not strongly correlated (R^2 = 0.0283 distance, R^2 = 0.0193 hurdle). Snout-vent length and runway condition were the only important factors in both the ability and behavior around movement, yet hydroperiod was not significant in either the movement hurdle (z = 1.25, p = 0.212) or movement distance (z = 0.23, p = 0.816). The opposite effect of ephemeral conditions with smaller size at emergence and subsequent increased growth rates likely reduced the significance of hydroperiod in the behavioral assay because of the spectrum of ages included (Range= 2-83 days after emergence, mean = 35 ± 19 days SD).

Discussion

The ability of an amphibian species to respond plastically to changing hydroperiods in seasonally-variable habitats is an essential life history adaptation, particularly in the face of changing climate. However, if an appropriate larval trait response carries over to fundamentally influence an individual’s ability to contend with stressors later in life, this response could be maladaptive. Our objective was to assess the carryover effects of larval hydroperiod permanence onto juvenile growth and movement in low- and high-stress terrestrial conditions. We found that two factors, individual *R. aurora* size and terrain condition, were the central predictors of individual movement behavior. The carryover effect of hydroperiod was expressed in both the size at emergence and compensatory growth of individuals soon after metamorphosis. We identified no direct correlation between hydroperiod and movement behavior as hypothesized. However, hydroperiod is directly related to the size of juveniles, which is the main factor determining movement behavior. Thus larval conditions, including hydroperiod, indirectly influence movement behavior.

Our experiment found that *R. aurora* from permanent hydroperiod conditions metamorphosed at a larger size than individuals reared in ephemeral hydroperiods (Figure 3.1). This pattern is consistent in species that can plastically modify larval developmental rates under stressful conditions (Denver et al., 1998; Morey and Reznick, 2004). Changes in larval duration has been one suggested explanation for the effects of hydroperiod (Morey and Reznick, 2004). We did not observe any difference in larval duration between treatments, which is supported by other observation of reduced size in drying conditions independent of changes in larval duration (Brady and Griffths, 2000; Mogali et al., 2017). However, these smaller sized individuals from ephemeral conditions then demonstrated increased growth rates immediately after emergence, possibly to compensate for suboptimal size at metamorphosis. Compensatory growth of smaller individuals exposed to stressful larval conditions has been observed in other frog species (Boone, 2005; Bouchard et al., 2016). The increased growth rates of the individuals from ephemeral conditions may explain why larval hydroperiod was not significant in our analysis of individual movement. Since our experiment included individuals from a wide emergence window (i.e. emergence dates ranged from 25 June to 24 September), the opposing effect of hydroperiod on emergence size and terrestrial growth created difficulty in deciphering the carryover effect directly. It should also be acknowledged that the relative different in sizes between ephemeral and permanent conditions is only ca. 4% after accounting for emergence timing, which match the magnitude of other studies (Searcy et al., 2014; Semlitsch, 1987). What is clear from our analysis is that larval hydroperiod has effects on movement of juvenile *R. aurora* by means of a trade-off in growth between the aquatic and terrestrial environment. This may be common for many species with multiple life history stages to escape drying conditions but requires long-term experiments to uncover fully.

We found body size to be a strong predictor of movement behavior. Size is a critical trait in amphibian biology from physical abilities to individual fitness (Earl and Whiteman, 2015; Van Allen et al., 2010; Walton, 1988), with snout-vent length being a simple measurement that encompassed much of the variation in size. In many amphibian species, larger individual size is often correlated with increased performance (Chelgren et al., 2006; Gomes et al., 2009; Yagi and Green, 2017), as observed in our results (Figure 3.3). Yet increases in snout-vent length were also correlated with increased movement probability (Figure 3.2). This result indicates that an individual’s behavior is also influenced by its physical size. One possible explanation for this effect is a change in the perceived cost of a condition relative to body size. Larger individuals can retain moisture more efficiently than small individuals (Levy and Heald, 2016), thereby making movements in dry conditions less risky. Another possibility is inherent differences in behavior that result in differences in size. Individuals with bold personalities can be more aggressive in resource acquisition resulting in differences in body size and these personality traits can also increase predisposition to explore new areas (Kelleher et al., 2018). Whatever the cause of these behavioral differences across a gradient of snout-vent length, this physical trait may be a useful metric for understanding individual movement potential in field contexts.

Terrain moisture is an important aspect of environmental condition that shapes the movement strategies of organisms that are sensitive to dehydration, such as amphibians and invertebrates. With our experimental design, we were able to examine the critical aspects of this behavior: initial decision to move and distance traveled (Martin et al., 2005). The effect of runway condition had predictable effects, such as wet conditions increasing the probability of movement over dry conditions (Figure 3.2). However, dry conditions that can pose significant physiological hazards to young amphibians increased movement distances. Movement may be more effective if individuals quickly traverse the drier terrain to find more hospitable habitat. In contrast, wet terrain conditions are less risky and have the effect of reducing the distance moved (Figure 3.3). Most research has found reduced movement in non-habitat (Eycott et al., 2012) with only occasional evidence for increased movement in inhospitable areas (planthopper - Haynes et al., 2006; damselfly - Pither and Taylor, 1998). However, as indicated by our results, there were several instances of amphibians moving more efficiently over simple and inhospitable habitat (Northern green frog - Birchfield and Deters, 2005; Natterjack toads - Stevens et al., 2004). While there is limited information about the terrestrial movement and habitat of *R. aurora*, there is anecdotal evidence that they are associated with aquatic habitat and moist forests while also moving substantial distances (Chan-McLeod, 2003; Haggard, 2000; Hayes et al., 2001). Amphibians with different habitat requirements or life-history could be expected to respond differently.

Changes in precipitation pattern and droughts likely will also influence the distributions of aquatic habitat and, by extension, amphibian populations and their connectivity (Cayuela et al., 2016a; Jaeger et al., 2014; Robson et al., 2011). Insights into carryover and direct effects of stress on juvenile movement behavior provide opportunities to inform management strategies. Beaver canals have been observed to influence the location and emergence of amphibians, making waterway modifications a potential strategy for spatial management of populations (Anderson et al., 2015). Amphibians' likely rely on rare long-distance movements for population connectivity (Semlitsch, 2008). Even small changes in the success of dispersing individuals or distances traversed will likely have great implication for population connectivity (Stevens et al., 2012). Our study informs this pattern by relating hydroperiod permanence with juvenile amphibian body size and growth rates with dispersal probability. The behavioral and developmental trait connections across this life history transition likely influence population connectivity.

This project looked at movement behavior in a simplified setting. However, amphibians have shown to change their movement behaviors based on ground cover and context (Cline and Hunter, 2014, 2016; Osbourn et al., 2014). Accounting for the accumulated impacts of stressors across an individual's development, including terrain complexity, is a key step in providing a complete understanding of these animals. How other stressors, such as terrestrial density, predator presence, or prey availability interact with hydroperiod and terrain conditions could add additional consideration to the movement decisions of these animals (Patrick et al., 2008; Rittenhouse et al., 2007; Vonesh and Warkentin, 2006). Evidence from other amphibian species have also found reduced growth rates in dry conditions creating potential multiplicative effects of environmental conditions, as size was the central determinant of movement (Charbonnier et al., 2018; Gomez-Mestre and Tejedo, 2005). Other research on carry-over effect in amphibians has supported the need for longitudinal studies (Charbonnier and Vonesh, 2015; Johansson et al., 2010; Yagi and Green, 2018). With this broader understanding, we would be better able to combine aquatic structure with terrestrial habitat management to provide for essential habitat components of threatened species (Bartelt and Klaver, 2017; Fellers and Kleeman, 2007).

Amphibian movement has been understudied despite its importance for population connectivity and dispersal of vulnerable species (Howell et al., 2018; Pittman et al., 2014; Zamberletti et al., 2018). Our study details some of the drivers of movement assessed in isolation which can be incorporated into predictions of *in-situ* movement, but there is still need for such knowledge to be explored and validated in field and population studies. There are still important aspects such as directionality and habitat settlement that would further our understanding of movement. In short, assessing movement as a holistic, ontogenetic system, will improve our understanding of this complicated behavior and the myriad factors influencing how an animal moves through life.

Acknowledgments

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Table 3.1 – Candidate model sets with included variables. All candidate models used runway movement distance as their response and included the random effect of enclosure and experimental treatment factors of larval condition, runway treatment, and runway assay number. The addition of each group of covariate variables were then compared against the base model using AIC.

Model	**Variables**	**ΔAIC**
BASE	Hydroperiod + Runway Condition + Run# + (Random effect of Enclosure)	26.3
Environmental Condition	*BASE* + experimental day + time of assay + ambient temp during assay.	30.1
Individual characteristics	*BASE* + SVL + body condition + days since emergence	0
Emergence characteristics	*BASE* + emergence SVL + emergence body condition + emergence day	12.4

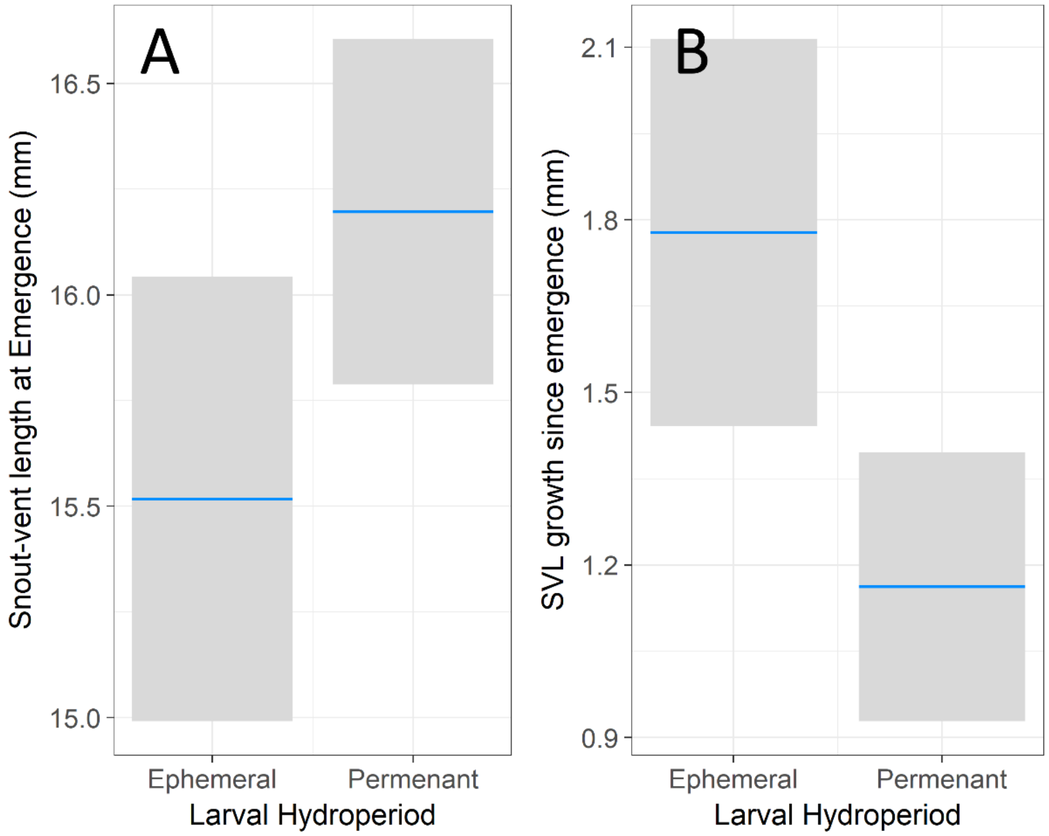

Figure 3.1 – The effect of hydroperiod on snout-vent length. The left panel (A) shows the effect of hydroperiod on emergence SVL after controlling for the emergence day. The right panel (B) shows the effect of hydroperiod on juvenile SVL growth during the first assay after controlling for emergence day, days since emergence, enclosure density. The blue bar represents the modelled response of an average individual with the 95% confidence interval in the shaded bar.

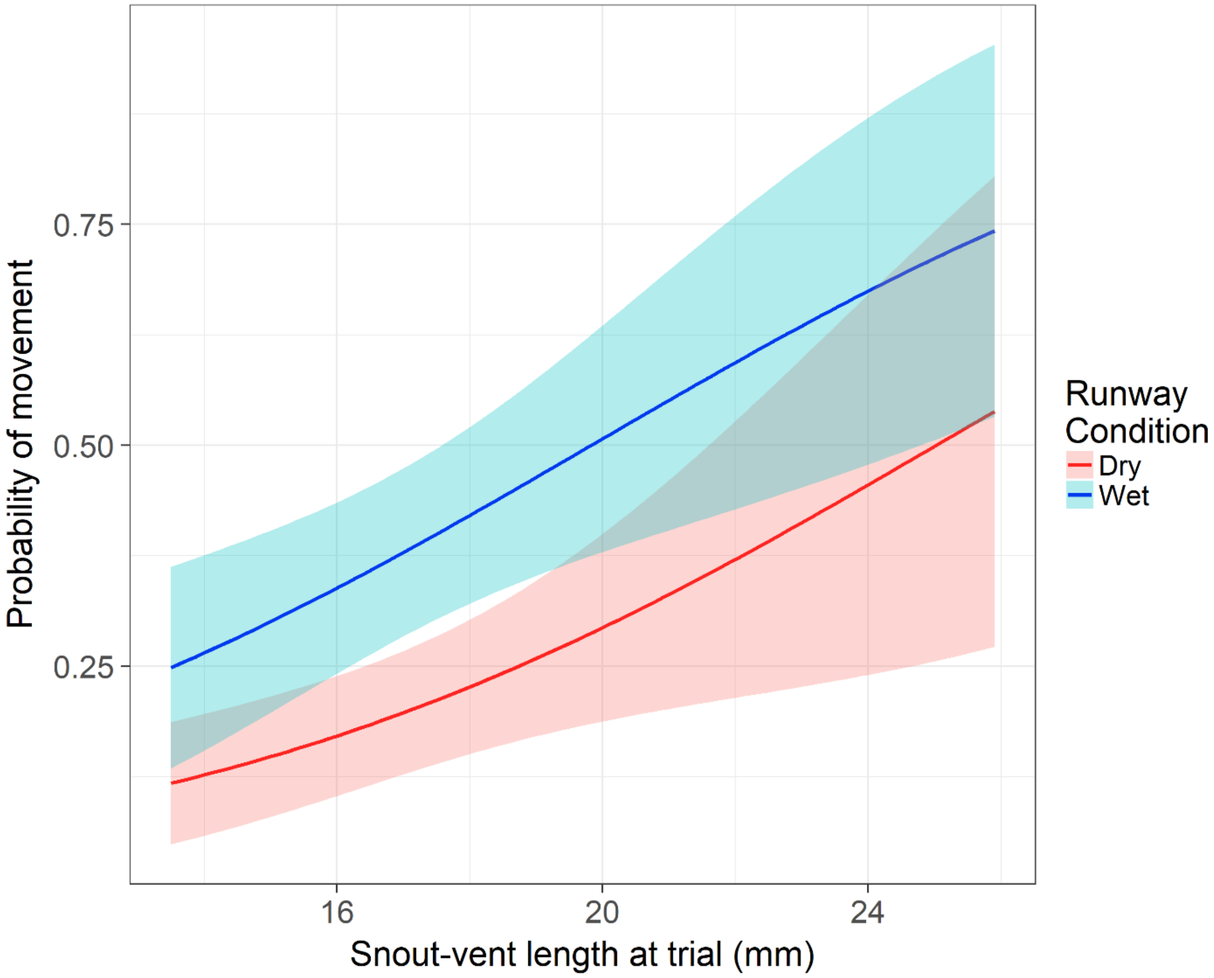

Figure 3.2 – The impact of snout-vent length and runway condition on probability of movement across the movement hurdle. Shaded areas represent the 95% confidence interval. Response is modelled off an individual from the permanent hydroperiod in their first runway assay with average body condition and time since metamorphosis.

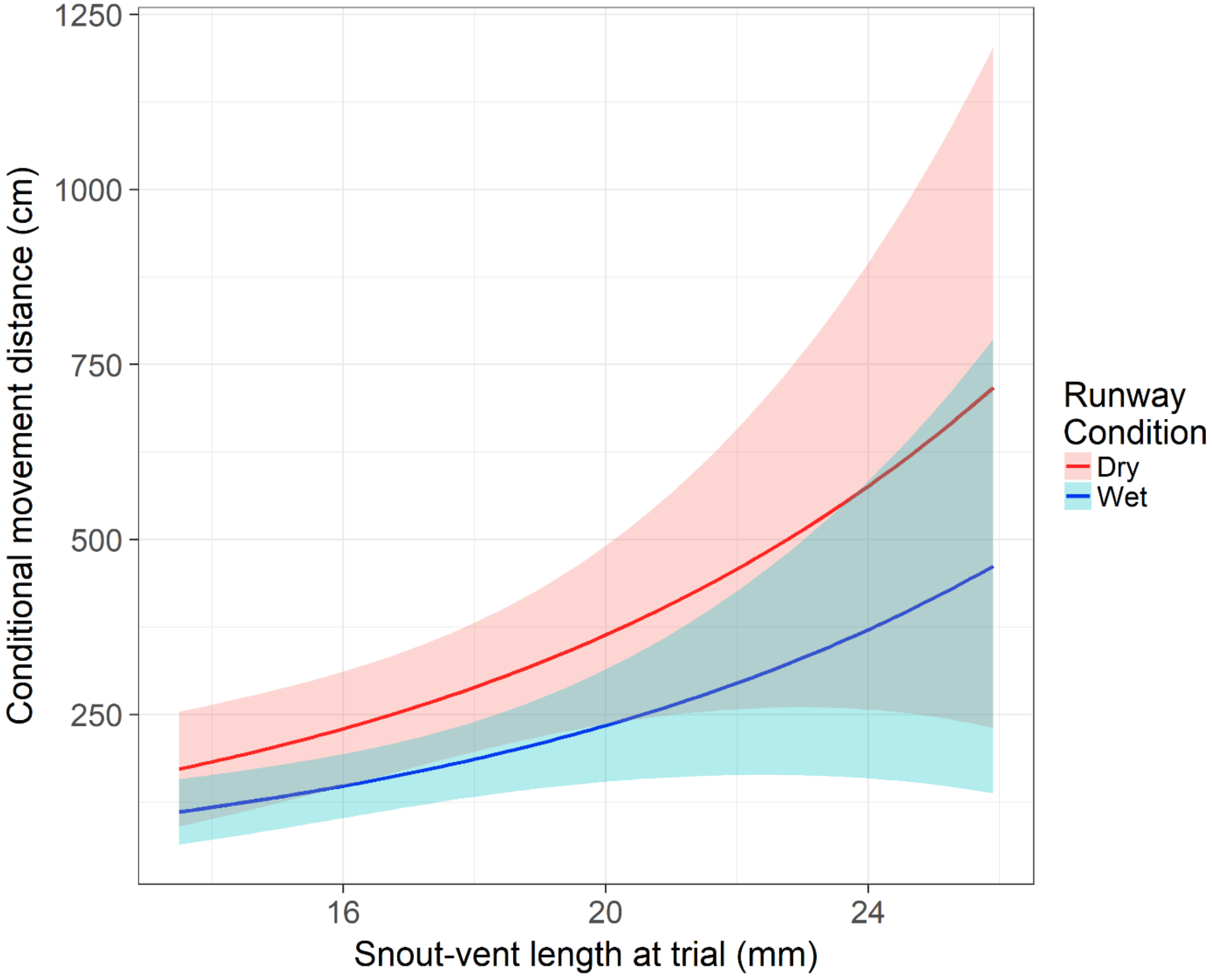

Figure 3.3 – The impact of snout-vent length and runway condition on movement distance after crossing the movement hurdle. Shaded areas represent the 95% confidence interval. Response is modelled off an individual from the permanent hydroperiod in their first runway assay with average body condition and time since metamorphosis.

JUMPING IN WITH BOTH FEET: EXPLORING FACTORS THAT SHAPE JUVENILE AMPHIBIAN MOVEMENT

CHAPTER 4 – THE ROLE OF AQUATIC PREDATOR EXPOSURE AND TERRESTRIAL ENVIRONMENT IN SHAPING THE MOVEMENT BEHAVIOR OF RECENTLY METAMORPHED FROGS

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Abstract

Exposure to predators in early life stages can alter behavioral and developmental traits of an individual across ontogeny. This is particularly important for bi-phasic amphibian species, as juvenile movement behavior can be shaped by carry-over effects of the larval environment and direct effects of terrestrial condition. We explored how aquatic predator exposure influenced juvenile morphology and movement behavior of Northern Red-legged Frogs (*Rana aurora*). This species can plastically modify larval growth, development, and behavior in response to aquatic environments. After metamorphosis, this species must then navigate an entirely novel, potentially hazardous, terrestrial environment. To quantify individual movement behavior, we used a combination of semi-natural enclosed runways and controlled-release powder tracking assays. We found a latent effect of aquatic condition, such that crayfish-exposed individuals were larger upon metamorphosis, and all predator-exposed individuals were larger relative to controls during our assays. Terrestrial conditions, however, was the most important factor shaping movement behavior. In the runway assay, individuals increased their movement distances in conditions with dry soil and low humidity. During the powder tracking assay, individuals increased their total movement distances in warm temperatures while path were straighter in cool dry conditions. In addition to the environmental influences, individual size was also an important determining factor with larger individuals moving longer distances during the powder tracking assay. Latent effects of aquatic conditions on terrestrial juveniles has been an expanding area of research in amphibian conservation but quantifying the relative importance of carry-over effects with direct environmental conditions is needed to understand the implications of sub-lethal stressors on movement.

Introduction

Evolutionary and ecological pressures are the drivers that shape life history strategies, but the dynamic nature of biological communities and environments often prevent a singular ideal adaptation. Plastic responses to changing environmental conditions, including bet-hedging and phenotypic plasticity, allow an organism to adapt by expressing different morphologies, behaviors, or development rates in response to shifting environmental stressors (Relyea, 2001a; Simons, 2014). However, there may be inherent physiologically or fitness costs to the organisms that plastically respond to environmental stress. Freshwater snails, for example, exhibiting inducible antipredator shell morphology and behaviors have associated reductions in growth rates (DeWitt, 1998). Plastic life history strategies allow organisms to trade off the benefit of improved response to an immediate stressor with a long-term cost. Antipredator responses can exchange reduced mortality risk with long term costs of reduced foraging and growth (Stoks et al., 2003).

The fitness costs of phenotypic plasticity may be even less apparent if they do not occur within a single life stage. Complex life histories allow organisms to specialize their response to distinct habitats, but may create latent, or carry-over, effects in subsequent life history stages (Orizaola and Braña, 2005; Pechenik, 2006). For example, expressed plasticity can incur costs that limit the ability of later life stages to accomplish stage-specific activities such as dispersal or reproduction (Benard and McCauley, 2008; De Block and Stoks, 2005). Alternatively, phenotypic plasticity can be determined by cues across life history transitions to affect behavior and dispersal, such as pea aphids which increase the production of offspring with dispersal-morphs when exposed to predators, or salamanders predisposed to disperse when raised in high density environments (Ousterhout and Semlitsch, 2018; Weisser et al., 1999). Insights into the expression of phenotypic plasticity and associated costs provide information about species ability to manage variation in climate and factors that have shaped their evolution (Thurman and Garcia, 2017; Weinig and Delph, 2001).

Animal movement is a initiated and constrained by a myriad of factors, some of which may be carried over from previous life history stages (Nathan and Giuggioli, 2013). These can be direct factors such as predation risk or interspecific competition shifting foraging areas (Carrascal and Alonso, 2006) or latent effects with conspecific alarm and predator cues reducing activity rates and increasing refuge use (Garcia et al., 2017). Changes in movement behavior can have significant implications on an individual's ability to access refuge, forage, or disperse to new habitats. Changing spatial distribution of individuals easily scales up to broader influences on community ecology (Warne et al., 2019). Examining the ontogenetic and environmental drivers of movement is particularly important in amphibians for two main reasons: movement has been an understudied aspect of their biology; and amphibians are a taxa of conservation concern (IUCN, 2014; Pittman et al., 2014). Amphibians have demonstrated phenotypic plasticity to a range of environmental conditions, including predator exposure (Altwegg, 2002) and water availability (Laurila and Kujasalo, 1999; Mogali et al., 2017). Further, latent effects of larval plasticity have been shown in post-metamorphic morphology (Relyea, 2001b), physiology (Bouchard et al., 2016), and movement ability (Van Buskirk and Saxer, 2001). As such, we have an opportunity to examine the relative importance of stressors across ontogeny on movement behavior and address specific mechanisms that shape individual fitness and dispersal (Benard and McCauley, 2008).

To assess immediate and latent effects on movement, we quantified morphological and behavioral responses of recently metamorphosed Northern Red-legged Frogs (*Rana aurora*) after larval exposure to predation risk and immediate exposure to dry habitat. Predator exposure can induce behavioral and phenotypic plasticity in larvae with effects that carry over through metamorphosis to impact juvenile morphology (Benard, 2004; Garcia et al., 2017; Nicieza et al., 2006). We hypothesized that aquatic predators would predispose individuals to undertake longer post-metamorphic movements in an attempt to access more hospitable breeding habitats (Buxton and Sperry, 2017). Past research has found that juveniles that experience aquatic predators increase their movement activity (Barbasch and Benard, 2011; Van Buskirk and Saxer, 2001). Further, predator-exposed larvae were predicted to develop into smaller juveniles (Capellán and Nicieza, 2007). Habitat drying during terrestrial movement events was also expected to decrease movement distances, with larger individuals moving farther along straighter paths.

Methods

Larval Exposure Treatments

Three *R. aurora* egg masses were collected from 3 independent wetlands in the Willamette Valley, Oregon for a total of nine clutches in January of 2016. Egg masses were transported to Oregon State University and placed in a temperature-controlled environmental chamber set at 12 °C with a 12L:12D photoperiod. Egg masses were transferred into individual 75L glass aquaria filled with de-chlorinated tap water and reared to hatching. Within 8 hours of hatching, larvae were transferred to 75L aquaria of de-chlorinated tap water and maintained in cohort groups. Larvae were reared until Gosner developmental stage 25, in which individuals are free swimming and no egg sac remained (Gosner, 1960) and fed 3:1 ratio of ground alfalfa and fish flakes *ad libitum* every other day. We changed water in larvae aquaria every 10 days.

On 31 March, all individuals were pooled and we randomly selected groups of 75 individuals and transferred to one of 30 semi-natural outdoor mesocosms located at the John L. Fryer Aquatic Animal Health Laboratory (44.575688, -123.240868). Mesocosms were randomly assigned a predator exposure treatment: control water, Red Swamp Crayfish (*Procambarus clarkii*) cue water, or juvenile Rainbow Trout (*Oncorhynchus mykiss*) cue water, with 10 replicates of each treatment. Each mesocosm was fitted with a tight-fitting mesh screen lid and 30% shade cloth was hung approximately 1.5m over the mesocosm tubs to reduced direct sun exposure.

Mesocosms (120 L HDPE stock tanks) were prepared two-weeks in advance by stocking 100 grams of dried and autoclaved oak leaves with 5 grams of rabbit chow in 100 liters of well-water. Mesocosm were then inoculated with natural algae and microorganism communities from 2L of pond water based on methods by Gervasi *et al.* (2013). Fixed water levels were maintained using standing pipe drains once cue water flows were initiated.

Predator cue exposure treatments were created with a flow-through system connecting mesocosms to predator stock tanks. On 2 April, cue water flows were initiated and continued for the duration of the experiment. Cue water lines consisted of continuous 1L/minute flows of effluent from 600 L stock tanks that contained either clean water, Red Swamp Crayfish, or juvenile Rainbow Trout. Rainbow Trout were selected as a representative native fish predator, while Red Swamp Crayfish are an invasive predatory species in Oregon that elicit antipredator behaviors in *R. aurora* (Pearl et al., 2003). The trout stock tank housed ~2500 grams of trout biomass and was fed BioClark 2.5mm pellets (Bio-Oregon). Because of intraspecific aggression and territorially, the crayfish tank only housed ~150 grams of crayfish biomass but fed the same diet to maintain consistency. Conspecific alarm cue (emulsified larval *R. aurora* in control water) was added to predator cue treatment stock tanks every other day to simulate predation risk (Garcia et al., 2017). The size and developmental stage of conspecific alarm cue animals advanced over the course of the experiment; therefore, cue concentration was not standardized but increased over time. Alarm cue concentration averaged 4.78g of biomass per liter with an initial rate of 1.55g/L in early April, increasing ~0.48g/L per week to a high of 9.1g/L in early July. No alarm cue was added to the control treatment.

We checked mesocosms every other day for metamorphosing individuals and collected individuals that at the end of the metamorphic window (Stage 46, Gosner, 1960). Collected individuals were measured (snout-vent length and mass) and individually marked with a unique color tag. Tagging with visible implant elastomer (Northwest Marine Technology, Inc.) consisted of 3 subcutaneous injections in the belly, right leg, and left leg (Bredeweg et al., 2019b; Govindarajulu et al., 2006; Swanson et al., 2013). Each individual was placed in a container with moist paper towel and transported to Lewis-Brown Horticultural Farm (44.551346, -123.215831). At Lewis-Brown, 20 individuals from the same larval-treatment were placed in 75L glass terrariums under a mixed oak canopy. Terrariums were assembled with moistened coconut husk bedding and were angled to create a pool of water on one end. Small sections of black HDPE drain pipe and dried grass were also provided for refuge. Individuals were fed an excess wingless fruit flies (*Drosophila melanogaster*) every other day. We collected individuals every other day for 3 weeks after the first individual completed metamorphosis on 21 June until 11 July when we had collected 218 individuals in total.

Juvenile Movement Assays

To quantify the movement behavior of juvenile frogs, we used a linear runway assay and a powder tracking assay. The runway assay was held on either dry or wet substrates and examined willingness to move as well as movement distance in a 30-minute window. The powder tracking assay examined path shape and movement ability during 30 minutes in an open field at night. These two assays always occurred in a 2-day sequence starting with the runway assay during the day, and the powder tracking assay at night the following day. This provided more than a full day of recover for individuals stressed during the runway assay.

Runway Assay

Runways (1 x 20m) were constructed at Lewis-Brown Farm using the same procedure as Bredeweg et al. (2019b). Four runways were constructed in pairs on level ground under dappled shade of surrounding trees. Each run had an exterior barrier of a single sheet of 7-mm white plastic attached to taunt wires at 75cm high along the perimeter. Inside this plastic sheeting, there was a 7cm layer of smoothed and compacted topsoil. This created a fully enclosed terrain to prevent individual escape. Dry or wet conditions were randomly assigned within each of the runway pairs. Conditions within a run were maintained during the experiment since wet runways would not dry quickly. Wet-assigned runs their entire length sprayed with well-water before each assay to the point of near saturation to minimize any standing water. Regardless of treatment, all runways had a release point (15cm disk of saturated moss) at the northeast end that was gently misted before each assay.

These assays were run starting on 28 July until 10 August during daylight hours. The start time of these assays ranged from 07:55 to 13:10h with an average of 10:15h. Individuals were tested in the runway assay in sets of 4 animals (2 in wet, 2 in dry runways) which were composed of one animal from each larval treatment group, and the fourth was rotated between groups to provide even representation of the treatments during the course of the trials. Individual animals were randomly selected within a terrarium, and terrariums of each treatment were run in sequence starting with the first established group. When selected, each individual was measured for snout-vent length and mass, then sequentially assigned to either a wet or dry runway condition based on treatment group. To start the assay, individuals were given a small dab of highly visible fluorescent powder (ECO Aurora Pink® Pigment, DayGlow Color Corp.) on their head to assist in relocation and then placed under a clay pot on the moss start location for a 5-minute acclimate period. After the acclimation period, the pot was remotely removed and individuals were given 30-minutes to move. After this time, individual final position was marked and distance from the runway start measured. Individuals were then moved to a separate temporary terrarium until their powder tracking assay.

Powder tracking assay

Powder tracking assays occurred in an adjacent agricultural field of plowed and smoothed soil in the evening the day after an individual's runway assay. Assays were held on 29 July to 11 August and were initiated after nautical dusk (21:57h on 29 July shifting to 21:36h on 11 August). All nights were free of precipitation. Animals were individually housed in perforated containers with moist paper towel until their release. Before a release, individuals were dusted in biosafe, water-soluble fluorescent tracking powder (ECO Pigments, Day-Glo Color Corp.), and allowed 5-minutes to acclimate on a petri dish lid under a plastic cover. The cover was removed after the acclimation period and each individual was given 30 minutes of free movement in the field. Releases were staggered over 30 minutes with release points spaced 10m apart and arranged along a line. A dim red light was only occasionally used when preparing an animal for release. At the end of the movement period, a UV light was used to relocate the individual, and a flag was placed at their final position. After all animals were collected, UV illumination visually revealed the tracks of the animals to allow for measurement of path total length and net displacement using measuring tapes.

Upon the completion of both assays, individuals were humanely euthanized with a solution of Tricaine Methanesulfonate (Leary et al., 2013). Euthanized animals were then imaged on a scaled gridded background for quantification of head width, forearm length, hind leg length, and body length in ImageJ (Boes and Benard, 2013; Johansson et al., 2010; Schneider et al., 2012). The Agrimet Weather Station (CRVO) was used for measurements of temperature and relative humidity during both the runway and powder tracking assays. These weather measurements were associated with the time and date of each individual's assays. All our procedures were done according to approved animal care and use protocol (ACUP# 4536 Oregon State University).

Statistical Analysis

We focused our analysis of three difference aspects of this experiment: juvenile morphology, runway assay behavior, and powder tracking assay behavior. The analysis of juvenile morphology was used to assess carry-over effects of larval condition and provided morphological covariates for the analysis of assay responses. We also used two blocking variables of mesocosm and assay group (day). Blocking by assay group encompassed variation in both the day of runway assay and night of powder tracking assay. Blocking by mesocosm was important as larval development was not independent within the same mesocosm. There were also 9 mesocosms that had low rates of metamorphosis (Less than 4 individuals: 2 control, 2 crayfish, and 5 trout), and were removed from the analysis. Of the 218 individuals that completed both assays in this experiment, only 186 individuals were used in the final analysis (Control = 58, Crayfish = 70, Fish = 57). Of the 32 animals removed, 19 were removed because of low mesocosm metamorphosis, 11 were removed as potential multivariate outliers, and 2 were removed for data errors. All statistical analyzes were performed in R (v3.5.0) and RStudio (v1.1.447) utilizing packages glmmTMB, car, visreg, plyer, DHARMa, mvnormtest, and mvoutlier (Breheny and Burchett, 2014; Brooks et al., 2017; Fox and Weisberg, 2011; Hartig, 2019; R Core Team, 2017; RStudio Team, 2016; Wickham, 2011).

Morphology

As body sizes scale, other measures of morphology for larger individuals will increase because of the strong correlation between morphological. To correct for these relationships, we used the residuals from a log-log linear regression of each trait with individual body length (Boes and Benard, 2013). This residual was multiplied by 100 to give a residual index of each trait independent of body length. We used the following seven response variables for our analysis of morphology: body length, body condition (transformed mass), relative leg length (transformed leg length), relative arm length (transformed forearm length), relative head width (transformed head width), relative emergence size (transformed emergence SVL), and emergence condition (transformed emergence mass).

We performed a MANOVA test to test for the effect of larval treatment on these seven response variables. Our data met most of the assumptions of this analysis but may violate the assumption of multivariate normality. Therefore, we elected to use Pillai's trace as our test statistic since it is robust to this violation (Olson, 1974). As a post-hoc test, we performed univariate ANOVA tests on each response variable using a Bonferroni adjustment for simultaneous inferences.

Runway Assay

There are two distinct aspects of an individual’s response in the runway assays: the decision to move away from the moist start location, and the distance moved down the runway for those that depart. Because of these two interrelated aspects, we used a mixed-effects hurdle model to analyze the behavior of individuals. The hurdle model framework allows the simultaneous fitting of a binomial logistical regression on the choice to depart the start location, and a conditional generalized linear model on distances moved by individuals (Falke et al., 2013). Animals that did not move more than 20cm from the start location (a 15cm disk of moss) were considered to have not moved down the runway. The predictor variables in this model were larval predator treatment, runway condition, ambient relative humidity, and the interaction of runway condition with relative humidity. Ambient temperature was another potential predictor, but was removed because of collinearity based on the variance inflation factor. Since movement ability in amphibians is strongly shaped by morphology, we included significant morphological traits from our earlier analysis as covariates. Continuous variables were all scaled by their variance and centered by their mean. The conditional model was fit with a truncated negative binomial error structure and a log-link and back transformed for interpretation. Within each of these models, we also included random effects to account for non-independence of larval mesocosm and assay group.

Powder Tracking Assay

Movement behavior was quantified by the total distance moved during the assay and a path straightness index. The straightness index provided a measure of movement effectiveness independent of distance moved and was created by dividing the net displacement of an individual's path by the total distance traveled. While there are finer-scale measures of path shape, the resolution of the powder trail did not allow for reliable measurement of turning angles required for these analyses (Benhamou, 2004). These two responses were analyzed using separate linear mixed-effects models with predictor variables of larval treatment, assigned runway condition, and runway movement choice. We, again, included covariates of significant morphological traits from our MANOVA analysis in addition to relative humidity, ambient temperature, and their interaction. While temperature was removed in the runway assay analysis, the variable inflation factor indicated these environmental conditions were not colinear at night for the powder tracking assay. As before, we included random effects of mesocosm and assay group in both models and continuous variables were scaled by their variance and centered by their mean. The measurements of total distance were log-transformed to account for non-normality and back transformed for interpretation, while the model of straightness index was untransformed.

Results

Morphology

Individual morphology varied between larval predator-exposure treatments (MANOVA, Pillai's Trace = 0.175, $\sim F_{14,360} = 2.466$, p = 0.0024). The post-hoc univariate ANOVAs indicated that this difference was driven by differences in body length and relative size at emergence (Table 4.1). Individuals from control conditions had the smallest body length, while both crayfish and trout treatments were 4.84% and 3.43% larger, respectively (Figure 4.1A). Individuals exposed to crayfish cue were also relatively larger at emergence compared to control and trout treatments (Figure 4.1F). A similar trend existed in relative leg length and emergence condition as observed in relative size at emergence; however, with the Bonferroni correction there was no difference (Figure 4.1C & G, Table 4.1). Relative body condition, arm length, and head width were not affected by larval treatment (Figure 4.1B, D, & E).

Runway Assay

Larval exposure treatment did not influence the willingness to move away from the start ($\chi^2(2) = 2.65$, $p = 0.266$) nor influence the conditional movement distance ($\chi^2(2) = 1.47$, $p = 0.480$). Similarly, the covariates of individual body length and relative size at emergence did not affect either movement choice (Body: $\chi^2(1) = 0.13$, $p = 0.715$; Emerg. Size: $\chi^2(1) = 0.29$, $p = 0.588$) or conditional distance (Body: $\chi^2(1) = 0.19$, $p = 0.663$; Emerg. Size: $\chi^2(1) = 0.61$, $p = 0.433$) models. We found an effect of terrestrial conditions on conditional movement distance, including runway condition ($\chi^2(1) = 6.68$, $p = 0.010$), ambient humidity ($\chi^2(1) = 20.6$, $p < 0.001$), and the interaction of these two ($\chi^2(1) = 6.15$, $p = 0.013$). If an individual moved down the runway, that animal would move the greatest distance in dry runway conditions when relative humidity was low (Figure 4.2). Movement choice was not influenced by runway conditions ($\chi^2(1) = 2.45$, $p = 0.118$), ambient humidity ($\chi^2(1) = 0.81$, $p = 0.367$), or their interaction ($\chi^2(1) = 1.11$, $p = 0.292$).

Powder Tracking Assay

Behavioral responses in the powder tracking assays, similar to results in the runway assay, were strongly affected by the ambient conditions. The total movement distance of individual in this assay were influenced by ambient temperature ($\chi^2(1) = 15.5$, $p < 0.001$). For each Celsius degree increase in temperature, movement distances increase by 12.7% (95% CI = 6.2 to 19.6%, Figure 4.3). The straightness index was also influenced by environmental conditions with significant effects of ambient temperature ($\chi^2(1) = 5.53$, $p = 0.018$), relative humidity ($\chi^2(1) = 8.81$, $p = 0.003$), and their interaction ($\chi^2(1) = 14.67$, $p < 0.001$). Individual path straightness was highest (most effective) in low temperatures and low humidity (Figure 4.4).

Total movement distance was influenced by an individual's body length ($\chi^2(1) = 12.58$, $p < 0.001$) and their willingness to move in the runway assay ($\chi^2(1) = 5.39$, $p = 0.020$). Movement distances increased on average by 11.7% (95% CI = 5.1 to 18.8%) for each millimeter increase in an individual's body length (Figure 4.3). Individuals that moved away from the start location in the runway assay reduced their total movement distance in this assay by 16% (95% CI = 2.8 to

28.7%, Figure 4.3). The effect of the movement choice from the runway assay also influenced the straightness index ($\chi^2(1) = 5.66$, $p = 0.017$), such that individuals that moved in the earlier assay had straightness indices that were reduced on average by 0.085 (95% CI = 0.015 to 0.156, Figure 4.5). There were no effects on total movement distance from larval exposure treatment ($\chi^2(2) = 0.63$, $p = 0.729$), runway assay condition ($\chi^2(1) = 0.94$, $p = 0.332$), relative size at emergence ($\chi^2(1) = 0.37$, $p = 0.543$), relative humidity ($\chi^2(1) = 2.21$, $p = 0.137$), or the interaction of humidity with temperature ($\chi^2(1) = 0.90$, $p = 0.343$). There were also no effects on the straightness indices from larval treatment ($\chi^2(2) = 3.34$, $p = 0.188$), runway assay condition ($\chi^2(1) = 2.64$, $p = 0.104$), individual body length ($\chi^2(1) = 0.83$, $p = 0.361$), or relative size at emergence ($\chi^2(1) = 0.00$, $p = 0.954$).

Discussion

Juvenile red-legged frogs exhibited phenotypic plasticity indicative of latent effects from larval predator exposure. The latent effect of larval predator treatments was observed in shifts in morphology (Figure 4.1). There was no evidence of a latent effect on movement behavior in our assays. In our runway assay, individual response was primarily determined by ambient humidity and the moisture condition of the terrain, with individuals in low humidity and dry soil moving the longest distances. The role of environment was again important in the powder tracking assay with ambient temperature and humidity effecting movement. Movements were longer in warmer conditions, and movement paths were straighter in cooler and dryer conditions. However, individual conditions also influenced movement in the context of the powder tracking assay, with larger individuals and those that did not move in the runway assay increasing their movement distances.

The latent effect on morphology larval resulted in larger body sizes and relative size at emergence for individuals exposed to invasive crayfish or native trout. These results support other research establishing latent effects of larval conditions on juvenile morphology in amphibians (Bouchard et al., 2016; Garcia et al., 2017; Relyea, 2001b; Tejedo et al., 2010; Van Buskirk and Saxer, 2001). However, the direction of this plastic response contrasted our hypothesis, as individuals in predator exposure treatments increasing individual size compared to control treatments. This may indicate the mechanism of the expressed plasticity may differ from reduced activity and foraging (Altwegg, 2002) and instead rely on development as an escape (Benard, 2004; Relyea, 2001a). Contrary to previous studies, we did not find carry-over effects on other aspects of juvenile morphology such relative leg lengths (Relyea, 2001b; Tejedo et al., 2010), body size (Vonesh and Warkentin, 2006), or behaviors such as activity rate (Barbasch and Benard, 2011; Van Buskirk and Saxer, 2001). Potential latent effects from stressful larval environments can also include changes in physiology that is less apparent in morphology (Bouchard et al., 2016). The long term effects of these induced shifts in body size are unclear, as compensatory growth in post-metamorphic individuals has been observed (Boone, 2005; Bredeweg et al., 2019b; Charbonnier et al., 2018).

Our results indicating that the role of individual size on movement only occurred in one assay contrasted other studies demonstrating strong relationships between individual body size and post-metamorphic movement (Beck and Congdon, 2000; Bredeweg et al., 2019b; Searcy et al., 2018; Yagi and Green, 2017). We did not find an effect of individual morphology or larval predator treatment on juvenile movement behavior in experimental runways. The lack of significant influence of movement behavior as a function of body size, a pattern that has been wildly observed in amphibian species (Beck and Congdon, 2000; Searcy et al., 2018; Yagi and Green, 2017), may be contributed to the result of limited variation in individual body size in our experimental animals. When we compare the distributions of individual sizes between our results and a similar experiment with the same species that documented an effect of individual size, our results here have less variety of size with individuals ranging from 16.3 to 23.8mm (range = 7.5mm) compared to 13.1 to 25.9mm (range = 12.8mm) by Bredeweg et al. (2019b, Figure 4.6). Having individuals that were more similar in size would have made the detection of movement behaviors more challenging. The cause of our reduced range of individual sizes compared with Bredeweg et al. (2019b) was likely the limited window of metamorphosis and subsequent post-metamorphic growth (Figure 4.7). The explicit variation in movement and dispersal behavior of individuals across the entire metamorphic window is an important area for further exploration (Schmidt et al., 2012).

While individual size or relative size at emergence did not influence directed movement in runways, individual morphology was important in shaping free movement behavior, with longer individuals moving farther distances. While this result fits the discussed expectations above, it is unclear as to why this result was only observed in the evening movement assay. The distinction could speak to differences in diurnal or nocturnal periods in changing relative movement phase of juvenile amphibians as discussed by Pittman et al. (2014). Additional information on the temporal activity of this species could inform the timing of normal activity. Individuals that did not move in our runway assay also moved further and straighter during the free movement assay. This could indicate some variability of an individual's propensity for movement in different contexts. While we did not explicitly measure personality in this project, the role of personality in shaping amphibian movement behavior has been gaining support (reviewed by Kelleher et al., 2018). Rather, we found that movement of individuals was primarily determined by environmental conditions, which is in line with observations of broad patterns of amphibian dispersal (Nowakowski et al., 2015; Peterman et al., 2014; Watling and Braga, 2015).

Environmental condition in our movement assays were the primary factors shaping individual response, with dry soil and atmospheric conditions increasing movement distance and path straightness. The importance of moisture in the environment on amphibian movement, dispersal, and survival is understandable given their sensitive physiology (Mitchell and Bergmann, 2016; Moore and Gatten, 1989; Watling and Braga, 2015). The association of long movements and straighter paths in dry conditions is somewhat counterintuitive for animals sensitive to desiccation. There is evidence that juvenile amphibians do not avoid dry habitats to the same extent as adults, and it is unclear if this functions as an adaptive form of movement or just naiveté (Janin et al., 2012). This behavior, however, does fit into a context of compensatory movement in harsh conditions that has been observed in amphibian movement speed (Haggerty et al., 2019), distance (Bredeweg et al., 2019b), and genetic connectivity (Peterman et al., 2014). Individuals in stressful, dry conditions were perhaps more motivated to move beyond these habitats in an attempt to find more suitable refuge.

The mechanisms by which biological systems plastically modify phenotypes in response to stressors in dynamic environments, an ability widely documented in larval amphibians, influence the dispersal and fitness on a broader scale of an organism's life history is an important area of continued research (Benard and McCauley, 2008). There are many opportunities to expand our understanding of post-metamorphic amphibian movements as this life-stage has been difficult to track *in situ* (Pittman et al., 2014). While we only found latent effects on morphology in our study, examination of how the various interacting aspects of individual traits, environmental conditions, and carryover from larval environments ultimately shape movement behavior is important for yet a broader challenge for advancing the understanding of amphibian ecology.

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Table 4.1 – Results from post-hoc ANOVA tests of morphological traits between larval treatment groups of control, crayfish predated, and rainbow trout predated.

Morphological Trait	Body Length	Body Condition	Relative Leg Length	Relative Arm Length	Relative Head Width	Relative Emergence Size	Emergence Condition
Sum of Squares	26.13	103.3	102.6	128.4	4.794	96.83	790.8
F2,185	8.3	0.65	1.66	0.8	0.22	5.67	3.69
p-value	0.002*	1	1	1	1	0.028*	0.187
p-values adjusted using a Bonferroni correction; asterix indicating significant values at the α = 0.05 level.							

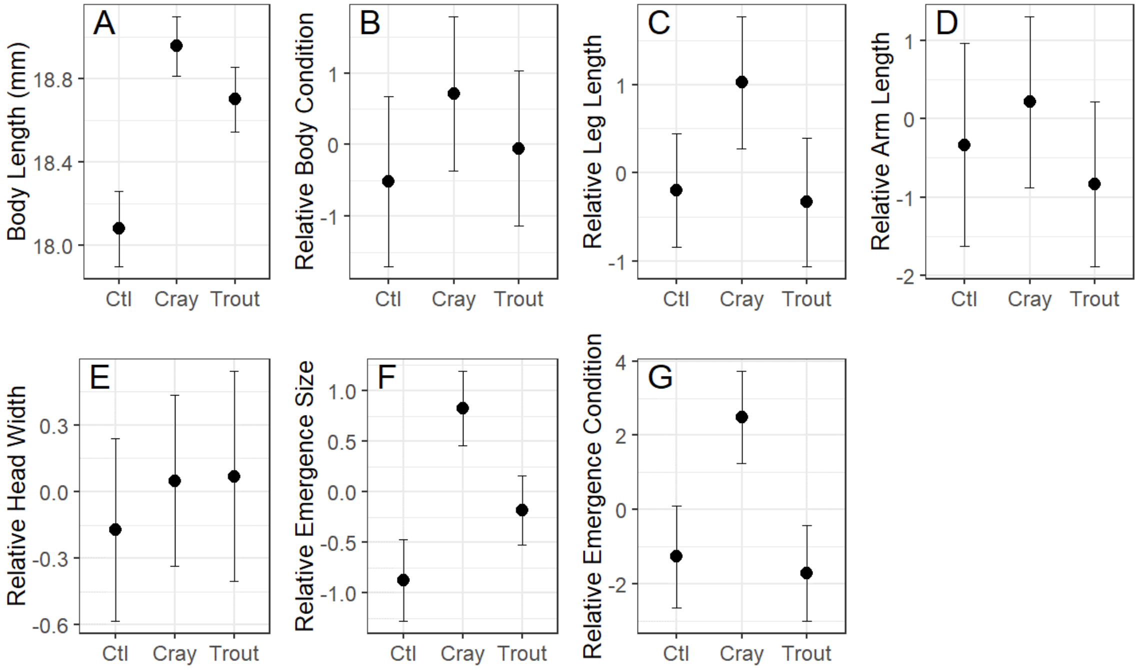

Figure 4.1 – Morphological traits of each larval treatment group (Ctl = control, Cray = crayfish predated, Trout = rainbow trout predated). Mean values are indicated by circles with error bars illustrating ± 1 standard error.

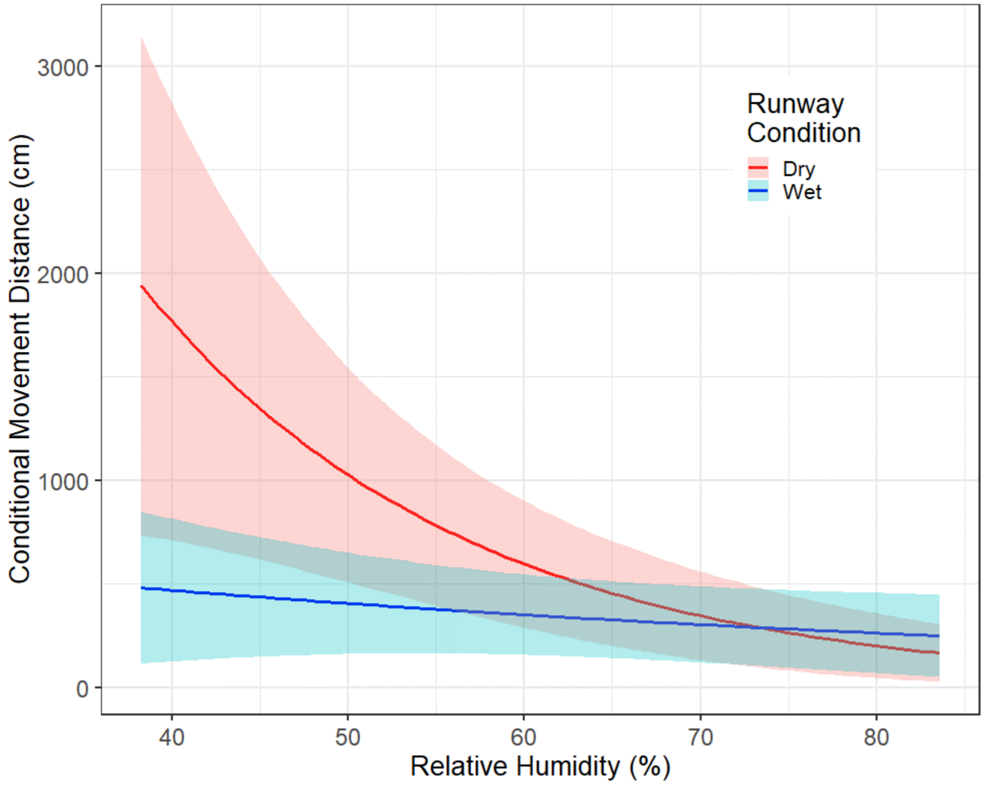

Figure 4.2 – Partial residual plots of the impact of ambient relative humidity and runway condition on the movement distance of those individuals that move from the start in the runway assay. Shaded areas represent 95% confidence intervals. Response is modelled based on an individual from the control treatment of average body length and relative size at emergence.

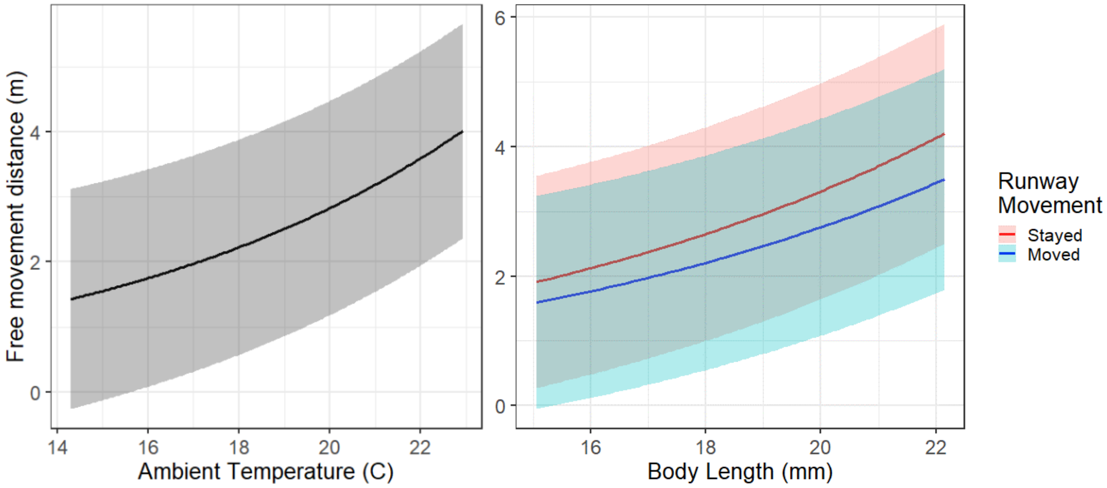

Figure 4.3 – Partial residual plots of the mean response in movement distance from the impacts of ambient temperature (left) and body length and runway behavior (right) in the powder tracking assay. Shaded areas represent 95% confidence intervals. Response is modelled based on an individual from the control treatment of average body length and relative size at emergence.

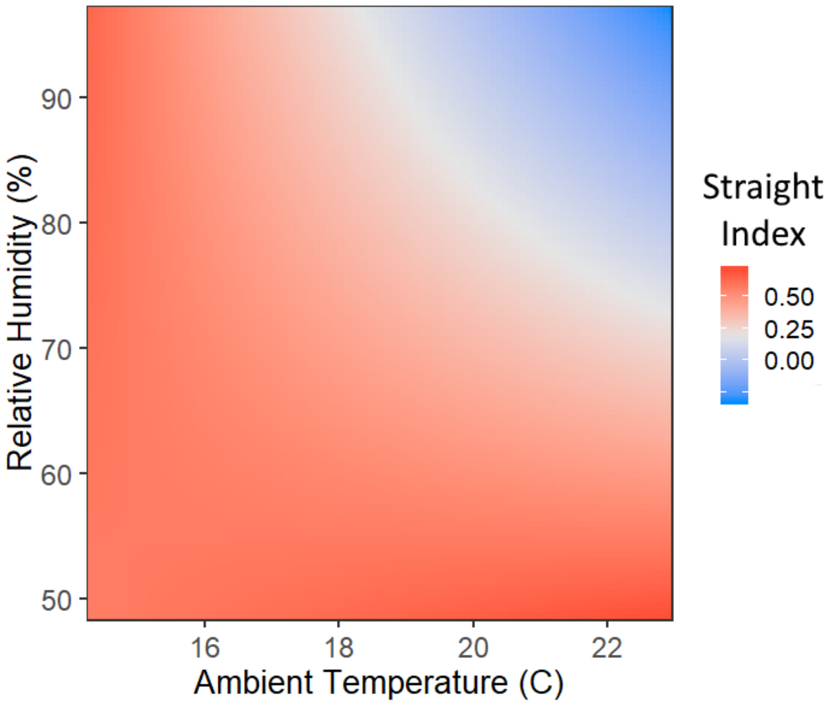

Figure 4.4 – Partial residual plots of the mean straightness index in the powder tracking assay based on the interaction of ambient temperature and relative humidity. The straightness index represents a ratio of net displacement with distance traveled; an index of 1 is a straight line, while a tortuous path approach can zero. The color represents the mean response with each combination of temperature and humidity. Response is modelled based on an individual from the control treatment of average body length and relative size at emergence with average temperature and humidity.

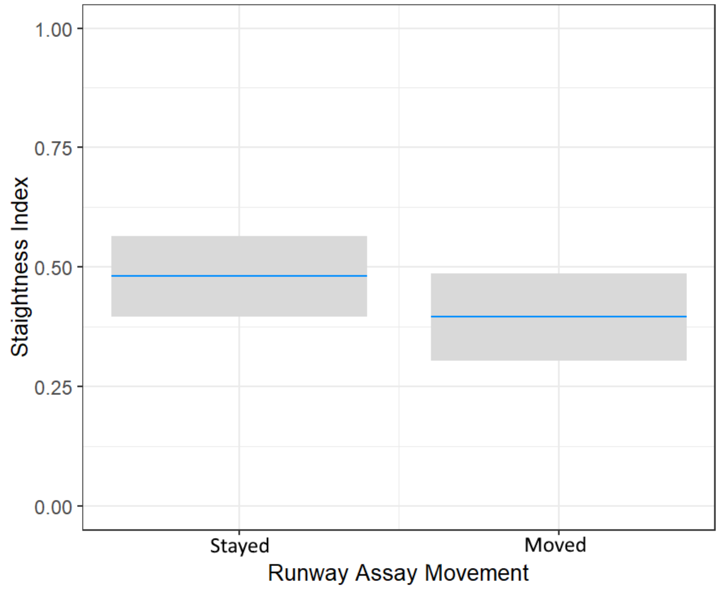

Figure 4.5 – Partial residual plots of the mean straightness index in the powder tracking assay based on the dispersal choice in the runway assay. The straightness index represents a ratio of net displacement with distance traveled; an index of 1 is a straight line, while a tortuous path approach can zero. Shaded areas represent 95% confidence intervals. Response is modelled based on an individual from the control treatment of average body length and relative size at emergence with average temperature and humidity.

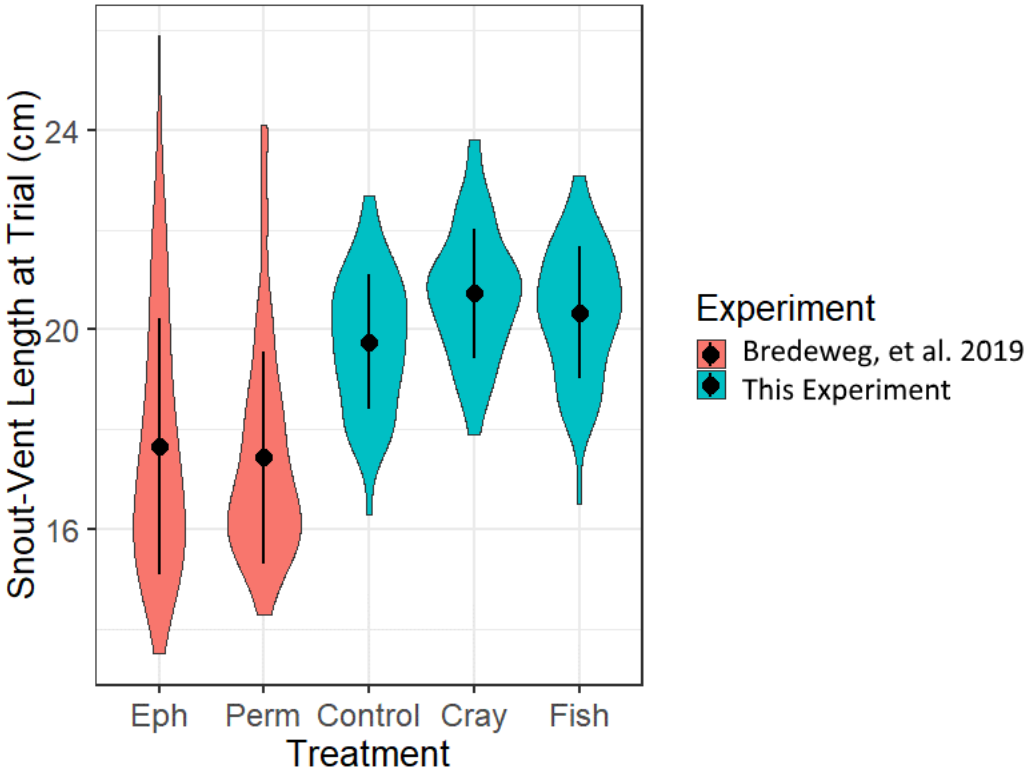

Figure 4.6 – Violin plots showing the distribution of individual size (Snout-vent length) between a similar experiment (Bredeweg et al., 2019b) in comparison to this experiment. Violin plots indicate the kernel density of sizes for each treatment level with the point and error bars showing mean value and standard deviation.

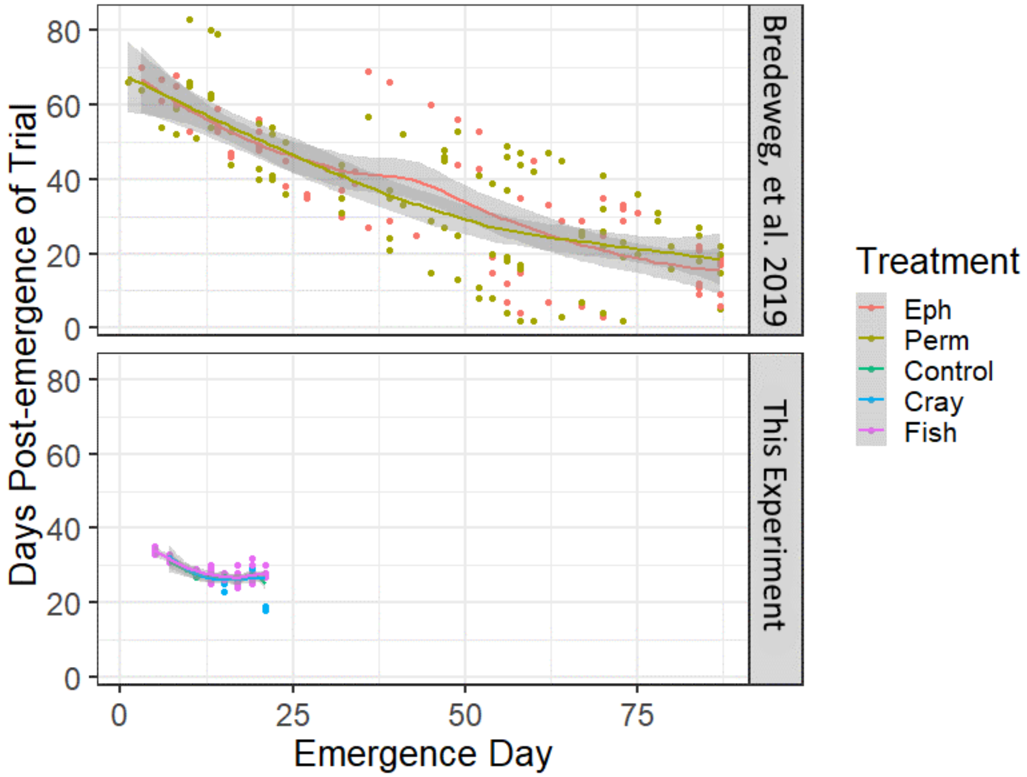

Figure 4.7 – Comparison of the metamorphic window and time elapsed post-emergence before behavioral trials of animals included with the top panel from a similar experiment (Bredeweg et al., 2019b) with this experiment shown on the bottom panel. In each experiment, emergence day was based of the date of the first animal to complete metamorphosis as Day 1. The colors represent the different treatments within each experiment and a best fit line using the LOESS method with a 95% confidence interval.

JUMPING IN WITH BOTH FEET: EXPLORING FACTORS THAT SHAPE JUVENILE AMPHIBIAN MOVEMENT

CHAPTER 5 – THE IMPACTS OF CHANGING CLIMATE ON AMPHIBIAN DISPERSAL AND POPULATION CONNECTIVITY IN A SIMULATED ENVIRONMENT

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Abstract

Movement is a fundamental process through which animals interact with their environment. However, the movement process may be influenced by environmental variability, including climate change. Climate change influences precipitation and, therefore, environmental conditions that influence species dispersal success. Amphibian species, a group that often inhabits isolated breeding habitat, are dependent on access to moist conditions in the terrain making them sensitive to shifting conditions. How conditions associated with climate change impact dispersal behavior of amphibian species will be important in determining how populations respond in a warming climate. To assess how climate change might influence population connectivity, we used the HexSim modeling framework to develop a spatially-explicit, individual-based model of juvenile Northern Red-legged Frogs (*Rana aurora*) movement behavior. Our model combines experimentally observed movement behavior with current and predicted future environmental conditions derived from three CHIMP5 global climate models (CNRM-CM5, HadGEM2-CC, and IPSL-CM5B-LR) to assess predicted changes of juvenile dispersal within a simulated landscape. Across all climate models, future populations had increased rates of surviving dispersers compared with past climate periods. However, this increase in total number of surviving dispersers was offset by reduced rates of effective dispersal that contribute to population connectivity. The timing of effective dispersers was also shifted to later in the season, which could have implications for exposure to higher temperatures or on overwinter survival. Projects such as this that integrate experimental evidence and population simulation are important for understanding the spatial ecology of amphibians in the face of a changing climate.

Introduction

The effects of climate change have been predicted to threaten as many as one in six species with extinction (Brook and Fordham, 2015; Urban, 2015). Climate scientists have developed a range of climate models of varying complexity, with a general consensus that average temperatures, precipitation, and extreme weather events will increase (Abatzoglou, 2013; Hardiman et al., 2012; Rupp et al., 2013; Taylor et al., 2012). However, determining the impacts of these changing climates on species has been a challenge as predicted responses can widely vary based on species ecology, biology, and available data (Brown et al., 2016; Fei et al., 2017).

Researchers have developed a variety of tools to assess the relative risk to species and their population response to climate change (Pacifici et al., 2015). Species distribution models (SDM), for example, represent a correlative approach that relates current or historic species distributions with an environmental niche, the characteristics of which can be projected into future climate conditions to evaluate climate impacts (Elith et al., 2010; Gerick et al., 2014; Mckelvey et al., 2011; Miller and Holloway, 2015). Alternatively, approaches incorporating species-level ecology and life-history characteristics, termed trait-based assessment, can evaluate climate vulnerability risk across large groups of species (Fei et al., 2017; MacLean and Beissinger, 2017; Pacifici et al., 2017; Pearson et al., 2014). The application of these tools can be used to priorities research for species at risk and manage for increase connectivity providing populations opportunities to track their preferred environmental niche (Hodgson et al., 2009, 2011).

In general, approaches to assessing climate impacts have focused on broad, landscape-level responses, often omitting important fine-scale and individually based mechanisms such as dispersal (Holloway et al., 2016; Stevens et al., 2014; Zurell et al., 2012), demography (Santini et al., 2016; Urban et al., 2016), physiology (Bozinovic and Pörtner, 2015; Gerick et al., 2014; Kearney and Porter, 2009), and evolutionary adaptation (Munday et al., 2013; Tung et al., 2018; Urban et al., 2014). Such coarse-scale approaches limit these model’s ability to project complex interactions that create non-additive climate impacts, as in the case of changing disease risk (Murray et al., 2013; Rohr et al., 2011) or the spread of invasive species (Gallien et al., 2012; Mainali et al., 2015; Rahel and Olden, 2008). Together, understanding the dynamics of community- and species-level responses to a changing climate can even create synergistic effects that would otherwise not be apparent (e.g., Mitton and Ferrenberg, 2012). In contrast, the use of mechanistic models to predict species responses provides an alternative approach that integrates biological detail that can better predict synergistic effects (Ehrlén and Morris, 2015; Loehle and LeBlanc, 1996; Singer et al., 2015).

For amphibians, species of conservation concern whose responses to climate change involves a myriad of life history, physical, and interactive adaptations, a mechanistic approach may be an informative appropriate even when limited data availability restricts the scope of these investigations (Blaustein et al., 2010; Urban et al., 2016). The majority of existing attempts to create mechanistic models of climate impacts have focused on characteristics of amphibian physiology (Davenport et al., 2017; Gerick et al., 2014; Hallman and Brooks, 2016; Velo-Antón et al., 2013). Changes to precipitation and temperature will be important factors as desiccation risk shapes both individual dispersal and population connectivity for amphibians (Peterman et al., 2014; Watling and Braga, 2015). Thus far, these mechanistic approaches have been hampered by the exclusion of broader organism ecology and dispersal behavior (Singer et al., 2015; Travis et al., 2013). This omission has largely been driven by the limited availability of dispersal and movement information for amphibian species, particularly for juveniles as the hypothesized stage of dispersal (Bredeweg et al., 2019a; Pittman et al., 2014; Sinsch, 2014). As a result, efforts to incorporate amphibian dispersal behavior into mechanistic models has relied on adult movements despite evidence that juveniles have unique responses to terrain compared to later life-stages (Bartelt et al., 2010; Janin et al., 2012). In addition to importance of dispersal to access new or isolated habitats, such movement is important in maintaining gene flow and hence species ability to respond to future changes (Caplat et al., 2016; Muñoz et al., 2016; Peterman et al., 2013a). New knowledge of juvenile amphibian movements (Chelgren et al., 2008; Cline and Hunter, 2014, 2016; Ousterhout and Semlitsch, 2018; Scott et al., 2013; Semlitsch et al., 2012), provides us an opportunity to revisit and enhance mechanistic climate change models for these species by incorporating movement behavior of juvenile amphibians.

To address these knowledge gaps, our objective was to evaluate how climate change will affect juvenile amphibian dispersal and therefore landscape-level population connectivity. To address this objective, we developed a mechanistic, spatially-explicit, individual-based model

(IBM) for the Northern Red-legged Frog (*Rana aurora*) in moist and dry conditions, that integrated experimentally derived movement behavior (Bredeweg et al., 2019b) and the HexSim modeling framework (Schumaker and Brookes, 2018). This integrated IBM will assess changes in dispersal behavior of an understudied life-stage of amphibians.

Methods

This project was developed in a spatially-explicit, flexible, individual-based modeling environment called HexSim (Schumaker and Brookes, 2018). This modelling framework utilizes a hexagon-shaped cell to provide additional complexity in movement behavior that is not constrained to a four-sided grid. Since our model is a simulated representation of the Northern Red-legged Frogs (R. aurora), we used species biology and experimentally derived conditional movement behavior data to parameterize our model.

Base Landscape

The landscape extent of this model consisted of 1000 rows of 1000 hexagons (87 hectares) with the scale of each hexagon measuring one meter in width. The landscape extent contained eight individual patches of habitat, each of which were 5000 hexagons (0.435 hectares) in size and uniformly constructed in circular shapes. These patches were arranged within the landscape to create both isolated and adjacent groups (Figure 5.1). Patches were similar in habitat suitability, and considered ‘habitat’ in a matrix of ‘non-habitat’ consistent with other patch-matrix landscape studies (Hein et al., 2004; King and With, 2002). This base landscape arrangement remained fixed for all simulation runs while the weather conditions changed based on the climate model and period.

Weather Data

Precipitation and temperature can vary across the extent of a species range. To account for such variability, we used weather information for thirty different locations within the range of *R. aurora*. For each of these locations, we the associated extract predicted temperature and precipitation projections of our climate models. The geographical range of *R. aurora* was sourced from IUCN Redlist data (International Union for Conservation of Nature & NatureServe, 2015). Because this species range data has a very course resolution, we further restricted our study extent to elevations below 1200 meters to match the natural history of the species (Lannoo, 2005). Within this area, we randomly selected 30 locations within the states of Washington, Oregon, and California (QGIS). For each of these random points, we extracted the associated weather variables from the MACAv2-METDATA dataset based on three climate models: CNRM-CM5 (hereafter: CNRM), HadGEM2-CC (hereafter HadGEM2), and IPSL-CM5B-LR (hereafter IPSL; Fairhead et al., 2016; Hardiman et al., 2012; Voldoire et al., 2013). These three specific global climate models were selected because they a encompassed a range of seasonal change in precipitation within the pacific northwest (Rupp et al., 2017). Climatic data was based on a statistical downscaling method (Multivariate Adaptive Constructed Analogs; Abatzoglou and Brown, 2012) of global climate model data (Coupled Model Intercomparison Project 5; Taylor et al., 2012). This downscaling method provided daily time-step precipitation for each climate model used (CNRM, HadGEM2, and IPSL). Additionally, this dataset relied on a modified method that utilized METDATA as observational training data (Abatzoglou, 2013). From this downscaled climate data, we extracted precipitation data and maximum daily temperature for each day between July 1 and November 30. This was done for each year within a 30-year window for historical (1970-1999) and future (RCP 8.5, 2070-2099) climate periods. We additionally extracted the total amount of precipitation from Jan 1st to June 30th for each location, climate period year, and climate model to provide a year-to-date (YTD) precipitation measure.

Based on the climate period and climate model for each simulation, one year in the 30-year range and one of the 30 locations were randomly selected. This selected point-year combination provided the specific weather data for the simulations (see below). Weather variables of interest included daily precipitation (mm), maximum daily temperature (°C), and YTD precipitation (mm). Weather conditions were input into the HexSim modeling framework through separate lookup tables for precipitation, temperature, and YTD precipitation to establish the environmental weather conditions for each step of each simulation. From these data lookup tables, the model assigned distinct conditions to environment based on the daily precipitation amount. Daily precipitation of greater than 1mm was considered ‘rain’ conditions, while less 1mm was considered ‘no-rain’ conditions. The general moisture of the environment was also considered in the model as either ‘wet’ (greater than 7mm precipitation in 7 days) or ‘dry’ (less than 7mm precipitation in 7 days). Maximum daily temperature and YTD precipitation were not used to set the environmental conditions but were used in other aspects of the simulated species phenology and survival.

Model Agent Structure

The model was developed around a daily time interval with one time-step representing a single day. This temporal scale was chosen because it fit the daily resolution of available climate data; weather data (see above) was adapted for this time step. The model was then run for 153 days starting on July 1st of a model year until November 30th thereby corresponding to a late summer metamorphic time period based on the phenology and development of *R. aurora*.

At the initiation of a simulation, 400 frogs were introduced to each of the eight distinct patches (3200 in total). Each patch represented an isolated breeding population. Mirroring the life history of anuran amphibians, simulated individuals were introduced as tadpoles and required to completed metamorphosis before dispersal. Individuals were assigned a given day to complete this transformation by drawing and rounding up values from a normal distribution (μ=day 16, σ^2=3.5). At the completion of metamorphosis, each individual was assigned their initial size (SVL at metamorphosis). An individual’s size was drawn from a normal distribution that was dependent on the emergence day (μ_0^{SVL}=20mm, σ^2=1). The distribution had a mean of 20mm on day 1 and this mean was reduced by 0.1mm per day over the emergence window. This reduction in emergence body size over the metamorphic window was done to mirror experimental data of *R. aurora* metamorphosis (Bredeweg et al., 2019b; Chelgren et al., 2006). Because winter and spring rainfall can also influence amphibian size at emergence through changes in hydroperiod (Blaustein et al., 2010), we assumed that increased amounts of precipitation would create longer hydroperiods and allow for increased growth of tadpoles and therefore larger size at metamorphosis (Tejedo et al., 2010). The initial mean size at emergence (μ_0^{SVL}) was shifted up or down by a magnitude of 10% of the year-to-date rainfall above or below the 1000mm. This threshold was set based on the 30-year (1970-1999) YTD precipitation average for January to July from the CNRM climate model. For example, if year-to-date rainfall was 1200mm (+20%) the initial mean size at emergence was increased to 20.4mm (+2%).

Conversely, if the year-to-date rainfall was 800mm (-20%) the initial mean size at emergence was reduced to 19.6mm (-2%).

Dispersal and Survival

After completion of metamorphosis, simulated individuals remained at the edge of their starting patch and were considered ready to disperse. At this point, each individual was assigned a day to begin their individual dispersal attempts. This dispersal initiation day was randomly drawn from a 100-day window beginning on July 30th. After completion of metamorphosis and before their departure from the patch, terrestrial individuals were allowed to grow. Growth for each individual was randomly drawn from a range between 0mm and 0.1mm per day. However, research on amphibians has shown that growth can be reduced in dry environments (Charbonnier et al., 2018; Gomez-Mestre and Tejedo, 2005). Therefore, in 'no-rain' conditions individual growth was restricted to a random amount between 0mm and 0.057mm (43% reduced range based on Gomez-Mestre and Tejedo, 2005).

Once the model reached the day an individual was assigned to begin its dispersal attempt, the ultimate departure from the patch was based on the current weather conditions. Dispersal probability from the patch was parameterized from the movement behavior of *R. aurora* observed in Bredeweg et al. (2019b): initiation of movement in moist condition was higher (44%) than in dry conditions (24%) and was strongly influenced by an individual's size (increased 16% for each additional 1mm SVL). Based on the weather conditions in the simulations, individual dispersal behavior was determined using the probabilities of 44% in 'rain' and 24% in 'no-rain' in combination with a sigmoidal function of body size ($p = 0.5 - 1/(1 + e^{-(SVL - \mu0\mathrm{SVL})*0.16})$). If an individual did not disperse on a given day, the process was repeated the following day until an animal dispersed.

Once dispersal was initiated, the dispersal process was modeled as a sequence of four components that occurred in a single day: (1) drawing a movement length from a log-normal distribution function, (2) scaling the movement length based on environmental conditions, (3) movement based on scaled movement length, and (4) environmentally determined survival. One set of these components (1-4) occurred for an individual each day they were dispersing. Assuming an individual survived each day, this sequence repeated the following day for a total of 6 days dispersing. Beginning on the third day and every day thereafter, individuals would assess their location at the end of the sequence. If they finished a day in habitat, they would stop dispersal behaviors and were considered ‘done’ with dispersal. Individuals that did not locate habitat at the end of those 6 dispersal days were considered unsuccessful and perished.

(1) The movement length was randomly drawn from a log-normal distribution function ($\mu=4$, $\sigma^2=1$). This distribution is common in individual movement (Gurarie, 2008), and has fit some amphibian movement observations (De Villiers and Measey, 2017). This movement of highest probability in this function is 20m which is well within the ability of juvenile *R. aurora*. This length was bound at a minimum value of 5 to prevent dispersing individuals from not moving.

(2) The movement length was then scaled based on the individual and environmental conditions. We parameterized individual behavior from experimental observations that quantified movement behavior of *R. aurora* based on conditions (36% reduced in wet conditions compared to dry) and individual size (individuals increased distance by 12% for each additional 1mm in SVL; Bredeweg et al., 2019b). Conditions in ‘no-rain’ were considered default while in ‘rain’ conditions, movement distance was reduced by 36% with a minimum value of five. Movement distance was also increased or decreased by 12% for each 1mm an individual was over or under μ_0^{SVL} (20mm). Finally, we assumed that hot conditions would reduce dispersal ability. We used the threshold of 22.5°C as the temperature of optimal movement (T_{opt}) based on the average of maximal acceleration and velocity from Gerick et al. (2014). Based on the model’s maximum daily temperature, movement distance was reduced by 10% per each °C over T_{opt}. If the maximum daily temperature for a given day was under the T_{opt} threshold, no temperature scaling was made.

(3) Individuals then moved in the landscape a distance determined by the modified movement length which was rounded down to the nearest integer (movement length=11.19, hexagons moved=11). All dispersal paths had moderately high path autocorrelation (75% over a period of 10 steps). During the first and second days of dispersal movement, the only influence of the landscape on movement was to direct

movement away from patch interior. Beginning on the third day of dispersal, individuals were redirect to any hexagons of habitat during their movement.

(4) To focus our model on dispersal behavior, we assumed that individual mortality is only a risk during the dispersal window. When individuals were within a habitat patch before dispersal or after completing dispersal, they were at no risk of mortality. The rate of mortality risk during dispersal was dependent on the environment and an individual's condition. When a model day had conditions of 'rain', 'wet', and the maximum daily temperature was less than 10°C over T_{opt} individuals had a 100% survival rate even during dispersal. In 'no-rain' rain conditions (daily rainfall less than 1mm), survival rates of dispersing individuals were reduced by 20%. In 'dry' conditions (less than 7mm of rainfall in 7 days), the survival rates of dispersing individuals were reduced by 20%. When maximum daily temperature was more than 10°C over T_{opt}, dispersing individual's survival rate was reduced by 10% for each 1°C over this higher threshold. Individual size is also important in determining risk of dehydration (Newman and Dunham, 1994; Scott et al., 2007). When environmental conditions were both 'no-rain' and 'dry', small individual's survival was additionally reduced by 10% for each 1mm they were under μ_0^{SVL}. These effects could combine additively with small individuals in 'no-rain', 'dry', and extremely hot conditions experiencing the lowest probability of survival.

Simulations and Data Extraction

We ran 1000 simulations of this IBM model for each climate period (Past: 1970-1999 and Future: RCP 8.5, 2070-2099) with each of the three climate models (CNRM, HadGEM2, and IPSL) for a combined 6000 simulations in total. During each model simulation, individuals recorded their phenological information (emergence day, dispersal day, individual size at emergence) in addition to aspects of their environment (natal patch ID, days spent dispersing, maximum daily temperature while dispersing, and final patch ID). This information was collated and extracted from the model run at the completion of the simulation. Additionally, by focusing on individuals that resettled in patches other than their natal patch, we could assess the specific behavior of those dispersing individuals that contributed to population connectivity in the landscape.

All model runs were verified to have run to competition using the associated log files for each simulation. Information from each simulation was extracted, summarized, and organized using R (version 3.5.0) and RStudio (version 1.1.447) statistical software (R Core Team, 2017; RStudio Team, 2016). Data analysis and graphs were created using *plyr* and *ggplot2* (Wickham, 2009, 2011).

Data Analysis

Climate-IBM Model Results

To examine the effect that predicted weather would have on the simulated *R. aurora* populations, we focused on two central aspects of the populations: how many animals were able to disperse, and when were they able to disperse. These aspects were used to understand what impacts we may expect on population connectivity and in dispersal phenology in future climates. To quantify these aspects, we used several response variables from the IBM simulations. We used the total number of surviving dispersers and the proportion of effective dispersers to address the dispersal success. The proportion of effective dispersers was a ratio of the number of individuals able to disperse and settle in patches other than their natal site to the total number of surviving dispersers. Since the number of effective dispersers was inherently related to the total number of surviving dispersers, this proportion from each simulation was the clearest way to examine this aspect of connectivity.

While the number of effective dispersers may be a more meaningful value for discussion of gene flow rates (Baguette et al., 2013), this value is inherently tied to the total number of surviving dispersers. In order to assess this value more directly, we fit a two-way ANCOVA model of number of effective dispersers based on the climate model, climate period, and total number of dispersers. Both effective dispersers and total number of dispersers were log transformed in the model and then back transformed for interpretation using the *effects* package in R (Fox and Weisberg, 2018). We included an interaction between climate model and climate period in the model structure. We also examined the timing of dispersal of those effective dispersers. In order to quantify this timing, we averaged the dispersal day of effective dispersers within each simulation (reported in ‘model days’ where day 1 is July 1st).

IBM Model Assessment

To explore how different precipitation states would impact the results of this IBM, we created two reference precipitation data sets: ‘Wet World’ and ‘Dry World’. Weather data in the ‘Wet World’ consisted of daily precipitation of 10mm while ‘Dry World’ had 0mm of precipitation. The effects of YTD rainfall and maximum daily temperature were removed to simplify model interpretation. These values created conditions of ‘rain’ and ‘wet’ every day in ‘Wet World’ while ‘Dry World’ had daily conditions of ‘no-rain’ and ‘dry’. The exact levels of precipitation are not as important to the model result since individuals in the simulation were only responding to the categorical precipitation measures (‘rain’/‘no-rain’ and ‘wet’/‘dry’). We ran 100 simulations in each of these worlds and assessed the simulations in the same manner as our Climate-IBM model. These precipitation conditions are not realistic scenarios but do speak to the differential behavior of individuals in this IBM.

IBM Sensitivity Analysis

Our IBM model focused on the end of metamorphosis and juvenile movement rather than a full lifecycle model. Regardless of this limited scope, it is still important to examine our model parameterization. For this analysis, we created three groups of variables: conditional weather thresholds, movement scaling and mortality variables, and general parameters. We focused on parameters that determined individual actions and condition-based movement activity. Changes in timing of development and phenology could also be an important aspect of amphibian response but was not the focus of this model approach (Brooks et al., 2019).

For every sensitivity assessment, we created a modified IBM scenario with one variable changed and ran 100 simulations. We then compared the modified IBM to an unchanged base IBM with 100 model simulations by examining our three response variables (number of surviving dispersers, proportion of effective dispersers, and dispersal timing for effective dispersers). In order to reduce the interannual variability and effect of location, all sensitivity model scenarios used the same weather conditions (climate model: CNRM, year: 1986, location: 48.2038922°N, 122.039967°W).

For our weather threshold variables (‘rain’ and ‘wet’ condition thresholds), we performed our sensitivity analysis using a range of potential values. For the threshold of daily precipitation controlling ‘rain’ conditions, we used values ranging from 0.25mm to 3.5mm (increments of 0.25mm). As this threshold increased, the amount of precipitation required for ‘rain’ conditions increase exposing individual to more ‘no-rain’ conditions.

To test the sensitivity of movement scaling and mortality parameters, we modified each variable ±10% and ±25%. The parameters included in this set were the effect of temperature to reduce movement, the added mortality of small individuals, increased mortality in high temperature, increased mortality in ‘no-rain’ conditions, and increased mortality in ‘dry’ conditions. This approach created 4 modified scenarios for each parameter to compare with our base model. We assessed the effect of each modification by the percent change in our three response variables (number of surviving dispersers, proportion of effective dispersers, and dispersal timing for effective dispersers).

The final set of general parameters were included in the sensitivity analysis since we felt they could be important in the IBM response but were less involved in the conditional-movement of individuals. The general parameters included in this set were the following: YTD precipitation threshold, T_{opt} movement threshold, T_{opt} mortality buffer, influence of YTD precipitation on SVL, movement distance distribution exp mean, path auto-correlation, SVL daily growth range. For these parameters, we created two modified scenarios for each variable adjusting the value ±10%. As for the movement scaling and mortality parameters, we assess the effects of each parameter using the percent change in each response variable.

Results

Climate-IBM Model Results

The total number of individuals that were able to disperse, survive, and resettle in any habitat was the first aspect of these simulations that we compared. During the past climate period, the climate model CNRM simulations has an average of 46.42 (SD = 17.72) total surviving dispersers which was less than the future climate period which has 50.48 (SD = 22.03) total dispersers. This trend of increased total dispersers in the future climate period was also see with past climates having an average of 44.48 (SD = 16.17) and 48.49 (SD = 21.02) individuals compared to future climates with 55.25 (SD = 23.35) and 56.49 (SD=23.09) for the HadGEM2 and IPSL models respectively (Figure 5.2). However, this pattern was reversed when we examined the percentage of effective dispersers in a simulation (Figure 5.3). The proportion of effective dispersers was lower in the future climate period with 21% (SD = 8%), 19% (SD = 8%), and 22% (SD = 8%) compared to the past climate period with 29% (SD = 8%), 28% (SD = 8%), and 28% (SD = 8%) respectively for CNRM, HadGEM2, and IPSL climate models. (Table 5.1)

There was a significant effect of the total number of dispersers on number of effective dispersers ($F_{1,5993} = 6098$, $p < 0.001$). There was no significant effect of climate model itself on the number of effective dispersers ($F_{2,5993} = 1.59$, $p = 0.203$). However, there were significant effects of climate period on the number of effective disperses ($F_{1,5993} = 393$, $p < 0.001$) and an interaction of climate period with climate model ($F_{2,5993} = 25.9$, $p < 0.001$). The number of effective dispersers in the future climate period was reduced compared to the past climate period, with the HadGEM2 climate model showing greatest reduction from 13.5 (95% CI = 13.2 to 13.8) effective dispersers in the past to 8.9 (95% CI = 8.7 to 9.1) in the future climate period (Figure 5.4).

In the CNRM climate model, the effective dispersers had a delayed dispersal timing with an average departure on model day 88.93 (SD = 10.58 days) in the past to 98.03 (SD = 10.82 days) in the future climate period (Table 5.1). The average timing of dispersal in the HadGEM2 climate model in the past climate period was on model day 90.25 (SD = 10.72 days) compared with the future which averaged model day 99.38 (SD = 10.5 days). The IPSL climate model had an average dispersal timing in the past of model day 90.2 (SD = 10.15 days) while the future climate period was on day 95.42 (SD = 10.58 days). These delays in dispersal timing were also observed in all climate models with the greatest delays of 9.13 and 9.1 days occurring in HadGEM2 and CNRM climate models respectively (Figure 5.5).

IBM Model Assessment

The ‘Wet World’ scenario had much higher total number of successful dispersers with a mean of 57.3 (SD = 6.8) dispersers per simulation compared to the ‘Dry World’ scenario with only 15.7 (SD = 4.1, Figure 5.6A). This measure encompassed all individuals that were able to disperse and resettle in habitat, irrespective of natal patch. The pattern in population connectivity was less extreme when we examined the success of those dispersers. The mean percentage of individuals dispersing to patches other than their natal site in the ‘Wet World’ was 27.2% (SD = 6.4%) while ‘Dry World’ was 36.1% (SD = 12.5%, Figure 5.6B). While there was potentially a difference in the dispersal timing for effective dispersers there was much more variability with the mean departure day occurring on model day 84.4 (SD = 7.4) in ‘Wet World’ compared to 88.4 (SD = 13.27) in the ‘Dry World’ (Figure 5.6C).

IBM Sensitivity Analysis

The most obvious effect of shifting the threshold of daily precipitation was an increase in the number of dispersers surviving (Figure 5.7A). There is a trend of increasing dispersal effectiveness across this range, however there is was no effect on the dispersal timing (Figure 5.7B & C). This increase in number of dispersers and slight effect in effectiveness may be the result of an increase in ‘no-rain’ conditions for movement which have longer step lengths than ‘rain’ conditions. The range of values we used for our threshold of ‘wet’ conditions ranged from 1mm to 13mm of precipitation in 7 days (increments of 1mm). The conditions within the model were increasingly ‘dry’ as the threshold for precipitation needed for ‘wet’ conditions increased. Shifting this threshold up caused a decrease in the number of surviving dispersers and a delay in the timing of dispersal (Figure 5.8A & C). There was no clear effect of this threshold on the proportion of effective dispersers (Figure 5.8B). The responses observed are likely tied to the increased mortality risk of dispersers in ‘dry’ conditions. The delay in dispersal timing is also associated with this mortality risk until there is consistent precipitation moving into fall.

Most of the scenarios with modified movement scaling and mortality parameters only minimally impacted the response variables (Table 5.2). A clear exception was the impact of mortality in ‘no-rain’ conditions which strongly impacted the total number of surviving dispersers. This response changed at a rate roughly proportional to the shift in the mortality rate in ‘no-rain’ conditions. The response variables were generally insensitive to changes in general parameters, however changes to the movement distance distribution and path auto-correlation had large impacts on the total number of dispersers and their rates of effectiveness (Table 5.3).

Discussion

Our evaluation of environmentally dependent dispersal behavior of juvenile amphibians revealed a decrease in the population connectivity in future climactic conditions across our landscape. Population connectivity in our landscapes was reduced in future climates compared to contemporary conditions as the result of a decrease in the proportion of dispersers that were effective in settling in non-natal patches (Figure 5.3). There was an observed increase in the total number of dispersers surviving (Figure 5.1), however the effect of this increase did not offset the lower rate of effective dispersal resulting in fewer individual effective dispersers in the future climate period (Figure 5.4). The reduction in the effective dispersal rates was also combined with a shift in the timing of effective dispersers later in the dispersal window in future time periods (Figure 5.5). There were some differences of effect sizes of response variables observed between the three global climate models (CNRM-CM5, HadGEM2-CC, and IPSL-CM5B-LR). However, the direction and general magnitude of these effects were not distinct.

The reduction in the population connectivity is likely not just the impact of drier conditions, but also the shift in movement behavior or individuals. Our comparison of simulations in the 'Wet World' and 'Dry World' climates, completely dry conditions had a stark reduction in the number of surviving dispersers and a slight increase in the proportion of effective dispersers compared to 'Wet World' simulations (Figure 5.6). In fact, 'no-rain' conditions would encourage longer dispersal distances and potential settlement in non-natal patches (Bredeweg et al. 2019b). The observed pattern of dispersal and population connectivity from our global climate model simulations is the result of balancing the longer dispersal movements of 'no-rain' conditions with the reduced mortality rates of precipitation (determent of 'rain' and 'wet' condition). The exposure to 'no-rain' condition itself is not enough to explain the future's reduction of population connectivity as there was no noticeable difference between the number of 'no-rain' days for effective dispersers in past and future climate periods (Figure 5.9). Our interpretation of the observed changes in population connectivity was driven by the loss of intermittent rainfall during the end summer into stretches of very low precipitation.

Amphibian species are broadly categorized as having "limited" dispersal ability, which makes them potentially more susceptible to the effects of a changing climate, habitat fragmentation, and genetic isolation (Gerick et al., 2014; Liebgold et al., 2018; Miller et al., 2015; Urban et al., 2013). From this standpoint, there are implications for the reduced population connectivity observed in this IBM for the persistence of amphibian species. The notion that all amphibians share a “limited” dispersal behavior, however, is likely an oversimplification that has been challenged by some genetic connectivity and metanalysis studies (Chan and Zamudio, 2009; Smith and Green, 2005). Even with more frequent dispersal and gene flow, a reduction in connectivity in the future could limit the ability for populations to adapt to changes in their climate or environment (Griffiths et al., 2010; Muñoz et al., 2016). The exact nature of the impact will likely be dependent on species-specific ecology since generalizing across amphibian species ignores differences in dispersal (Richardson, 2012).

The projected changes in climate for the Pacific Northwest by the end of the century on average involve an increase in annual temperature, a moderate increase in annual precipitation, and a shift in precipitation for drier summers and wetter winters (Rupp et al., 2013, 2017). However, when these coarser climate models are statistically downscaled to more relevant scales for animals (days), applying two-stage movement behaviors in ‘rain’ and ‘no-rain’ conditions with organismal survival creates this emergent response in our IBM simulations (Abatzoglou and Brown, 2012; Bredeweg et al., 2019b). For example, in our model, although there was no inherent change in an individual’s developmental phenology between climate periods in this model, the observed shift in the timing of dispersal was solely the result of dispersal success and survival. However, upon examinations of implications of this shift on the environment experienced during dispersal, the average daily maximum temperatures experienced by dispersers has a strong seasonal pattern that also changes with climate period (Figure 5.10). Individuals in the future climate, on average, experienced hotter days during their dispersal, even with their delayed departure, than their counterparts in the past climate period. Such variation could have other consequences for survival including reduced immune function (Raffel et al., 2006) and risk of toxicant susceptibility (Hallman and Brooks, 2016).

The kind of emergent response observed in our model represents the underlying value of mechanistic models to understand the implications of biological behavior in a changing environment (Pacifici et al., 2015; Urban et al., 2016). Nonetheless, data requirements for mechanistic models require both an appropriate understanding of a species ecology paired with an suitable scale of environmental data (Lynch et al., 2014; Shepard et al., 2013a; Zeigler and Fagan, 2014). The interpretation and inference of model results always will be limited by data quality, but can allow for the interaction of realistic biology with a dynamic environment (Rose et al., 2014; Spiegel et al., 2017). Mechanistic approaches have also been applied in combination with trait- and correlative-based to demographic responses and movement to broader-scale investigations (Santini et al., 2016; Singer et al., 2015). For example, incorporating dispersal into species distribution models allows for assessment of a species ability to sense and adapt to variation in its environmental niche (Duckett et al., 2013; Holloway et al., 2016; Zurell et al., 2012). This variety of approaches has increased options to incorporate organism dispersal and improve the assessment of ecological climate impacts (Pacifici et al., 2015; Travis et al., 2013).

The sensitivity analysis of our IBM also highlighted two areas in our model that are likely sources of variation where data quality should be improved: movement distance and environmentally dependent mortality. The importance of movement distance parameterization is understandably important when assessing dispersal, but field-based empirical data will rely on advancements in tracking technologies. Our understanding of environmentally-dependent mortality may prove to be even more elusive than tracking juvenile amphibians. It is understandable that desiccation in the landscape is an important factor shaping amphibian movement and it has been established that it impacts population connectivity (Peterman et al., 2014; Watling and Braga, 2015). However, the actual water loss is dependent of specific microhabitats and individual behavior which leave our best approximation of desiccation risk to plaster models (Peterman et al., 2013b; Seebacher and Alford, 2002; Tingley and Shine, 2011).

Like all simulation models, assumptions adopted for our IBM provide direction for future research. In addition to using a simulated landscape for our simulations, there was no distinction between aquatic breeding and terrestrial habitat. While our simulated landscape is much more emblematic of a simple metapopulation model, a landscape with distinct aquatic breeding and territorial habitat types would encapsulate a more-complex illustration of amphibian life history (Nakazawa, 2015). Additional efforts also may consider the seasonal dynamics of aquatic habitats that can change relative isolation and structural connectivity of water bodies (Smith et al., 2018). Furthermore, our IBM focused on the dispersal movements immediately after metamorphosis; however there is some conjecture that juvenile individuals may undertake movements throughout development to result in dispersal across multiple years (Pilliod et al., 2002; Semlitsch, 2008). It has also been proposed that adaptation to changing climates by amphibians will likely involve plasticity, a well-documented ability to alter behavior, physiology, or morphology, which was not incorporated in detail in our IBM (Tejedo et al., 2010; Thurman and Garcia, 2017). Our inclusion of a type of phenotypic plasticity with year-to-date (YTD) precipitation modifying individual emergence size has not been observed in all amphibian species and therefore may not capture other aspect of demographic change by seasonal precipitation (Benard, 2015; Cayuela et al., 2016b). In addition to plasticity, an examination of this system through an evolutionary lens with trait-selection would also be important as aspects of evolutionary response have been identified as vital for climate adaptation (Munday et al., 2013; Tung et al., 2018; Urban et al., 2014).

This is the first individual-based model for amphibians that uses empirically-derived juvenile movement data for parameterization. Additionally, our model uses movement behaviors that are depending on environmental conditions that are more representative of realistic animal movements (Hoffman et al., 2006; Shepard et al., 2013b). From our analysis, the observed changes in connectivity of just one portion of the amphibian life history is an exciting result, but we have the opportunity to expand and refine this IBM to address some of the simplifying assumptions made. Examining environmental conditions and weather affecting dispersal and movement is a difficult aspect of movement ecology, however the application of experimental-scale work to this IBM has provided an opportunity to explore this science on a scale that is relevant for population and landscape ecology.

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We would like to thank Dr. Jenny Urbina for her feedback and support in this project. Our thanks to the ROOTS support team at Oregon State University for their assistance with computer support, network access, and remote desktop connections. We would like to thank by the following the funding agencies for their support of climate models and data access: Regional Approaches to Climate Change (REACCH), the Climate Impacts Research Consortium(CIRC) and the Northwest/SouthEast Climate Science Centers(NWCSC,SECSC).

Table 5.1 – The average responses of populations in each climate model in both the past (1970-1999) and future (2070-2099) climate periods. There were 1000 simulations per treatment combination. Response variable were calculated from a single simulation and then averaged within a treatment. Values in parentheses are the standard deviations.

		Climate Model		
		CNRM-CM5	**HadGEM2-CC**	**IPSL-CM5B-LR**
		Total Number of Dispersers		
Climate Period	**Past**	46.42 (17.72)	44.48 (16.17)	48.49 (21.02)
	Future	50.48 (22.03)	55.25 (23.35)	56.49 (23.09)
		Percentage of Dispersers Effective		
	Past	29% (8%)	28% (8%)	28% (8%)
	Future	21% (8%)	19% (8%)	22% (8%)
		Departure Day of Effective Dispersers		
	Past	88.93 (10.58)	90.25 (10.72)	90.2 (10.15)
	Future	98.03 (10.82)	99.38 (10.5)	95.42 (10.58)

Table 5.2 – Results of sensitivity analysis of select model variables. Variables selected were thought to be important to the model response with limited experimental or observational evidence to be based on. As such, sensitivity of the model to changes in variables were done at both ±10% and ±25%. One hundred simulations for modified models were compared to a base simulation using the CNRM-CM5 climate model. All simulations used the same average climate year (1986) with the same GPS point (48.2038922°N, 122.039967°W). Values shown are the percent change in the average of each response variable (average number of dispersers, average proportion of dispersers effective, and average effect dispersers departure date).

	Variable and Base Value				
	Effect of Temp to Reduce Movement	Added Mortality of Small Individuals	Increased Mortality in High Temps	Increased Mortality in 'No-Rain' Conditions	Increased Mortality in 'Dry' Conditions
	10%	10%	10%	20%	20%
Shift	**Average Number of Dispersers**				
25%	-2.62%	-3.64%	-2.66%	-21.81%	-9.84%
10%	-1.35%	-3.81%	-3.52%	-10.60%	-5.23%
-10%	-1.62%	-0.67%	-2.26%	9.24%	1.95%
-25%	-2.55%	-0.02%	-1.15%	27.00%	10.35%
	Average Proportion of Dispersers Effective				
25%	-2.01%	3.96%	0.89%	1.56%	-0.89%
10%	3.36%	-1.70%	2.28%	2.30%	-2.36%
-10%	0.39%	-1.65%	4.12%	4.43%	-1.81%
-25%	4.01%	-1.10%	6.25%	4.18%	0.64%
	Average Effective Dispersers Departure				
25%	0.77%	1.53%	-0.44%	-4.07%	1.26%
10%	-1.36%	0.91%	-0.59%	-1.54%	1.59%
-10%	-0.86%	-1.55%	0.27%	0.60%	-1.93%
-25%	-0.82%	0.64%	0.26%	1.46%	-2.68%

Table 5.3 – Results of sensitivity analysis of select general model variables. Sensitivity of the model to changes in variables were done at ±10%. The 100 simulations for modified models were compared to 100 base simulation using the CNRM-CM5 climate model. All simulations used the same average climate year (1986) with the same GPS point (48.2038922°N, 122.039967°W). Values shown are the percent change in the average of each response variable (average number of dispersers, average proportion of dispersers effective, and average effect dispersers departure date).

	Variable and Base Value						
	YTD Precip. Threshold	T_{opt} Movement Threshold	T_{opt} Mortality buffer	Influence of YTD Precip. on SVL	Movement Distance Distribution Exp Mean	Path Auto-correlation	SVL Daily Growth Range
	1000mm	22.5°C	10°C	10%	4	75%	0.1mm
Shift	**Average Number of Dispersers**						
10%	-0.89%	0.95%	-2.77%	-1.02%	-29.37%	-14.56%	-0.71%
-10%	-0.11%	0.51%	-2.08%	-2.24%	39.66%	14.45%	-3.88%
	Average Proportion of Dispersers Effective						
10%	4.50%	0.02%	1.17%	4.89%	39.64%	19.03%	5.40%
-10%	3.67%	-0.33%	-0.44%	4.23%	-28.22%	-12.92%	-4.90%
	Average Effective Dispersers Departure						
10%	1.27%	0.48%	-0.45%	-0.31%	-2.97%	-0.28%	-0.87%
-10%	-1.34%	-0.33%	-0.88%	-1.53%	-1.43%	0.35%	-1.54%

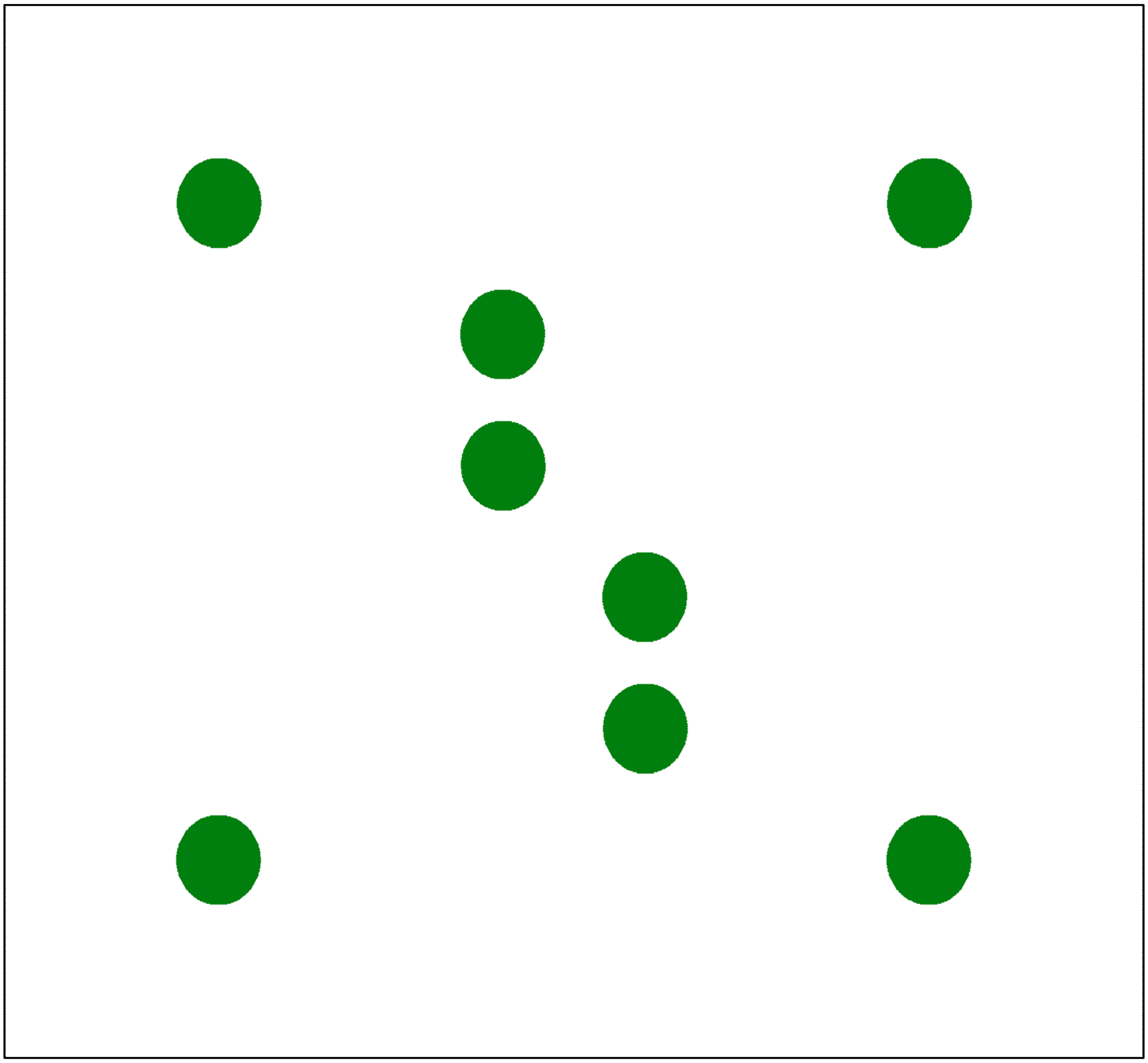

Figure 5.1 – Diagram of simulated landscape used in simulations. The size of the landscape was 1000 rows of 1000 hexagons with each Hexagon being 1m wide. Habitat patches (shown in green) were circular areas of 5000 hexagons (0.435 hectares).

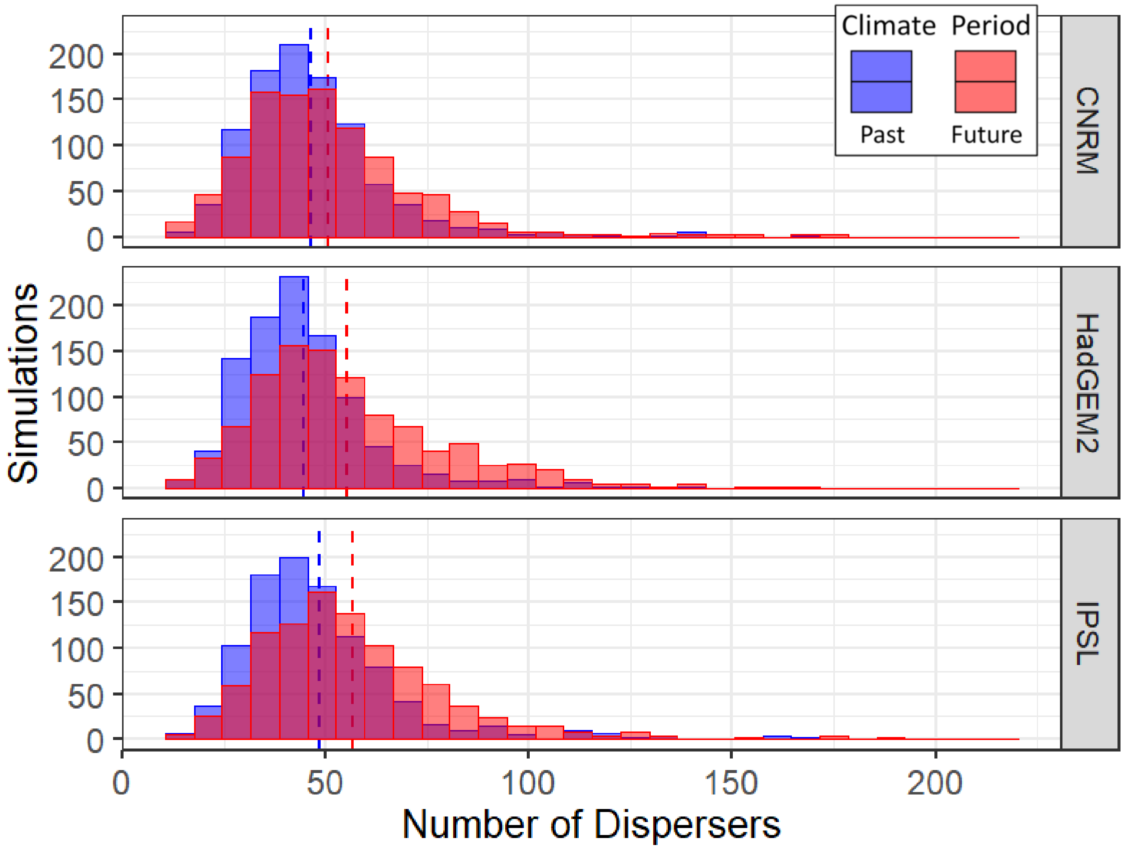

Figure 5.2 – Histogram of the number of surviving dispersers for Past (blue) and Future (red) climate periods for each climate model. The dashed vertical lines represent the average number of dispersers for all simulations in a climate period and model combination. The number of simulations (y-axis) is indicative of relative frequency with a total of 1000 simulations per climate period and climate model.

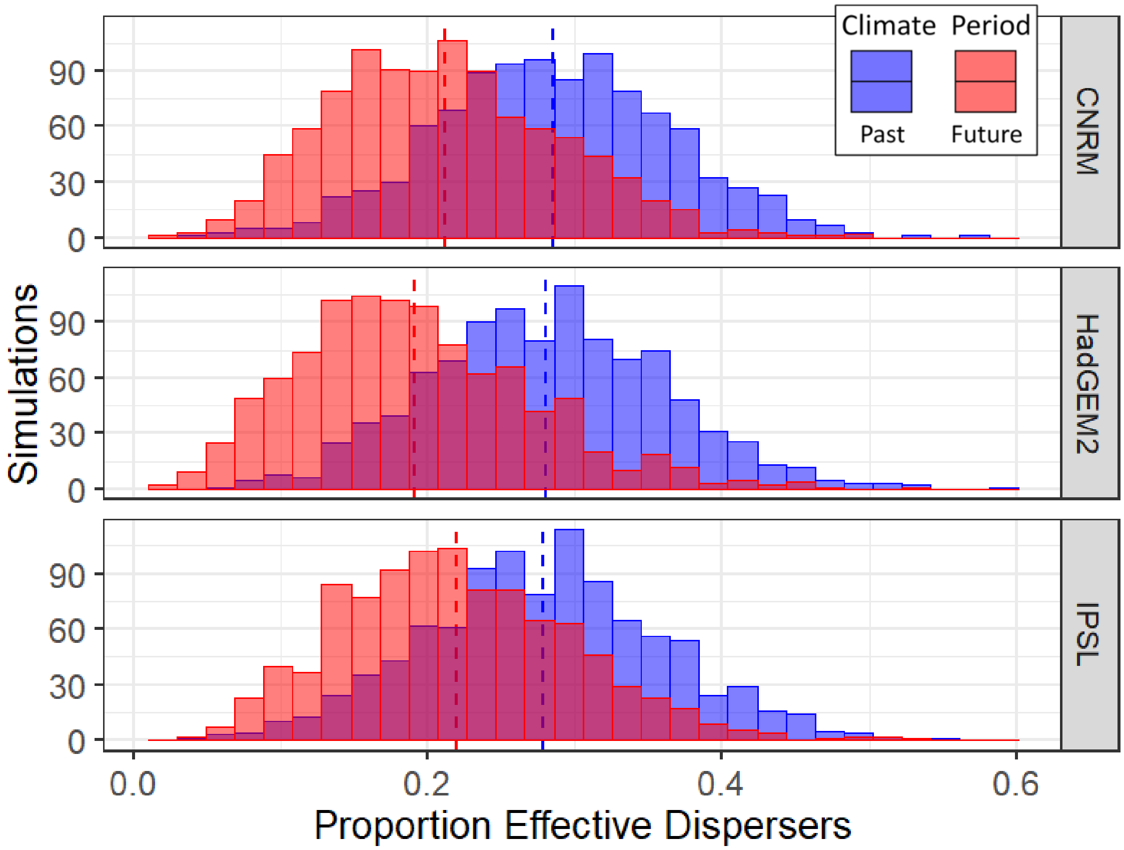

Figure 5.3 – Histogram of the proportion of effective dispersers per number of surviving dispersers for Past (blue) and Future (red) climate periods for each climate model. The dashed vertical lines represent the average proportion of effective dispersers for all simulations in a climate period and model combination. Effective dispersers were individuals that were able to disperse to populations other than their natal site. The number of simulations (y-axis) is indicative of relative frequency with a total of 1000 simulations per climate period and climate model.

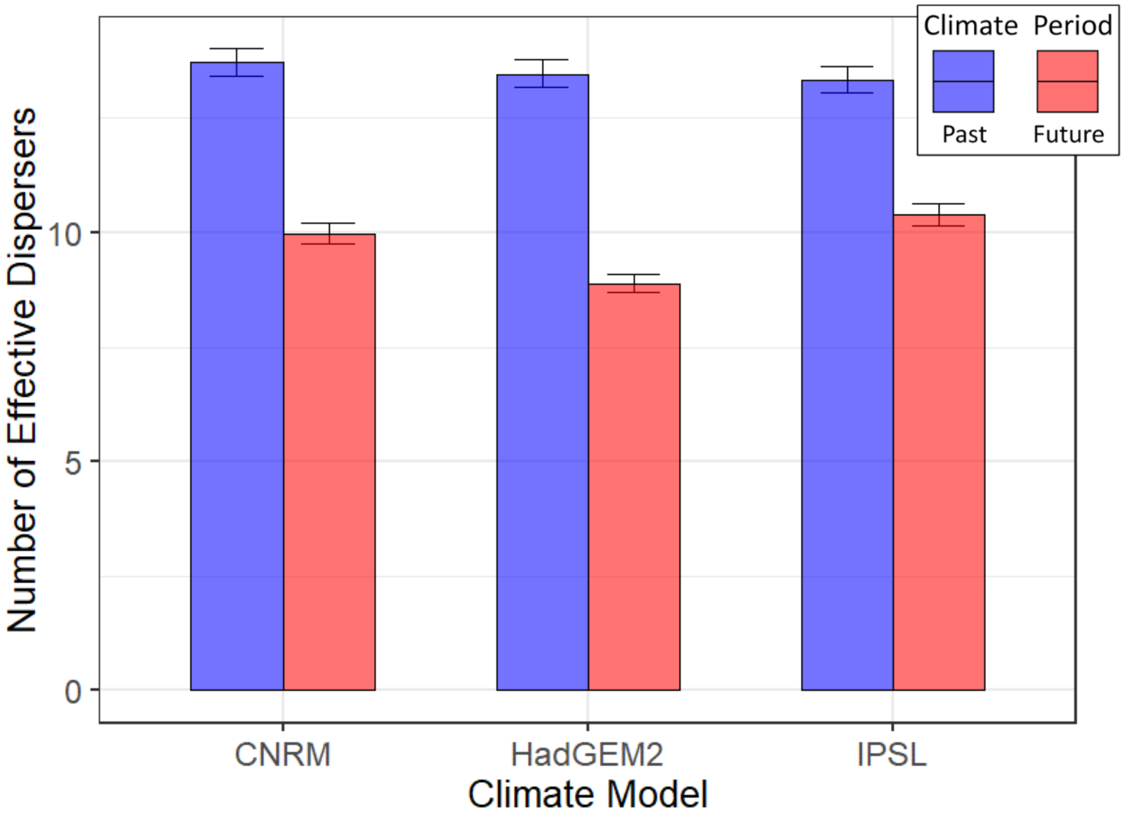

Figure 5.4 – An effects plot showing the number of effective dispersers predicted per simulation after controlling for the total number of dispersers for each climate model in the Past (1970-1999) and Future (2070-2099) climate periods. Bars represent modelled mean response and the error bars representing the 95% confidence interval.

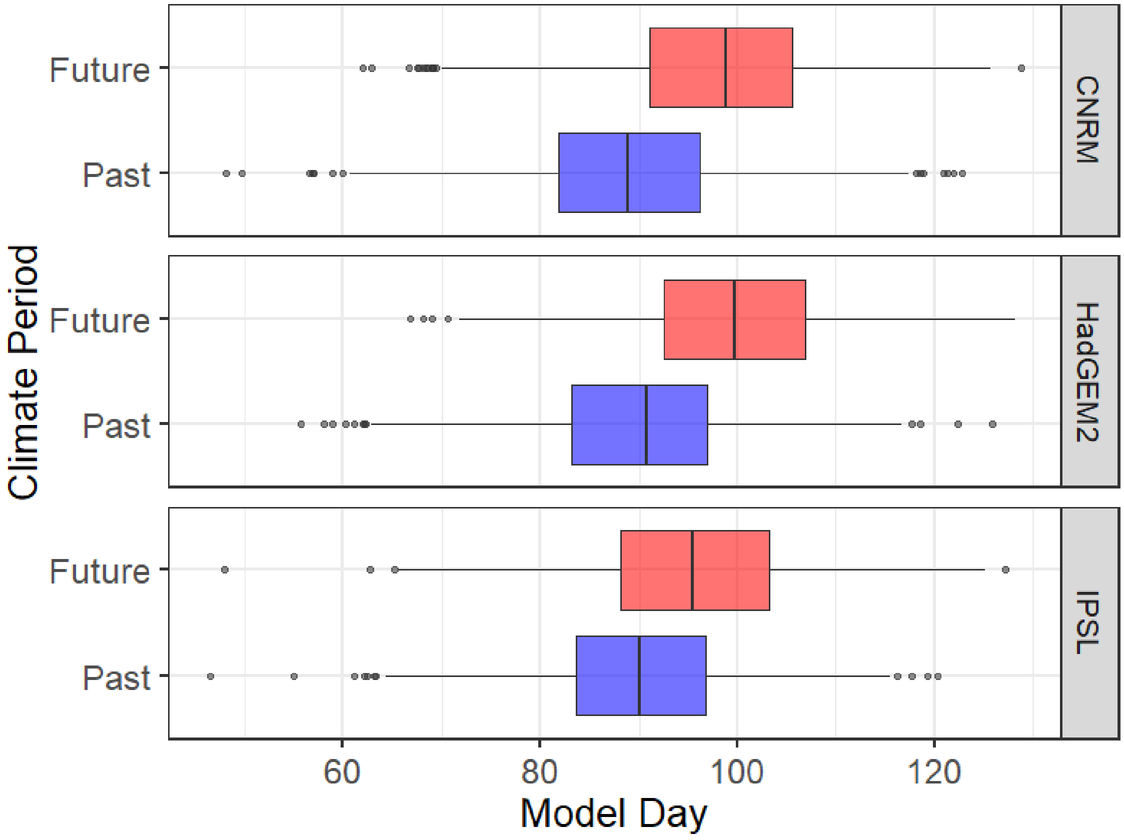

Figure 5.5 – Boxplot of effective dispersers timing of dispersal for Past (blue) and Future (red) climate periods for each climate model. The model ran from July 1st (Day 1) until November 30th (Day 153). Each climate period and climate model has 1000 simulations that are summarized within the boxplot. Boxplot areas represent the 25% to 75% quartile (inner quartile range) with the median value as the central line. Boxplot whiskers represent 1.5 times the inner quartile range with outliers shown as points.

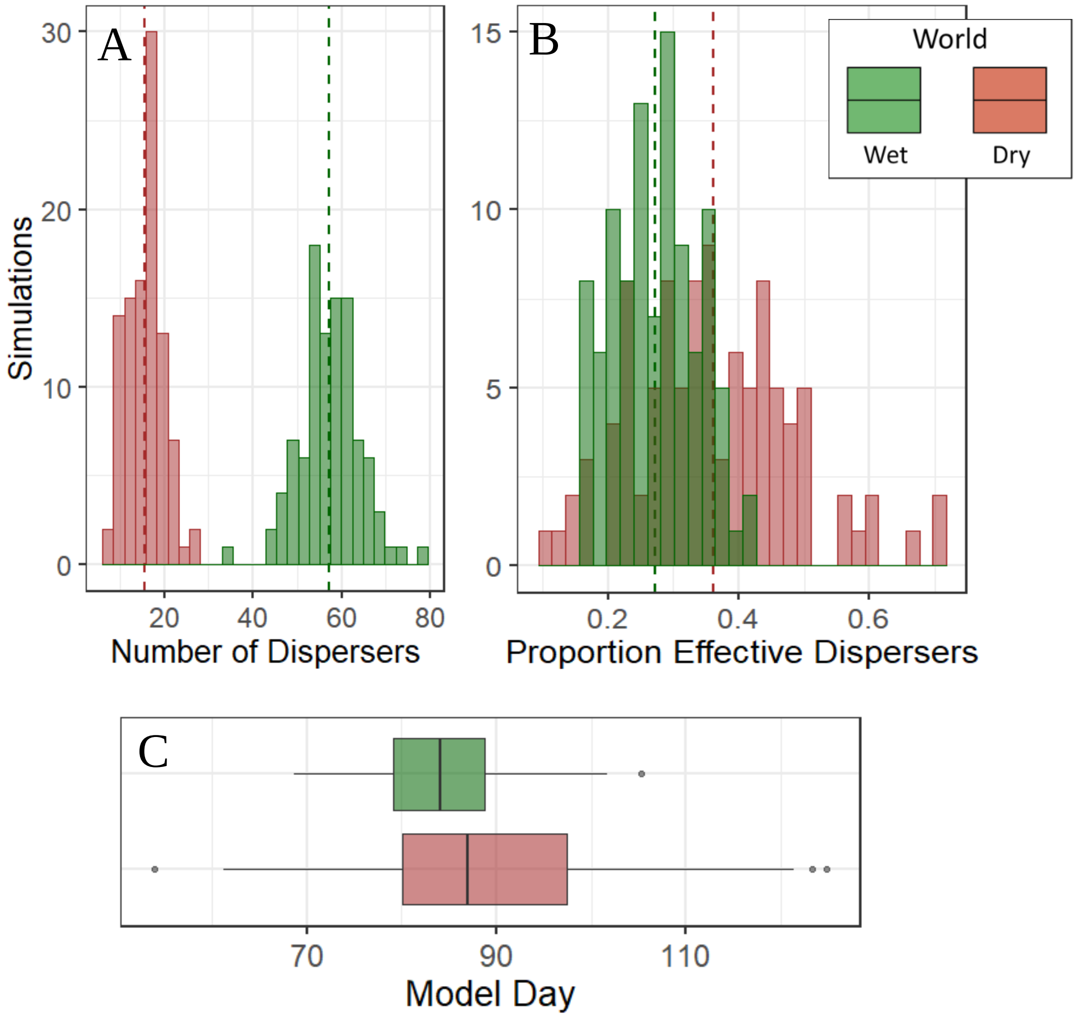

Figure 5.6 – Histograms of the number of surviving dispersers (A), the proportion of effective dispersers per number of surviving dispersers (B), and boxplot of dispersal timing for effective dispersers (C) in ‘Wet World’ (green) and ‘Dry World’ (brown). The dashed vertical lines represent the respective average number of surviving dispersers (A) and proportion of effective dispersers (B) for all simulations in each world. Effective dispersers were individuals that were able to disperse to populations other than their natal site. ‘Wet World’ simulations had ‘rain’ and ‘wet’ conditions every day while ‘Dry World’ simulations had ‘no-rain’ and ‘dry’ conditions; either version had any influence from maximum daily temperature or YTD precipitation. The number of simulations (y-axis) is indicative of relative frequency with a total of 100 simulations for each world.

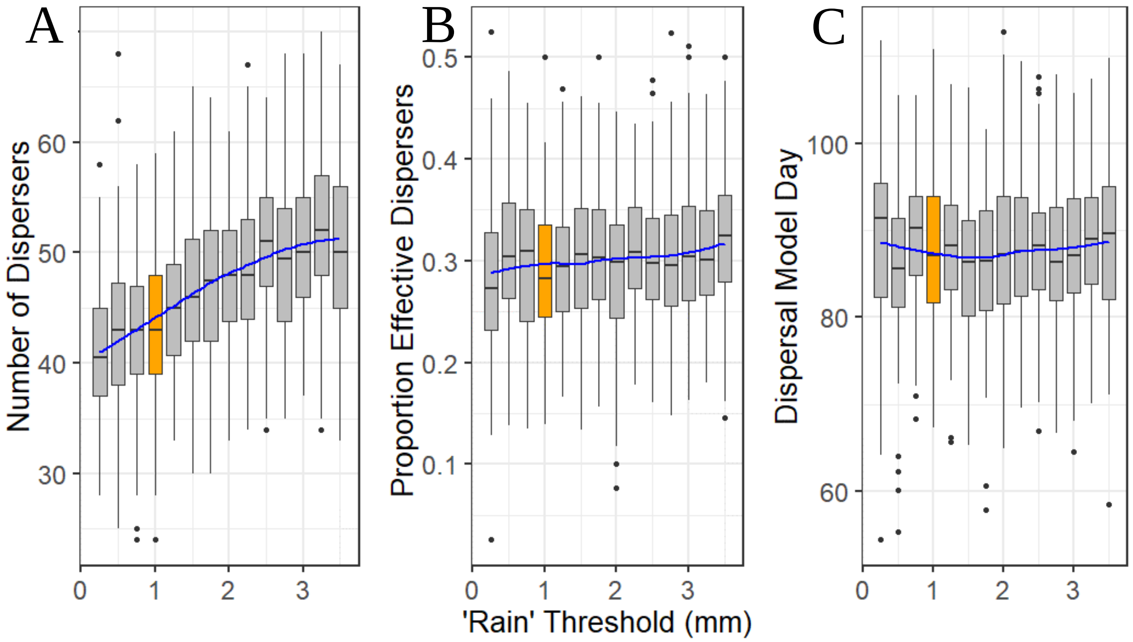

Figure 5.7 – Sensitivity analysis of the ‘Rain’ threshold value showing boxplots of the number of surviving dispersers (A), the proportion of effective dispersers per surviving dispersers (B), and dispersal timing for effective dispersers (C). The yellow highlighted boxplot (1mm precipitation) represents the base value of the IBM used in the full analysis. Each scenario across the range of ‘Rain’ threshold values had 100 simulations that are summarized within each boxplot. All simulations used the same climate model (CNRM-CM5), average climate year (1986), and the same GPS point (48.2038922°N, 122.039967°W). Boxplot areas represent the 25% to 75% quartile (inner quartile range) with the median value as the central line. Boxplot whiskers represent 1.5 times the inner quartile range with outliers shown as points. The blue lines are the best fit lines using the LOESS method.

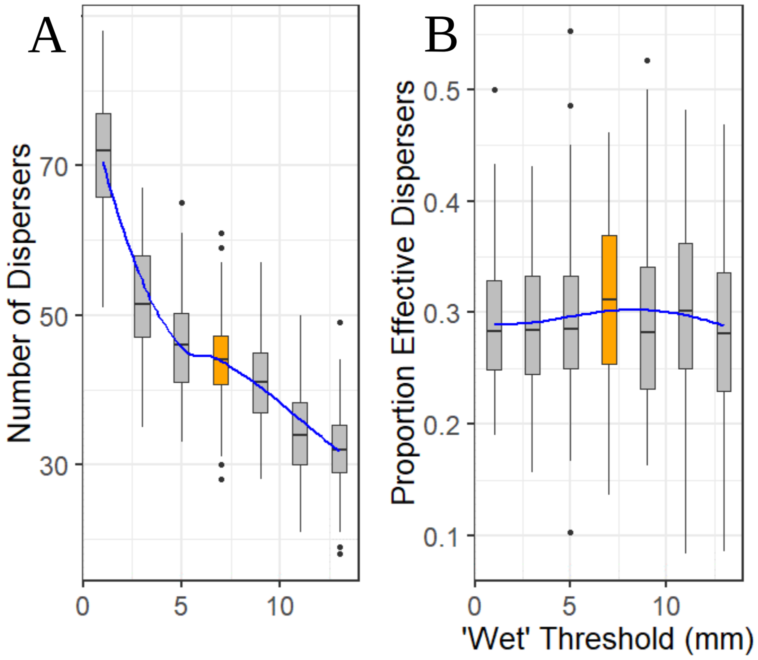

Figure 5.8 – Sensitivity analysis of the ‘Wet’ weekly threshold value showing boxplots of the number of surviving dispersers (A), the proportion of effective dispersers per surviving dispersers (B), and dispersal timing for effective dispersers (C). The yellow highlighted boxplot (7mm precipitation in 7 days) represents the base value of the IBM used in the full analysis. Each scenario across the range of ‘Wet’ threshold values had 100 simulations that are summarized within each boxplot. All simulations used the same climate model (CNRM-CM5), average climate year (1986), and the same GPS point (48.2038922°N, 122.039967°W). Boxplot areas represent the 25% to 75% quartile (inner quartile range) with the median value as the central line. Boxplot whiskers represent 1.5 times the inner quartile range with outliers shown as points. The blue lines are the best fit lines using the LOESS method.

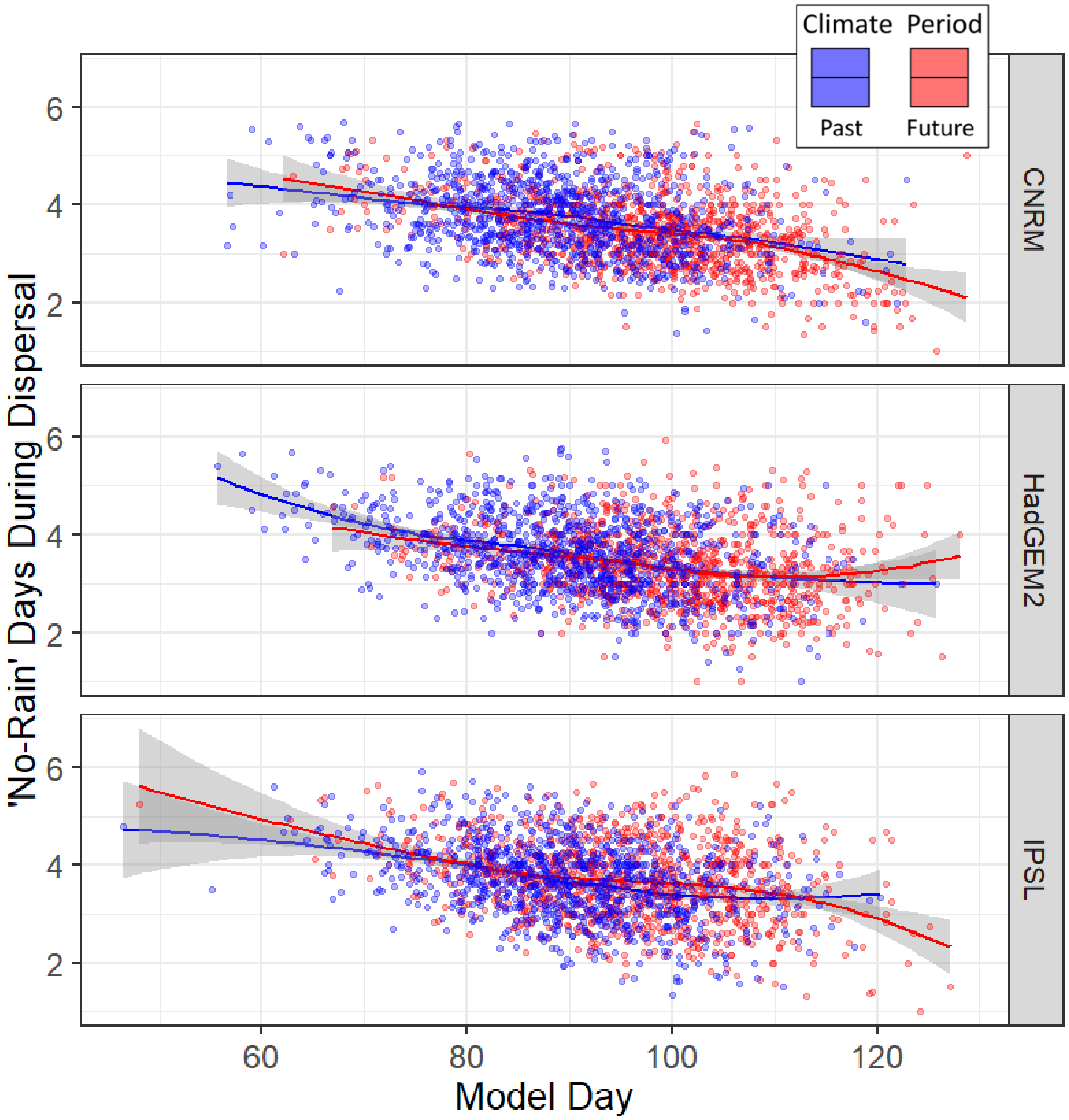

Figure 5.9 – Graph of average ‘no-rain’ conditions during dispersal movements of effective dispersers with associated timing of dispersal. Each point represents a simulation average with color indicating climate period each climate model: Past (blue) and Future (red). The model ran from July 1st (Day 1) until November 30th (Day 153). Lines for each climate period are the best fit lines using the LOESS method with grey band representing the 95% confidence interval.

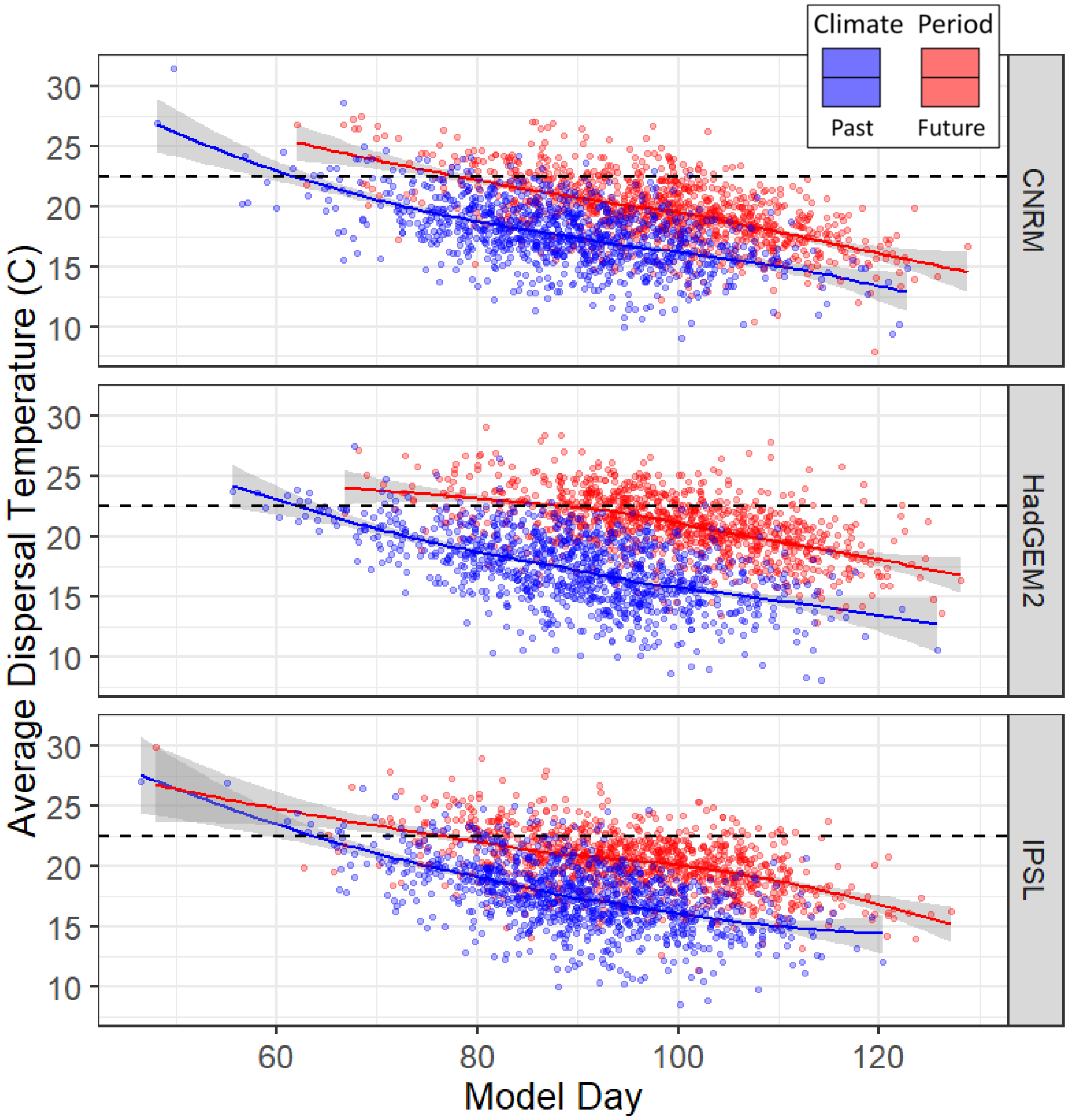

Figure 5.10 – Graph of average maximum daily temperature during dispersal movements of effective dispersers with associated timing of dispersal. The dashed horizontal line represents the temperature of optimal movement (T_{opt}) based Gerick et al. (2014). Each point represents a simulation average with color indicating climate period each climate model: Past (blue) and Future (red). The model ran from July 1st (Day 1) until November 30th (Day 153). Lines for each climate period are the best fit lines using the LOESS method with grey band representing the 95% confidence interval.

JUMPING IN WITH BOTH FEET: EXPLORING FACTORS THAT SHAPE JUVENILE AMPHIBIAN MOVEMENT

CHAPTER 6 – CONCLUSIONS

Movement is integral to the existence of any animal species. With their biphasic life history, the movement of recently metamorphosed juvenile amphibians from their breeding habitat represents a major change in their distribution and the potential challenges of an unfamiliar terrain. Thus, this natal dispersal presents an additional life history transition that will likely determine their long-term success and survival.

The movement ecology of amphibians has been an understudied aspect of their ecology, but may be very important in determining their persistence in the landscape (Sinsch, 2014). Yet, the movement behavior of juveniles is an area that has implications for a sensitive life-stage and one with implication for population connectivity (Pittman et al., 2014). Given the challenges of studying the movement of these animals in their natural habitats, in this dissertation I have worked to expand the understanding the movement behavior of juvenile frogs. At this life stage, individuals have not spent extensive time in terrestrial environments, and the environment and experiences that could be influencing their movements are derived over time as larval tadpoles (Eakin et al., 2019). Because of this potential carryover from aquatic environment to terrestrial behavior, I have investigated movement while exploring latent effects from larval stressors (O’connor et al., 2014).

Projects in this dissertation have examined the response of individual movement behavior between species, with larval stressors, and with terrestrial conditions. I have also explored the implications of these behaviors in project future climates. However, these efforts are contributions to a field that still has huge opportunity for additional work and synthesis. While developing and executing my research projects, I have found two aspects that are important for future study and further advancement of this research topic: breadth of experimental design and movement *in situ*. I will address how future study of each of these aspects will create further opportunities to advance our knowledge of movement ecology.

Experimental Design

A primary tool in scientific investigation is the use of controlled experiments. This approach allows for the manipulation of factors of interest. However, the clarity of this method can become challenging when working with a natural organism. For example, size at metamorphosis is a common response variable in experiments with amphibians. However, my experiments with the Northern Red-legged Frog (*Rana aurora*) have found a natural pattern related to morphology, such that the first individuals to complete metamorphosis being the largest, with decreasing body size as the metamorphosis window continues. Depending on the breadth of metamorphic window captured, the variability within a replicate can be amplified. This singular response of individual size then becomes entangled with timing of metamorphosis. Even more importantly, individuals that emerge at different times across the metamorphic window may have alternate strategies for success (Schmidt et al., 2012). For researchers, the use of these response variables requires the use of co-variates and potentially focusing on a sub-set of individuals that share a life history strategy (Ousterhout and Semlitsch, 2018). The additional detail of these factors complicates the statistical analysis but use of multiple-response analysis or model selection on a subset of variables provide advanced statistical approaches to manage these complex questions. The explicit inclusion of metamorphic timing provides an opportunity to assess different life history trajectories.

In addition to complications across the metamorphic window, another challenge with experimental design in amphibians is the non-independence of one individual across metamorphosis. Aspects from morphology to animal personality have been linked between larval tadpoles and post-metamorphic juveniles (Pechenik, 2006; Wilson and Krause, 2012; Yagi and Green, 2017). The ability to track individual identity is important to account for non-independence of observations across the metamorphic window but would provide a project much more information as to effects of treatments. One option to achieve this would be raising individuals in isolated containers (Beck and Congdon, 2000). While this is a technically simple solution, it can create a logistical challenge since not every animal will successfully metamorphose, requiring a large number of animals to care for. Another potential method for tracking individual across metamorphosis is the use of visible implant elastomers (VIE). This is an approach that has been used in this dissertation, and can provide unique IDs with placement coding or alphanumeric VIE tags (Clemas et al., 2009; Kaiser et al., 2009). Unfortunately, the movement of VIE tags across metamorphosis can create unreliable identification of individuals outside of batch marking which make it a risky method (Brannelly et al., 2013; Campbell Grant, 2008). Injectable passive Integrated Transponder (PIT) tags are another potential technique to track individuals across metamorphosis (Ousterhout and Semlitsch, 2018; Welsh-Appleby, 2014). This is the most reliable approach but does have limitations based on the ratio of tag to body size and the need for specialized equipment. Based on the size of the species in question, if the equipment can be acquired, the use of PIT tags may be the most appropriate method, assuming future advancements in PIT tag size.

Movement in situ

Movement of animals in natural environments is an aspect that is difficult to replicate in controlled settings, making the importance of tracking animals in natural or semi-natural habitats invaluable. The ability to track animals often falls into two distinct camps: individual tracking or population tracking (Holyoak et al., 2008). Individual-level tracking is important for examining path choice, between-individual variation, and environmental factors that shape individual movement propensity. Population-level tracking, on the other hand, is important for population demographics and landscape level effects. Each of these tracking methods have important qualities and the choice of method will largely be determined by the question of the study.

Amphibians in general, and particularly juveniles, have small bodies with moist skin that creates many issues with traditional technologies for individual tracking. Attachment of UHF radio tags has been used but is limited by tag and animal body size biasing these studies to adult individuals (Garwood and Welsh, 2007). The use of PIT tags in the field has been one reasonably successful method. The implementation of this is largely based on the organization of the antenna arrays since detection is dependent on an animal in close proximity to the antenna to be detected. PIT tagging in combination with a mobile scanning antenna has also been used to track individual movements within enclosed runways for semi-natural movements (Ousterhout and Semlitsch, 2018). The use of harmonic direction finders is another method that has been proposed for the relocation of individuals in the field, however, this approach does not provide a unique

ID, requiring the additional capture of an animal and the use of the PIT tag or alphanumeric VIE (Borzee et al., 2018; Popescu et al., 2012b). Individual tracking, regardless of size, can be performed using repeated fluorescent powder application, however this method relies on clearly flowing individual track (e.g., no hopping) and is limited by the time powder remains on the animal (Roe and Grayson, 2008). Tracking individuals in natural environments provides opportunities to answer questions about movement from a mechanistic perspective, if the system utilized fits within these logistical constraints.

With some landscape-scale questions, however, it is more important to examine not only the movements of individuals, but also of populations. For small animals such as amphibian, studies using capture-mark-recapture (CMR) dominate for tracking population movements. The efficacy and ethics of toe-clipping has necessitated the use of alternative tagging methods for CMR studies (Clemas et al., 2009). Like individual tagging, batch marking with VIE or the use of PIT tags are both potential tagging options for CMR. PIT tagging is useful to track individual recaptures but can be cost prohibitive. There have been some alternative batch tagging methods that use enriched nitrogen isotopes or fluorescent calcein that can be applied to larval tadpoles and be maintained after metamorphosis (Andis, 2018; Scott et al., 2015). These CMR methods provide a useful approach that is well established across many disciplines of ecology, however there is some evidence that some “fat-tailed” distribution patterns of amphibians can cause issues with CMR studies by underestimating long distance movements (Sinsch, 2014). Investigations on functional dispersal and connectivity of populations, without the use of tagging, can be performed with the construction of new breeding ponds to allow for natural colonization (Searcy et al., 2018). Alternatively, the application of landscape genetics approaches have been important in assessing functional connectivity (Coster et al., 2015; Nowakowski et al., 2015; Spear and Storfer, 2008). However, these approaches cannot assess contemporary effects of changing landscapes, can be costly, and are best used in combination with other information about population movement and demographics (Frei et al., 2016; Safner et al., 2010).

Regardless of the methods used, well designed scientific endeavors can piece apart the effects of various factors on movement behavior of individuals and populations. While the reductive approach of science has been key to understanding complex ecological systems, we may need to rethink our approaches on how to use this information. IUCN red list estimates that 40% of amphibian species around the world are threatened with extinction (IUCN, 2014). The reasons behind declining populations of amphibian species are linked to a combination of pathogens, environmental pollutants, exposure to UV-B, invasive species, habitat fragmentation, habitat modification, and changing climates (Whitfield et al., 2016). Without explicit research into these issues, even mechanistic models will not be able to accurately predict non-additive interactions of these stressors. With the current state of crisis in biodiversity, there is need to synthesize the impact of these factors in a more holistic fashion. Movement behavior of individuals and populations is an important piece in shaping the response of species and populations to many of these stressors (Pittman et al., 2014). By organizing this suite of stressors around a central biological process, like movement, may provide a process to address these broader questions of conservation. The disjointed nature of scientific investigation is important for academic freedom and exploring the breadth of ecology, but we may require research efforts that entail a step-by-step method to address the global declines of amphibian species.

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