

MOVEMENT ECOLOGY OF JUVENILE POND-BREEDING  
SALAMANDERS: IMPLICATIONS FOR THE MANAGEMENT AND  
CONSERVATION OF AMPHIBIAN POPULATIONS

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by

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MOVEMENT ECOLOGY OF JUVENILE POND-BREEDING  
SALAMANDERS: IMPLICATIONS FOR THE MANAGEMENT AND  
CONSERVATION OF AMPHIBIAN POPULATIONS

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## ABSTRACT

Human-induced habitat change is widely regarded as a primary factor threatening the persistence of species. One major consequence of habitat alteration is its effect on the movement behavior of individuals. Animal movement is often strongly influenced by habitat type; knowledge of the strength, direction, and variation inherent in species' behavioral reactions to novel or altered habitat is crucial for identifying the mechanistic causes of population or metapopulation dynamics, and for maximizing the effectiveness of conservation and management practices. Natal dispersal is an important mechanism by which species mitigate the effects of unpredictable variation in the spatial distribution of resources and is critical to many species' spatial dynamics. Habitat alteration impacts the spatial patterning of resources and the risks associated with searching for resources. Spotted salamanders (*Ambystoma maculatum*) are forest-dependent, pond-breeding amphibians with complex life cycles. Spotted salamanders metamorphose and move out of aquatic habitat with limited knowledge of the terrestrial habitat. I used a combination of empirical studies of juvenile spotted salamander movement and individual-based modeling to investigate the influence of habitat amount and arrangement on juvenile salamander survival.

I quantified the fine-scale movement behavior and search strategies of recently-metamorphosed spotted salamanders in three different habitat types (field, early successional forest, and forest) and at varying distances from both hard (field and forest) and soft (early successional forest and forest) edges using fluorescent

powder tracking. I found that salamanders moved straighter and with fewer turns through field habitat compared to both forest and early successional habitat. I found that movement in forest was well approximated by a correlated random walk. I combined powder-tracking with drift fence mark-recapture to investigate both short and long-term movement decisions. Individuals were released in grassland habitat 5, 10, 20, and 35 meters from a forest edge lined with drift fences. I found significant initial orientation toward forest of individuals released 5 and 10 meters from the forest, and random orientation at 20 and 35 meters, indicating either a small perceptual range or decreasing motivation to move towards forest with distance. My empirical work found that juvenile pond-breeding salamanders exhibit considerable variation in natal dispersal behaviors such as speed of movement, path linearity, and settlement propensity. Habitat alteration and landscape change may alter the benefits associated with different movement strategies.

Using individual-based simulation techniques, I developed a movement model of initial natal dispersal in juvenile salamanders using empirical data to parameterize movement tendencies. I investigated the consequences of behavioral decisions in differing habitat modification scenarios, altering the amount and distribution of habitat within the landscape. I found that different movement strategies were optimal under different habitat modification scenarios. Increasing habitat clumping lowered the probability that dispersers would find habitat across all ranges of behaviors. The strength of movement bias toward habitat had a

significant effect on the probability of individuals locating habitat. When density-dependent mortality was not included in the model, higher movement bias maximized the probability of locating habitat. When density-dependent mortality was included in the model, blind movement (no movement bias) was optimal. The configuration of habitat affected the movement strategy that generated the lowest probability of locating habitat under density-dependence. The degree to which movement bias affected the probability of locating habitat differed based on assumptions of habitat clumping. My results indicated that the amount and configuration of habitat surrounding wetlands affect optimal movement behavior, and habitat managers should consider the configuration of habitat surrounding wetlands when designing conservation measures.

## **CHAPTER 1**

# **THE MOVEMENT ECOLOGY OF JUVENILE POND-BREEDING AMPHIBIANS**

### **INTRODUCTION**

Movement is a fundamental aspect of an organism's biology (Nathan et al. 2008), affecting the spatial and temporal scale of an organism's interactions with other organisms, resources, and the environment. The spatio-temporal dynamics of populations are dependent on the movement mechanisms employed by individuals in conjunction with the structure of the landscape and the availability and predictability of resources (Clobert et al. 2001, Mueller et al. 2011). The study of animal movement often involves some aspect of the animal's movement path. These movement paths are the observable outcome of a confluence of interacting factors, including the internal state of the animal (e.g. physiological condition and motivation), the external environment (e.g. resource distribution or predator density), and the sensory and motion capacity of the individual (Nathan et al. 2008). Understanding the processes underlying the movement decisions of animals yields insight into population-level patterns observed in nature and increases the ability to predict population and species'-level responses to habitat alteration (Fahrig 2007, Hawkes 2009, Knowlton and Graham 2010). Despite the importance of movement behavior to species persistence, there remain critical gaps in our

understanding of movement processes across a range of taxa (Clobert et al. 2009, Hawkes 2009, Romero et al. 2009).

Pond-breeding amphibians are dependent on temporary habitats that are clumped in space (Gill 1978, Trenham et al. 2001). As a result of a relatively high rate of breeding pond extinctions that occur naturally in the landscape, dispersal ability has a profound impact on pond-breeding amphibian persistence (Trenham et al. 2001, Werner et al. 2009). Population dynamics are therefore highly susceptible to the effects of habitat fragmentation that impedes dispersal (Cushman 2006, Laan and Verboom 1990, McDonough and Paton 2007). Juveniles are widely regarded to be the primary long-distance dispersers in pond-breeding amphibian populations (Berven and Grudzien 1990, Gamble et al. 2007, Gill 1978, Griffiths et al. 2010), and population persistence is sensitive to survival at this life stage (Harper et al. 2008). Despite this, we know relatively little about the movement behavior of juvenile amphibians as they make initial movements in terrestrial habitat.

Nathan et al (2008) proposed a unifying paradigm of animal movement that emphasized linking movement patterns to specific behavioral modes defined by the goals of movement. For example, an animal escaping a predator may increase survival by maximizing net displacement within a certain amount of time, yielding a linear movement path. The same animal foraging within a territory may exhibit highly tortuous movement in order to exhaustively search an area while minimizing net displacement. The movement path of this animal will be composed of fundamentally different movement patterns that result from different movement

goals (predator avoidance or foraging). Within any specific movement mode, animals may move either systematically or randomly. Systematic movement often requires some degree of spatial memory or navigational capacity, and consists of strategies such as circular systematic search, directed movement (linear paths over scales larger than the native scale of movement), or foray searching (Bell 1991, Conradt et al. 2003, Nams 2006). These types of movement are fundamentally nonrandom and are employed to maximize success at obtaining a movement goal. For example, animals living in areas with unpredictable food resources maximized the probability of survival by employing systematic searching to efficiently search an entire area (Mueller et al. 2011). Random movement is often observed in animals that do not have spatial memory or sophisticated navigational abilities and are moving at spatial scales larger than their perceptual ranges, such as long-distance dispersers. As a result of the variety of movement mechanisms employed by organisms, interpretation of movement paths should be sensitive to the spatial and temporal scale of movement goals.

For many species, natal dispersal is a complex but critical movement phase that may dictate the spatial dynamics of populations (Clobert et al. 2009). Previous research has emphasized that natal dispersal may be composed of multiple movement modes that yield alternative movement patterns (Delgado et al. 2009, Yackulic et al. 2011). Currently, many landscape-level models of metapopulation dynamics make simplifying assumptions about movement behavior, such as the use of least-cost pathways or random movement to describe dispersal, even though

model outcomes are highly sensitive to assumptions about movement behavior (Fahrig 2007, Hawkes 2009). Understanding the behavioral mechanisms generating these movement patterns will aid in the development of models that better predict or explain landscape-level patterns observed in nature.

Few studies have sought to connect movement patterns to the movement goals of amphibians during natal dispersal, even though such an approach may be critical to our understanding of amphibian persistence in altered landscapes. Juvenile pond-breeding amphibians emerge from the aquatic environment naïve to the distribution and abundance of resources in the terrestrial environment and are heavily affected by external conditions as a result of their susceptibility to predation and desiccation (Rohr and Madison 2003, Rothermel and Luhring 2005). Initial movement into terrestrial habitat constitutes a substantial ecological bottleneck for amphibian populations. For example, as few as 17% of juvenile spotted salamanders survive one year after metamorphosis even in high quality habitat (Rothermel and Semlitsch 2002). Therefore, the behavioral decisions of juveniles at this life stage have important implications for survival and population persistence, especially in fragmented landscapes where mortality risks are high. Explicit investigation of the movement patterns of juveniles will aid in developing mechanistic movement models that can predict the ability of amphibians to behaviorally mitigate the effects of environmental perturbations.

Osborn (2012) proposed a conceptual framework of hypothesized movement modes of juvenile pond-breeding amphibians. In the following, we

adhere to his conceptual framework and review the ways in which internal and external factors may interact to affect observed amphibian movement patterns and how those movement patterns may be described in a movement modeling framework.

## PRE-EMERGENCE PHASE

The pre-departure phase primarily describes the timing and initial orientation of juvenile departure from a natal pond. Because entire cohorts of populations emerge from what is ostensibly a single location within the landscape (the natal pond), juvenile behavioral responses to external factors such as habitat arrangement in close proximity to the natal pond can affect the survival of large numbers of individuals. However, we know relatively little about what information is used by juveniles to make initial departure decisions. There is not currently a strong consensus on the degree to which juveniles acquire and respond to information about terrestrial habitat while in the pre-departure phase, or the role of temporal variation in weather conditions, making this a critical area for future research. We identify two movement modes within the pre-departure phase: pre-emergence mode and wait mode.

Pre-emergence mode is defined as the behavioral stage at which newly metamorphosed amphibians remain in the natal pond, move to shallower water along the pond edge, and assess conditions pertaining to movement into terrestrial habitat. Previous studies have found that juveniles position themselves toward

terrestrial habitat while in the aquatic habitat. For example, Hayward et al. (2000) speculated that newt larvae begin orientation towards surrounding terrestrial habitat prior to metamorphosis (Hayward et al. 2000). Patrick et al. (2007) observed that wood frog larvae (*Lithobates sylvatica*) in natural natal ponds oriented toward terrestrial habitat while within the wetland. When the authors transplanted larvae to experimental pools, the emerging juveniles maintained their original orientations acquired at their pond of origin. The ability of the juvenile wood frogs to maintain orientations after translocation suggests that some species are capable of directional orientation, as has been documented extensively in newts (Diego-Rasilla et al. 2008). Juveniles are motivated to leave the natal pond to find a terrestrial settlement location with high quality habitat, low density of conspecifics, low predator densities, and in proximity to a breeding site. Energy reserves (Beck and Congdon 2000, Scott et al. 2007) resulting from the quality of aquatic larval habitats are likely the most significant internal factor affecting juvenile decisions during this movement mode, and important external factors may consist of climatic conditions such as rainfall, wetland water level, and densities of conspecifics or predators.

Immediately following metamorphosis and emergence, juvenile amphibians often make initial movements into terrestrial habitats at night during or directly after rainfall (Maazerolle 2001, Todd and Winne 2006). If environmental conditions for movement are poor, juveniles may remain at the pond edge. Wait mode is the behavioral stage at which juveniles stay at the natal wetland until

environmental or internal conditions are ideal for movement. The timing of juvenile departure is dependent on assessments of the trade-off between the heightened desiccation risk of terrestrial movement in dry conditions (Rittenhouse et al. 2009, Rothermel and Luhring 2005, Tingley and Shine 2011) and a number of documented risks near the natal pond, such as depletion of energy reserves (Scott et al. 2007), predation (Pittman et al. in review, Rittenhouse et al. 2009), density effects (Berven 2009, Harper and Semlitsch 2007), and loss to time to locate suitable settlement habitat. Because of these costs, juveniles do not remain in wait mode indefinitely and will move into terrestrial habitat even under poor environmental conditions, such as droughts (Rothermel 2004). Such trade-offs are integral to animal movement and may drive the transitions between different movement modes (Clobert et al. 2001, Zollner and Lima 2005). Conditions affecting the initial orientation and timing of departure during the pre-departure phase likely contribute much to the success of juvenile amphibian movements in terrestrial habitats.

The initial orientations of juvenile movements out of ponds are likely to be largely random with respect to terrestrial habitat quality, although this may vary among species. On the whole, juveniles have limited ability to sense terrestrial habitat from the pond, and some generalist species may not exit the natal pond with affinity for any particular habitat type. Previous research has found that the overall orientations of departing juveniles are often nonrandom at single ponds (Jenkins et al. 2006, Patrick et al. 2007, Rittenhouse and Semlitsch 2006, Rothermel 2004,

Timm et al. 2007); however, the mean direction of exiting juveniles is not usually correlated with terrestrial habitat quality (but see(Patrick et al. 2007, Walston and Mullin 2008). Studies have found that although adult emigration post breeding is highly nonrandom and directed toward high quality terrestrial habitat, juvenile orientation is generally less concentrated and uncorrelated with terrestrial habitat quality. Therefore, orientations of departing juveniles are likely generated by small-scale climatic or topographic features along the pond edge that dictate juvenile spatial arrangement in the pre-departure phase, while adult orientation is more likely dictated by spatial memory of terrestrial refugia (Madison 1997).

During the pre-departure phase, juveniles may make foray searches into terrestrial habitat before final departure, a movement strategy which has been observed in multiple other organisms (Conradt et al. 2003). Foray loops are fundamentally nonrandom movement (but see (Crone and Schultz 2008)), in which individuals move into novel landscapes, acquire information, and return to a home or safe location. This process facilitates information acquisition and increases the likelihood that individuals choose the most favorable direction to travel during departure. While dispersers of numerous other species make foray loops into novel habitat (Conradt and Roper 2006, Cox and Kesler 2012, Kesler and Haig 2007, Schliehe-Diecks et al. 2012), there is little direct evidence that juvenile amphibians employ this search strategy extensively. However, numerous amphibian mark-recapture studies provide indirect evidence concerning foray searching; these studies document the occurrence of ‘reversals,’ or animals that depart from a natal

pond or release location and are recaptured back at the natal site some time later (Osbourn 2012, Popescu and Hunter Jr 2011, Rothermel and Semlitsch 2002). In these studies, not all individuals reverse, and the proportion of reversals seems to be negatively correlated with terrestrial habitat quality; juveniles are more likely to travel back to the pond if the terrestrial habitat is of lower quality. It is unclear, however, whether these movement bouts are true, nonrandom foray searches, as there is little data on the fate of individuals that reverse back to the wetland. For example, juveniles may reverse in order to escape poor environmental conditions and may not use information acquired in a previous foray to choose subsequent movement bearings.

Foray searching is unlikely to be prevalent among all pond-breeding amphibian species. Most species that perform foray search return to home locations where risk of mortality is low. Wetland edges have high densities of predators and conspecifics, and the risk of mortality directly around the wetland edge may be high. For example, Pittman et al. (in review) found that approximately 23% of juvenile ringed salamanders (*Ambystoma annulatum*) making initial movements into terrestrial habitat were consumed by anuran predators, with the highest mortality rates occurring within 5 m of the wetland edge (Pittman et al. in review). Rittenhouse et al (2009) also found that wood frog (*Rana sylvatica*) mortality due to predation was highest closest to breeding ponds. Foray searching therefore may incur significant costs because it increases the amount of time juveniles spend in areas with high predator densities and the amount of time that individuals spend

moving on the surface, subject to desiccation and loss of energy. Therefore, amphibian species with high vagility and low rates of desiccation may be expected to employ this search strategy the most consistently. We therefore predict foray searching to be more prevalent in juvenile anurans than salamanders because juvenile anurans tend to have higher vagility than juvenile salamanders (Osbourn 2012). Studies specifically targeting prospecting behavior in amphibians are necessary to identify the extent to which this search strategy is used.

#### INITIAL JUVENILE MOVEMENT PHASE

The initial juvenile movement phase consists of three movement modes: away mode, directed mode, and settlement mode. These behavioral states are defined by the extent to which individuals respond to external factors during movement and the spatial scale over which they make movement decisions relative to motion and sensory capacity (Fig. 2). Overall, we hypothesize that juveniles depart from natal ponds with low responsiveness to habitat and high movement rates and shift into behavioral states with higher responsiveness to habitat and slower rates of movement later in the movement path. The primary goals of amphibians during the initial juvenile movement phase are to escape the high rates of predation at the pond edge, to minimize density effects, and to locate suitable settlement habitat.

Juveniles in away mode are the least responsive to terrestrial habitat quality, and they make movement decisions on a large spatial scale relative to their

perceptual range. They do not exhibit boundary behavior and may therefore be likely to enter inhospitable areas. The benefits of this behavioral state are in maximizing net displacement from a natal pond, expediting escape from areas with the highest densities of predators and competitors, and, when employed at large scales, locating new breeding ponds. For example, Pittman et al. (2013) found that approximately 23% of juvenile ringed salamanders (*Ambystoma annulatum*) making initial movements into terrestrial habitat were consumed by anuran predators, with the highest mortality rates occurring within 5 m of the pond edge. Because juveniles are the least responsive to habitat quality during away mode, movement patterns may be described as basic Brownian motion, or diffusion (Boone et al. 2006), and may be modeled discretely using random walks (Codling et al. 2008, Conradt and Roper 2006, Schwarzkopf and Alford 2002). Random walks describe movement as a series of steps and turning angles drawn from a distribution, where each successive turning angle is independent of the previous turning angle. At the most basic level, this type of movement is common in animals that are not responsive to environmental features and which are not employing spatial memory or navigational mechanisms during movement (Codling et al. 2008, Haefner and Crist 1994). However, random walk models can be modified to incorporate different levels of behavioral complexity such as changes in step size or directional persistence (correlation of turning angles) with habitat type or risk level. Employment of random walk and diffusion models often involves the analysis of fine-scale movement data (Turchin 1998) or mark-recapture data (Ovaskainen

2004, Reeve et al. 2008) to estimate distributions of path components or diffusion coefficients and to test that observed movement patterns fit random walk expectations. For example, the movement paths of animals employing systematic searching (such as foray loops or large-scale orientation) are not well approximated by random walk models, and goodness of fit can be tested explicitly by comparing observed and expected net movement rates (Benhamou 2004, Kareiva and Shigesada 1983, Nams 2006). Analysis of fine-scale amphibian movement data within the context of random walk models will help researchers test hypotheses concerning the spatial memory and navigational abilities of juvenile amphibians (Nams 2006), estimate the scale at which juveniles make movement decisions (Papastamatiou et al. 2011), and develop mechanistic models of amphibian movement (McClintock et al. 2012).

Relevant movement parameters during away mode include mean step sizes (spatial scale over which individuals make single movement decisions) and the distribution of turning angles, both of which likely vary with habitat type (Gillies et al. 2011), the perceptual range of the individual (Olden et al. 2004, Pe'er and Kramer-Schadt 2008), and genetically-based behavioral tendency (Cote et al. 2010). Additionally, internal factors such as energetic reserves and vagility of species may impact movement parameters during away mode. Tortuosity of the movement path may be modeled by specifying the mean vector length of turning angle distributions (Codling et al. 2008, Haefner and Crist 1994). Relatively small differences in turning angle distributions may have large impacts on the efficacy of

different search strategies relative to movement goals (Zollner and Lima 1999), and risks encountered by individuals may also heavily affect optimal movement behavior (Fahrig 2007, Zollner and Lima 2005). Amphibians with low vagility likely move linearly to decrease the amount of time spent in close proximity to the pond edge and to maximize the energy efficiency in displacing themselves from the natal site. For example, Pittman (2013) found that juvenile spotted salamander movement in forested habitat approximated random walks with high correlation of turning angles. Alternatively, amphibians with high vagility may not be limited by energy or time and may move more tortuously during away mode because the costs associated with searching previously-visited areas are lower (Roznik and Johnson 2009, Roznik et al. 2009, Zollner and Lima 1999).

The extent to which juveniles respond to habitat features during movement away from their natal site likely increases the longer an animal has been moving, as has been shown explicitly in other species such as juvenile owls (Delgado et al. 2009). Jenkins et al. (2006) found that salamander orientation differed significantly at 3 m from the pond edge versus 30 m from the pond edge. Orientation at 30 m was predicted by habitat quality, while orientation at 3 m was not, indicating a shift in responsiveness to habitat. Additionally, Rittenhouse et al. (2006) found that while juvenile spotted salamanders oriented non-randomly toward low-quality habitat during initial emergence from the natal pond, the majority reversed toward high-quality habitat later in the movement path. Juveniles lose energy and time before sunrise as they move in the terrestrial habitat, increasing the risks associated

with blind movement and the likelihood that individuals shift into a more habitat-responsive behavioral state.

As juveniles become more responsive to habitat features during movement, they shift from away mode into directed mode. Individuals in this movement mode respond to habitat features at large spatial scales in relation to the species' perceptual range. Directed mode is characterized by higher path sinuosity, lower movement speed, and higher responsiveness to habitat characteristics than away mode (Fig. 1). Individuals in directed mode are likely to display edge-mediated movement behavior and may be less willing to enter poor-quality habitat (Demaynadier and Hunter Jr 1999, Popescu and Hunter Jr 2011). This movement can be characterized using correlated random walk models with the inclusion of a bias parameter toward important habitat features (Bartoń et al. 2009, Chapman et al. 2007, Crone and Schultz 2008, Haddad 1999). The strength of bias and the habitat features to which juveniles are sensitive are areas of research that may greatly impact our understanding of juvenile dispersion in terrestrial habitat and may be particularly critical for habitat management and conservation decision-making.

The timing of the switch between away mode and directed mode is likely dependent on species characteristics such as vagility, external environment, and the internal state of individuals (e.g., energy storage; Colbert et al., 2009)(Clobert et al. 2009). Species with higher vagility may spend less time in directed mode because they are able to search a large amount of habitat within a short amount of time and

biasing movement towards habitat may not be necessary for locating habitat (Bartoń et al. 2009, Bartoń et al. 2012, Zollner and Lima 1999). Higher vagility and greater responsiveness to habitat may partially explain the higher movement tortuosity and greater frequency at which green frogs (*Rana clamitans*) cross forest/non-forest boundaries than spotted salamanders (Osbourn 2012). Within species, the timing of the switch from away to directed mode is likely driven by internal and external factors influencing the benefits to settlement, such as remaining energetic reserves (Rémy et al. 2011), individualized motivation such as behavioral tendency (Cote et al. 2010, Sih et al. 2004), or the quality of previously-visited habitats (Clobert et al. 2009). For example, individuals that stay in away mode for the longest time are more likely to be long-distance dispersers than individuals that shift to directed mode early during initial dispersal. For an animal to be a long distance disperser, the individual must pass over quality habitat, which necessitates a lower responsiveness to habitat and a higher degree of boldness than individuals that respond to habitat and settle (Rehage and Sih 2004).

After directed mode, juveniles shift into settlement mode. This type of movement is characterized by high responsiveness to habitat features. Juveniles in this behavioral mode are responsive to habitat features such as moisture gradients, burrows, and coarse woody debris at fine spatial scales relative to their perceptual range. Pittman (2013) found that juvenile spotted salamanders moved on top of the leaf litter for the majority of their movement path before presumably shifting into settlement mode, at which point they moved underneath leaf litter and typically

found a stopping location within a 1 m radius. Although this type of movement is fundamentally non-random, these movements may be approximated using a pure random walk or a random walk with low correlation of turning angles and short step sizes. The shifts in behavioral states from away mode to directed mode to settlement mode may occur in a single night or may encompass multiple nights and juveniles may transition between behavioral states multiple times before final settlement. For example, juveniles may find a temporary location for settlement after the first night of movement and move again in subsequent nights when environmental conditions are favorable (Osbourn, 2012). Multistate random walk models may be used to simulate long-term amphibian movement using a series of biased and correlated random walks that define different movement modes (McClintock et al., 2012). Transitions between behavioral states occur probabilistically using various internal and external covariates dictating the risks and benefits to movement. This movement modeling approach will allow a more sophisticated interpretation of amphibian movement paths, generate hypotheses for the fitness consequences of movement behavior, and improve the prediction of the effects of landscape change on both local and metapopulation dynamics.

#### ESTABLISHMENT OF HOME RANGE

After juveniles have chosen a final settlement location, they establish home ranges. Amphibian home ranges are typically small, and individuals may be highly philopatric to even small-scale refugia such as logs, burrows, or trees (Johnson et

al. 2007, Pittman et al. 2008, Vasconcelos and Calhoun 2004). After settlement, movement consists of short foraging bouts and longer distance breeding migrations. Movement during foraging bouts is highly biased toward settlement locations. Movement models that incorporate memory or cognitive maps may approximate amphibian home-range behavior (Moorcroft 2012, Van Moorter et al. 2009).

## ADULT MIGRATIONS

In subsequent years following the establishment of a home range, juveniles continue to grow and eventually join an adult breeding population that migrate seasonally to and from a breeding pond typically on the scale of <1000 m (Semlitsch and Bodie 2003). There is a lack of attempts to theoretically model amphibian migrations, perhaps because of a bias of scale compared to other vertebrates. Some species or individuals may also migrate between home ranges and overwintering sites (Semlitsch 2008). Long-distance migrations to breeding locations are driven by memory or possibly even external cues such as conspecific trailing (Malmgren, 2002). Therefore, movement is nonrandom and highly directed toward breeding ponds and to overwintering locations after breeding (Jenkins et al., 2006 (Semlitsch 1998). The targeted movement of individuals toward known locations is a fundamental difference between the migration movement phase and initial juvenile movement. Modeling of movement during migrations should therefore incorporate spatial memory and potentially large-scale orientation mechanisms toward breeding sites (Mueller et al. 2011).

## DISPERSAL IN HUMAN-ALTERED LANDSCAPES

Juvenile movement decisions have consequences for both short-term survival and long-term fitness. The amount of time that individuals spend in away, directed, or settlement mode greatly affects the risks that they encounter during dispersal and potential fitness benefits. For example, a juvenile whose movement path is dominated by movement in settlement mode will likely settle close to the natal pond. This individual may have a smaller chance of dying from desiccation or loss of energy, but may also encounter higher rates of predation and may be affected by greater density effects and associated low juvenile survival (Harper et al., 2008). However, this individual will not incur great energetic costs during breeding migrations. A juvenile that spends the greatest amount of time in directed mode will settle within migration distance to the natal wetland and will likely be less susceptible to predation and density effects after settlement. This individual may maximize the chance of finding high-quality habitat a moderate distance away from the natal wetland. This individual will incur costs from the amount of time spent moving on the surface during dispersal and the distance traveled during breeding migrations. An individual that spends the greatest amount of time in away mode will incur significant energetic costs during movement and will increase the chance of entering unsuitable habitat and dying. However, this individual will also have the greatest likelihood of colonizing or locating a new breeding site with high fitness benefits.

Habitat alteration changes the risks and benefits associated with different movement modes and associated behavioral decisions (Fahrig 2007). For example, loss of habitat may increase the risks associated with away mode, and individuals may have higher survival by shifting to directed or settlement mode quickly during dispersal. However, movement that is highly responsive to habitat in clumped or fragmented landscapes may create high-density areas, which may increase time to maturity and lower growth rates of juvenile amphibians (Harper and Semlitsch 2007, Patrick et al. 2008). While remaining at natal wetlands may increase the chances of survival in altered landscapes, dispersal to new wetlands may also yield high fitness benefits. For example, theoretical models have found that evolutionary rescue is possible for butterfly species impacted by habitat fragmentation. In simulations, butterflies evolved to disperse farther in fragmented landscapes despite the high risk of movement because the long-term fitness benefits to colonizing newly available habitat outweighed the short-term survival benefits of remaining philopatric (Heino and Hanski 2001). Understanding the factors that affect amphibian movement decisions and the costs to those decisions will aid in understanding amphibians' ability to behaviorally and evolutionarily mitigate the effects of habitat alteration.

## CONCLUSIONS

Juvenile amphibian natal dispersal is a multi-stage process during which individuals vary movement speed, responsiveness to habitat features, and

propensity of settling based on internal state and the external environment (Fig. 1). Although the movement mode framework described in this paper is a discrete interpretation of what is more likely to be a continuous behavioral spectrum, the use of subdivided behavioral modes could be a useful first step in categorizing and interpreting amphibian movement data. The mechanistic movement modeling framework outlined in this paper can generate relevant hypotheses as to the survival consequences of different movement strategies and the external or internal conditions that dictate the outcome of different movement modes. Currently, many studies of amphibian movement are large-scale, pattern-oriented approaches that only indirectly address underlying movement mechanisms. Adhering to this framework will aid future studies place amphibian movement data into a larger explanatory framework that could help identify gaps of knowledge and guide new avenues of research. Understanding how, under what conditions, and to what extent juveniles respond to habitat features and internal state during dispersal will aid in developing realistic, predictive models of amphibian movement that can be used to further conservation and management efforts and will add to theory about how movement mechanisms during dispersal impact population persistence in altered landscapes.

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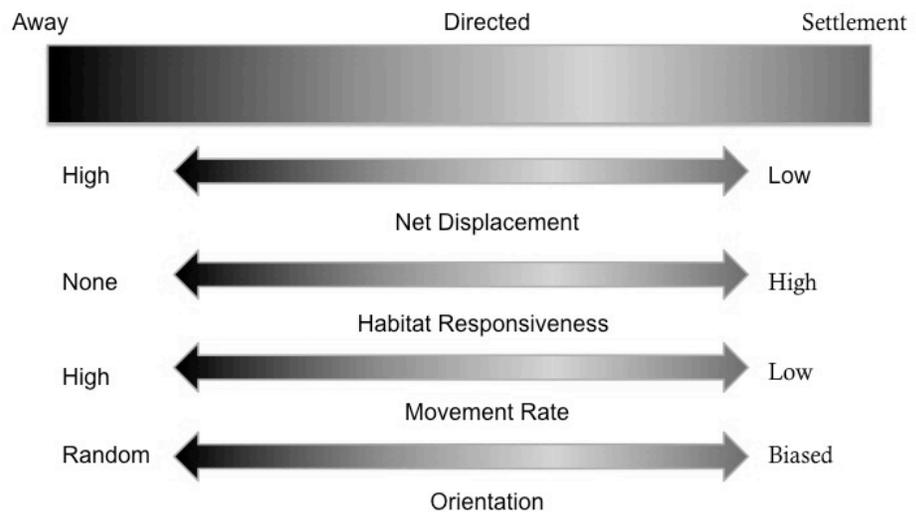
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Figure 1. Behavioral modes and characteristics of associated movement parameters during the initial movement phase.

# Movement Mode



## CHAPTER 2

### HABITAT TYPE AND DISTANCE TO EDGE AFFECT MOVEMENT BEHAVIOR OF JUVENILE POND-BREEDING SALAMANDERS

#### ABSTRACT

Behavioral strategies of natal dispersers in response to human-altered habitat have far-reaching implications for functional connectivity and local population dynamics. Spotted salamanders (*Ambystoma maculatum*) are forest-dependent, pond-breeding amphibians which metamorphose and disperse out of aquatic habitat with limited knowledge of the terrestrial habitat. We quantified the fine-scale movement behavior and search strategies of recently-metamorphosed spotted salamanders in three different habitat types (field, early successional forest, and forest) and at varying distances from both hard (field and forest) and soft (early successional forest and forest) edges using fluorescent powder tracking. We found that salamanders moved straighter and with fewer turns through field habitat compared to both forest and early successional habitat. Salamanders significantly oriented movement toward forest habitat when released in the field and when released on the edge between the forest and field. We found that salamander movement in the forest and early successional forest was not significantly different from a correlated random walk; however, a subset of salamanders showed directed movement at spatial scales ranging from 25 – 300 cm. Based on these results,

dispersing spotted salamanders exhibit strong edge-mediated behavior when differences between habitats are stark (forest and field) and can perceive forest habitat from distances of at least 10 m. These results indicate that dispersing juvenile salamanders exhibit reasonable behavioral rules when moving through habitat types of differing quality. Knowledge of these behavioral rules will improve predictions of the effects of habitat type and configuration on amphibian survival and dispersion in altered landscapes.

## INTRODUCTION

Human-induced habitat change is widely regarded as a primary factor threatening the persistence of species (Laurance 2008). One major consequence of habitat alteration is its effect on the movement of individuals (Clobert et al. 2009, With et al. 1997). Animal movement is often strongly influenced by habitat type; the strength, direction, and variation inherent in species' behavioral reactions to novel or altered habitat during dispersal have implications for population dynamics, and knowledge of this behavior may aid in maximizing the effectiveness of conservation and management practices (Hawkes 2009).

Natal dispersal is an important mechanism by which species mitigate the effects of unpredictable variation in the spatial distribution of resources and is critical to many species' spatial dynamics (Clobert et al. 2001). The population-level effects of the movement of individuals is the result of both the species' movement behavior and the composition of the habitat through which it is moving.

Habitat alteration impacts the spatial patterning of resources and the risks associated with searching for resources. Simulations have shown that certain search strategies employed by dispersers yield higher probabilities of encountering resources than others (Zollner and Lima 1999), and searchers may not always increase long term energy gain by responding to the spatial pattern of resources even if it is detectable (Klaassen et al. 2006). The impacts of habitat alteration on natal dispersal may be especially strong in species with complex life cycles, as individuals have no previous experience of the habitat into which they are dispersing and may employ standardized search strategies to maximize the probability of encountering suitable habitat. Search strategies employed by species with complex life cycles may therefore not always be optimal in relation to the spatial structure of habitat in altered landscapes (Fahrig 2007).

Pond-breeding amphibians are particularly sensitive to habitat alteration because populations are naturally spatially clumped in the landscape and movement among populations is necessary to maintain regional persistence (Cushman 2006, Marsh and Trenham 2001). Search strategies, orientation ability, and the spatial scale over which individuals make movement decisions have profound impacts on the effectiveness of management strategies aimed at minimizing fragmentation effects, such as the creation of corridors (Gillies et al. 2011, Haddad 1999), stepping stones (Kramer-Schadt et al. 2011), or the delineation of core habitat size (Johnson and Semlitsch 2003). Initial movement of juveniles out of wetlands is an important movement phase for pond-breeders because local population persistence

is sensitive to juvenile survival (Harper and Semlitsch 2007), and juveniles are often the primary inter-population dispersers (Berven and Grudzien 1990, Gamble et al. 2007, Gill 1978, Griffiths et al. 2010). Habitat loss and fragmentation increase the influence of movement strategies on juvenile survival by truncating the breadth of behavioral variation that yields the highest likelihood of successful dispersal. Despite its importance, movement strategies employed by amphibians in response to altered habitat during initial movement out of wetlands remain poorly understood.

Spotted salamanders (*Ambystoma maculatum*) are pond-breeding, forest-dependent amphibians in which juveniles are primary dispersers between populations (Gamble et al. 2007, Gill 1978). Recently-metamorphosed spotted salamanders make initial movements out of natal wetlands on the scale of 20 – 50 m (Osborn 2012). Mortality during this initial movement phase is considerable; approximately 17% of spotted salamanders survive one year after metamorphosis (Rothermel and Semlitsch 2002, 2006). Documented causes of mortality during include desiccation (Rothermel and Semlitsch 2002, Rothermel and Luhring 2005), predation (Rittenhouse et al. 2009), depletion of energy (Scott et al. 2007), and density effects (Harper and Semlitsch 2007, Patrick et al. 2008, Rittenhouse and Semlitsch 2007). Spotted salamanders have lower survival in open-canopy as opposed to closed-canopy habitat (Rothermel and Semlitsch 2002), and spotted salamander occupancy in ponds is highly dependent on the amount of forested habitat surrounding ponds (Porej et al. 2004, Skidds et al. 2007). Additionally,

mark-recapture experiments have shown that juveniles are more likely to be relocated in forested as opposed to field habitat (Patrick et al. 2008, Rittenhouse and Semlitsch 2006). While it is clear that habitat strongly affects the survival and location of spotted salamanders, the behavioral mechanisms underlying these observed patterns are currently unknown.

In this study, we determined the effects of habitat type and distance to habitat boundaries on juvenile spotted salamander movement behavior. Specifically, we quantified movement patterns and orientation of recently-metamorphosed spotted salamanders released on and at varying distances from both hard and soft forest edges. We predicted that salamanders would orient movement toward forest habitat and away from both field and early successional habitat. We also predicted that salamanders would move straighter through low-quality habitat, and would make more turns and settle after shorter distances in forest habitat. Understanding how habitat type affects juvenile spotted salamander movement will aid in predicting the effects of habitat loss to amphibian populations and improve management practices.

## METHODS

### *Study Area*

This study was conducted at Daniel Boone Conservation Area (DBCA, 1,424 ha) in Warren County, MO. DBCA is characterized by mature second-growth forest dominated by oak and hickory tree species in the canopy and sugar maple in the

understory. Small grassland clearings (~5 hectares) are maintained within DBCA through bi-annual mowing and consist of native warm season grasses such as Big Bluestem (*Andropogon gerardii*) and Indiangrass (*Sorghastrum nutans*).

We conducted this study at two pond locations within DBCA, situated ~500 m apart. Each pond was located within approximately 200m of two land use types: early successional forest (5 years post clearcutting, hereafter referred to as ‘early successional’) and open grassland habitat (hereafter referred to as ‘field’). The early successional patches were ~2.11 ha in size, and the field patches were approximately 1 ha in size. Both the habitat types were bordered by mature second-growth forest. Clearcutting of the early successional areas took place in March 2004, and all marketable timber >25cm DBH was removed. Timber <25 cm DBH was felled and left on the ground. We considered the borders between early successional and mature forest ‘soft edges’ and the borders between field and mature forest ‘hard edges’ for this study.

### ***Salamander collection and release design***

We collected metamorphosed salamanders from drift fences surrounding the two ponds and from cattle tanks stocked with 8 egg masses collected from small, ephemeral pools within 100m of the ponds. Salamanders were held in containers with damp moss until conditions were ideal for release and tracking, which were defined as: 1) within 24 hrs of, but not concurrent with, a rain event, 2) when minimum nightly temperatures were above 10 degrees Celsius, and 3) within 2 weeks of the individual’s metamorphosis. We released salamanders no later than

one hour after sunset, usually between 2030 and 2200 hrs. Salamanders were not released during a rain event in order to prevent loss of the powder trail. However, individuals were released soon after a rain event when the ground was wet and relative humidity was high. Previous studies have found that salamanders readily disperse from wetlands under these conditions (Rothermel 2004). Research has also shown that recently-metamorphosed salamanders will make natal dispersal movements up to 9 days after a rain event (S. Pittman, unpublished data). We therefore believe that the behavior of individuals in this study was consistent with behavior during initial natal dispersal.

We released salamanders in line transects perpendicular to the edge consisting of five release points: 10 m in the field or early successional forest (-10), 5 m in the field or early successional forest (-5), directly on the edge (0), 5 m into the forest from the edge (5), and 10 m into the forest from the edge (10; Fig. 1, Table 1). Each transect was positioned a minimum of 5 m from any other transects during the experiment. We performed a maximum of 2 transect releases in a single night (10 animals total). Salamanders were randomly assigned to release points at the soft or hard edge closest to the salamander's natal wetland. We placed salamanders underneath release enclosures for approximately 10 minutes to allow animals to acclimate to the environment and to reduce the likelihood of observing artificial release responses (Turchin 1998). We lifted the release chamber by pulling the end of a string attached to the release chamber from a distance of at least 3 m in order to minimize the influence of observer orientation in salamander

movement decisions. We recorded relative humidity, ground temperature, soil temperature, and ambient air temperature at each release location at the time the salamanders were placed under the release chamber.

Fluorescent powder was used to track the continuous movement of salamanders after release. Directly prior to release, we covered the posterior half of salamanders with pink, orange, or green fluorescent pigment. Color of pigment was alternated along a release transect to reduce the likelihood of two identically-colored paths intersecting. Fluorescent powder has been used successfully in previous studies to track short-term movements of small amphibians (Eggert 2002, Graeter et al. 2008, Roberts and Liebgold 2008, Roe and Grayson 2008). Previous work has shown that the pigment does not affect survival or level of cutaneous respiration in newts and ambystomatid salamanders (Orlofske et al. 2009, Roe and Grayson 2009); therefore, we do not think it likely that powder affected the movement behavior of animals in this study.

### ***Salamander tracking and mapping***

We returned 4-5hrs following release and followed fluorescent powder trails left by the salamanders with an ultraviolet light (Arachnid A14, Blacklight.com, Volo, IL). Pilot experiments found 4 hrs to be sufficient time for salamanders to move and settle (S. Pittman, unpublished data). We applied powder to a subset of 35 animals that settled in the forest or early successional habitat and tracked these animals for an additional night in order to determine whether animals maintained movement bearings for subsequent nights.

We returned the following day and positioned flags at each turning point in order to map the movement path as a series of consecutive moves, or ‘steps’. We designated turning points and move lengths with the approach suggested by Turchin et al (1998). We aggregated a section of the path into one step if the intermediate spatial positions of the path fell within 15 cm from a perpendicular straight line connecting the beginning of the path section and the end of the path section. This methodology allows an observer to categorize paths into discrete steps objectively while minimizing unconscious observer bias (Turchin 1998). We recorded the distance and bearing from each turning point to 1) the release location, 2) the end point of the path, and 3) the closest point along the edge. We used these data to convert paths to x-y coordinates for evaluation of movement path parameters, response to habitat boundaries, and search strategies.

### ***Data Analysis***

#### *Orientation Propensity*

We used circular statistics to test whether salamanders significantly oriented movement according to the bearing of the forest perpendicular to the edge. We used Rayleigh’s test to determine whether orientation significantly deviated from a random distribution for each release distance (Batschelet 1981, Fischer 1993). We used the V-test to determine whether salamander orientation was significantly different from a hypothesized mean angle (bearing towards the forest, perpendicular to the edge). We analyzed the vanishing bearing of any animal that moved a net distance greater than 1 m.

### *Estimation of Movement Path Parameters and Search Strategy*

Movement paths of juvenile salamanders were analyzed using the software program Fractal 5.0 (Nams 1996). For each path with a total distance greater than 5 m and a minimum of 5 steps, we determined: path linearity (net distance moved/total distance moved), mean step size, and concentration of turning angles (k).

We additionally tested each movement path used in the previous analyses for goodness of fit to a correlated random walk (CRW; (Nams and Bourgeois 2004)). This test compared the net squared displacement (square of the distance between the individual's position after  $n$  moves and starting point; (Benhamou 2004, Kareiva and Shigesada 1983)) of each movement path with predictions of net squared displacement based on a CRW model using the test statistic  $CRW_{Diff}$ , determined by,

$$CRW_{Diff} = \frac{1}{k} \sum_{n=1}^k \frac{R_n^2 - E(R_n^2)}{n^2 l^2 - E(R_n^2)}$$

where  $R_n^2$  represented the observed mean net squared displacement for number of  $n$  consecutive moves,  $E$  was the expected mean net squared displacement according to the CRW model described by Kareiva and Shigesada (1983), and  $l$  was the mean step length. If  $CRW_{Diff} > 0$ , the animal moved farther than predicted by a CRW, while if  $CRW_{Diff} < 0$ , the animal moved more tortuously than a CRW. We ran the  $CRW_{Diff}$  test at both the species level (where errors are based on among-path variation) and at the individual level (where errors are based on within-path

variation).

We additionally tested for directed movement in salamander paths using the scaling test for orientation employed by Nams (2006). The test assumed that animals undergoing directed movement move distances farther than predicted by a CRW at larger spatial scales. Therefore, we resampled movement paths at a range of spatial scales and measured  $CRW_{Diff}$  at each scale. If  $CRW_{Diff}$  was significantly positive, we concluded that animals employed directed movement at that spatial scale. Animals that did not employ directed movement should show  $CRW_{Diff}$  values that were not significantly different from 0 at all spatial scales. We set the minimum spatial scale to be the smallest path resolution recorded in this experiment (15 cm) and the maximum to be 10 m.

#### *Comparison of Movement Path Parameters in Different Habitats*

We compared the mean step length and linearity (net displacement / total path length) of movement paths among individuals moving in different habitat types (forest, early successional forest, and field) and at different edges using a two-way analysis of variance with edge location (Edge) and habitat type (Habitat) as explanatory factors. We analyzed the first 5 m total distance of each movement path for comparisons. In this way, we controlled for differences in path detection and potential changes in movement objectives as individuals moved longer distances. We performed the Shapiro-Wilk normality test for both step length and linearity, and log transformed both step length and linearity to achieve normality. When ANOVA results were significant, we used Tukey's Honestly Significant

Differences Test (HSD) for pairwise comparisons between treatments. We used R for all ANOVA and circular statistical tests (R Development Team 2012) and  $\alpha = 0.05$  as a standard for significance.

## RESULTS

Out of a total of 200 released salamanders, three movement paths were not definitively identified and therefore were not included in analyses. The size of salamanders used in this experiment was 30.9 mm (SE = 2.8) from the tip of the snout to the posterior end of the vent. The mass of salamanders in this experiment was 0.93 g (SE = 0.30). The longest movement path recorded was 50.10 m net distance and a total distance of 53.44 m. Mean recorded path length was 5.67 m (SE = 0.41,  $n = 50$ ) in the field, 10.95 m (SE = 1.70,  $n = 42$ ) in the early successional habitat, and 10.65 m (SE = 1.05,  $n = 84$ ) in the forest (Table 2), excluding animals that settled within 1 m of the release location ( $n = 21$ ). However, these estimates likely underestimate actual movement distances, as animals that moved farther were less likely to be relocated (Table 1, Table 2). Overall, 50% of salamanders were relocated at the end of the tracking session (98 out of 197). However, habitat type affected relocation probability (Table 1); salamanders released in field habitat were 46% less likely to be relocated at the end of the first tracking night ( $t = 6.47$ ,  $df = 4$ ,  $P = 0.003$ ), and were less likely to settle within 1 m of the release location (Field:  $n = 0$ , Early Successional:  $n = 6$ , Forest:  $n = 15$ ). In forest and early successional habitat, 61% of salamanders were relocated (94 out of

155), and there was no difference in relocation probability between individuals released in forest and early successional habitat ( $t = 0.54$ ,  $df = 4$ ,  $P = 0.614$ ).

### ***Habitat-Specific Movement Behavior***

Mean step lengths and path linearity of salamanders differed significantly among habitat types (step length:  $F(2,134) = 9.683$ ,  $P < 0.001$ , Table 3; path linearity:  $F(2,132) = 3.125$ ,  $P = 0.047$ ; Table 4). Using Tukey's HSD Test, we found that salamanders in the field exhibited longer step lengths (mean = 1.32 m, SE = 0.104 m) than salamanders released in the forest (mean = 0.846 m, SE = 0.042 m,  $P < 0.001$ ) or early successional habitat (mean = 0.90 m, SE = 0.08 m,  $P = 0.008$ ).

Although we found an overall treatment effect, we failed to detect significant pairwise differences between treatments at the  $\alpha = 0.05$  level using Tukey's HSD Test for path linearity. However, pairwise differences between field and early successional and forest habitat were approaching significance (field and early successional: Tukey's HSD:  $P=0.074$ ; field and forest:  $P = 0.076$ ). We did not find a difference in step lengths (Tukey's HSD:  $P = 0.799$ ) or path linearity (Tukey's HSD:  $P = 0.909$ ) among individuals moving in the forest and the early successional habitat.

### ***Movement Over Multiple Nights***

A subset of 35 salamanders that settled under logs or leaf litter after the first night of tracking was tracked for a second night. Twenty-four out of 35 of these individuals did not move a net distance greater than 1 m the second night and remained in the settled habitat until a rain event. Seven out of the 9 salamanders

that did move more than 1 m the second night were tracked to burrows. The final two salamanders that moved the second night were tracked to leaf litter, and remained in these locations until a rain event, after which they were not recaptured. We found that the orientations of the 9 individuals that moved a second night were highly correlated (V-test:  $p < 0.001$ ) with orientation the first night, indicating that the bearings of individuals the first night affected bearings in subsequent nights of movement.

### ***Orientation***

Salamanders at 0 m, -5 m, and -10 m release locations along hard edges exhibited target-oriented movement toward forest habitat: 0 m (mean vector length ( $r$ ) = 0.48, Rayleigh's test:  $P = 0.004$ , V-test:  $P = 0.001$ ,  $n = 18$ ), -5 m ( $r = 0.385$ , Rayleigh's test:  $P = 0.03$ , V-test:  $P = 0.004$ ,  $n = 23$ ), and -10 m ( $r = 0.31$ , Rayleigh's test:  $P = 0.04$ , V-test:  $P = 0.05$ ,  $n = 19$ ), with angles corrected so that  $0^\circ$  was toward the forest, perpendicular to the edge (Fig. 3A-C). Salamanders released within the forest at hard edges did not significantly orient away from the field habitat: 5 m ( $r = 0.256$ , Rayleigh's test:  $P = 0.29$ , V-test:  $P = 0.942$ ,  $n = 19$ ), 10 m ( $r = 0.177$ , Rayleigh's test:  $P = 0.61$ , V-test:  $P = 0.29$ ,  $n = 16$ ) (Fig. 3D-E). The orientations of salamanders released at soft edges were randomly distributed: -10 m ( $r = 0.256$ , Rayleigh's test:  $P = 0.63$ , V-test:  $P = 0.492$ ,  $n = 17$ ), -5 m ( $r = 0.246$ , Rayleigh's test:  $P = 0.52$ , V-test:  $P = 0.774$ ,  $n = 15$ ), 0 m ( $r = 0.199$ , Rayleigh's test:  $P = 0.58$ , V-test:  $P = 0.795$ ,  $n = 14$ ), 5 m ( $r = 0.246$ , Rayleigh's test:  $P = 0.52$ , V-test:  $P = 0.774$ ,  $n = 17$ ), and 10 m ( $r = 0.187$ , Rayleigh's test:  $P = 0.63$ , V-test:  $P = 0.415$ ,  $n$

= 13) (Fig. 4A-E). Additionally, salamanders did not orient toward natal ponds or cattle tank locations (V-test:  $P = 0.54$ ).

### ***Search Strategy***

At the species level, juvenile spotted salamanders utilized a CRW ( $CRW_{Diff} = 0.595$ ,  $P = 0.1617$ ,  $n = 84$ ), with a mean step size of 1.20 m (SE = 0.06 m) and a mean k value of 0.703 (SE = 0.018) when moving through forest or early successional habitat (Fig. 3, Fig. 5A-B). However, at the individual level, 23% of salamander paths did significantly deviate from CRW (19 out of 84; Fig. 6A-B). Of these, 95% yielded  $CRW_{Diff} > 0$  and therefore moved farther distances than predicted by a CRW (18 out of 19; Table 5). When we re-sampled these paths at a mean step size of 1.2 m, 68% of the paths did not deviate from a CRW, indicating that the original mean step sizes calculated for these paths may have been smaller than the native scale of movement (Nams 2006). Additionally, 42% of salamander paths showed some evidence of directed movement, at scales ranging from 25-300 cm (Fig. 5A-B, Table 5).

Nine salamander paths through field habitat did not cross a habitat boundary and were long enough to include in this analysis. We found that salamander movement through field was not significantly different than a CRW ( $CRW_{Diff} = 0.389$ ,  $P = 0.7852$ ,  $n = 9$ ), with a mean step size of 1.62 m (SE = 30 cm) and a mean k value of 0.804 (SE = 0.04).

## DISCUSSION

Elucidating behavioral rules that predict organisms' spatial ecology in altered landscapes requires species-specific, bottom-up approaches to the study of movement (Romero et al. 2009). The fine-scale search strategies of juvenile salamanders documented in this study provide behavioral mechanisms underlying the patterns observed in previous mark-recapture and occupancy studies (Demaynadier and Hunter Jr 1998, 1999, Rittenhouse and Semlitsch 2006, Skidds et al. 2007), with important implications for management of pond-breeding amphibian populations in altered landscapes. This study found that salamanders moved straighter through field habitat than forest or early successional habitat and biased movements strongly toward forest, indicating that recently metamorphosed amphibians exhibit reasonable movement rules during initial movement out of ponds to minimize time spent in unsuitable habitat.

Salamanders released in early successional and mature forest showed random overall orientation in response to habitat boundaries, and individuals employed search strategies with highly correlated turning angles. In accordance with previous studies on spotted salamander habitat use, the majority of salamanders settled underneath leaf litter, underneath coarse woody debris, or inside of burrows (Madison 1997, Rothermel and Luhring 2005). Because the majority of individuals remained in these locations for multiple days or until a rain event, the chosen settlement locations were important to survival. Animals that did move more than 1 m in subsequent nights maintained movement bearings exhibited

in the first night of movement. Thus, salamander movement the first night was important to both salamander survival and to salamander dispersion over multiple nights of movement. This behavior suggests that dispersing salamanders use energy reserves to maximize net displacement from wetlands as opposed to exhaustively searching areas immediately around wetlands for suitable microhabitat.

Responsiveness to habitat affects the likelihood of an animal finding suitable habitat and the amount of time spent searching for habitat (Bartoń et al. 2009, Kramer-Schadt et al. 2011, Pe'er and Kramer-Schadt 2008). Salamanders released in the field oriented movement bearings toward the forest from distances of 10 m away and exhibited longer step sizes and higher path linearity than individuals in forest or early successional habitat. Because juvenile salamanders bias movements toward mature forest in field habitat, ponds situated on hard habitat edges or within a certain distance of forested habitat may not necessarily have low juvenile recruitment because juveniles can behaviorally mitigate the impact of the location of unsuitable habitat; they would likely utilize corridors or stepping stones to minimize time spent in suboptimal habitat, and field habitat may constitute a dispersal barrier (Rittenhouse and Semlitsch 2006). However, high habitat responsiveness may also increase salamander density in habitat patches close to natal ponds and limit the functional connectivity of populations in fragmented landscapes (Patrick et al. 2008).

We did not detect a significant difference in step size or path linearity between early successional and forest habitat, and juveniles moved randomly with

respect to habitat boundaries when released in these habitats. These results suggest that early successional forest may not act as a dispersal barrier for spotted salamanders. However, early successional forest may act as an ecological trap if patches are of a sufficient size and fail to provide the resources needed for survival. Previous studies have found that abundance in early successional habitat is significantly lower than mature forest for lungless salamanders (Hocking et al. 2013) and wood frogs (Popescu et al. 2012), which could correspond either to differences in survival or to differences in behavioral responses to the habitat. Although spotted salamanders did not orient away from early successional forest in this study, more research is required to determine whether spotted salamanders behave differently in early successional forest over longer temporal scales.

At the species level, spotted salamander movement through field, early successional, and mature forest was adequately described by a CRW, providing evidence supporting the use of CRWs in amphibian movement models (Boone et al. 2006) and suggesting that juvenile amphibians may not use systematic searching behavior during initial dispersal (Bell 1991). However, this study additionally shows that movement models should incorporate habitat-specific movement and boundary behavior, even for initial movement out of wetlands. Numerous studies have concluded that an understanding of animal behavioral rules is required to yield accurate predictions of functional connectivity or population viability in altered habitat (Knowlton and Graham 2010, McClintock et al. 2012, Reeve et al. 2008, Yackulic et al. 2011). Movement models incorporating edge behavior and

habitat-specific movement will have the ability to predict the consequence of spatial arrangement of habitat on population persistence and implement effective strategies to improve connectivity of populations.

In conclusion, this study indicates that salamanders adopt highly correlated random walk search strategies, that they alter movement behavior in habitat of differing quality, that they are able to detect and orient movement toward forest habitat when released in field habitat, but that they do not respond to subtler differences between habitat types (mature and early successional forest) and behaviorally orient movement toward the higher-quality habitat. Locally, salamander populations may be boosted by increasing the amount of high quality forested habitat directly surrounding wetlands and minimizing clearcutting surrounding wetlands (Semlitsch et al. 2009), as juveniles may not avoid this suboptimal habitat after succession has occurred. At the landscape scale, dispersing spotted salamanders are likely to avoid open habitat from urban or agricultural development, which may limit functional connectivity but increase the survival of juveniles in existing populations. Research on juvenile amphibian movement patterns in relation to habitat type and edges over longer temporal scales will provide further insight into effects of landscape change on amphibian population distributions.

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Table 1. Number of salamanders released and relocated at each distance and percentage of individuals that moved net distances greater than 1m from release locations.

| Release Location | Number Released | Percentage of Salamanders Relocated (%) | Percentage of Paths Longer than 1 m (%) |
|------------------|-----------------|---|---|
| <b>Hard Edge</b> |                 |   |   |
| -10              | 19              | 15.8                                    | 100                                     |
| -5               | 23              | 21.7                                    | 100                                     |
| 0                | 19              | 63.2                                    | 84.2                                    |
| 5                | 23              | 52.2                                    | 87.0                                    |
| 10               | 21              | 71.4                                    | 76.2                                    |
| <b>Soft Edge</b> |                 |   |   |
| -10              | 19              | 52.6                                    | 89.5                                    |
| -5               | 19              | 68.4                                    | 78.9                                    |
| 0                | 18              | 44.4                                    | 77.8                                    |
| 5                | 18              | 64.7                                    | 94.4                                    |
| 10               | 18              | 72.2                                    | 72.2                                    |

Table 2. Mean observed movement distances (net and total) of all salamanders that moved more than 1 m. Numbers in parentheses indicate standard errors.

| Habitat            | Total Distance Moved |                 |    |                | Net Distance Moved |                |    |                |
|--------------------|----------------------|-----------------|----|----------------|--------------------|----------------|----|----------------|
|                    | n                    | Mean            | n  | Mean           | n                  | Mean           | n  | Mean           |
| Field              | 50                   | 5.88<br>(0.83)  | 10 | 5.35<br>(0.73) | 50                 | 5.67<br>(0.41) | 10 | 5.14<br>(0.39) |
| Early Successional | 42                   | 10.95<br>(1.7)  | 27 | 8.72<br>(1.34) | 42                 | 9.40<br>(2.05) | 27 | 7.00<br>(1.38) |
| Forest             | 84                   | 10.65<br>(1.05) | 60 | 9.06<br>(0.97) | 84                 | 9.32<br>(1.16) | 60 | 7.73<br>(1.04) |

Table 3. Analysis of Variance table of step sizes for salamanders that moved total distances greater than 5m. Habitat type (Habitat) significantly influenced step size.

|              | Degrees of<br>freedom | Sum of<br>Squares | Mean Sum<br>of Squares | F value | P-value |
|--------------|-----------------------|-------------------|------------------------|---------|---------|
| Habitat      | 2                     | 0.972             | 0.486                  | 9.683   | <0.001  |
| Edge         | 3                     | 0.0985            | 0.0328                 | 0.6542  | 0.5817  |
| Habitat*Edge | 2                     | 0.0319            | 0.0319                 | 0.6361  | 0.5309  |
| Residuals    | 134                   | 6.726             | 0.0502                 |         |         |

Table 4. Analysis of Variance table of path linearity (net distance/ total distance) of individuals that moved total distances greater than 5m. Habitat type significantly affected path linearity.

|              | Degrees of<br>freedom | Sum of<br>Squares | Mean Sum<br>of Squares | F value | P-value |
|--------------|-----------------------|-------------------|------------------------|---------|---------|
| Habitat      | 2                     | 4.665             | 2.332                  | 3.125   | 0.047   |
| Edge         | 3                     | 1.029             | 0.3429                 | 0.460   | 0.7111  |
| Habitat*Edge | 2                     | 0.118             | 0.0591                 | 0.0792  | 0.9239  |
| Residuals    | 132                   | 98.516            | 0.7463                 |         |         |

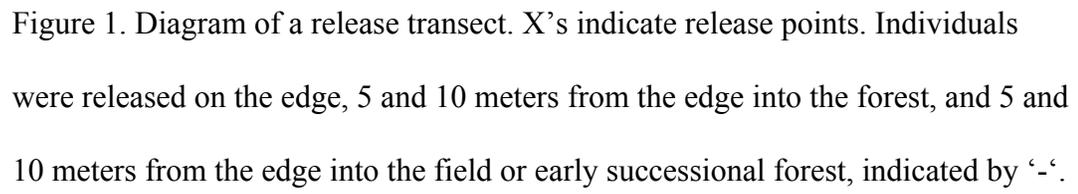
Table 5.  $CRW_{Diff}$  values and scale of directed movement for all individuals that showed evidence of directed movement or that had significant  $CRW_{Diff}$  values. Significant p-values are followed by an asterisk. Significantly positive  $CRW_{Diff}$  values represent salamanders that moved farther than predicted by CRW, while significantly negative  $CRW_{Diff}$  values represent salamanders that moved more tortuously than a CRW.

| ID    | $CRW_{Diff}$ | P-value | Scale of Directed Movement (cm) |
|-------|--------------|---------|---------------------------------|
| MA101 | 0.720        | 0.281   | 100                             |
| MA105 | -1.503       | 0.036*  | N                               |
| MA106 | 0.962        | 0.051*  | 100                             |
| MA110 | 0.470        | 0.004*  | N                               |
| MA113 | 1.351        | 0.051*  | N                               |
| MA151 | 0.566        | 0.124   | 100                             |
| MA152 | 1.004        | 0.089   | 50                              |
| MA156 | 0.395        | 0.774   | 60                              |
| MA157 | 0.858        | 0.007*  | 90                              |
| MA162 | 0.391        | 0.260   | 50                              |
| MA167 | 0.749        | 0.038*  | 50                              |
| MA170 | 1.200        | 0.038*  | 40                              |
| MA181 | 1.124        | 0.199   | 100                             |
| MA182 | 1.129        | 0.123   | 250                             |
| MA183 | 1.021        | 0.054*  | 70                              |
| MA184 | 0.955        | 0.146   | 100                             |
| MA185 | 0.835        | 0.015*  | 50                              |
| MA187 | 0.525        | 0.315   | 100                             |
| MA188 | 0.396        | 0.496   | 100                             |
| MA190 | 0.612        | 0.050*  | 200                             |
| MA191 | 1.253        | 0.043*  | 150                             |
| MA192 | 0.576        | 0.391   | 80                              |
| MA194 | 0.642        | 0.011*  | N                               |

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|       |        |         |     |
|-------|--------|---------|-----|
| MA196 | 2.134  | 0.194   | 100 |
| MA198 | -0.275 | 0.633   | 150 |
| MA199 | 0.590  | 0.012*  | 300 |
| MA27  | 1.145  | 0.094   | 60  |
| MA50  | 1.544  | 0.054*  | N   |
| MA57  | 1.000  | 0.054*  | 80  |
| MA58  | 0.954  | 0.555   | 70  |
| MA61  | 0.919  | 0.013*  | 30  |
| MA62  | 0.461  | 0.620   | 100 |
| MA67  | 0.598  | 0.164   | 50  |
| MA82  | 0.473  | 0.027*  | 50  |
| MA96  | 0.598  | <0.001* | 100 |

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Figure 1. Diagram of a release transect. X's indicate release points. Individuals were released on the edge, 5 and 10 meters from the edge into the forest, and 5 and 10 meters from the edge into the field or early successional forest, indicated by '-'.  


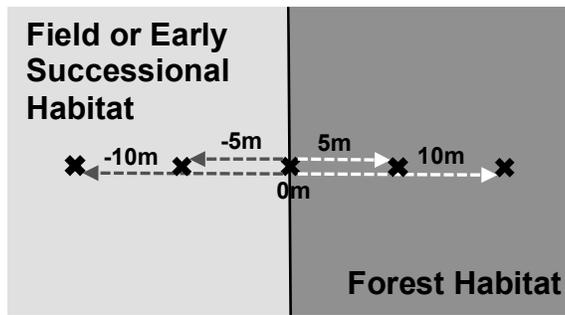


Figure 2. Histogram of mean step sizes (cm) for each salamander moving through field, forest, and early successional habitat. Notice that the frequency distribution of step sizes for salamanders released within the field habitat is skewed toward longer step sizes than salamanders released in forest and early successional habitat.

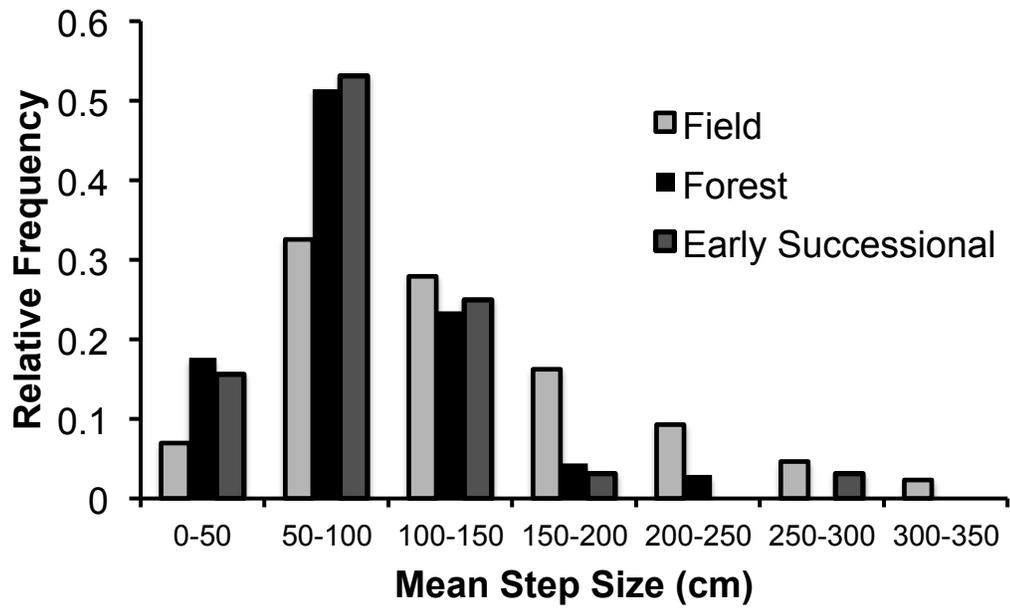
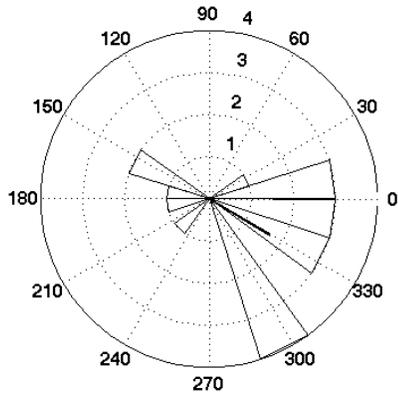
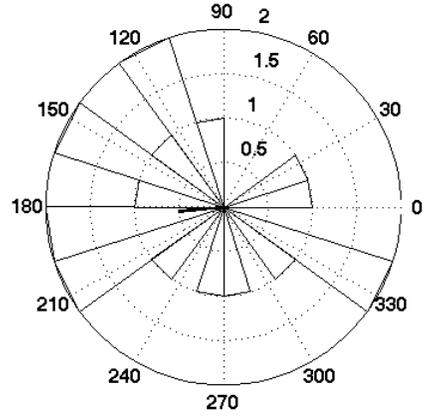


Figure 3. Orientation of juveniles released varying distances from forest/field edges (hard). Bold solid lines indicate mean direction and the length of the line corresponds to mean vector length. Length of wedges indicates percentage of animals whose orientation fell within the designated 20-degree bin. Orientations have been standardized so that 0 degrees refers to the direction of the forest, perpendicular to the edge.

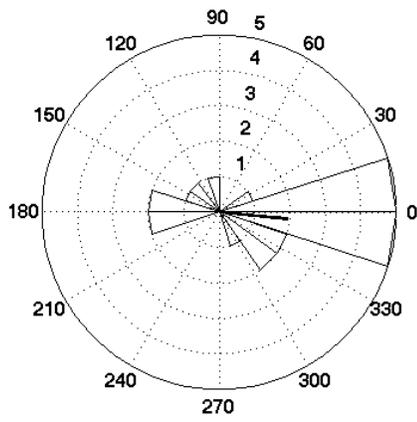
a) 10 m - field



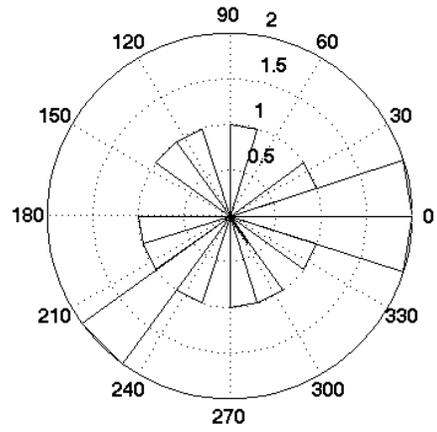
d) 5 m - forest



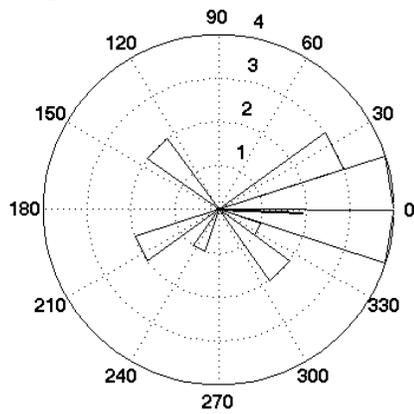
b) 5 m - field



e) 10 m - forest

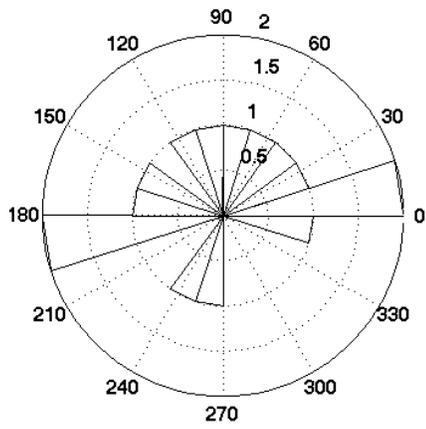


c) Edge

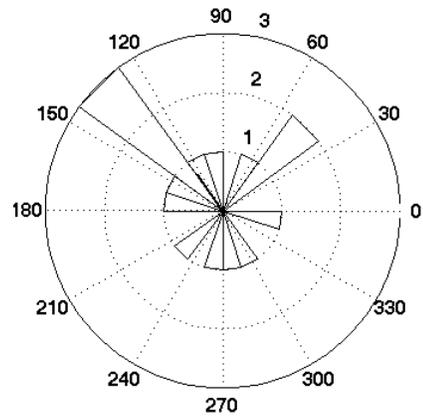


Figures 4. Orientation of juveniles released varying distances from forest/early successional edges (soft). Bold solid lines indicate mean direction and the length of the line in relation to the radius of the circle corresponds to mean vector length ( $\rho$ ). Length of wedges indicates number of animals whose orientation fell within the designated 20-degree bin. Orientations have been standardized so that 0 degrees refers to the direction of the forest, perpendicular to the edge.

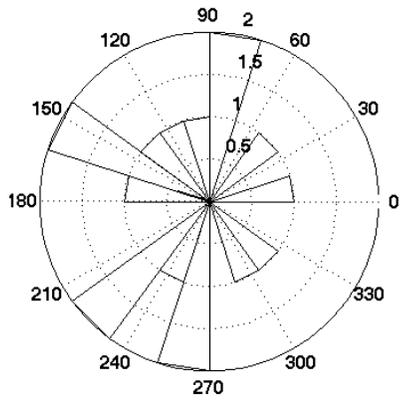
a) 10 m – early successional



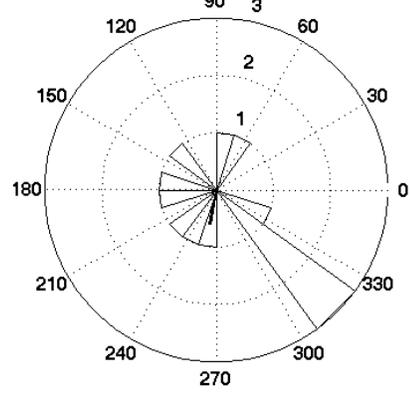
d) 5 m - forest



b) 5 m – early successional



e) 10 m - forest



c) Edge

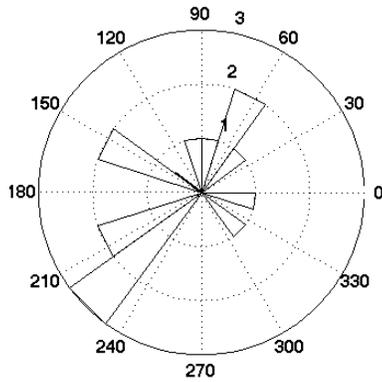
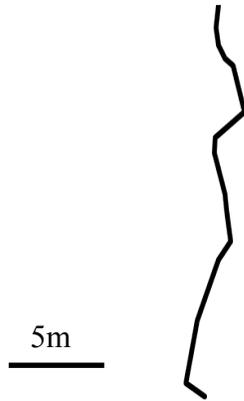


Figure 5. Example of (a) movement path that showed no evidence of directed movement at any spatial scale and (b) graph showing  $CRW_{Diff}$  at different spatial scales (cm). This path was not significantly different than a CRW:  $CRW_{Diff} = 0.555$ ,  $P=0.297$ , mean step size=1.43m,  $k=0.89$ .

a)



b)

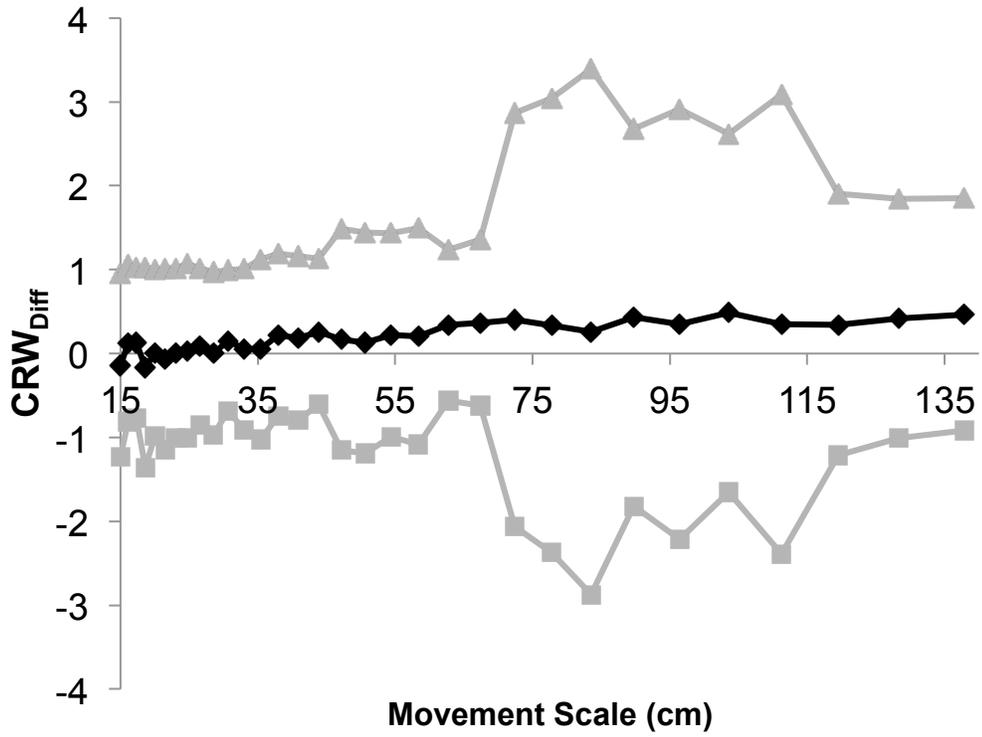
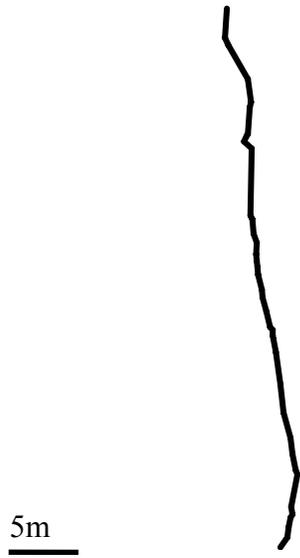
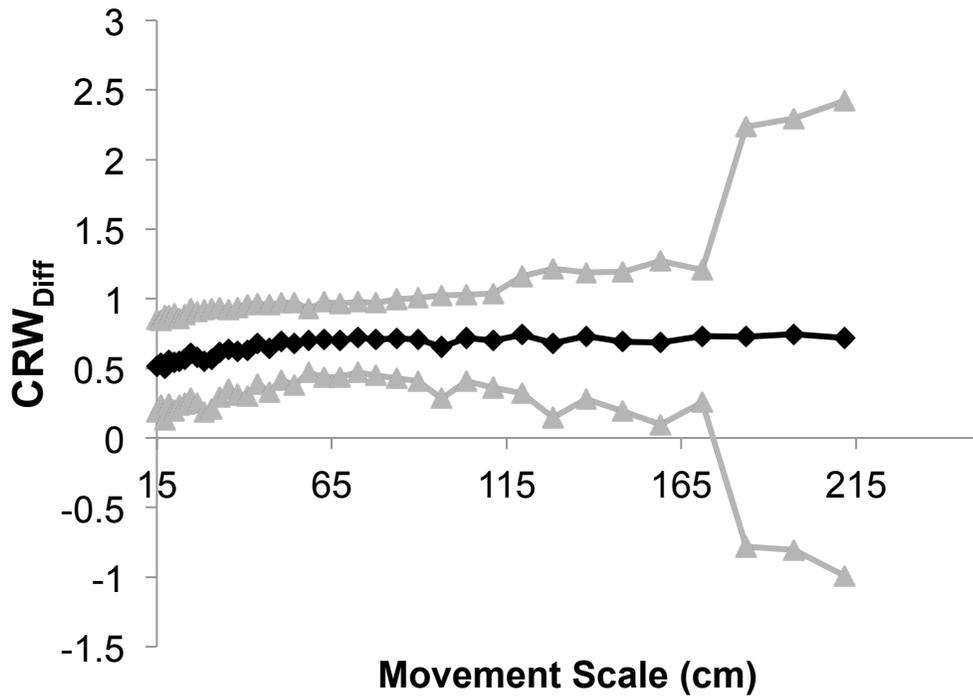


Figure 6. Example of (a) movement path that showed evidence of directed movement at scales between 40cm and 190cm and (b) graph showing  $CRW_{Diff}$  at different spatial scales (cm). This path moved significantly farther than would be predicted by a CRW model:  $CRW_{Diff} = 0.612$ ,  $P=0.05$ , mean step size=1.44 m,  $k=0.86$ .

a)



b)



## CHAPTER 3

### IMPORTANCE OF MOVEMENT BIAS IN PREDICTING THE EFFECTS OF HABITAT LOSS ON THE SURVIVAL OF JUVENILE POND- BREEDING AMPHIBIANS

#### ABSTRACT

Factors affecting the movement behavior of pond-breeding amphibians making initial movements in terrestrial habitat are currently poorly understood. Behavioral decisions of juvenile pond-breeding amphibians have a large impact on survival and may influence population persistence both at the local and regional levels. Habitat fragmentation affects the survival consequences of movement behavior, thus increasing the need to identify and understand both the external and internal factors affecting the movement decisions of juveniles. We performed experimental releases of juvenile spotted salamanders (*Ambystoma maculatum*) 5, 10, 20, and 35 m from forest and investigated factors affecting the likelihood of individuals reaching the forest. We measured the initial orientation of juveniles using fluorescent powder tracking, and we recaptured individuals at the forest using drift fences. Orientation data was used to create a simple movement model of spotted salamander initial movement away from a natal pond. Juveniles significantly oriented toward the forest at 5 and 10 m, and both initial movement bearing and size of the salamander influenced success at reaching the forest. The inclusion of

movement bias toward habitat in movement models significantly affected the probability of juveniles finding habitat and the efficacy of different search strategies. These results illustrate that understanding factors affecting fine-scale movement of animals at critical life stages can improve our ability to predict the effects of habitat loss to species.

## INTRODUCTION

Habitat loss and fragmentation affect the persistence and spatial dynamics of species in part by influencing the likelihood of individuals locating suitable habitat (Olden et al. 2004, Heinz and Strand 2006). Animals searching for resources are limited by both motion and sensory capacity (Barbraud et al. 2003, Nathan et al. 2008, Rémy et al. 2011) and employ strategies to maximize the likelihood of finding suitable habitat (Zollner and Lima 1997, Conradt et al. 2003, Delgado et al. 2009). The efficiency of search strategies is dependent on the spatio-temporal structure of resources (Clobert et al. 2001, Kinezaki et al. 2010). Changes in the configuration of habitat patches can vastly affect the survival consequences of movement behavior, thus influencing metapopulation dynamics, population persistence, and adaptation (Alderman et al. 2005, Fahrig 2007, Knowlton and Graham 2010).

Models designed to predict the effects of habitat or landscape configuration on species persistence and spatial dynamics often make simplifying assumptions about animal movement that can have significant impacts on model outcomes

(Heinz et al. 2006, Clobert et al. 2009, Hawkes 2009). An understanding of the movement mechanisms important to model outcomes could be critical for evaluating the effectiveness of management efforts or predicting the impacts of habitat alteration. For example, Pe'er and Kramer-Schadt (2008) found that incorporating perceptual range of forest into connectivity models for the Eurasian lynx (*Lynx lynx*) doubled the predicted likelihood of immigration success. Numerous other studies have shown that basic knowledge about species' movement responses to habitat can lead to a better understanding of the effectiveness of management strategies aimed at influencing population connectivity (Lima and Zollner 1996, Revilla and Wiegand 2008), such as corridors (Haddad 1999), stepping stones (Kramer-Schadt et al. 2011), and wildlife crossings (Woltz et al. 2008, Pagnucco et al. 2011).

Although pond-breeding amphibians are integral components of a range of ecosystems, relatively little is known about their movement and sensory capacities, especially during initial emigration out of natal ponds. Movement behavior during dispersal is particularly critical to population processes over a range of spatial and temporal scales (Clobert et al. 2001, Delgado and Penteriani 2008, Clobert et al. 2009). Dispersal affects local population dynamics by influencing rates of immigration and emigration (Bell et al. 2005, Gamble et al. 2007), metapopulation dynamics through probability of recolonization and rescue (Brachet et al. 1999, Heino and Hanski 2001, Heinz et al. 2006, Clobert et al. 2009), and evolutionary processes by dictating the degree and directionality of gene flow and adaptation

(Westley 2011). Initial dispersal of juvenile pond-breeding amphibians away from natal wetlands represents a substantial ecological bottleneck, with as few as 17% of juvenile spotted salamanders (*Ambystoma maculatum*) surviving one year after metamorphosis (Rothermel and Semlitsch 2002). Because juveniles are often the primary long-distance dispersers in amphibian populations (Gill 1978, Berven and Grudzien 1990, Gamble et al. 2007), understanding juvenile movement behavior is the first step toward understanding metapopulation dynamics and the mechanisms by which population persistence is affected by habitat loss and fragmentation.

Spotted salamanders (*Ambystoma maculatum*) are forest-dependent, pond-breeding amphibians that make initial movements out of natal wetlands after metamorphosis on the scale of 20-50 m (Osbourn 2012). Because juvenile spotted salamanders have relatively low vagility and specific habitat requirements, they may be highly susceptible to the arrangement of habitat surrounding natal ponds. How animals alter movement based on habitat and risk is an integral component of their search strategies, along with factors such as the degree of boundary behavior, perceptual range, and movement path tortuosity (Cantrell et al. 2006, Romero et al. 2009, Mueller et al. 2011). For example, perceptual ability and responsiveness to habitat affect both the likelihood of an animal locating suitable habitat and the amount of time spent searching for habitat (Olden et al. 2004). The addition of perceptual range and habitat responsiveness into movement models may greatly affect their predictive capacity and their success at guiding management efforts (Pe'er and Kramer-Schadt 2008, Prevedello et al. 2010). By explicitly identifying

the effect of distance to habitat on the movement of juvenile amphibians, we can better predict the extent to which amphibians can behaviorally mitigate the effects of habitat loss (Fischer and Lindenmayer 2007).

To determine the degree to which emigrating salamanders bias their movements in response to habitat, we performed experimental releases of recently-metamorphosed juvenile spotted salamanders at different distances from forest-field edges. We monitored the initial movement bearings of juvenile salamanders using fluorescent powder tracking. Using mark-recapture, we determined the extent to which initial bearing, size, and distance to forest affected their success at reaching the forest. We used movement data to develop a simple movement model of juvenile emigration from natal wetlands to investigate the effects of movement behavior on the probability of juvenile salamanders locating suitable habitat under different assumptions about the distance of the natal pond from a forest edge.

## METHODS

### *Experimental Set-Up*

We conducted this study along replicate forest-pasture edges at the Mark Twain National Forest in Boone County, MO, USA. The pastures were characterized by Big Bluestem (*Andropogon gerardii*) and fescue (*Festuca sp.*), and the forests were dominated by mature, second-growth oak (*Quercus sp.*) and hickory (*Carya sp.*) in the overstory and sugar maple (*Acer saccharum*) in the understory. We conducted this study at two separate locations along forest edges

facing different cardinal directions (east, north, and west facing edges). At each of the two sites, we released salamanders 5 m, 10 m, 20 m, and 35 m from forest edges (Fig. 1), and we released salamanders at five release locations at each distance from the forest edge (20 total release locations). We installed plastic silt fencing along the edge of the forest, and installed pitfall traps (4 L metal cans) every 5 m along the edge of the silt fencing. Free-ranging animals encounter the fence, move along the edge of the fence, and are captured in the pitfall traps along the fence edge (Gibbons and Semlitsch 1982). The pitfall traps contained a damp sponge to prevent desiccation of animals caught in the traps.

### ***Capture and Handling***

We collected late-stage spotted salamander larvae from an ephemeral pond < 500 m from the release locations. We raised salamander larvae in outdoor cattle tanks at a nearby University of Missouri research facility in Boone County, MO, USA. We checked cattle tanks nightly for metamorphosed salamanders. Recently-metamorphosed salamanders were housed in containers with damp sphagnum moss in an indoor laboratory at the University of Missouri with controlled temperature (22°C). Animals used in the experiment were released within two weeks of their metamorphosis. We individually-marked each salamander using toe clipping, and we determined the snout-to-vent length of each salamander prior to release.

We released a maximum of 50 salamanders in a night, directly after sunset. We released salamanders within 12 hours of a rain event, when the ground was wet and relative humidity was high. We did not release salamanders during a rain event

to prevent loss of the powder trail. Previous studies have found that salamanders readily disperse from wetlands under these conditions (Rothermel 2004, Vasconcelos and Calhoun 2004, Todd and Winne 2006). We randomly assigned salamanders to release sites and locations on the night of release. Salamanders were placed underneath plastic cups that acted as release enclosures for approximately 20 minutes to allow animals to acclimate to the environment and to reduce the likelihood of observing artificial release responses (Turchin 1991). We lifted the release chamber from a distance of at least 3 m to minimize the influence of observer orientation in salamander movement decisions.

We released a total of 388 salamanders from 26 June to 3 August 2010. We used fluorescent powder (DayGlo Color Corp, Cleveland, OH) to track the continuous movement of salamanders after release. Prior to release, we covered the posterior half of salamanders with pink, orange, or green fluorescent pigment. Color of pigment was alternated among release locations to reduce the likelihood of two identically-colored paths intersecting. Fluorescent powder has been used to track short-term movements of small amphibians (Graeter et al. 2008, Roberts and Liebgold 2008) and does not affect survival or cutaneous respiration in newts and ambystomatid salamanders (Orlofske et al. 2009, Roe and Grayson 2009). Therefore, we do not think it likely that powder affected the movement behavior of animals in this study.

We returned 24 hours following release and followed the powder trails deposited by salamanders for the initial 2-3 m total distance using ultraviolet lights

(Arachnid A14, Blacklight.com, Volo, IL). We determined the net bearing of the powder trail using a compass. We checked the pitfall traps every morning from 26 June to 31 October 2010.

### ***Data Analysis***

#### *Orientation*

We used circular statistics to test whether salamanders significantly oriented movement according to the bearing of the forest perpendicular to the edge closest to the salamander release location (Batschelet 1981, Pe'er and Kramer-Schadt 2008). For salamanders released at locations equidistant from the two forest edges, we used the mean of the two bearings as the target bearing. We used Rayleigh's test to determine whether orientation significantly deviated from a random distribution for each release distance. We used the V-test to determine whether salamander orientation was significantly different from a hypothesized mean angle (bearing towards the forest, perpendicular to the edge). We used MatLab (MATLAB version 7.10.0 Natick, MA: The Mathworks, Inc., 2010) to graph the data and determine whether data adhered to statistical assumptions. The release distances at which salamanders significantly oriented movement toward the forest were considered to be within the salamander's perceptual range of the forest, while release distances at which salamander movement bearings were random were considered to be outside of the perceptual range of the forest. We directly compared the distributions of animals released within and outside of the perceptual range of

the forest to determine whether orientation distributions were significantly different using the Watson-Williams test (Batschelet 1981).

#### *Recapture at Forest Edge*

We used simple logistic regression to determine the probability that individuals were recaptured at the forest edge based on predictor variables (Table 1). We used an information-theoretic approach to investigate *a priori* models predicting the factors affecting salamanders successfully being recaptured at the forest edge. We compared models using Akaike's information criterion (AIC), adjusted for small sample size (AICc) to evaluate relative support for each model and to identify the most parsimonious model for the data (Burnham & Anderson 2002). The model with the lowest AICc value and the highest weight was selected as the best model for the data.

We evaluated seven models in this study (Table 2), including a null model (intercept-only). Each model except the null model included the WEATHER predictor (Table 1), which was a set of the three predictor variables: 1) maximum temperature one day after release, 2) total rainfall 24 hrs before and after release, and 3) the interaction of temperature and rainfall. Numerous studies have concluded that amphibian movement is highly dependent on weather variables such as temperature and rainfall (Vasconcelos and Calhoun 2004, Todd and Winne 2006). We therefore decided *a priori* to include these predictors in each model. CPROB refers to the probability of capture in terms of the percentage of area

around the release location that was encompassed by fences and was also incorporated into all models following Rothermel (2004).

We were principally interested in the effects of initial movement bearing and release distance on probability of capture at the forest edge. We used the orientation data gathered through powder tracking to assess two primary types of models: one which included Euclidean distance (DIST) as an explanatory variable and one which included the coarser-scale explanatory variable of release within or outside of an hypothesized perceptual range (PERCEP) as an explanatory variable. We defined initial bearing (BRNG) as whether the initial orientation of the salamander was toward or away from the forest closest to the salamander release location. We used R to run the logistic regression analysis (R Development Team 2012).

### ***Model Development***

We analyzed the strength of salamander orientation (mean resultant length) at different distances from the forest in this study. We additionally analyzed data on the strength of orientation in a separate study on juvenile spotted salamander orientation toward forest (Chapter 2, Pittman 2013). In Pittman (2013), the authors tracked the continuous movements of juvenile spotted salamanders on and at different distances from forest/field edges (Chapter 2). We used the strength of orientation (mean resultant length) at each edge as a replicate, and we calculated the mean and 95% confidence intervals (CI) of the mean resultant length of bearings at 5 and 10 m in the current study and 0, 5, and 10 m in the separate study

(Pittman 2013). We used these data to describe a linear relationship between distance from forest and movement bias towards forest. We additionally identified linear relationships for the upper and lower 95% confidence intervals (CI) for each distance from forest. We developed a simple movement model of salamanders emigrating from natal ponds. Salamander movement was modeled as a correlated random walk (CRW) with a wrapped Cauchy distribution of turning angles (Zollner and Lima 1999) and constant step size (1 m, Appendix C). The parameter  $r$  described the kurtosis of the distributions from which turning angles were drawn. The  $r$  parameter varied between 0 and 1, with 1 being a completely straight movement path and 0 being a uniform distribution of turning angles. We used results from Pittman (2013) to parameterize the turning angle distribution and step size of the CRW (Appendix C). For identifying the effects of path straightness on probability of reaching the forest, we used  $r$  values of 0.5, 0.7, and 0.97 based on a representative range of values observed in Pittman (2013; Chapter 2).

We were specifically interested in predicting the influence of movement bias on probability of reaching the forest edge. Therefore, we evaluated two types of models, one which included a bias parameter ('informed'), and the other which did not include a bias parameter ('blind'). The bias parameter was built into the model as the degree to which salamanders chose a movement bearing according to the bearing of the forest. The bearing that the animal chose at each time step was a weighted average of the bearing of the previous step (plus random error drawn

from the wrapped Cauchy distribution) and the bearing toward the forest, following:

$$\varphi_t = (1 - \beta)(\varphi_{t-1} + \gamma_t) + \beta\delta_t$$

Where  $\varphi_t$  is the bearing at time  $t$ ,  $\beta$  is the strength of bias based on distance from forest,  $\gamma_t$  is the turning angle drawn from the wrapped Cauchy distribution at time  $t$ , and  $\delta_t$  is the bearing toward the forest at time  $t$  (Crone and Schultz 2008, Bartoń et al. 2009).

We evaluated the effects of assumptions about movement bias and path straightness on predictions of the likelihood of salamanders reaching forest habitat. Salamanders in our simulations moved a fixed distance of 100 m total, with 1 m step sizes (Osbourn 2012, Pittman 2013). The total distance moved was the greatest net distance that a salamander moved in a single night in Osbourn (2012). Salamanders were given a random initial orientation drawn from a uniform distribution of initial bearings (1-360 degrees) for the first step away from the natal wetland. We recorded the location of each salamander at each time step through the 100 m path. The natal wetland was located a specific distance from a straight line that represented the ‘forest.’ Salamanders that crossed into forest habitat at any point along the 100 m path were considered ‘successful’ in reaching the forest. We ran the model 100 times for each set of movement parameters and distance to forest (0-30 m, at 1 m intervals). We present the mean number of salamanders that

successfully reached the forest in the 100 simulations. Inferential statistics were not used to evaluate model outcomes because sample sizes were large enough that most observed differences in outcomes were statistically significant (Zollner and Lima 1999).

#### *Model validation*

We used independently-collected data of juvenile salamander captures to determine whether our movement model generated realistic salamander movement. Rothermel (2004) performed an experiment in which spotted salamanders emigrated from experimental pools different distances from forest edges (5, 10, 25, and 50 m) and were captured along the forest-field edge. We used Rothermel's capture data as a pattern with which to compare the informed and blind movement models. We simulated a landscape with configuration of edges and natal ponds similar to those in Rothermel (2004), where two edges intersected at 90 degrees and release locations were equidistant from the two edges. We used an  $r$ -value of 0.9 and mean step size of 1.2 m as CRW movement parameters based on salamander movement in the field in Pittman (2013), and salamanders moved a total of 100 m during the simulations. If a salamander crossed into forest habitat at any point along the 100-m movement path, we considered this successful emigration. We compared the percent decrease in the number of animals reaching the forest at each pond distance between Rothermel (2004), a blind movement model, an informed movement model, and upper and lower 95% CI movement models. We did not use pure

number of captures from Rothermel (2004) because drift fences did not have perfect capture success in her study.

## RESULTS

### *Orientation*

We found that salamanders exhibited target-oriented movement behavior at release distances of 5 m (V-test:  $P < 0.001$ , mean resultant length: 0.25,  $N = 88$ ) and 10 m from forest habitat (V-test:  $P = 0.05$ , mean resultant length: 0.14,  $N = 97$ ), but salamanders oriented randomly at 20 m (V-test:  $P = 0.96$ , mean resultant length: 0.022,  $N = 92$ ) and 35 m (V-test:  $P = 0.75$ , mean resultant length: 0.062,  $N = 74$ ) from the forest edge (Fig. 2). We designated animals released at 5 and 10 m distances from the forest to be ‘within’ perceptual range and those released at 20 and 35 m to be ‘outside’ of perceptual range of the forest. We found that the distribution of bearings of animals released within and outside of perceptual ranges were significantly different (Watson-Williams,  $F = 4.49$ ,  $P = 0.0348$ ).

### *Capture at Fence*

Of the 388 salamanders released in this study, 107 were recaptured at the forest fences. The model that best predicted capture at forest edge included perceptual range, size of salamander, and initial bearing ( $w_i=0.885$ ; Table 2). We calculated parameter estimates and odds ratios for each explanatory variable in the best-supported model (Table 3). We found that animals were 1.6 times more likely to be captured at the forest edge if they were released within their perceptual range

of the forest and were 2.5 times more likely to be captured at the forest edge if their initial movement bearing was in the direction of the nearest forest edge. For every 1 mm increase in SVL, the salamander was 1.2 times more likely to be captured at the fence. Therefore, larger animals were more likely to be captured than smaller animals. Size of the animal could affect either physiological ability to move or motivation to make directed movement in suboptimal habitat. We found that size of salamander was negatively correlated with the deviation between initial movement bearing and bearing toward the location of capture at fence (Pearson  $R = -0.60$ ,  $P = 0.048$ ), suggesting that body size may affect search strategy.

### ***Movement Model***

Using the mean resultant lengths from this study along with those from Pittman (2013), we identified a relationship between distance from forest and movement bias toward habitat, defined as:

$$\beta = -0.032 * D + 0.5 \quad \text{Informed Model}$$

where  $D$  is distance from forest (Fig. 3). We additionally computed the upper and lower 95% CIs around each mean and generated two upper and lower CI bias relationships (Fig. 3), defined as:

$$\beta = -0.044 * D + 0.8 \quad \text{Upper 95\% CI}$$

$$\beta = -0.019 * D + 0.2 \quad \text{Lower 95\% CI}$$

We found that the informed model predicted the capture results of Rothermel (2004) as well as a blind movement model (Fig. 4).

The incorporation of bias into models of salamander movement affected the predicted probability of successful dispersal. The informed and blind movement models yielded a maximum of 46% difference in probability of reaching forest (Fig. 5). In the blind movement models, optimal path straightness values were dependent on distance of natal pond from the forest (Fig. 6). Overall, the straightest movement paths yielded the highest probability of salamanders reaching forest both in the blind and informed movement models. In the informed movement model, straighter movement paths always generated higher probabilities of reaching forest (Fig. 6A). In the blind movement model, straighter paths were suboptimal when the natal ponds were positioned close to the forest (Fig. 6B).

## DISCUSSION

These results demonstrate that habitat and internal state play a critical role in the movement behavior of juvenile amphibians, with direct implications for amphibian survival and dispersion in heterogeneous landscapes. This study found that juvenile spotted salamanders moved towards forest habitat from distances of up to 10 m, but that individuals released 20 m from forest either could not detect or were unmotivated to make directed movements toward forest. The relatively small perceptual range documented in this study combined with low vagility suggests that juvenile pond-breeding salamanders have limited ability to behaviorally mitigate the effects of habitat loss surrounding natal ponds.

### ***Orientation***

While this study found strong evidence for spotted salamander orientation towards forest, previous research on juvenile spotted salamander orientation in relation to forest has yielded conflicting results (Rothermel 2004, Rittenhouse and Semlitsch 2006, Walston and Mullin 2008). For example, Rothermel (2004) captured juvenile spotted salamanders emigrating from natal ponds in fields and did not find that juveniles oriented bearings toward forests. Rittenhouse and Semlitsch (2006) found that juveniles emigrated from a natal pond positioned on a forest-field edge irrespective of the position of the forest, but juveniles released in the field oriented back toward the forest nonrandomly. Walston and Mullin (2008) found that juvenile spotted salamanders initially moved toward the forest as they were exiting natal ponds. The seemingly contradictory nature of these studies may be partially explained by distinguishing the goals of different behavioral modes during initial movement out of wetlands (Osbourn 2012). Research suggests that juveniles experience high levels of predation and competition immediately upon exiting natal ponds (Jenkins, McGarigal & Timm 2006; Patrick, Calhoun & Hunter Jr 2007). Species with limited vagility (such as salamanders) may therefore move linearly away from a natal wetland irrespective of terrestrial habitat conditions for the first few meters post-emergence (Rothermel 2004) and change movement bearings toward habitat later in the movement path (Rittenhouse and Semlitsch 2006). For example, Jenkins et al (2006) found that juvenile salamanders initially departing wetlands did so irrespective of terrestrial habitat quality, but shifted bearings

toward higher quality habitat later in the movement path. In this study, salamanders were released by the researchers and were not exiting natal ponds; therefore the natal pond did not act as a negative cue for salamander movement, and individuals were therefore more likely to move towards quality habitat.

### ***Success at Reaching Forest***

Our mark-recapture study found that a combination of external and internal factors affected salamander success at reaching the forest. The primary external factor tested was distance from forest. Release within or outside of the salamander's perceptual range was a better predictor of reaching forest than was Euclidean distance, suggesting that movement models based on a species-specific view of the landscape may increase the ability to estimate functional connectivity of amphibians in fragmented landscapes (Fischer and Lindenmayer 2007, Laurance 2008). Because the juvenile life stage is important for both local population dynamics and long-distance dispersal, fine-scale movement and risk-taking strategies of juveniles may have a large impact on the outcomes of predictive models.

The internal factors tested in this study were initial movement bearing (motivation) and body size (physiological condition). Juveniles that initially moved in the direction of the forest were 2.5 times more likely to reach the forest than juveniles that initially moved away from the forest. Because initial movement bearing was a strong predictor of success at reaching forest, juvenile spotted salamanders likely maintain relatively straight movement paths, which is consistent

with previous studies on fine-scale spotted salamander movement (Pittman 2013) and mark-recapture studies finding a low incidence of reversals between habitats (Osbourn 2012). Size of salamander was also a significant predictor of successful dispersal, with larger animals more likely to reach the forest than smaller animals. Size of salamander likely affects the physiological condition of the organism in terms level of energy reserves and rate of desiccation (Scott et al. 2007, Tingley and Shine 2011). However, the mechanism underlying the influence of size on movement success warrants further investigation. Larger animals may have been more successful at reaching forest either as a result of better physiological condition allowing animals to travel farther and faster (Claussen et al. 2000), or by influencing the search strategies employed by animals during movement. Our study found a slight but significant negative relationship between size of salamander and response angle (difference between initial movement bearing and bearing to capture location) among those captured at the forest edge, indicating that smaller animals moved more tortuously than larger animals. This result indicates that the size of the animal may affect actual movement strategy. Smaller animals may have attempted to find habitat within a small radius in order to preserve energy, and therefore these animals may have responded to habitat at a finer scale than animals making longer-distance movements e.g. (Osbourn 2012). The influence of body size on risk-taking strategies are well documented in other species (Rémy et al. 2011, Hemptinne et al. 2012) and should be considered in relation to pond-breeding amphibian dispersal decisions.

### *Movement Model*

Results from our movement model highlight the importance of assumptions about movement behavior to predictions of juvenile survival and dispersion in fragmented landscapes. Assumptions about turning angle correlation and degree of bias towards the forest greatly affected the likelihood of individuals reaching the forest even at small spatial scales. The inclusion of bias in the movement model affected the influence of path straightness on probability of reaching the forest. Straighter movement paths always increased the probability of locating habitat if the salamander could perceive the forest. However, straight movement paths were suboptimal at close distances if the animals could not perceive forest habitat. The benefits of the informed strategy decreased the farther the forest was positioned outside of the animal's perceptual range. The benefits of the informed strategy were also dependent on path straightness. For example, an animal that moved tortuously garnered the largest benefit to informed movement versus blind movement at spatial scales around the distance of the perceptual range, but the benefits to informed movement decreased precipitously outside of the perceptual range. Straighter movement paths yielded lower peak benefits to the informed strategy, but moderate benefits to informed movement were observed for wetlands positioned as far as 30 m from the forest (Fig. 6).

There is likely considerable variation among individuals in movement tendencies and responsiveness to habitat during dispersal (Clobert et al. 2009, Chaput-Bardy et al. 2010). Habitat fragmentation truncates the breadth of

behavioral variation leading to successfully finding habitat, and alters the risks and benefits associated with movement parameters (Fahrig 2007). Our movement model illustrates how behavioral decisions during movement may contribute to salamander survival, especially when habitat is highly clumped or spatially separated from the natal wetland. Salamanders that are highly responsive (high movement bias) to habitat may be more likely to survive in the short term by finding habitat quickly upon exiting natal ponds. However, longer-term persistence of amphibian populations requires long-distance dispersers that would likely exhibit high boldness and low responsiveness to habitat (Sih et al. 2004, Cote et al. 2010) and whose movement may approximate the blind movement model. Habitat loss and fragmentation increase the amount of time that individuals spend in hostile habitat and therefore increase the risk to blind dispersal strategies. Animals with low vagility (such as spotted salamanders) may therefore display significant negative responses to habitat loss at both local and landscape scales in part by individuals employing suboptimal movement behavior.

### ***Conclusions***

A combination of internal and external factors influenced the movement decisions of juvenile amphibians. The movement model indicated that assumptions about movement behavior impacted predictions of successful emigration even at small spatial scales. Because population persistence is sensitive to assumptions about juvenile survival, models that oversimplify behavior may yield inaccurate estimates of population persistence. A basic understanding of fine-scale movement

behavior during the juvenile dispersal phase will increase our ability to predict the consequences of habitat fragmentation to amphibian populations.

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Table 1. Definition and description of covariates used in the logistic regression analysis.

| Variable | Description  |
|----------|--|
| Percep   | Release location in relation to perceptual range: whether an animal was released at 5 or 10 m (within) or 20 or 35 m (outside) from forest |
| Distance | Straight-line distance (m) between release location and nearest forest edge  |
| SVL      | Snout to vent length (mm) of salamanders at time of release  |
| Weather  | Total rainfall, maximum temperature 24 hours before and after release, and interaction   |
| Brng     | Initial bearing: to forest vs away from forest   |

Table 2. Results of simple logistic regression. Percep was a better predictor of capture at fence than Distance.

| Model                           | No.<br>parameters | AIC    | AICc  | Akaike<br>weight |
|---------------------------------|-------------------|--------|-------|------------------|
| Percep+Cprob+Weather+SVL+Brng   | 7                 | 395.5  | 395.9 | 0.885            |
| Distance+Cprob+Weather+SVL+Brng | 7                 | 399.7  | 400.5 | 0.108            |
| PercepRange+Cprob+SVL+Weather   | 6                 | 406.38 | 406.7 | 0.004            |
| Distance+Cprob+SVL+Weather      | 6                 | 407.82 | 408.2 | 0.002            |
| PercepRange+Cprob+Weather       | 5                 | 414.79 | 415.0 | 0.000            |
| Distance+Cprob+Weather          | 5                 | 415.64 | 415.9 | 0.000            |
| Null                            | 1                 | 431    | 431.0 | 0.000            |

Table 3. Parameter estimates and odds ratio for each parameter in the best-fit logistic regression model.

| Parameter | Estimate | Odds ratio | 95% Confidence |      |
|-----------|----------|------------|----------------|------|
| Percep    | 0.48     | 1.60       | 1.00           | 2.17 |
| Cprob     | -0.73    | 0.52       | 0.27           | 0.82 |
| Prcp      | 0.91     | 2.47       | 1.38           | 5.37 |
| Temp      | 0.99     | 2.71       | 1.37           | 4.52 |
| SVL       | 0.18     | 1.20       | 1.07           | 1.34 |
| Bearing   | 0.92     | 2.51       | 1.51           | 4.24 |
| Temp*Prcp | -0.03    | 0.97       | 0.95           | 0.99 |

Figure 1. Diagram of half of the release locations along the forest-field edge.  
Release locations are replicated for the other half of the diagram, yielding 20  
release locations per edge.

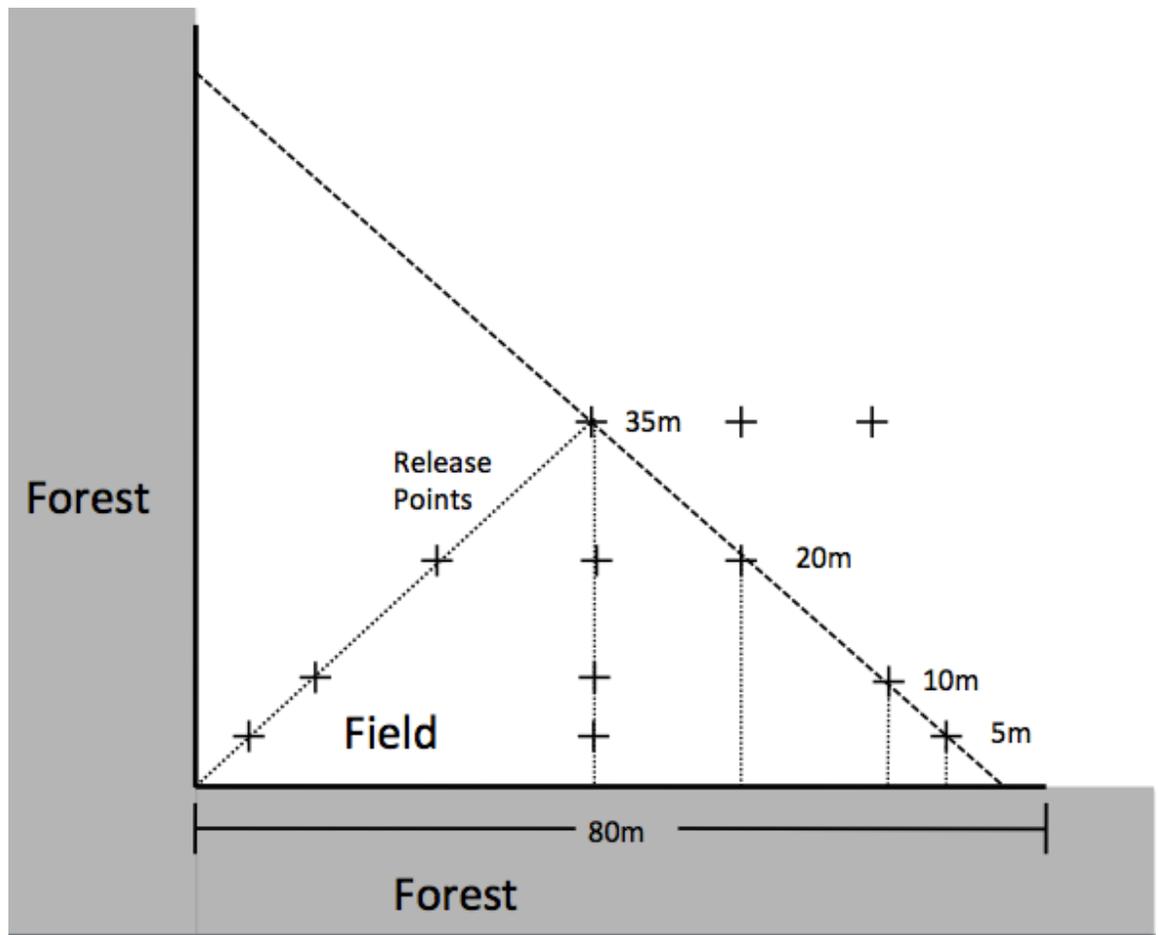
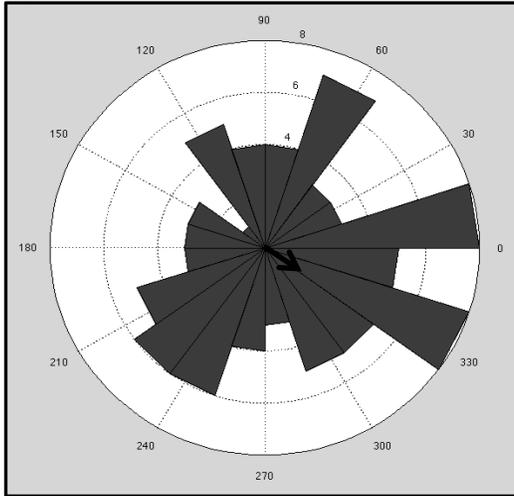
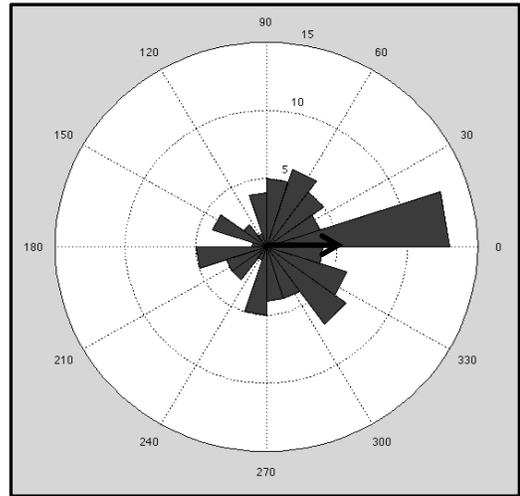


Figure 2. Distribution of initial bearings in relation to the forest for salamanders released 5 m (B), 10 m (A), 20 m (D), and 35 m (C) away from the forest. In each graph, 0 degrees corresponds to the direction of the forest. Black arrows correspond to mean resultant vectors of the distribution. Length of vector in proportion to radius of the circle corresponds to the strength of orientation and the direction of the vector corresponds to mean direction of movement.

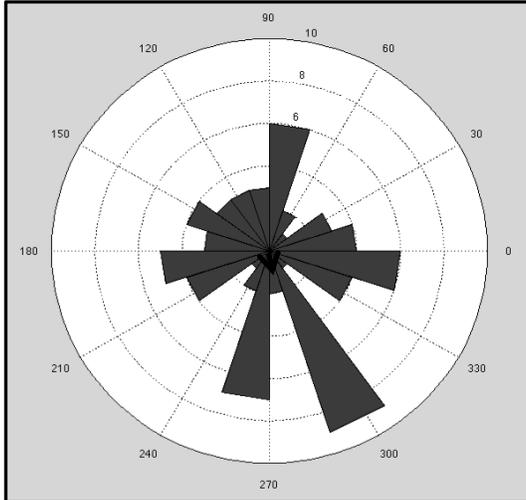
A)



B)



C)



D)

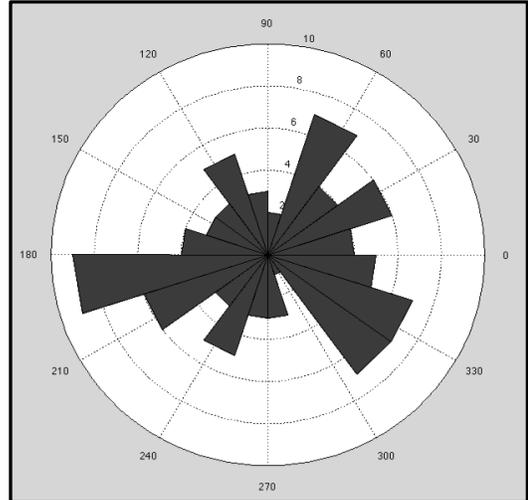


Figure 3. Relationship between the strength of orientation toward forest and distance from forest based on the current study and Pittman (2013). We used the relationship between distance from forest and strength of orientation to simulate juvenile spotted salamanders moving out of wetlands.

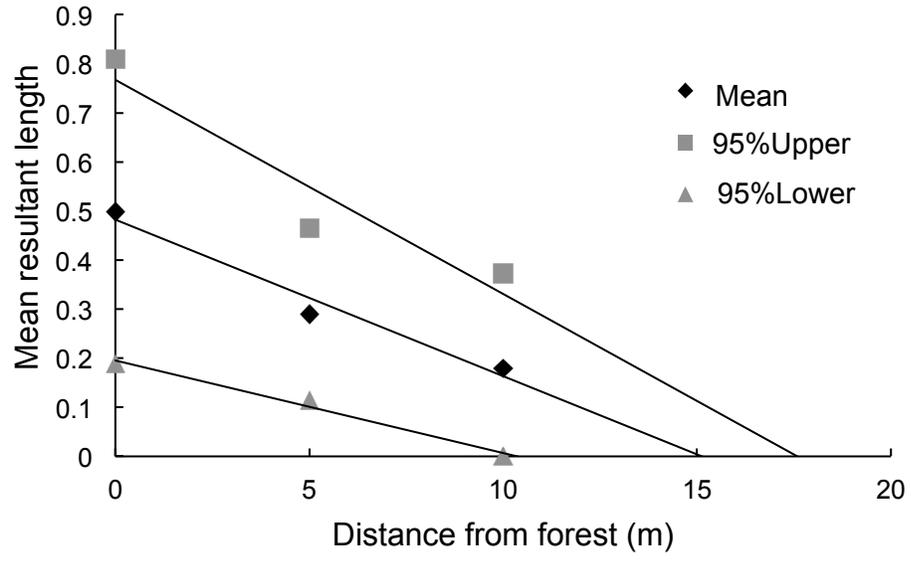


Figure 4. Comparison of patterns of capture between Rothermel (2004) and the informed and blind movement models. Including bias in the movement model provided reasonable outputs compared to independently-collected recapture data of spotted salamanders by Rothermel (2004).

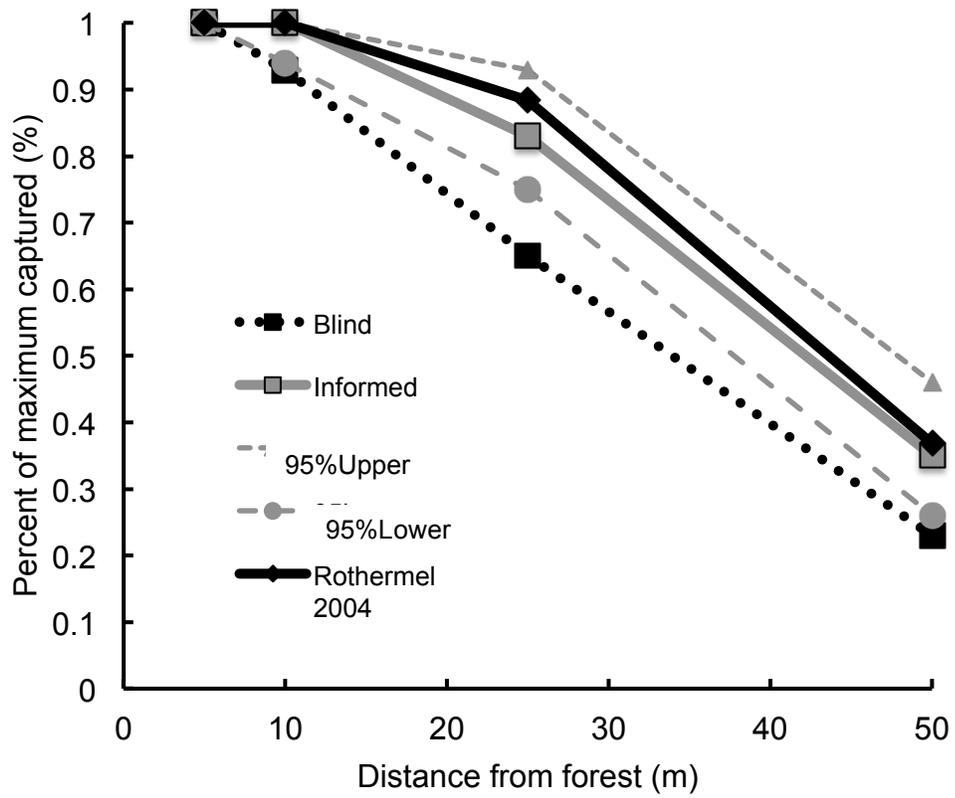


Figure 5. Probability of dispersing salamanders reaching forest. The benefits to informed movement decreased the farther the animal was located from the forest, but more than doubled the probability of finding the forest at distances of 30 m.

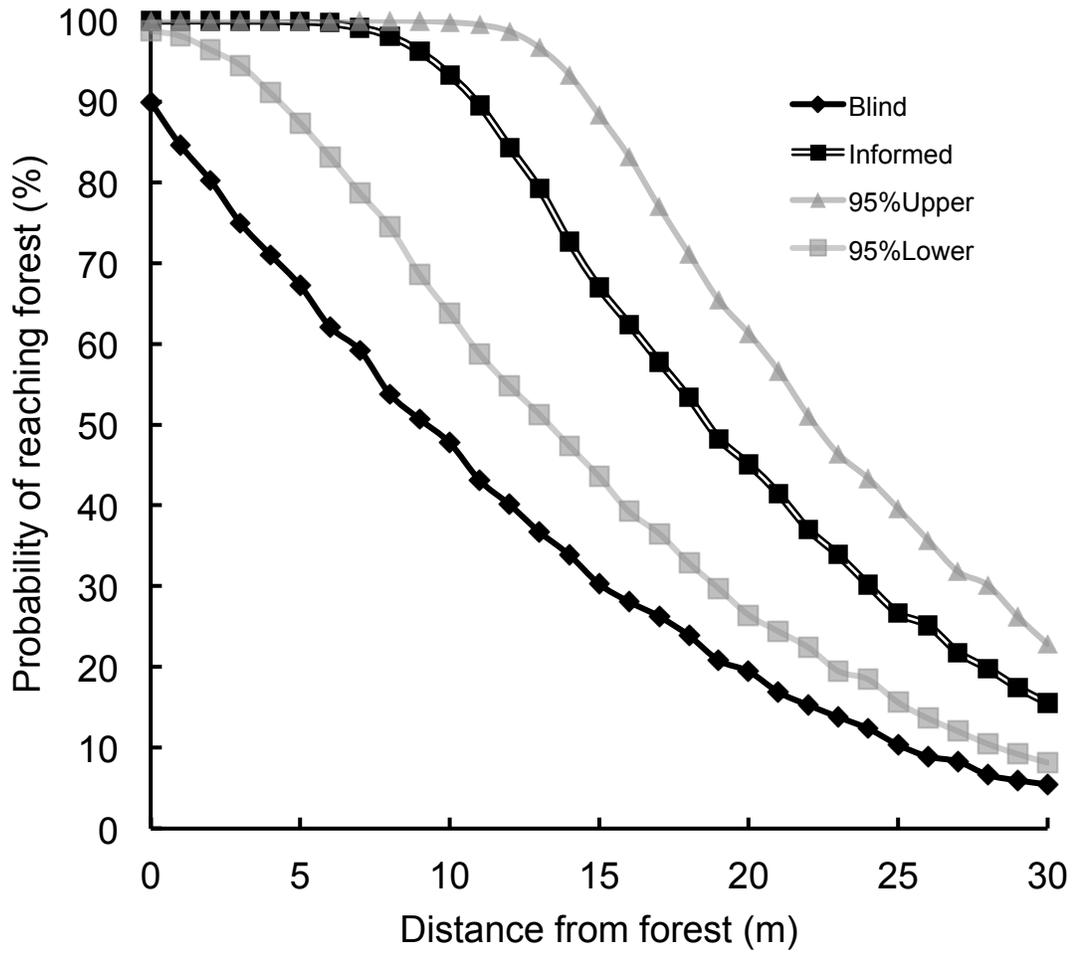
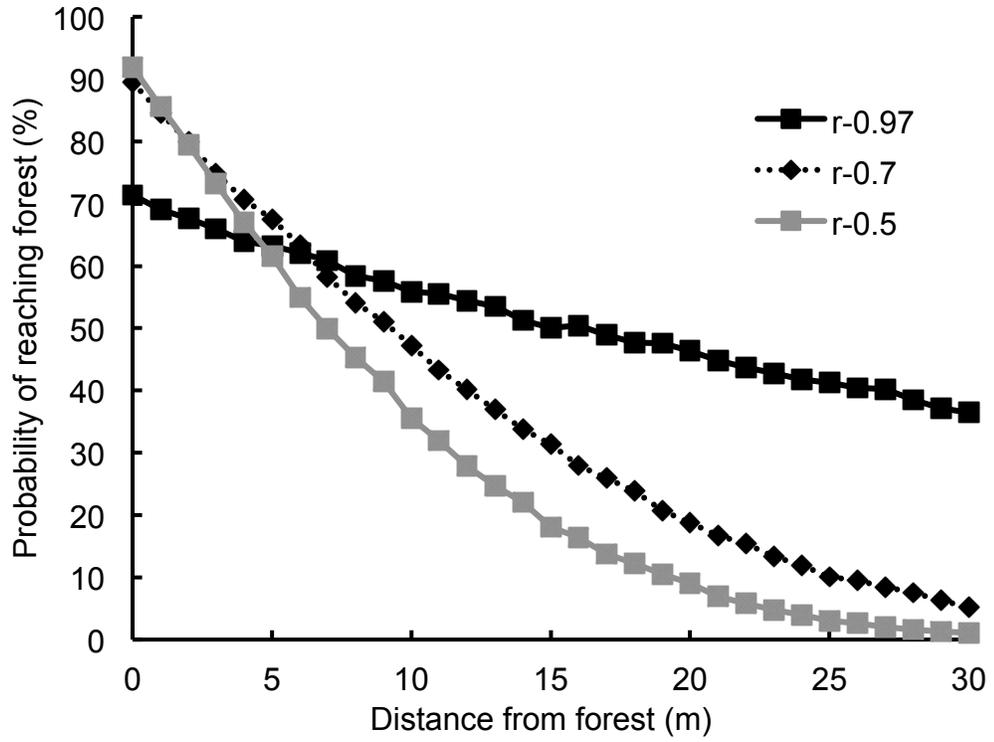
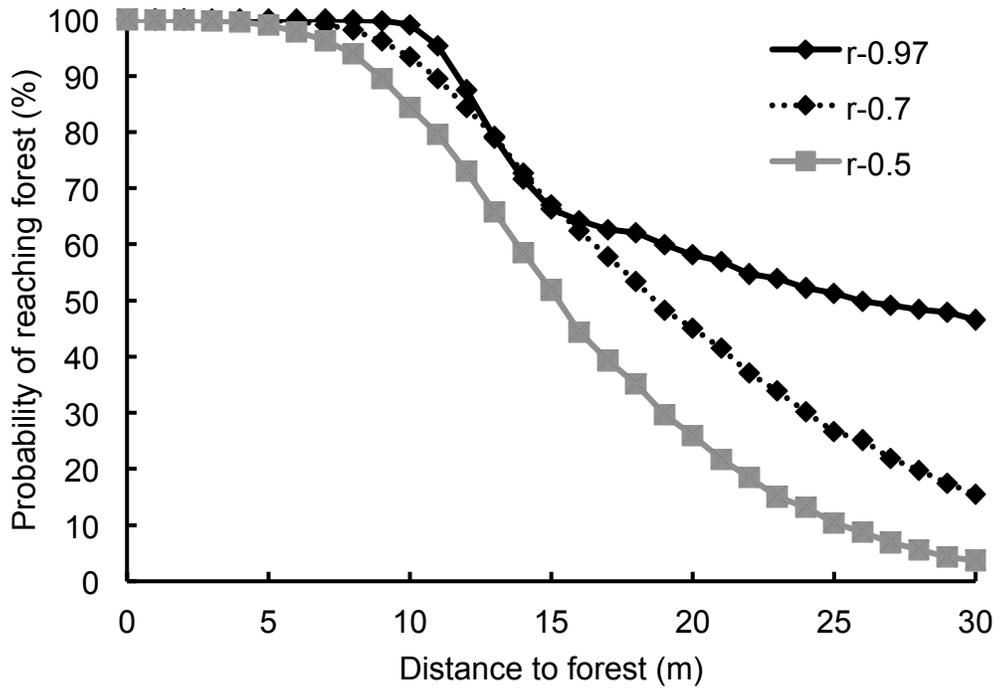


Figure 6. The effects of path straightness on blind (A) and informed (B) movement. The influence of path straightness on probability of finding habitat is affected by the inclusion of bias. Straighter paths were always more successful for animals that could perceive the forest.

A)



B)



## CHAPTER 4

# SIMULATING THE IMPORTANCE OF MOVEMENT BEHAVIOR TO JUVENILE POND-BREEDING AMPHIBIANS IN ALTERED LANDSCAPES

### ABSTRACT

Movement behavior and search strategies influence the spatiotemporal dynamics of individuals and populations. Understanding the survival consequences of movement strategies may increase our ability to predict the effects of land use change on animal populations and increase the effectiveness of conservation and management practices. The population dynamics of pond-breeding amphibians are sensitive to juvenile survival rates, and juveniles are widely considered to be the primary inter-population dispersers. We know relatively little about the movement behavior of juvenile salamanders and how individuals balance the risks and benefits to movement. We used a simple movement modeling framework to investigate the effects of habitat amount and arrangement on the survival consequences of amphibian movement behavior. We explicitly investigated two behavioral parameters: path straightness and movement bias towards habitat. We used data on the fine-scale movement of juvenile spotted salamanders (*Ambystoma maculatum*) to parameterize an individual-based movement model. Habitat amount and configuration had a large impact on the likelihood of an individual locating habitat. Inclusion of density-dependent mortality changed optimal movement

behavior of salamanders and influenced the effects of habitat configuration on the effectiveness of search strategies. Habitat loss and fragmentation alter the consequences of animal movement behavior. An understanding of the behavioral decisions of juveniles could have large impacts on predictions of amphibian persistence in fragmented landscapes.

## INTRODUCTION

The ability of species to persist in altered landscapes is at least partially dependent on movement behavior and vagility (Laan and Verboom 1990, Knowlton and Graham 2010). Habitat alteration may change the risks and benefits to different movement strategies and result in different movement strategies maximizing the likelihood of survival (Kokko and Sutherland 2001, Heinz et al. 2006). The movement parameters of individuals, such as path straightness and response to habitat, are subject to natural selection because they influence survival and fitness, and therefore, movement of some species may be suboptimal when the distribution and abundance of resources change rapidly (Fahrig 2007). Suboptimal movement behavior may yield lower rates of survival than would be predicted with models that do not incorporate species-specific movement ability and sensory capacity (Hawkes 2009). Explicit investigation of the influence of movement parameters on survival under different assumptions about the abundance and distribution of resources is difficult in experimental settings but may be

accomplished through the use of simulation models that define behavioral parameters of interest and control the amount and distribution of habitat.

Mechanistic movement models can aid in understanding and predicting the consequences of habitat fragmentation and alteration to species, facilitating conservation planning and informing habitat management strategies (Alderman et al. 2005, Kramer-Schadt et al. 2011). These movement models are often individual-based, and many use random walks to describe the movement of individuals within real or theoretical landscapes (Codling et al. 2008, Hawkes 2009, Zollner and Lima 1999, McClintock et al. 2012). At the most basic level, random walks are the discrete representation of basic diffusion, where individuals move through space in discrete time steps and the bearing of each movement step is independent of the bearing of the previous movement step. Animal movement is often more realistically described using correlated random walks, for which turning angles are drawn from distributions where small turn angles are more likely than large turn angles, and the bearing of a step is dependent on the bearing of the previous step. The tortuosity of correlated random walks can be defined by specifying the mean resultant length of the distribution of turning angles (Kareiva and Shigesada 1983), and is an important determinant of dispersal processes. Basic correlated random walks assume that movement is not dependent on habitat components. However, numerous studies have found that organism movement path parameters change in different habitat types (Schtickzelle et al. 2007, Daniel et al. 2010). More recently, research has shown that incorporating movement bias and perceptual ranges into

models can increase their predictive capacity and usefulness in conservation planning (Fraker and Luttbeg 2012, Bartoń et al. 2009, Pe'er and Kramer-Schadt 2008). Multistate correlated random walk models have been developed that incorporate behavioral complexity, such as including movement bias toward or away from particular habitat types and specifying movement parameters such as step size and path straightness based on habitat type or level of energy reserves (McClintock et al. 2012). These flexible models require species-specific behavioral data for parameterization, but may increase the ability of models to explore the consequences of animal movement decisions in different landscape scenarios.

Pond-breeding amphibians are good model organisms for investigating the effects of habitat loss and arrangement on survival because their ecology and spatial ontogeny dictate that the short-term, small-scale movement decisions of juveniles have major consequences for both local and metapopulation processes. For example, juveniles have high rates of mortality in the first year post-metamorphosis and are widely considered to be the primary inter-population dispersers (Gill 1978, Gamble et al. 2007). Local population dynamics are also highly sensitive to juvenile survival rates (Harper et al. 2008). Because entire annual cohorts of populations emerge into the terrestrial habitat from what is essentially a single location within the landscape (the natal pond), the movement responses of juveniles to habitat directly around the natal pond will have implications for the survival and dispersion of all juveniles within the population.

The spatiotemporal structure of risk influences optimal movement and search strategies (Zollner and Lima 2005, Bonte et al. 2012). Con-specific density and competition are likely to be important external factors affecting the survival of juvenile amphibians. Amphibian density decreases with distance from natal ponds (Rittenhouse and Semlitsch 2007, Berven 2009), and juveniles are susceptible to negative effects of competition, such as decreased survival and increased time to maturity (Harper and Semlitsch 2007, Patrick et al. 2008, Berven 2009). Amphibians provide a model system for simulating the effects of density on optimal search strategies because the spatial structure of density dependence is likely to be relatively consistent among all pond-breeding amphibian populations (highest density close to the natal pond) (Rittenhouse and Semlitsch 2007). This scenario likely provides a consistent selective pressure to the movement behavior of dispersing juveniles. When the optimal behavior for finding habitat differs from the optimal behavior for mitigating some predictable risk, behavioral trade-offs may occur that could become maladaptive behavioral responses when resource distribution differs from expected (Fahrig 2007).

Using information on the movement behavior of juvenile spotted salamanders (*Ambystoma maculatum*), we developed models to predict the ability of juvenile amphibians to locate suitable habitat during initial movement out of natal wetlands under different assumptions about the configuration and abundance of habitat. Specifically, we determined the effects of path tortuosity and movement bias on success at locating habitat and show how habitat abundance and

configuration affect the relative benefit of different movement strategies. We additionally investigated the effects of density-dependence on optimal movement behavior in simulated salamanders.

## METHODS

We developed an individual-based simulation model to investigate the influence of movement parameters on the success of individuals at reaching suitable habitat in landscapes with different amounts and configurations of habitat. Simulations took place on maps composed of cells and moving individuals were located in continuous space. Movement behavior was parameterized using previous research on the fine-scale movement behavior of juvenile spotted salamanders (Pittman 2013, Chapters 2 and 3). Simulation models were coded and executed in MatLab (MATLAB version 7.10.0 Natick, MA: The Matworks, Inc., 2010). Each simulation took 38s on an Intel core i7 processor.

### *Landscape Simulation*

We generated realistic, theoretical distributions of habitat using neutral landscape models and percolation theory (With and King 1999, With et al. 1999), which have previously been used extensively in studies of the effects of habitat arrangement on population dynamics and dispersal (Gardner et al. 1987). Fractal landscapes were produced as segmented fractional Brownian surfaces based on the mid-point displacement theorem and the diamond-square algorithm (Gardner et al. 1987). Landscapes were binary and consisted of 1024 by 1024 cells. Each habitat cell was

defined as representing 20 x 20 cm of space. All habitat within the landscape was generated within a circle with a radius of 512 units (Fig. 1). Using fractal landscapes, we varied habitat amount ( $p$ ) and habitat configuration ( $H$ ) independently, yielding replicate landscapes with statistically identical properties. Habitat configuration was defined by the Hurst exponent of the fractional Brownian motion. The Hurst exponent ( $h$ ) varied between 0 and 1, with 1 being a landscape with a high degree of clumping and 0 being a landscape with diffusely-spaced habitat (Fig. 1). We generated landscapes with six levels of habitat abundance (1, 10, 20, 30, 40, and 50%) and two levels of clumping ( $H = 0.3$  and  $0.9$ ). The clumping values were chosen to represent different, plausible configurations of available habitat. Therefore, we investigated a total of 12 landscape treatments. A new landscape was generated for each replicate simulation.

### ***Movement Model***

We simulated individuals moving according to a correlated random walk with varying degrees of path straightness and movement bias toward habitat. Individuals began moving from the same location at the center of each map, and 100 individuals were simulated in each model run. Each individual was given an initial starting angle drawn from a uniform distribution (1 – 360 degrees) and moved 1 m (or 5 map units) at each time step. This mean step size was based on the average of the step sizes observed for all spotted salamanders studied ( $n = 97$ ) in Pittman (2013, Chapter 2). Each individual was assigned a set of two movement parameters at the beginning of the simulation: a path straightness value and a value for

movement bias. The mean vector length ( $r$ ) of the wrapped Cauchy distribution was used as a measure of path straightness (Zollner and Lima 1999, Haefner and Crist 1994). Mean vector length varies between 0 and 1, with 1 being a completely straight movement path (all turning angles drawn are 0) and 0 being a uniform distribution of turning angles between 180 and -180 degrees. We simulated individuals with  $r$ -values of 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, and 0.99. The  $r$ -values represent the range of  $r$ -values observed for spotted salamanders in Pittman (2013, Chapter 2, Appendix C); the mean  $r$ -value observed in Pittman (2013, Chapter 2, Appendix C) was 0.7. At each movement step, the individual combined the bearing of the previous step with the turning angle drawn from the assigned distribution to determine the subsequent movement bearing.

The bias parameter was defined as the degree to which an individual biased movement toward a particular habitat cell. Each cell within the landscape was defined as either 'habitat' or 'nonhabitat.' At every time step, each simulated individual determined the straight-line distance between its current location and any habitat cell within a 20 m radius. The individual determined the distance and bearing to the closest habitat cell, and biased their movement toward that particular habitat cell. A linear function described the relationship between the strength of the movement bias (mean vector length) and the distance to the habitat cell. The slope of the linear function was calculated from previous research on spotted salamander orientation toward forest edges (Pittman 2013, Chapter 3). The bias parameter was defined by the intercept of the linear function describing the relationship between

distance to habitat and strength of orientation described in previous studies (Eq. 1, Fig. 3):

$$\beta = -0.032 * D + B \quad (1)$$

where  $\beta$  is the degree to which salamanders move according to the bearing of habitat,  $D$  is straight-line distance from habitat (Pittman, 2013) and  $B$  is the intercept determining the mean vector length of movement at 0 m away from habitat. The movement bearing of each individual at each time step was a weighted average of the previous bearing (plus turning angle drawn from the wrapped Cauchy distribution) and the bearing toward the nearest habitat cell (Eq. 2):

$$\Phi_t = (1 - \beta)(\Phi_{t-1} + \gamma_t) + \beta * \vartheta_t \quad (2)$$

where  $\Phi_t$  is the bearing at time  $t$ ,  $\gamma_t$  is the turning angle drawn from a wrapped Cauchy distribution at time  $t$ ,  $\vartheta_t$  is the bearing toward the habitat at time  $t$ , and  $\beta$  is the strength of bias based on distance from habitat. We simulated individuals with 9 values for the bias parameter: 0 (no movement bias), 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, and 0.8 (Fig. 2). We simulated individuals with every combination of the two behavioral parameters of interest: path straightness ( $r$ ) and movement bias ( $B$ ). Therefore, we simulated a total of 81 movement strategies in 12 different landscape scenarios.

Each animal moved for a total of 102 steps, and the step sizes were constant at 1 m (Pittman 2013, Osbourn 2012, Appendix C). If the animal stopped within 5 map units (1 m) of a habitat cell, the animal was treated as surviving and successfully reaching habitat.

### *Incorporation of Density-Dependence*

We investigated the influence of density on optimal movement behavior of simulated salamanders by incorporating a penalty for stopping in the same location as another individual. One animal survived in each  $1 \times 1 \text{ m}^2$  area of space; this value was chosen based on previous research on the effects of density on juvenile anuran survival after one year (Harper and Semlitsch, 2007). We assumed that each individual settled in the final habitat patch that it encountered along its movement path. For each combination of habitat amount, configuration, and behavioral strategy, we simulated both a density-independent and density-dependent scenario. We additionally modeled a landscape with 100% habitat coverage in order to determine the effects of path straightness on survival when density was the only source of mortality.

### ***Simulations***

The number of animals that were successful in reaching habitat was calculated for each simulation. This number was identical to the number of animals surviving in simulations that did not include density dependence; each animal that reached habitat survived even if that animal settled in the same location as another animal. For simulations that included density-dependent processes, one animal survived per  $1 \times 1 \text{ m}^2$  area (Harper and Semlitsch, 2007). Because more than one animal could settle in a particular  $1 \times 1 \text{ m}^2$  area but only one could survive, the number surviving in density-dependence simulations was always a proportion of the number of animals that located habitat. For the low clumped landscape treatment ( $h = 0.3$ ),

each combination of movement strategy and habitat amount was replicated a minimum of 20 times. For the high clumped landscape treatment ( $h = 0.9$ ), each combination of movement strategy and habitat amount was replicated 100 times. We present the mean of the outcomes of each treatment.

### ***Analysis***

We analyzed the effects of behavioral strategy on the number of salamanders reaching habitat separately for each landscape treatment in the density-independence simulations. For each landscape treatment, we used linear regression models to determine whether behavioral strategy affected the number of animals reaching habitat. For the density-dependence simulations, we did not have specific hypotheses as to the relationship between the number of animals surviving and behavioral parameters. We therefore used a grid search approach to identify the behavioral strategies that maximized and minimized survival. We used Wilcoxon rank sum tests to determine whether two different behavioral strategies significantly differed within landscape configuration treatments. All statistical analyses were performed in R (R Development Core Team 2012) and an alpha of 0.05 was used as a standard for significance.

## RESULTS

### ***Density-Independence***

We found that simulated salamanders were able to behaviorally mitigate habitat loss under certain landscape treatments. Under density-independence, the

movement strategy with the highest path straightness and the highest bias was expected to always yield the highest probability of finding habitat. All regression models showed that movement bias and path straightness had a significant effect on the number of salamanders locating habitat (Table 1). However, the importance of movement behavior to dispersal success varied based on both habitat amount and configuration (Table 1; Fig. 3). In low-clumped habitat ( $h = 0.3$ ), we found that even under low habitat abundance scenarios (1%), salamanders with the straightest movement paths and highest bias parameters had over 95% survival on average. However, the consequences of suboptimal movement in this landscape scenario was also high; individuals with the highest tortuosity and lowest bias had survival rates of 20% on average (Fig. 3). Under this landscape treatment, movement behavior had a high impact on survival. However, when habitat abundance was 20%, almost all individuals reached habitat regardless of behavioral strategy (Fig. 3); the blind strategy with the highest path tortuosity yielded an average of 94% of animals finding habitat under 20% habitat abundance.

High clumping ( $h = 0.9$ ) led to lower rates of juvenile survival in all habitat amount scenarios than did low clumping (Fig. 3). At 1% habitat, survival rates in the high clumping treatment were not strongly dictated by behavior; few individuals survived under all movement strategy scenarios (mean = 17%; range = 0 – 43%). At 1% habitat, the number of animals locating habitat was not significantly related to movement bias ( $P = 0.34$ ), but was positively affected by path straightness ( $P = 0.0005$ ). At 10% habitat, survival rates were higher (mean =

34%; range = 11 - 77%) but much lower than survival rates for individuals in the low clumping treatments (mean = 89%, range = 79 - 100%). Landscape treatments with greater habitat amounts yielded increasing survival of the behavioral strategy with highest movement bias and path straightness (Fig. 4). However, even under the 50% habitat abundance scenario, the cost to suboptimal movement was high; 60% of animals survived with the strategy with the highest path tortuosity and lowest bias, while 100% of animals with the straightest paths and highest bias survived (Fig. 4). Therefore, suboptimal movement of salamanders could reduce survival probabilities by as much as 40% even when habitat comprised 50% of the landscape.

### ***Density-Dependence***

In 100% habitat landscapes, straighter movement paths yielded higher survival because individuals were less likely to settle in the same location as other individuals the farther they moved away from the natal wetland. However, at the highest path straightness values ( $r > 0.97$ ), survival decreased because individuals that exited the pond at the same bearing as other individuals settled in the same location: some random movement was necessary to enable individuals to utilize more of the available landscape (Fig. 5).

Across all landscape treatments, the inclusion of density-dependence yielded different optimal movement strategies from the density-independent models; blind movement typically had higher survival rates than movement with high movement bias. However, habitat configuration yielded differing optimal

movement strategies under density-dependence. In landscapes with little habitat clumping (hereafter “low clumped”), blind, straight movement was optimal (Fig. 6). As habitat amount increased, more tortuous movement paths with low movement bias also yielded high survival estimates (Fig. 6). The movement strategy that minimized survival was the highest path straightness and highest movement bias ( $r = 0.99$ ,  $B = 0.8$ ).

In landscapes with highly clumped habitat (hereafter “high clumped”), straighter paths were almost always better than more tortuous paths (Fig. 7). As habitat amount increased, movement bias played a larger role in salamander survival, with lower movement bias yielding higher survival. However, the strength of the effects of movement bias on survival was not as strong in high clumped landscapes as low clumped landscapes. Habitat configuration affected the behavioral strategy yielding the lowest likelihood of survival. In high clumped landscapes, the behavioral strategy that minimized survival was that with the highest tortuosity and lowest movement bias ( $r = 0.2$ ,  $B = 0$ ; Fig. 7). Alternatively, in low clumped landscapes, the straightest movement paths with the highest movement bias minimized survival ( $r = 0.99$ ,  $B = 0.8$ , Fig. 6). We found that these two behavioral strategies yielded significantly different survival probabilities across habitat amounts for both the low clumped landscapes ( $P = 0.05$ ) and the high clumped landscapes ( $P = 0.05$ ). In high clumped landscapes, the search strategy that maximized survival probability without density dependence actually

minimized survival probability when density-dependent mortality was incorporated ( $r = 0.99$ ,  $B = 0.8$ ).

## DISCUSSION

Emigration of juvenile amphibians from natal ponds is a critical process for amphibian populations (Semlitsch 2008). The majority of empirical studies on initial movement of juveniles out of natal ponds are conducted at scales that cannot address the mechanistic bases of decreased juvenile survival in altered landscapes (Cushman 2006). By simulating the dispersal of recently-metamorphosed spotted salamanders using fine-scale behavioral data, we generated predictions of the survival consequences of movement strategies and the effects of habitat amount and distribution on optimal movement behavior. The low clumped habitat scenario presented in this study likely describes the distribution of microhabitat in continuous forest surrounding natal ponds, while the high clumped scenario is more likely to describe microhabitat distribution in fragmented landscapes, where available habitat is congregated in one area. In all simulations, the configuration of habitat greatly impacted salamander survival; low clumped scenarios yielded higher survival than high clumped scenarios across behavioral strategies and habitat abundances. The inclusions of density-dependent mortality increased the benefits of blind movement and suggests that assumptions about risk may drastically alter the movement strategy yielding the highest likelihood of survival.

Degradation of forested habitat occurs as a consequence of changes in land use that increase the influence of edge or matrix habitat (Ries et al. 2004), species invasions that disrupt ecosystems (Crooks 2002), or forestry practices that impact habitat quality, such as clearcutting (Semlitsch et al. 2009), burning (Humphries and Sisson 2012), or increases in soil compaction (Semlitsch et al. 2007, Osbourn 2012). These practices may impact the amount of quality habitat available to juvenile amphibians exiting natal ponds and increase the clumping of resources, thus altering habitat distribution and the survival consequences of behavioral strategies. Our study illustrates the need to understand movement behavior in order to predict survival in degraded or fragmented landscapes. We also demonstrate that assumptions about costs to settlement, such as density dependence or independence, have strong impacts on predictions of optimal movement strategy. Models that make implicit assumptions about behavior based on plausibility or expert opinion may reach erroneous conclusions about the effects of changes in land-use on juvenile survival and dispersion.

Juvenile salamanders exit natal ponds with limited knowledge of the terrestrial habitat and have limited ability to acquire information during emigration movements as a result of low vagility that limits the area that they are able to search before initial settlement (Osbourn 2012). Because juveniles may have limited ability to adjust search strategies based on acquired information, individuals may emerge from the pond with pre-defined behavioral strategies that are a consequence of a variety of interacting factors such as physiological condition

(Scott et al. 2007), climatic conditions on the night of movement (Todd and Winne 2006), and genetic tendency (Sih et al. 2004). Understanding how the survival consequences of hypothesized behavioral strategies change based on the distribution of resources may therefore aid in identifying causes of population declines and guide avenues of future behavioral research. Our simulations revealed that path straightness and movement bias affected probabilities of juvenile amphibians locating habitat more strongly under certain landscape configurations than others. For example, under low clumping scenarios, over 90% of individuals of all behavioral types were able to locate habitat when as little as 10% of the landscape was suitable. This is explained by the fact that individuals were moving in landscapes in which habitat was likely to be located close to the pond in any direction. Alternatively, when habitat was highly clumped, individuals may be unable to locate habitat if they initially move out of the wetland in the wrong direction. Because individuals in these simulations have relatively low vagility, the initial bearing out of the natal pond greatly impacted the portion of the landscape that individuals were able to search. If an individual initially traveled away from a habitat clump, it was unlikely to reach another during the simulation in highly clumped landscapes.

Currently, the degree to which amphibians exit the natal pond in relation to terrestrial habitat quality is poorly understood, and studies offer contradictory conclusions as to the effects of the location of high-quality terrestrial habitat on juvenile orientation. For example, two studies on spotted salamander dispersal from

natal ponds indicated that terrestrial habitat quality did not impact initial movement bearings (Rothermel 2004, Rittenhouse and Semlitsch 2006), while a separate study on spotted salamanders did detect significant movement toward quality habitat (Walston and Mullin, 2008). Studies on wood frogs (*Rana sylvatica*) in Maine also found that initial bearing away from natal ponds was influenced by habitat quality (Patrick et al. 2007, Demaynadier and Hunter 1999). As habitat is degraded and the arrangement of habitat changes, understanding factors affecting initial movement bearing of juveniles out of natal wetlands may become critical to understanding and preventing population declines. More research is needed on factors affecting initial orientation out of wetlands across a range of amphibian species and across geographic regions.

The inclusion of density-dependent costs in the model altered the effects of habitat configuration on optimal movement strategies. In the density-independent model, the straightest movement paths with the highest movement bias always generated the highest probabilities of survival. The inclusion of density dependence generated benefits to blind movement strategies in both clumped and non-clumped habitat scenarios. For both high and low clumped landscapes, low movement bias and high path straightness yielded the greatest likelihood of survival. High movement bias yielded lower survival than blind movement strategies because individuals moving with high bias were likely to locate the same nearby habitat cell as other individuals. Blind movement allowed individuals to bypass habitat close to the pond that other animals were likely to locate as well. Blind movement was

necessary for individuals to locate habitat outside of the highest density areas close to the natal wetland. However, the configuration of habitat influenced the benefits to blind movement. In highly clumped landscapes with low habitat abundance, straighter movement was generally better than more tortuous movement, but bias did not have a great impact on survival. Survival was dependent more on path straightness than movement bias. With increasing amounts of habitat, blind movement was better among the straightest movement paths. However, the benefits to blind movement were lost if individuals moved more tortuously.

Alternatively, in the low clumped landscapes, survival was more dependent on level of bias than path straightness across the range of habitat amounts investigated. In low habitat abundance landscapes, the benefits to straight movement were high regardless of level of bias. However, with increasing habitat abundance, the benefits of blind movement outweighed the benefits to straight movement. For example, when habitat abundance was 50%, a behavioral strategy with  $r = 0.7$  and  $B = 0$  (moderate straightness, no bias) was better than a strategy of  $r = 0.99$  and  $B = 0.5$  (high straightness, moderate bias). This result suggests that there may be a strong selective pressure to move blindly for juvenile amphibians initially exiting natal ponds because the likelihood that a habitat location is occupied is lower the farther the individual travels from the natal site.

The importance of density dependence in determining the consequences of movement highlights the sensitivity of movement behavior to assumptions about movement risk. Interestingly, the behavioral strategy that maximized survival in the

density-independent simulations was the worst movement strategy when density-dependence was included in the model in low clumped landscapes. The primary goal of juvenile pond-breeding salamanders exiting natal ponds is to find suitable terrestrial habitat. Because the quality of habitat is affected by densities of conspecifics (Patrick et al. 2008, Harper and Semlitsch 2007), juveniles may maximize the probability of finding suitable habitat by ignoring habitat quality close to the wetland. However, this strategy is highly suboptimal in landscapes with low habitat abundance and high clumping. In landscapes where habitat is not highly clumped, the benefits to the blind movement strategy are high and the costs to tortuous movement are lower. However, in high clumping scenarios, the benefits to blind movement decreased and straighter movement paths were optimal regardless of habitat amount.. Juveniles exiting natal ponds may therefore not always behave in a way that maximizes the chance of locating suitable habitat in relation to the amount and arrangement of habitat, which could cause reduced survival and population persistence.

Our study investigated only scenarios in which all individuals emerged from the aquatic habitat with the same behavioral strategy. While this assumption does not affect the density-independent conclusions, it may influence the results of the density-dependent scenarios because the survival outcome is highly dependent on the behavior of other individuals in the population. Additionally, the strength of the outcome will change by varying the number of animals leaving the natal pond in the simulations as well as assumptions about the strength of density dependence.

However, the overall pattern observed in this study is highly relevant, as individuals in nature are likely to encounter other cohorts of amphibians at a higher rate close to the natal pond (Rittenhouse and Semlitsch 2007).

Theoretical studies have found that species experiencing high movement or dispersal risks should evolve the ability to perceive and respond to habitat from a distance (Heinz and Strand 2006, Olden et al. 2004, Bartoń et al. 2009). Because amphibians are highly susceptible to environmental conditions and therefore incur high movement costs, it is likely that they would benefit from greater perceptual ranges and habitat responsiveness. However, blind movement, especially of juveniles, may be adaptive under some circumstances, such as upon exiting the natal pond. Amphibian populations at ponds situated on or near poor-quality habitat may therefore incur reduced juvenile survival if juveniles do not avoid the poor-quality habitat. Research investigating edge responses of juveniles are therefore necessary for the parameterization of accurate movement models. For example, least cost methods of modeling population connectivity implicitly assume that individuals choose the path of least cost more than they choose other potential movement routes. Management strategies that place the highest conservation priorities on 'least-cost' paths without an understanding of how animals make movement decisions may not maximize the efficacy of management practices. For example, the creation of corridors increases dispersal rates only if animals use the dispersal corridors (Haddad 1999). Explicit investigation of movement behavior along edges and in different habitats can therefore provide insight into the

usefulness of these management practices for amphibians (Berggren et al. 2002, Haddad 1999, Pittman 2013).

Animals move in such a way as to balance the benefits and costs associated with movement. The consequences of movement behavior change as landscapes are altered, and species may not behave in predictable or adaptive ways when the benefits and risks to movement are altered. Our study illustrates that survival may be highly sensitive to movement behavior, and this sensitivity likely increases with greater habitat change. A sound understanding of the behavioral parameters important to survival and how habitat change alters the risks associated with those behaviors will improve conservation and management efforts and our understanding of the ability of species to respond to landscape change.

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Table 1. Linear regression results for each density-independent landscape treatment and coefficients related to behavioral parameters.

| Habitat  | Habitat | Bias   | Straightness |                |         |
|----------|---------|--------|--------------|----------------|---------|
| Clumping | Amount  | Coeff. | Coeff.       | R <sup>2</sup> | P-value |
| Low      | 1       | 55.2   | 48.33        | 0.89           | P<0.001 |
| Low      | 10      | 23.8   | 21.3         | 0.78           | P<0.001 |
| Low      | 20      | 14     | 9.5          | 0.69           | P<0.001 |
| Low      | 30      | 8.8    | 8.2          | 0.52           | P<0.001 |
| Low      | 40      | 0.36   | 0.77         | 0.17           | P<0.001 |
| Low      | 50      | 0.28   | 0.27         | 0.09           | P=0.009 |
| High     | 1       | 4.4    | 16.8         | 0.13           | P=0.001 |
| High     | 10      | 21.6   | 36.5         | 0.54           | P<0.001 |
| High     | 20      | 36.3   | 39.3         | 0.84           | P<0.001 |
| High     | 30      | 33.7   | 37.9         | 0.82           | P<0.001 |
| High     | 40      | 30.8   | 33.9         | 0.84           | P<0.001 |
| High     | 50      | 28.3   | 27.3         | 0.82           | P<0.001 |

Figure 1. Examples of different habitat clumping scenarios in generated fractal landscapes.

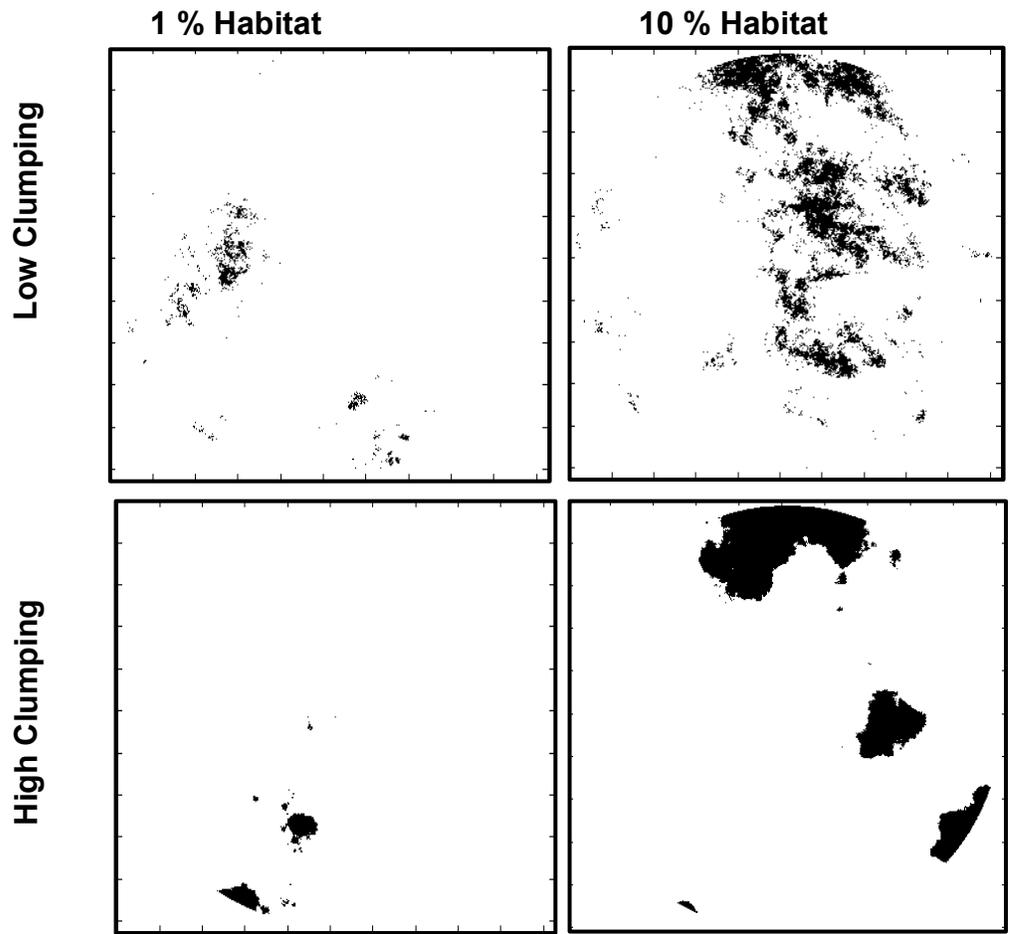


Figure 2. Linear relationship between distance from habitat and strength of orientation towards forest. The bias parameter ( $B$ ) was defined as the intercept of this linear function and ranged between 0 (blind movement) and 0.8. The slope of the linear relationship was the same among all levels of bias. The range of intercepts used in this study were based on data from Pittman (2013). The black line represents the mean of orientation strengths found in Pittman (2013) and the gray lines represent upper and lower limits to the  $B$  parameter.

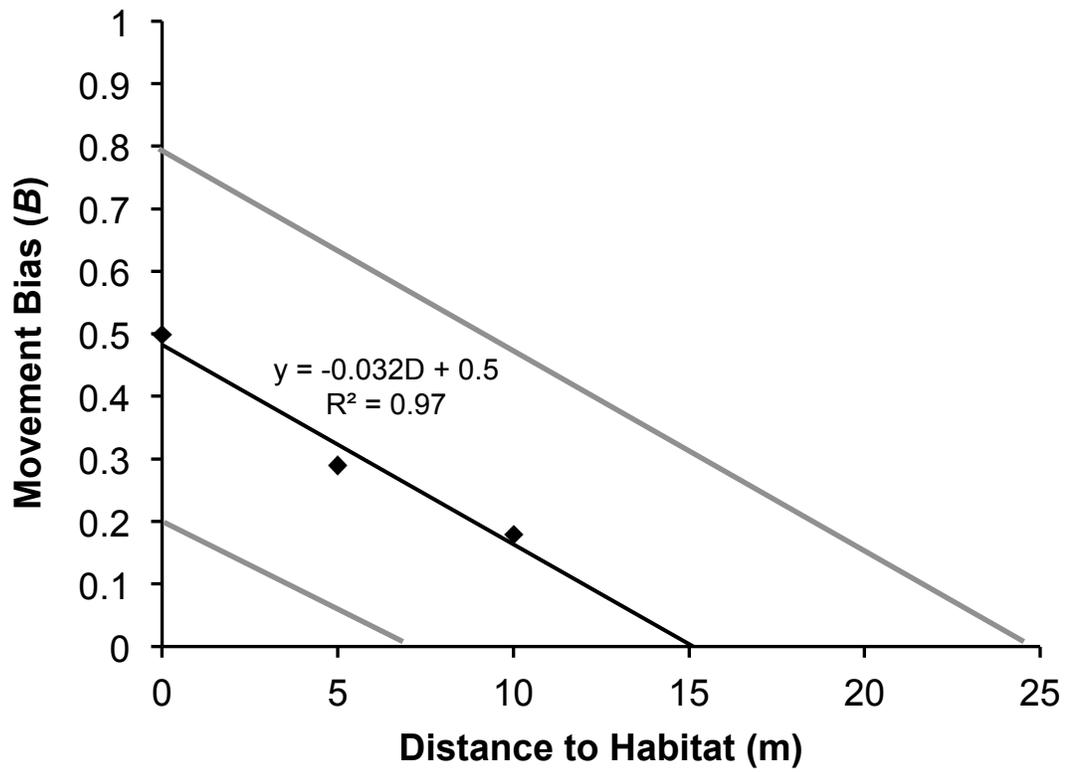


Figure 3. Mean survival estimates of salamanders with each behavioral strategy in four different landscape scenarios.

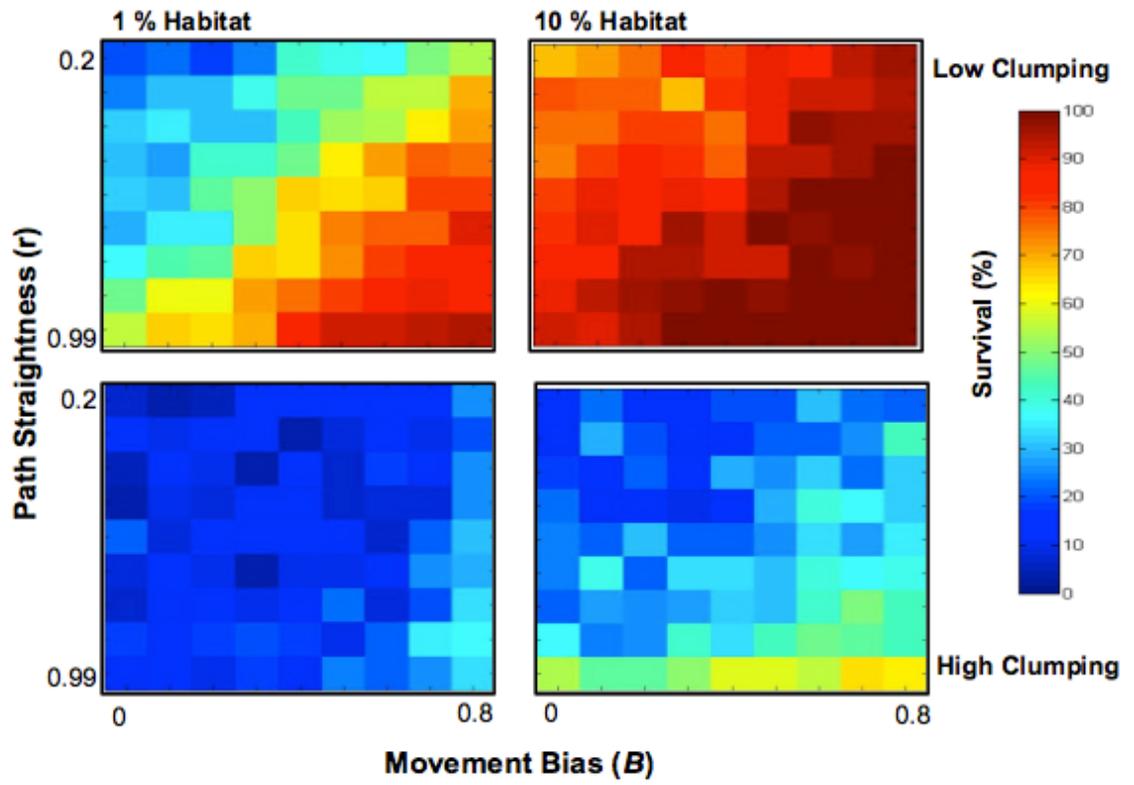


Figure 4. Mean survival estimates of each behavioral strategy in highly clumped landscapes with different habitat amounts.

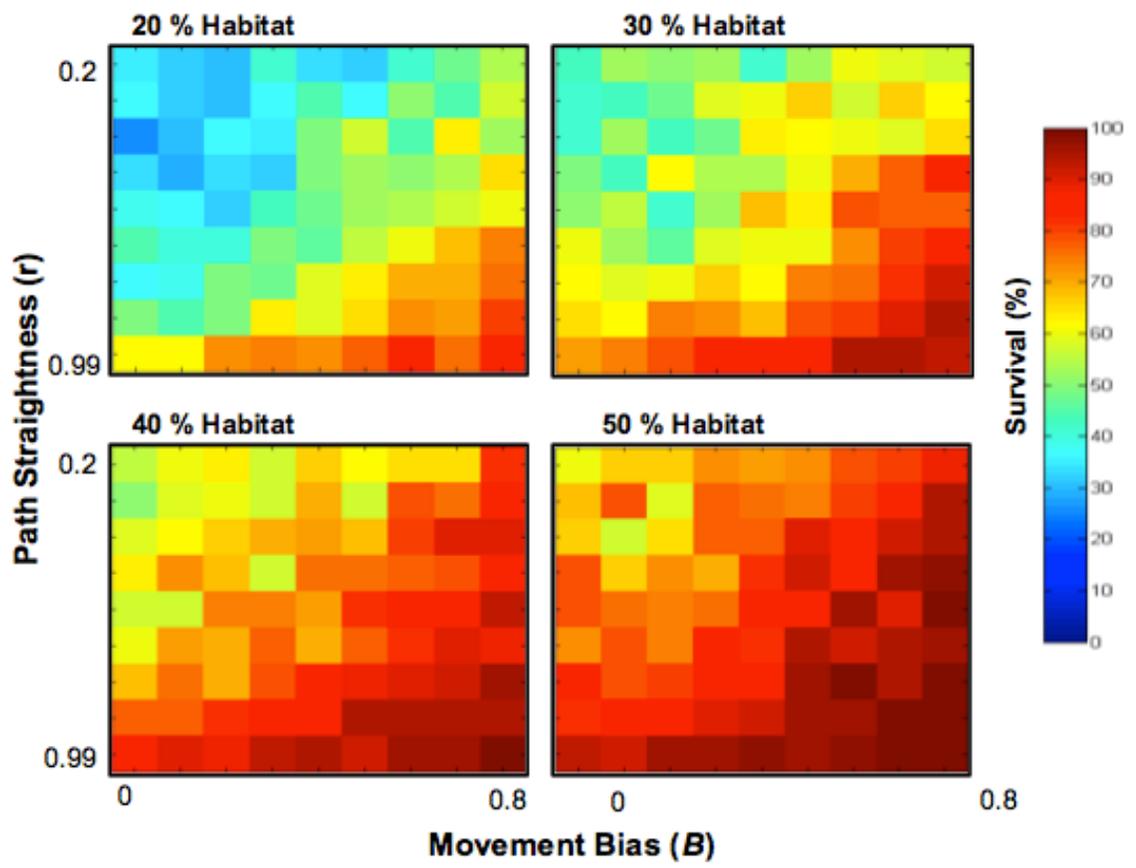


Figure 5. Effects of path straightness on survival in landscapes with 100% habitat under the assumption of density-dependence.

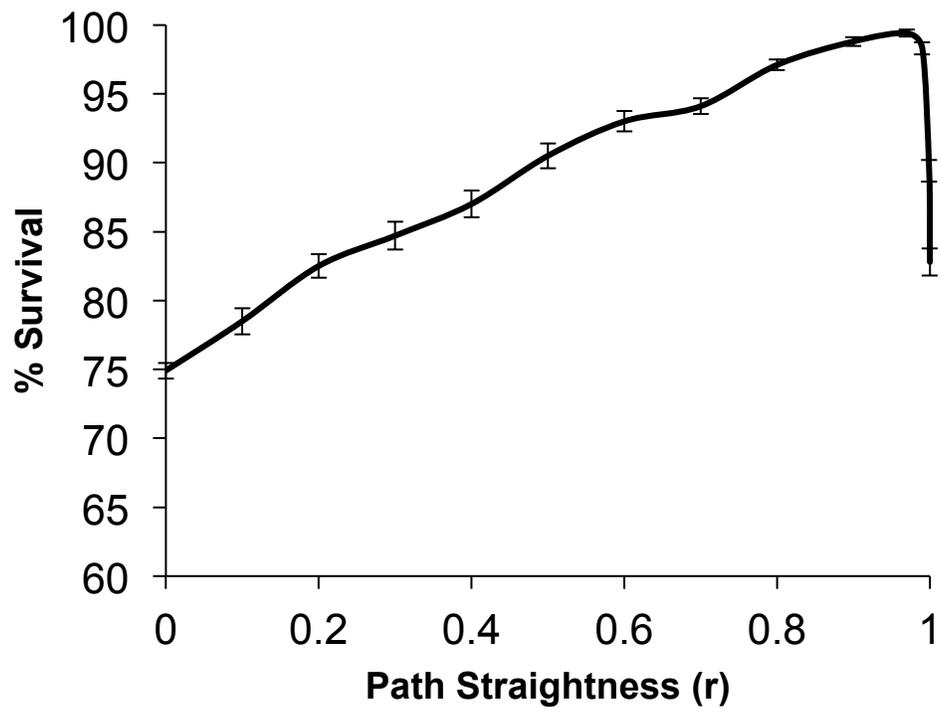


Figure 6. Effects of habitat abundance on optimal movement behavior of juveniles under the low clumping landscape treatment and the assumption of density-dependent mortality.

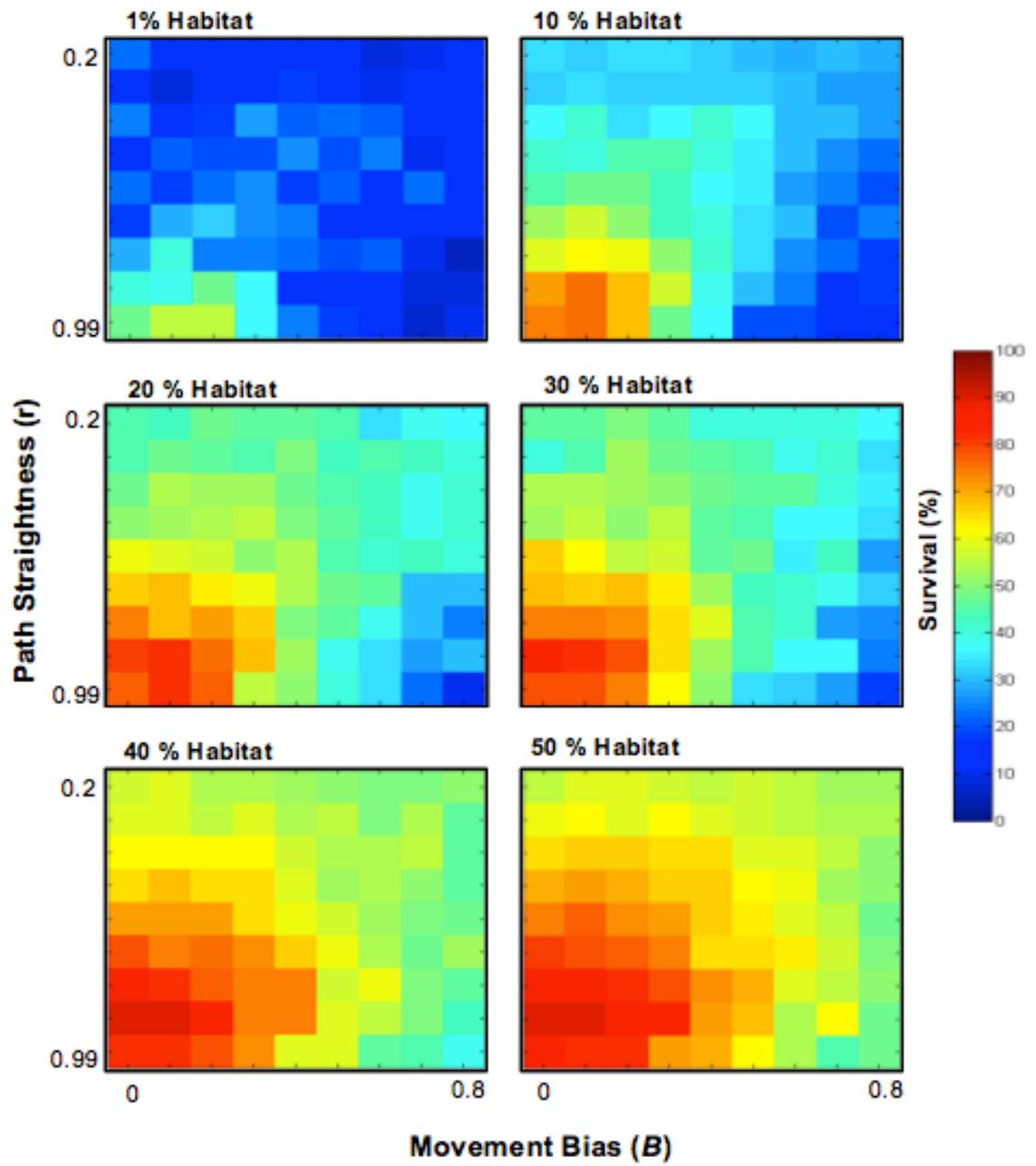
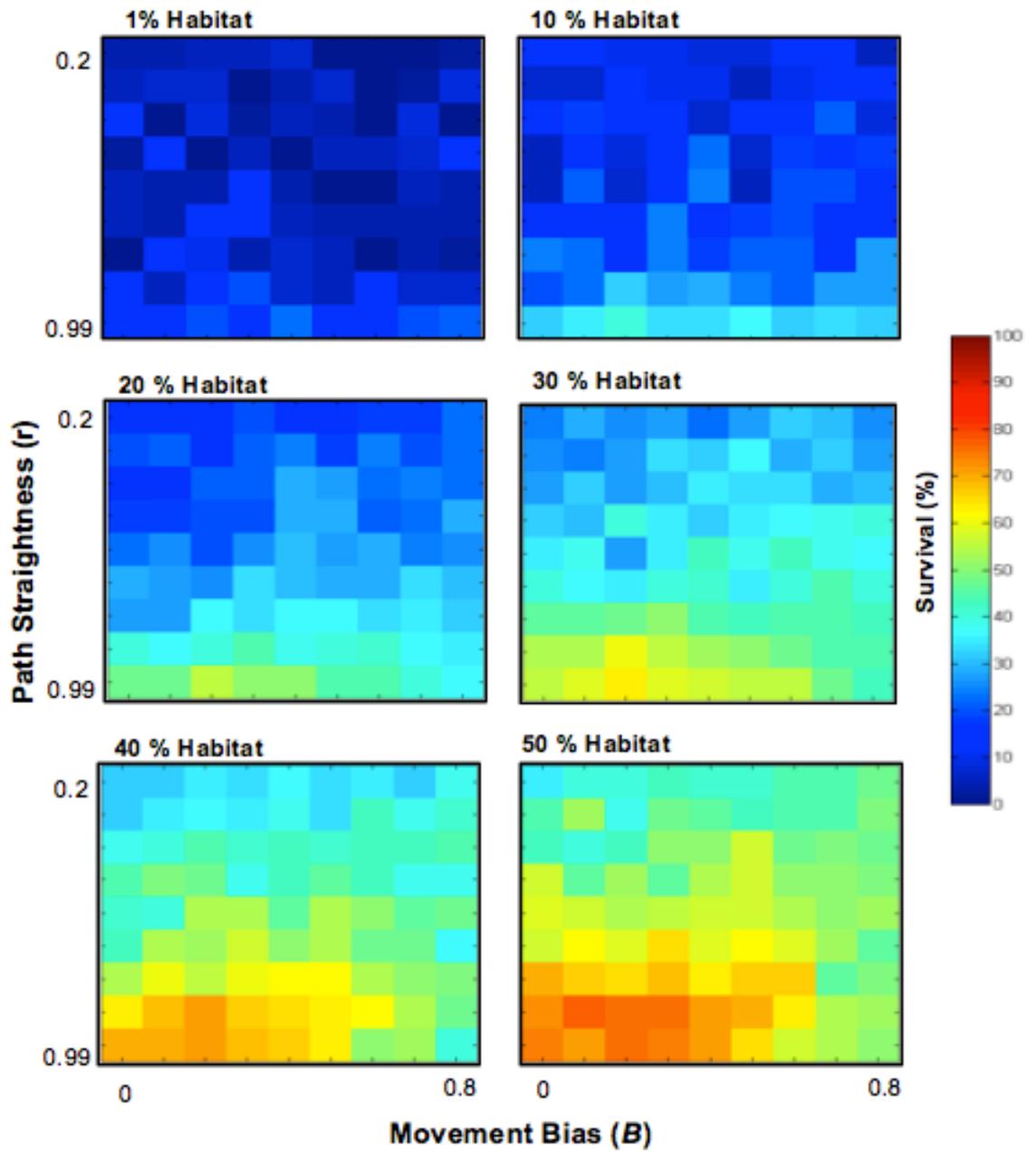


Figure 7. Effects of habitat amount on optimal movement behavior in salamanders under the high clumping landscape treatment and the assumption of density-dependent mortality.



## CHAPTER 5

### CONCLUSIONS, SUMMARY OF RESULTS, AND FUTURE DIRECTIONS

The movement behavior of amphibians may affect the consequences of habitat loss and degradation to local and metapopulations. Juvenile movement is a particularly important process because juveniles are the primary interpopulational dispersers for most pond-breeding amphibian species. Juvenile amphibians are heavily susceptible to external environmental conditions and have limited knowledge of terrestrial habitat conditions upon exiting natal ponds. Habitat loss and alteration increase the risks associated with movement, with potentially significant negative effects on population connectivity and juvenile survival. Effective conservation of pond-breeding amphibian populations necessitates an understanding of how proposed management strategies impact populations, and management aimed at increasing the viability or connectivity of populations in the face of habitat alteration depends on how animals alter movement in response to different types of land use. Multiple factors may influence the movement behavior of individuals, including external factors such as habitat quality or climatic conditions and internal factors such as level of energetic reserves or previous experience. Understanding how juveniles assess and respond to the costs and benefits associated with movement provides a mechanistic basis for movement behavior and may help generate predictions for how individuals and populations respond to habitat alteration.

## SUMMARY OF RESULTS

### ***External and Internal Factors Affect Movement Path Parameters:***

1. Habitat type influences movement behavior of juvenile spotted salamanders (Chapter 2). Juveniles moved straighter and with longer step sizes through field habitat than early successional or mature forest habitat.
2. Distance to habitat influences the directional movement of juvenile amphibians (Chapter 2 and 3). Juveniles significantly oriented toward forest habitat from distances of up to 10 m away. Therefore, juvenile spotted salamanders exhibited strong boundary behavior.
3. Juvenile amphibians do not alter movement in response to all habitat boundaries (Chapter 2). Juveniles detected stark differences in habitat type (forest and field) but did not respond to subtler differences in habitat types (forest and early successional forest).
4. Internal state influences the dispersal behavior of spotted salamanders. Smaller salamanders were less likely to successfully reach forest habitat (Chapter 3). Additionally, size of salamanders was negatively correlated with path straightness, indicating that the internal state of juveniles may influence their search strategies.

### ***Movement Modeling***

1. Juvenile spotted salamander movement paths are approximated by correlated random walk models (Chapter 2). At the individual level, a

portion of juveniles moved significantly farther than predicted by a correlated random walk model, signifying that some individuals maximize net displacement from the release location. For modeling purposes, correlated random walks may represent a good description of initial juvenile movement out of natal ponds.

2. Step size and correlation of turning angles depend both on external factors (habitat type) and internal state (size of salamander). Movement parameters needed to define correlated random walk models should be dependent on spatially-explicit factors such as habitat type and distance to habitat. Additionally, internal state should be incorporated into movement models as it likely affects risk-taking and search strategies of juvenile amphibians.
3. Biased correlated random walk models generate plausible movement behavior of juvenile spotted salamanders and may be more realistic and useful in predictive models than pure correlated random walks (Chapters 3 and 4). However, parameterization of bias in correlated random walk models necessitates empirical data on both the strength of bias and the habitats to which juvenile amphibians respond.

### ***Efficacy of movement strategies***

1. The amount and arrangement of habitat heavily influences the survival consequences of movement strategies (Chapter 4). Based on the behavioral variation observed in the field, spotted salamanders can behaviorally

mitigate the effects of habitat loss to a certain extent, depending on habitat arrangement.

2. When habitat is highly clumped and competition is not considered, salamanders can achieve > 90% chance of survival by moving straight and with the highest levels of movement bias when habitat amount is at least 20%.
3. When habitat arrangement is not clumped, salamanders have > 90% chance of survival by moving straight with the highest movement bias in landscapes with as low as 1% habitat. However, when habitat amount is < 10%, the consequence of suboptimal movement is high.
4. The strength of movement bias towards habitat affects the influence of path straightness on the probability of finding habitat (Chapter 3 and 4).  
Straighter movement paths are always optimal if salamanders can perceive habitat. If salamanders cannot perceive habitat from a distance, more tortuous movement paths are optimal if habitat is located closer to natal wetlands.
5. Density-dependence changes the optimal movement behavior of salamanders and mediates the effects of habitat configuration on juvenile salamander survival (Chapter 4).
6. When habitat is low clumped and density-dependence is present, the greatest probability of finding habitat was straight, blind movement

(Chapter 4). As habitat amount increases, path straightness is less important for survival than the strength of movement bias.

7. When habitat arrangement is highly clumped and density-dependence is present, the greatest probability of finding habitat was straight, blind movement (Chapter 4). However, as habitat amount increases, path straightness is more critical to survival than the strength of movement bias.
8. Because habitat arrangement, amount, and assumptions about movement risk affect the optimal movement strategies of juvenile amphibians, juveniles may not behave optimally when any of these factors is altered (Chapter 4). Therefore, predictive models that assume that juveniles behave optimally may generate erroneous predictions of population responses to habitat alteration and the effectiveness of management strategies.

## APPENDIX A

### **PREDATION OF JUVENILE RINGED SALAMANDERS (*AMBYSTOMA ANNULATUM*) DURING INITIAL MOVEMENT OUT OF PONDS**

Shannon E. Pittman, Michael S. Osbourn, Dana Drake, Raymond D. Semlitsch

#### ABSTRACT

Natal dispersal is often accompanied by substantial risks to survival, which may dictate the movement behavior of individuals. For pond-breeding salamanders, initial natal dispersal is accompanied by an ontogenetic habitat shift, and individuals are naïve to terrestrial surroundings and accompanying movement risks. Although there have been numerous studies on the effects of habitat type on amphibian movement and survival, few studies have directly documented predation risk to free-ranging, newly-metamorphosed salamanders. We tracked the movements of 124 Ringed Salamanders (*Ambystoma annulatum*) at four ponds and found that 23% were consumed by anuran predators during initial movement in terrestrial habitat. These results document that predation may constitute a substantial risk to pond-breeding salamanders after metamorphosis and should be considered in studies analyzing the survival consequences of movement behavior.

## INTRODUCTION

Dispersal behavior is driven by tradeoffs between risks and benefits associated with movement (Clobert et al. 2001, Nathan et al. 2008, Delgado et al. 2010). Understanding risks animals face during dispersal is critical to explaining and analyzing observed movement patterns (Clobert et al. 2001, Nathan et al. 2008, Pe'er and Kramer-Schadt 2008). For many species, initial movement away from natal locations is accompanied by substantial risks to survival as a result of individuals' lack of experience in the new environment, small body size relative to conspecifics, and novel antagonistic interactions with heterospecifics (Barbraud et al. 2003, Yoder et al. 2004, Chaput-Bardy et al. 2010). The ways that individuals mitigate the risks associated with natal dispersal may have important implications for the spatial dynamics of the species (Barbraud et al. 2003, Zollner and Lima 2005).

Relatively little is known concerning the initial movements of juvenile pond-breeding amphibians out of ponds, even though this life stage is widely acknowledged to be critical to population regulation (Harper et al. 2008). Dispersing juvenile amphibians undergo an ontogenetic habitat shift (aquatic to terrestrial habitat) and are subject to high mortality during the first year post metamorphosis (Rothermel and Semlitsch 2002). Documented causes of mortality include energy depletion (Scott et al. 2007), desiccation (Rothermel and Luhring 2005), density effects (Harper and Semlitsch 2007, Rittenhouse and Semlitsch 2007, Berven 2009), and predation (Rittenhouse et al. 2009). Numerous studies

have found that habitat quality surrounding ponds influences juvenile survival and the duration and directionality of juvenile movements (e.g. deMaynadier and Hunter 1999, Rittenhouse and Semlitsch 2006, Popescu and Hunter 2011). However, few studies have directly documented predation of juveniles during initial movement in terrestrial habitat, and there is currently little evidence to address the question of whether predation represents a significant risk factor to dispersing pond-breeding amphibians.

Pond-breeding salamanders make initial movements away from ponds on the scale of 20-50 m, and the choices that individuals make during this initial phase of dispersal have profound implications for future survival (Osbourn 2012). For example, recently-metamorphosed salamanders are susceptible to predation by larger anurans. Search strategies during initial movement out of natal ponds are often considered solely in relation to their effectiveness in locating quality habitat; few studies acknowledge the potential of predation pressure to dictate optimal search strategies, largely because relevant data on predation risk are scarce. Because terrestrial amphibian density is negatively correlated with distance from ponds (Rittenhouse and Semlitsch 2007), predation pressure by anurans is likely highest closest to the pond. Therefore, we hypothesize that juvenile amphibians face high predator densities immediately upon exiting ponds after metamorphosis (Madison 1997).

In this study, we used fluorescent powder tracking to follow the movements of recently-metamorphosed Ringed Salamanders (*Ambystoma annulatum*) away

from natal ponds to document the occurrence of predation, the identity of predators, and the locality of predation events in relation to the pond.

## METHODS

This study was conducted at Daniel Boone Conservation Area (DBCA, 1,424 ha) in Warren County, MO. DBCA is characterized by mature second-growth forest dominated by oak and hickory tree species in the canopy and sugar maple in the understory. The study took place at four small permanent ponds within DBCA. Each of the four ponds was surrounded by a closed-canopy forest and consisted of identical amphibian communities (Hocking et al. 2008).

We captured late-stage Ringed Salamander larvae from the ponds and raised the larvae in cattle tanks within 500 m from the natal ponds. We collected metamorphosed salamanders from the cattle tanks and held them in containers with damp moss until conditions were ideal for release and tracking, which were defined as: (1) within 24 hrs of, but not concurrent with, a rain event; (2) when minimum nightly temperatures were above 10°C; (3) within 2 weeks of the individual's metamorphosis. Salamanders were released at the pond from which they were collected as larvae between May and July 2011. We released up to 10 salamanders in a night between 2030 and 2200 hrs, soon after a rain event when the ground was wet and relative humidity was high. Previous studies have found that salamanders readily disperse from ponds under these conditions (Rothermel 2004) and make dispersal movements up to 9 days after a rain event (S. Pittman, unpubl. data). We

therefore believe that the behavior of individuals in this study approximated that of individuals initially moving from their natal ponds.

During salamander releases, we placed salamanders approximately 20 cm from the edge of the pond, under upside-down clay flowerpots spaced a minimum of 5 m apart. The clay pots served as release enclosures and allowed animals to acclimate to the environment for approximately 20 minutes prior to release. To minimize the influence of observer orientation in salamander movement decisions, we lifted the release chambers from a distance of at least 3 m.

Directly prior to release, we covered the posterior half of salamanders with pink, orange, or green fluorescent powder (DayGlo Color Corp, Cleveland, OH) to enable us to track continuous movement of salamanders after release. By alternating pigment color, we reduced the likelihood of two identically-colored paths intersecting. Fluorescent powder has been used successfully in previous studies to track short-term movements of small amphibians (Eggert 2002, Graeter et al. 2008, Roberts and Liebgold 2008, Roe and Grayson 2008). Previous work has shown that the pigment does not affect survival or level of cutaneous respiration in newts and ambystomatid salamanders (Rittenhouse and Semlitsch 2006, Orlofske et al. 2009, Roe and Grayson 2009). Therefore, we do not think it likely that powder affected the movement behavior of animals in this study.

Two hours after release we returned and used ultraviolet lights (Arachnid A14, Blacklight.com, Volo, IL) to locate and follow powder trails deposited by salamanders. We followed trails until we located the salamander, the trail was lost,

or the trail ended at a predator with traces of fluorescent powder on its mouth or evidence of an obvious predation event (Fig. 1). We identified the species of the predator and measured the distance between the predation event and the edge of the pond. Predators were identified as ‘unknown anuran’ if the powder trail post-predation exhibited a pattern indicative of anuran movement (such as hopping behavior).

## RESULTS

Of the 124 salamanders tracked for this study, 29 were consumed by predators (23%), 33 were relocated alive (27%), and 62 were not found on the surface at the end of their trails (50%). Predation rates were comparable among the four ponds (Range: 17%–25%). Salamanders were predated by Green Frogs (*Rana clamitans*; 52%; n = 15), Bull Frogs (*Rana catesbeiana*; 17%; n = 5), and unknown anurans (31%; n = 9). The majority of predation events occurred within 5 m of the pond edge (Fig. 2; Table 1). The mean percentage predation per meter did not decrease with distance from pond between 6–15 m (Table 1).

## DISCUSSION

This study found that anuran predators present a substantial risk to Ringed Salamanders during initial movement away from natal ponds. Overall, approximately 23% of salamanders were consumed by predators in this study, and predation events occurred up to 15 m from the pond edge. The predation

documented also represents a minimum estimate of actual number of predation events, as a considerable proportion of salamanders were not relocated and their fates were unknown.

Studies documenting the terrestrial movement of amphibians after metamorphosis often analyze movement in relation to habitat type and structure (deMaynadier and Hunter 1999, Jenkins et al. 2006, Popescu et al. 2012). While habitat plays a profound role in amphibian movement decisions, predation risk may also influence movement behavior and search strategies. Both theoretical and empirical studies have found that predation risk has potentially large impacts on the consequences of prey movement decisions (Zollner and Lima 2005, Rittenhouse et al. 2009, Fraker and Luttbeg 2012). For example, Rittenhouse et al. (2009) found that Wood Frog (*Lithobates sylvaticus*) survival was highly influenced by movement strategy; Wood Frogs that remained close to the pond were more likely to die as a result of predation.

Juvenile salamanders likely behave in response to both habitat quality and predation risk under the limitations of movement and sensory capacity. Rittenhouse and Semlitsch (2007) found that terrestrial amphibian density is highest closest to breeding ponds and decreases substantially 30 m from the pond edge. We found that the highest proportion of predation events occurred close to the natal pond (0–5 m) and decreased slightly at distances farther than 5 m from the pond edge. We did not detect differences between predation rates 6–10 m and 11–15 m from the pond, but sample sizes at these distances were small. Linear

movement perpendicularly away from the pond edge should minimize the time that salamanders spend in areas with the highest predator densities. It is possible that during initial movement bouts into terrestrial habitat, juveniles have an evolved propensity to move linearly away from the pond regardless of acquired information in order to reduce predation risk (Jenkins et al. 2006, Patrick et al. 2007).

Studying the movement decisions of juvenile amphibians based on an incomplete accounting of risk may yield incorrect or misleading conclusions about the survival costs of movement behavior. Movement in response to predation risk may not be the best search strategy for locating ideal habitat for settlement, especially in fragmented areas or areas with highly clumped habitat. Movement behavior that is optimal for reducing predation risk may therefore appear maladaptive when considered in the context of locating settlement habitat. Future studies of juvenile salamander movement should seriously consider the impact of predation pressure on movement decisions during initial movement out of ponds in order to garner a more comprehensive understanding of the basis of amphibian behavior.

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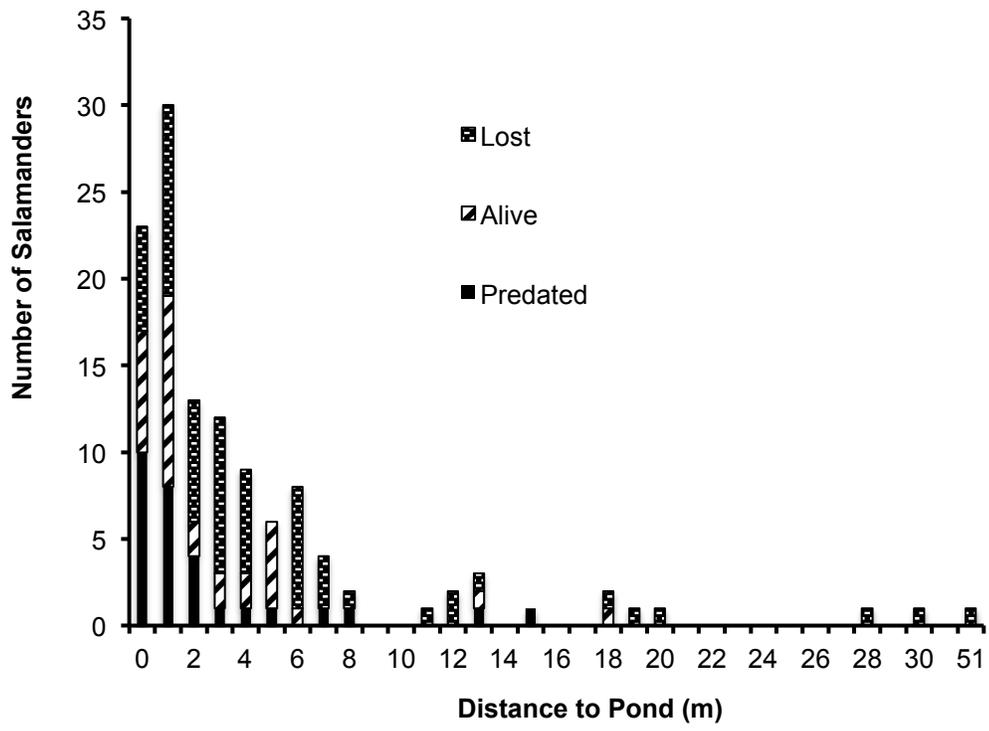
Table 1. Predation events based on distance from the pond. ‘Number present’ refers to the number of salamanders that traveled at least the minimum distance from the pond. ‘Number predated’ refers to the number of salamanders that were consumed by anurans within the distance from pond range. The ‘% predated/meter’ indicates the mean percentage of animals that were consumed at each meter within the distance range indicated.

| Distance from Pond (m) | # Present | # Predated | % Predated/m |
|------------------------|-----------|------------|--------------|
| 0 to 5                 | 124       | 25         | 4.9          |
| 6 to 10                | 27        | 2          | 2.4          |
| 11 to 15               | 13        | 2          | 3.2          |

Figure 1. Green Frog (*Rana clamitans*) after predation event. (Photographed by Dana Drake)



Figure 2. Fate of salamanders according to distance from pond. 'Lost' represents salamanders which were not located at the end of the trail, 'alive' represents salamanders that were located alive on the surface, and 'predated' represents salamanders which were consumed.



## **APPENDIX B**

### **RISK OF DESICCATION AFFECTS MOVEMENT BEHAVIOR OF JUVENILE POND-BREEDING SALAMANDERS**

Shannon E. Pittman, Amber Pinnell, Brett Spatola, and Raymond D. Semlitsch

#### **ABSTRACT**

Internal and external factors may interact to affect the movement behavior of individuals. Juvenile pond-breeding salamanders are particularly susceptible to environmental conditions during initial movement out of wetlands. However, the ways in which juveniles mitigate risk during natal dispersal is not currently well understood. We tested the effects of desiccation risk and body size on the movement behavior of juvenile spotted and ringed salamanders under controlled laboratory conditions. We found that desiccation risk and body size significantly affected the movement behavior of juvenile spotted salamanders. We found that juvenile ringed salamanders moved significantly more in the high risk treatment than the low risk treatment, but body size did not impact ringed salamander movement decisions. We conclude that the ways that the external environment and internal state impact movement decisions may be species specific. Fine-scale behavioral data is therefore required to understand species' responses to habitat alteration that affects animal movement.

## INTRODUCTION

Resource acquisition often requires animals to explore hostile or suboptimal environments, and animals employ a wide variety of behavioral strategies to minimize the risk associated with this movement (Bonte et al. 2012). How animals alter movement to mitigate risk influences population and spatial dynamics occurring across a range of spatiotemporal scales. Human-induced habitat alteration changes the level and types of risks encountered by animals during movement (Fahrig 2007). The impact of habitat alteration on species persistence is dependent on the ways in which animals assess and respond behaviorally to movement risks (Knowlton and Graham 2010).

Body size relative to conspecifics is often an important correlate of physiological condition and a phenotypic characteristic fundamental to animal movement capacity (Mech and Zollner 2002, Delgado et al. 2010). Because optimal movement strategies are affected by movement capacity, body size is often assumed to be a significant mediating factor in individual responses to movement risk (Hempton et al. 2012, Claussen et al. 2000). Animals undergoing ontogenetic habitat shifts into novel environments face substantial risks to survival. Because these animals are naïve to the environment and associated risks, behavioral strategies to mitigate risk may not always be proportional to actual risk. Naïve animals moving into anthropogenically-altered habitat may not employ movement

strategies that maximize the likelihood of survival, which could yield population-level dynamics that are more sensitive to the type and level of habitat alteration than would be predicted based on the animal's physiological capacity for movement alone (Fahrig 2007).

Pond-breeding salamanders have complex life cycles, with an aquatic larval stage and a terrestrial adult stage, and are sensitive to the quality of the terrestrial habitat surrounding wetlands (Dodd Jr and Cade 1998, McDonough and Paton 2007, Popescu and Hunter Jr 2011). Spotted salamanders (*Ambystoma maculatum*) and ringed salamanders (*Ambystoma annulatum*) are forest dependent and undertake initial movements out of wetlands on the spatial scale of 50-100 m (Osbourn 2012). The risks encountered by recently-metamorphosed salamanders during this initial movement phase are substantial, and behavioral strategies in response to risk may have important effects on the likelihood of survival (Rittenhouse and Semlitsch 2006, Rothermel and Semlitsch 2002). Additionally, juveniles are considered to be the primary inter-population dispersers for many pond-breeding amphibian species (Gill 1978, Berven and Grudzien 1990, Gamble et al. 2007), so factors affecting survival at this life stage will have implications for metapopulation dynamics and gene flow. Documented movement risks include desiccation from evaporative water loss (Rittenhouse et al. 2008), predation (Rittenhouse et al. 2009), density effects (Patrick et al. 2008, Berven 2009), and depletion of energy (Scott et al. 2007).

Human-induced habitat alteration increases the risk associated with amphibian movement, particularly the risk of desiccation. Habitat alteration for urban or agricultural development is often accompanied by decreases in canopy cover, soil moisture, and ground cover (Fischer and Lindenmayer 2007), which negatively impact the survival of juvenile amphibians (Harper and Semlitsch 2007, Rittenhouse et al. 2008). Previous studies have also shown that juvenile pond-breeding salamanders have lower survival in grassland and agricultural habitat than forest habitat (Rothermel and Semlitsch 2002, Veysey et al. 2009), as well as higher rates of desiccation (Graeter et al. 2008). Mark-recapture studies have additionally shown that habitat quality affects movement and settling behavior by juvenile spotted salamanders (Osbourn, 2012). However, the fine-scale behavioral mechanisms for these effects are unknown (Osbourn, 2012). A mechanistic approach to amphibian behavioral responses to desiccation risk may aid in explaining and predicting patterns occurring at larger scales.

The ways in which salamanders respond behaviorally to desiccation risk and how internal factors such as body size affect decisions will determine the extent to which they are able to behaviorally mitigate the effects of habitat loss and alteration. In this study, we measured the behavioral responses of individuals to different risks of desiccation. We tested the influence of desiccation risk on movement behavior in two species of salamanders, spotted salamanders (*Ambystoma maculatum*) and ringed salamanders (*Ambystoma annulatum*), by controlling levels of desiccation and observing movement in indoor enclosures.

We predicted that higher levels of desiccation would result in higher overall rates of movement.

## METHODS

### ***Capture and Handling***

One hundred and twenty juvenile spotted salamanders (*Ambystoma maculatum*) and sixty juvenile ringed salamanders (*Ambystoma annulatum*) were used in this experiment. We collected salamander egg masses from Mark Twain National Forest in Boone County, MO, USA (spotted salamanders) and Daniel Boone Conservation Area in Warren County, MO, USA (ringed salamanders) and raised salamander larvae in outdoor cattle tanks at a University of Missouri-Columbia research facility in Columbia, MO, USA. We checked cattle tanks nightly for metamorphosed salamanders. Recently-metamorphosed salamanders were housed in containers with damp sphagnum moss in an indoor laboratory at the University of Missouri-Columbia with controlled temperature (25C). Animals used in the experiment were tested within 4 weeks of their metamorphosis. Because salamander movement typically occurs at night, we conducted all trials at night using a red light for observation.

### ***Experimental Design***

To determine the effect of desiccation level on salamander movement, we randomly assigned animals to one of four desiccation treatments for spotted salamanders: 0% body weight lost (control – fully hydrated), 5% body weight lost

(low risk), 10% body weight lost (medium risk), and 15% body weight lost (high risk), and two desiccation treatments for ringed salamanders: 0% body weight lost (control – fully hydrated) and 15% body weight lost (high risk). Thirty spotted and ringed salamanders were assigned to each of the treatments. To apply these treatments, we removed each salamander from its housing container, weighed it, and placed it within a covered, rounded container. Salamanders were held in these containers devoid of moisture to allow desiccation to occur. We weighed salamanders periodically depending on the size of the salamander and the assigned level of desiccation. Pilot studies were used to determine approximate rate of salamander water loss based on body size. When salamanders approached the appropriate weight, they were placed on the scale and body weight was continuously monitored until the correct weight was attained.

Salamanders that were assigned to the control treatment were placed in rounded, covered containers with 5-mm of water at the bottom, which prevented desiccation. We randomly assigned each control animal to be held in these containers for one of three amounts of time, each corresponding to the average amount of time to desiccation for each of the low, medium, and high risk treatments. We could therefore correlate time spent in desiccation container and handling time with movement behavior in order to ensure that differences in movement behavior observed in the trials were a result of differences in desiccation level and not differences in handling time.

We observed salamander movement behavior for 20 min at 25°C within 310 cm by 10 cm plastic enclosures. The bottom and sides of the enclosures were lined with outdoor carpeting (100% Eco-fi polyester Nonwoven material with backcoating, 3mm pile height Delour). We used outdoor carpeting instead of soil to line the enclosures because soil stuck to the bodies of the salamanders, which prevented accurate estimation of salamander weight immediately following the experiment. The outdoor carpeting that we used in this experiment mimicked soil but did not stick to the bodies of the salamanders during movement. We replaced the carpeting between each trial to prevent conspecific scent from affecting movement decisions.

After desiccation, we carefully placed the salamander at one end of the movement enclosure. We recorded the time to first movement (movement latency), position of animal along the length of the enclosure every 3 min, and the time and position of the animal at the end of each continuous movement bout. The response variable of interest was total distance moved from the beginning to the end of the 20-min trial. We determined the location of the salamanders within the enclosures by marking the sides of the enclosures at equal distances, and by observing a measuring tape set along the side of the enclosure.

We observed 2 animals at a time with a dim red light, each in a separate enclosure. If the salamander moved the entire length of the enclosure, we prodded the salamander's tail once to provide incentive for the animal to move down the length of the enclosure again. Observers were oriented behind the enclosure, with

the salamander facing away from the observer when it was initially introduced to the enclosure. At the end of the 20 min trial, we weighed the salamanders and placed them in containers with water to speed rehydration. After a minimum of 10 min in the rehydration container, we placed the salamanders within their housing containers. No animals died as a result of this experiment.

### ***Data Analysis***

We analyzed the effects of desiccation level and body size on total distance moved in spotted and ringed salamanders. For spotted salamanders, we analyzed the effects of desiccation treatment, body size (mass), and the interaction between treatment and body size on total distance traveled using linear models. For ringed salamanders, we used ANOVA to analyze the effects of the desiccation on total distance moved with desiccation as a factor and body mass as a covariate. We plotted the data to ensure the assumption of normality and all statistical tests were conducted in R. We additionally tested for the effects of handling time on movement rates of salamanders in the control treatments using ANOVA.

## **RESULTS**

Mean mass of spotted salamanders in this study was 0.89 (SE = 0.02), while the mean mass of ringed salamanders in this study was 1.22 mm (SE = 0.06).

Multiple linear regression of the combined influence of treatment, body size, and treatment x body size showed that spotted salamander total movement was a positive linear function of body size ( $P = 0.026$ ) and the interaction of desiccation

level and body size ( $P = 0.001$ ), and a negative function of desiccation level ( $P = 0.021$ ; model  $R^2 = 0.44$ ; Fig. 1A-D). We additionally found that desiccation treatment significantly affected movement in ringed salamanders ( $P < 0.001$ ), but body size did not ( $P = 0.60$ ). Ringed salamanders in the high risk treatment moved an average of 888 cm ( $SE = 56$ ) while ringed salamanders in the control treatment moved 415 cm ( $SE = 41$ ). Additionally, handling time did not affect the movement behavior of either ringed ( $P = 0.3$ ) or spotted salamanders ( $P = 0.4$ ).

## DISCUSSION

Results from this study provide evidence that desiccation level and body size affect movement strategies employed by juvenile salamanders, and behavioral responses may be highly species-specific. Larger spotted salamanders responded to high desiccation risk with increased movement, while smaller spotted salamanders moved less, likely in an attempt to conserve water. Mass was not a significant factor affecting movement in ringed salamanders, but animals in the higher risk treatment moved significantly more than animals in the control treatment. Our study provides evidence that seemingly small differences in body size can have substantial impacts on risk-taking strategies of juvenile amphibians for some species.

Juvenile spotted salamanders vary in body size upon metamorphosis (Shoop 1974, Harper and Semlitsch 2007), and our study indicates that body size may influence both the physiological capacity and motivation for movement in

terrestrial habitat. Because juvenile amphibians typically disperse from natal wetlands during favorable weather conditions, body size may not impact distance moved from a natal site in high-quality habitat. However, body size may impact the degree to which juveniles cross unfavorable habitats, such as open-canopy fields or roads (Rittenhouse and Semlitsch 2006, Cosentino et al. 2011), and during unfavorable, dry weather.

Body size was not a significant factor in determining the response of juvenile ringed salamanders to desiccation risk. Ringed salamanders were larger on average than spotted salamanders, and as a consequence may have lost water at a slower rate. Additionally, juvenile ringed salamanders move farther than spotted salamanders upon metamorphosis based on mark-recapture studies in the field (Osbourn 2012). Therefore, ringed salamanders may attempt to mitigate risk by locating higher-quality habitat through displacing themselves from the low-quality area, while spotted salamanders may attempt to wait out the high-risk conditions. These alternative risk-mitigation strategies may have different impacts on the spatial dynamics of populations in altered landscapes. While ringed salamanders may be more likely to cross poor-quality habitat, they also may have higher mortality by encountering poor-quality conditions at a higher rate. Spotted salamanders may be less likely to cross poor-quality habitat which may limit the functional connectivity of populations. However, juvenile spotted salamanders may also be less likely to suffer mortality from movement through suboptimal habitat.

Results from our study support the idea that movement behavior may be determined by both internal and external conditions (Nathan et al. 2008). However, the degree to which internal and external factors affect movement may also be highly species-specific. Species-specific behavioral data may vastly improve our understanding of the proximate effects of habitat alteration to the persistence and functional connectivity of amphibian populations.

#### ACKNOWLEDGEMENTS

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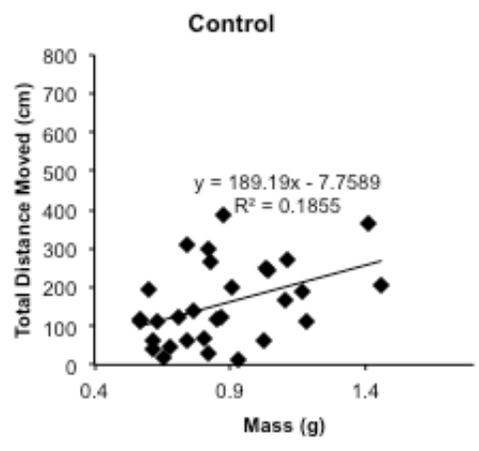
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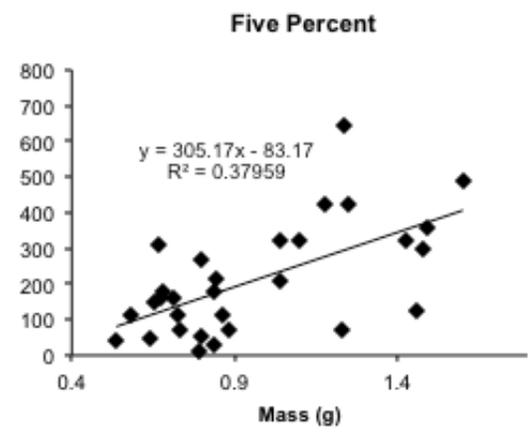
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Figure 1. Effects of mass on movement of juvenile spotted salamanders (*Ambystoma maculatum*) in response to differing desiccation risks.

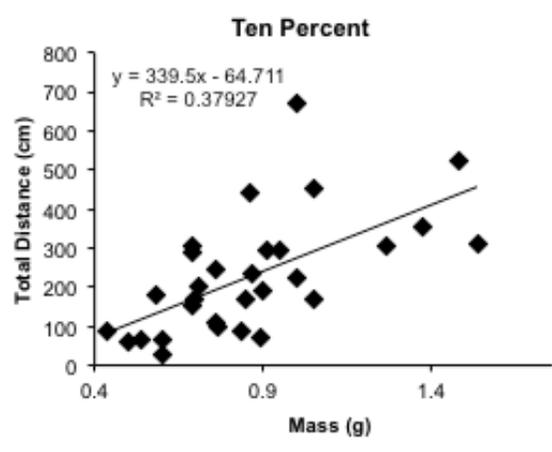
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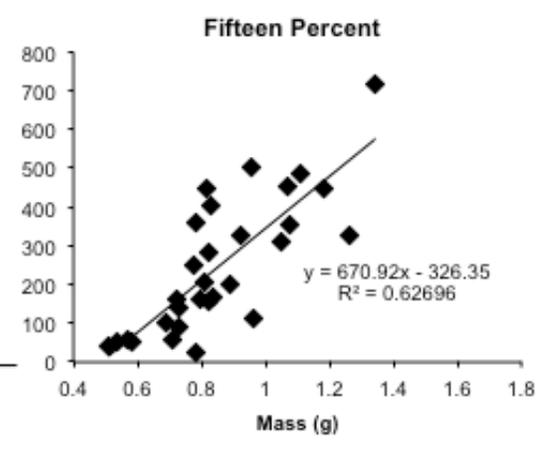
B)



C)



D)



## APPENDIX C

### BEHAVIORAL DATA USED TO PARAMETERIZE MOVEMENT MODELS

Figure 1. Histogram of r-values for individual salamanders in Chapter 2.

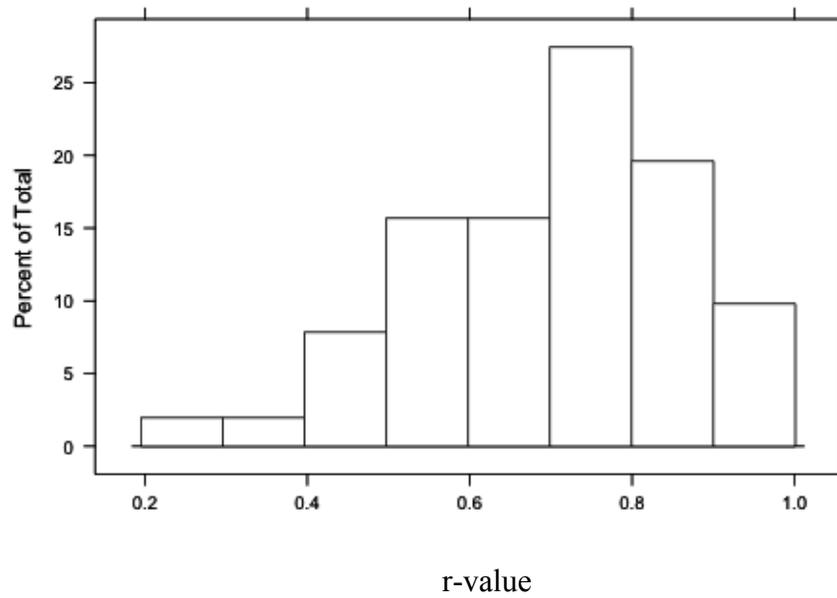
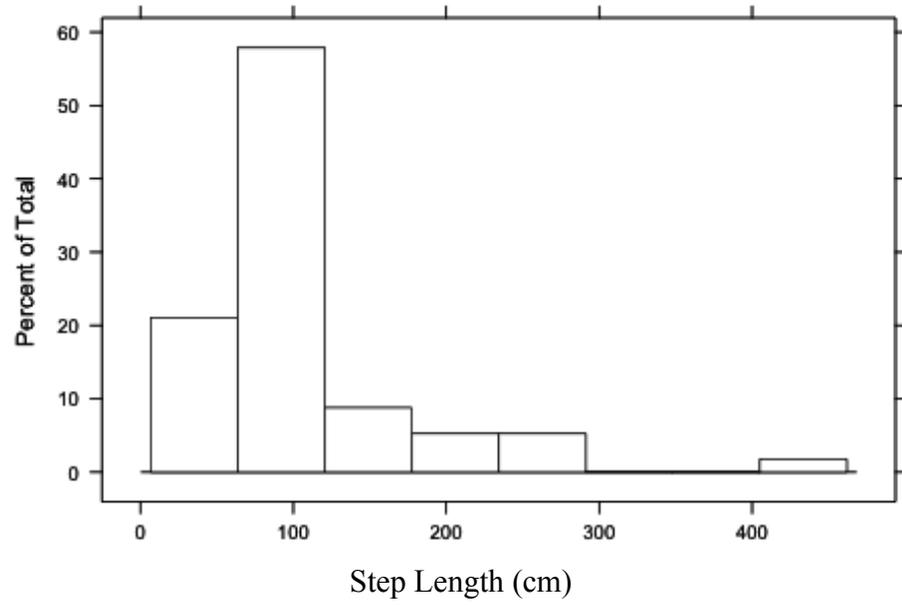


Figure 2. Histogram of step lengths for individual salamanders in Chapter 2.



## VITA

Shannon Pittman was born on April 27, 1986 in Birmingham, Alabama. In 2004, she graduated from Groton School, where Dr. David Black first introduced her to amphibian biology through an independent research project on ambystomatid salamanders. While in high school, Shannon attended ecology-focused summer programs at Dauphin Island Sea Laboratory in Alabama and Mountain Lake Biological Station in Virginia. She earned a B.S. in Biology from Davidson College in 2008. While at Davidson, Shannon worked extensively in the laboratory of Dr. Michael Dorcas studying the ecology of a wide range of reptile and amphibian species, with independent research projects on the ecology of gray treefrogs, bog turtles, and diamondback terrapins. She additionally spent three months in 2006 studying abroad at the School for Field Studies in Queensland, Australia, where she learned about rainforest ecology and restoration. Shannon began graduate school at the University of Missouri in 2008 under the mentorship of Dr. Raymond Semlitsch. She earned a Ph.D. from the Division of Biological Sciences in May 2013. She will be conducting post-doctoral research in the laboratory of Dr. James Forester at the University of Minnesota in St. Paul, Minnesota. In the future, she would like to continue studying animal movement ecology to improve conservation and management practices.