INITIAL JUVENILE MOVEMENT OF POND-BREEDING AMPHIBIANS IN ALTERED FOREST HABITAT

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Doctor of Philosophy

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by

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The undersigned, appointed by the dean of the Graduate School, have examined the dissertation entitled

INITIAL JUVENILE MOVEMENT OF POND-BREEDING AMPHIBIANS IN ALTERED FOREST HABITAT

presented by Michael S. Osbourn,

a candidate for the degree of doctor of philosophy,

and hereby certify that, in their opinion, it is worthy of acceptance.

Professor Raymond Semlitsch

Professor James Carrel

Professor Lori Eggert

Professor Dylan Kesler

To all those without whose support I could not have made it this far.

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ABSTRACT

The initial juvenile movement phase represents the first stage of the multi-phase process of natal or juvenile dispersal and is particularly crucial as individuals encounter novel habitats and are highly vulnerable to mortality. For many amphibian species, juveniles represent the primary dispersal stage and therefore have a disproportionate influence on population dynamics and persistence. My objective was to investigate how alterations in forest habitat quality impact initial juvenile movement success and behavior. To this end, I conducted a mark-recapture study of juvenile Spotted Salamanders (*Ambystoma maculatum*) and Green Frogs (*Lithobates clamitans*) emerging from natal ponds within experimental forest arrays. Each array contained four treatment quadrants (2.11 ha each) containing a control, partial cut, burned clearcut, or unburned clearcut. I determined movement success and identified individual behaviors by analyzing the proportion of juvenile recaptured at drift fences located at 0 m, 20 m, and 50 m from the natal pond, in each quadrant.

The partial cut accounted for over half (53%) of the total Spotted Salamander recaptures in 2008, followed by the control and burned clearcut (20% each), and the unburned clearcut with the fewest (7%). Green Frogs also showed a significant effect of forest treatment, with 54% of recaptures occurring in the control followed by the partial cut (35%), burned clearcut (7%), and unburned clearcut (4%). While we recaptured significantly more Spotted Salamanders at 20 m than 50 m, there was no distance effect with Green Frogs. A significantly greater proportion of both Spotted Salamander and Green Frog juveniles initially moving through open-canopy habitats switched to forests. Nearly all recaptured salamanders originally released into partial cuts were recaptured there (97% treatment fidelity) and only 3 % switched to other habitats, whereas in unburned clearcuts 61 % switched habitats. Green Frog juveniles showed 96% and 68% fidelity to the control and partial cut, respectively. In clearcut treatments, 74% and 87% of Green Frogs switched to forest treatments from the burned and unburned treatments, respectively.

I next sought to identify how fine-scale habitat quality affected juveniles' decisions to cease moving away from their natal pond, select a refuge, and settle. By using experimental enclosures, I attempted to isolate the effects of forest canopy and microhabitat manipulations on salamander settling decisions relative to unmanipulated forest controls. I employed generalized linear mixed models to examine the effects of canopy cover (closed or open), microhabitat (control, compacted soils, high coarse woody debris, high burrow density), temperature (weekly mean ˚C), weekly total rainfall amount (cm), and body size (mass; g) on the probability of settling. The analyses for both species revealed strong effects of habitat quality on this key decision. Specifically, in the open canopy control, *A. maculatum* and *A. annulatum* had 10% and 30% decreased probability of settling, respectively, compared to the closed canopy control. *Ambystoma annulatum* were 24% less likely to settle in compacted soil. The responses to the increased refuge density appear to be species-specific. While microhabitat quality did not impact the settling probability of *A. annulatum,* for *A. maculatum*, the probability of settling increased 18% and 25%, respectively, under conditions of high burrow density and high coarse woody debris.

This study provides empirical evidence that initial juvenile movement is affected by habitat quality. By releasing thousands of individually marked juveniles, I was also able to record previously undescribed behaviors. This study increases our understanding of individual-level movement responses and provides valuable insights for better predicting patterns of movement at larger scales.

CHAPTER 1

THE MOVEMENT ECOLOGY OF JUVENILE POND-BREEDING AMPHIBIANS

Michael S. Osbourn

INTRODUCTION

Nathan et al. (2008) proposed a conceptual framework for examining the lifetime movements of organisms as a series of phases associated with fulfillment of particular goals. The movement paths of individuals are determined by an interaction among internal state, movement capacity, navigational capacity, and external factors (Nathan et al. 2008). By subdividing movement phenomena into distinct movement phases we can begin to identify processes and relate them to patterns observed at larger scales. For animals, the goal of a movement phase could be, for example, foraging, predator evasion, breeding migration, or long-distance dispersal. Each movement phase involves trade-offs in terms of fitness (Zollner and Lima 2005) and produces discernible patterns when measured at varying spatiotemporal scales throughout the lifetime of an individual (Fryxell et al. 2008, Nathan et al. 2008; Figure 1).

When viewed at a fine scale, often multiple behavioral states or “movement modes” can be identified within each movement phase (Fryxell et al. 2008, Getz and Saltz 2008, Nathan et al. 2008). Shifts between movement modes are thought to be initiated by changes in an individual’s internal state and/or external factors (Nathan et al. 2008). Multiple movement modes should be advantageous in heterogeneous landscapes, allowing individuals to respond adaptively to variations in habitat quality.

Movement modes therefore enable animals to optimize movement success while balancing trade-offs between movement rate, searching, or vigilance with energy reserves, predation risk, or desiccation risk (Zollner and Lima 2005, Wiens 2001).

The importance of dispersal to ecological and evolutionary processes is well documented; however it persists as a significant gap in our understanding of ecology (Ronce 2007). For many species complexity, condition dependence, and limitations of current tracking technology have contributed to a lack of fine-scale empirical data concerning dispersal (Massot et al. 2002, Clobert et al. 2009). Also contributing to our lack of understanding is the traditional tendency to over-generalize dispersal as a uniform movement phenomenon rather than a multi-staged process (Bowler and Benton 2005). Further encumbering our attempts to elucidate the processes and patterns of dispersal is the wide-spread ambiguity and inconsistent use of terminology within dispersal literature (Bowler and Benton 2005). Since our focus is on pond-breeding amphibians, we have adopted the terminology as defined by Semlitsch (2008). Dispersal differs from migration in that it is the one-way movement of individuals from their natal site to a new site for breeding, whereas migration is the two-way movement of individuals between resource patches. The most conspicuous migratory movements of pond-breeding amphibians are adult breeding migrations between terrestrial home ranges and breeding wetlands. Far less visible are the movements of newly-metamorphosed juveniles into terrestrial habitats. Currently, it is not possible to distinguish which individuals will ultimately move to new breeding populations (dispersers) from those that will establish terrestrial home ranges within their natal population range (emigration). Because of this uncertainty, we have chosen to avoid the use of the terms “dispersal” or “emigration” when discussing this first terrestrial stage in amphibians. By using the outcome-neutral label of “initial juvenile movement” we seek to avoid confusion while focusing attention on this critical stage in animal movement.

The initial juvenile movement phase represents the first stage of the multi-phase process of natal dispersal or juvenile emigration. This is a particularly crucial phase for juvenile animals which may have ramifications in terms of population persistence. Juveniles are highly vulnerable to mortality as they encounter novel habitats with only very limited knowledge about the locations of resource patches (Lucas et al. 1994, Alberts and Altmann 1995, Delgado et al. 2009). Unlike adults, juveniles lack prior experience moving through habitats and have more limited perceptual ranges (Zollner and Lima 2005). For many species, initial juvenile movement is an ecological bottleneck in which high mortalities greatly reduce the number of individuals before they have had an opportunity to establish individual home ranges or disperse to a new breeding population. The post-fledging movements of juvenile birds (e.g. White and Faaborg 2008) and the movements of salmon fry emerging from their redd into the water column (e.g. De Garcia Leaniz et al. 2000) are examples of initial juvenile movement. The challenge of initial juvenile movement can be further compounded by an ontogenetic habitat shift (e.g. juvenile pelagic seabirds, sea turtles, and amphibians; Janzen 1993, Huyvaert and Anderson 2004, Semlitsch 2008, respectively).

Pond-breeding amphibians provide an excellent study system for investigating initial juvenile movement. While there are obvious differences in life-history and behavior among the various taxa of pond-breeding amphibians, such as newts (Salamandridae), toads (Bufonidae), mole salamanders (Ambystomatidae), true frogs (Ranidae), tree frogs (Hylidae), narrow-mouthed toads (Mycrohylidae), and spadefoot toads (Scaphiopodidae), they all have a complex life cycle (aquatic larval stage and terrestrial juvenile and adult stage), centered around a breeding/natal wetland. The requirement of aquatic habitat for early life-stages results in spatiotemporal concentration of juveniles at natal wetlands following metamorphosis, providing a predictable source of test subjects. Also, their limited movement distances mean that they can be studied at much smaller scales than many other vertebrate taxa. Amphibians' are also sensitive to changes in habitat quality because of their high susceptibility to evaporative water loss while moving through terrestrial habitats (Jørgensen 1997). For most pond-breeding amphibian species, juveniles represent the primary dispersal life stage (Semlitsch 2008). Because of the dynamic nature of breeding/natal wetland quality, juvenile dispersal plays a vital role in rescue and recolonization of ponds following local extinctions or bottlenecks (Marsh and Trenham 2001). As a result, the movement success of juveniles can have a disproportionate influence on local population and metapopulation dynamics. It is also important that we continue to identify the mechanisms of global amphibian declines (Stuart et al. 2004), particularly in light of the recognition of habitat loss and alteration as the leading contributor (deMaynadier and Hunter 1995, Gardner et al. 2007).

Traditionally, many studies of amphibian movement have focused on the outcomes of movement without considering the behavioral state of individuals, while studies focusing on individual behavior have often failed to place those behaviors within a larger fitness context. As a result the literature on juvenile amphibian movement and orientation occasionally appears contradictory and contains examples of both random and non-random initial orientation, and examples of forest-associated species both entering and avoiding open-canopy habitats. By applying the movement ecology conceptual framework of Nathan et al. (2008) we can begin to put these apparent contradictions into context. The concept of movement modes can explain some of these contradictions by attributing differing outcomes to different behavioral states.

By dissecting amphibian life-time movements into phases driven by specific goals (Figure 1) and then further identifying behavioral movement modes within each movement phase (Figure 2), we can develop a more accurate understanding of amphibian movements. We recognize pre-departure, initial juvenile movement, and home range establishment as the fundamental movement phases of natal dispersal and juvenile emigration for pond-breeding amphibians. By examining fine-scale, individual-level responses of juvenile amphibians, we can begin to elucidate the mechanisms underlying patterns seen at higher scales of organization (Wiens 1993, Haddad 1999, Morales et al. 2010). In this introductory chapter, we have attempted to integrate empirical findings and observations from the literature into a movement ecology conceptual framework following Nathan et al. (2008), Bowler and Benton (2005), Clobert et al. (2009), and Bonte et al. (2012). In the following, we outline potential movement phases and accompanying movement modes for juvenile pond-breeding amphibians. Ultimately this approach should inform the development of predictive models to aid in conservation and management of populations and species.

The pre-departure phase

The initial juvenile movement phase is preceded by the pre-departure phase. The goal of the pre-departure phase is to prepare for initial juvenile movement. Newly metamorphosed amphibians may forage, grow, and increase energy reserves while waiting for optimal movement conditions. Juvenile pond-breeding amphibians also establish their initial orientation during this phase. The pre-departure phase is composed of one to three discernible movement modes, including an obligate aquatic “pre-emergence” mode and facultative terrestrial “waiting” and “prospecting” modes.

Pre-emergence mode

The pre-emergence movement mode represents a distinct shift from aquatic-larval to post-metamorphosis behavior. During this transition period metamorphosing amphibians move to the shallow margins of their natal wetland and begin to perceive near-pond terrestrial habitats and select where to emerge. Information gathered at this time may help juveniles establish their initial orientation, and possibly their terrestrial movement trajectories before leaving the water.

Amphibians establish a “Y-axis orientation” as larvae, whereby they orient perpendicular to the shore and move along an axis between shallow pond margins and deep water (Ferguson and Landreth 1966). Depending on the species, orientation along the Y-axis can be accomplished through several sensory mechanisms including a sun compass (Adler 1976), polarized light (Taylor and Adler 1973, Taylor and Auburn 1978, Auburn and Taylor 1979), and magnetic compass (Phillips 1998, Deutshlander et al. 2000, Freake et al. 2002). This is important for many species that establish a fixed reference point or internal map for terrestrial navigation away from their natal pond, and to later aid their return as breeding adults (see Sinsch 1987). Larvae and metamorphs during this stage may also develop a scent profile for their natal pond. For example, McGregor and Teska (1989) demonstrated an attraction by immigrating adult Spotted Salamanders to the scent of their breeding pond and hypothesized that this recognition was established as juveniles before departure.

There is also evidence that larval amphibians position themselves at pond margins adjacent to favorable terrestrial habitats. Hayward et al. (2000) speculated that newt larvae begin orientation towards surrounding terrestrial habitat prior to metamorphosis. This trend was confirmed by Patrick et al. (2007), when they observed that Wood Frog larvae (*Lithobates sylvatica*) in natural natal wetlands oriented in the direction of predominant forest cover. When the authors transplanted larvae to experimental pools, the emerging metamorphs maintained their original orientations acquired at their pond of origin. Pre-emergence behavior ends with the completion of metamorphosis and emergence from the natal wetland. At this point individuals decide whether to wait, explore, or depart.

Wait Mode

The timing of metamorphosis is affected by complex interactions among multiple factors and does not necessarily coincide with optimal terrestrial conditions (Wilbur and Collins 1973, Semlitsch et al. 1988). Juveniles typically time their movements to coincide with warm rainy or humid nights (Todd and Winne 2006, Timm et al. 2007a, Hocking et al. 2008); however, metamorphosis may force many individuals to transition to terrestrial habitats regardless of whether environmental conditions are suitable for movement. Immediately following metamorphosis, juvenile amphibians must often wait at the interface between water and land until conditions are optimal for terrestrial movement. More-aquatic species such as Green Frogs (*Lithobates clamitans*) or Bullfrogs (*L. catesbeiana*) wait in the emergent vegetation, in the shallow margins of the pond. Some species are easily observed waiting to depart such as recently metamorphosed Southern Leopard Frogs (*L. sphenocephalus*) congregating in the grassy areas surrounding wetlands (M. Osbourn pers. observ.). More-terrestrial species, such as ambystomatid salamanders, are often overlooked while waiting under terrestrial cover objects within several meters of the pond edge (M. Osbourn pers. observ.).

The timing and size of individuals at metamorphosis likely is an important factor determining the duration a juvenile will wait to depart their natal pond. Chelgren et al. (2008) found that the propensity of juvenile Northern Red-legged Frogs (*Lithobates aurora*) to wait for rainfall before moving increased with decreasing body size. Because of the negative relationship between desiccation rate and body size in amphibians (Newman and Dunham 1994), choosing to wait at the natal wetland and grow before moving overland could be a beneficial strategy for small individuals. Chelgren et al. (2008) also found that waiting for rainfall decreased with increasing time to metamorphosis, perhaps due to greater development in individuals with prolonged larval periods (Pough and Kamel 1984, Buckley et al. 2005). Pond drying later in the season may also effect the duration of waiting.

Waiting too long to move can be costly. Competition for limited refuges and predation pressure is often high for juvenile amphibians near the wetland (Osbourn unpubl. data). These pressures likely result in high mortalities of individuals waiting for optimal weather for terrestrial movement. Shoop (1974) reported finding dead, desiccated Spotted Salamander (*Ambystoma maculatum*) metamorphs in mud and debris next to their pond. There is also evidence of juvenile amphibians opting to move rather than remain next to their wetland during prolonged dry periods. Rothermel (2004) reported that a large number of Spotted Salamander metamorphs moved from their ponds during prolonged dry periods. We also observed this tendency at our drift fence arrays (Chapter 2). The decision of when to move involves balancing trade-offs among the competing pressures of energetic limitations, predation, and competition, against the heightened desiccation risk of terrestrial movement in dry conditions. Such trade-offs are integral to animal movement and likely drive the transitions between different movement modes (Wiens 2001, Zollner and Lima 2005). Juveniles may reach a physiological threshold at which the costs of continued waiting outweighs the costs of moving.

Prospecting mode

Recent metamorphs may conduct limited information gathering prior to departing pond-edge habitats. Prospecting allows individuals to sample surrounding habitats prior to departure and is a well-described behavior in birds (e.g. Cox and Kesler 2012). During “prospecting mode”, juveniles make brief forays into nearby terrestrial habitats accumulating information about potential movement habitats and orientations (see Conradt et al. 2003). There is very little documentation of this behavior in amphibians and its occurrence may be highly species-specific. It is likely that individuals alternate repeatedly between prospecting and wait modes before they depart from near-pond habitats. Prospecting may enable juvenile amphibians to locate the highest-quality refuges in which to wait for rain or forage prior to departure. Because of the added energetic investment required and desiccation risk, this movement mode may be too costly for smaller individuals or some species. Individuals must balance the advantage of increased familiarity with surrounding habitat against depleted energy reserves and increased exposure to predators and desiccation. Prospecting may occur primarily in more-vagile taxa such as ranid frogs. For example, juvenile Green Frogs have been observed moving back and forth repeatedly between their pond and adjacent habitats before departure (M. Osbourn pers. observ.)

Initial orientation

Pond-breeding amphibians likely establish initial orientation during the pre-departure phase. The direction of first movements away from the natal wetland plays an important role in movement success of juvenile amphibians navigating through novel terrestrial habitats. Depending on the interplay of multiple internal and external factors, initial orientation may appear either random (uniform) or nonrandom (directional). Roznik and Johnson (2009) observed Gopher Frogs (*L. capito*) initially orienting randomly from natal ponds, however when they encountered heterogeneous terrestrial habitat they directed their orientations toward areas of higher habitat quality. Many studies, however, have shown nonrandom initial orientation to be the norm (e.g. Stenhouse 1985, Sinsch 1990, Vasconelos and Calhoun 2004, Patrick et al.

2007). Nonrandom initial orientation may indicate selection for favorable terrestrial habitat, however the cues associated with this behavior are not well understood (Dodd and Cade 1998, Rothermel 2004).

Walston and Mullin (2008) provided evidence that juvenile amphibians oriented in the direction of greatest forest cover. Other studies, however, suggest that factors determining nonrandom initial orientation are more complex and vary among sites or shift among years at the same site (Jenkins et al. 2006, Timm et al. 2007b, Homan et al. 2010). Given the limited perceptual ranges of juvenile salamanders (5-10 m, S. E. Pittman, unpubl. data), it is most likely that they are orienting towards near-pond, fine-scale microhabitat features, such as moisture gradients, herbaceous vegetation structure and composition, and microtopography, rather than larger-scale habitat features. Rothermel (2004), for example, found that Spotted Salamander metamorphs initially oriented nonrandomly, however their orientations did not correspond with the direction of suitable terrestrial habitat. When juvenile amphibians must wait for rainy conditions at the pond edge, rather than departing directly at emergence, their initial orientation may then correspond with the location of near-pond temporary refuges exploited during wait mode.

The initial juvenile movement phase

For pond-breeding amphibians, initial juvenile movement begins on wet nights following metamorphosis, when juveniles emerge from their natal pond with the goal of moving into terrestrial habitats and eventually establishing a home range. Juveniles may complete initial juvenile movement after their first night movement pulse or it may require multiple nights to reach their goal. During the initial pulse, juveniles have very limited information regarding the location of suitable movement habitat and refuges. It is likely that individuals continuing initial juvenile movement for multiple nights refine their search image of suitable microhabitat as they accumulate experience. They may use a series of different refuges as temporary “stepping stones” until a long-term settling location is chosen. Also, as conditions change, some individuals may abandon newly established home ranges that prove unsuitable for long-term settlement and resume movement. In species where philopatry is high (e.g. 91% in Marbled Salamanders, *Ambystoma opacum*; Gamble et al. 2007), most juveniles stop moving away from their natal pond and settle within the migratory range of their natal population. For a small yet vital minority (9%; Gamble et al.

2007), initial juvenile movement develops into true natal dispersal when individuals settle outside of their natal population and join the breeding migrations of a new population.

Departure

If conditions are optimal for overland movement, juveniles may transition directly to the initial juvenile movement phase immediately following emergence. Evidence of “direct departure” is provided by observations of salamander metamorphs with gill stubs or frogs still absorbing their tails moving in terrestrial habitats (M. Osbourn pers observ.). Depending on conditions, many juveniles will wait for rain (or the drop in barometric pressure preceding a rain) before departing. The timing of departure is likely highly condition-dependent and for some species and individuals “delayed departure” may be advantageous. Others, however, may be forced to stop waiting and depart during an extended dry period once a physiological threshold is reached (e.g. dwindling energetic reserves). Competition for limited moist refuges near the natal pond may also force some individuals to move when environmental conditions are not ideal.

Away Mode

The first behavioral state experienced by juvenile amphibians departing their natal wetland is “away mode”. Once this movement mode is initiated juveniles move rapidly away from their natal pond, ignoring potential refuges in favor of speed and greater distance traveled. Their movement trajectory remains largely unaltered from their initial orientation, producing relatively straight movement paths with few stops and turns. Away mode enables vulnerable juveniles to get as far away as possible from the predation and competition pressures of their natal pond during their first night of movement. With the exception of avoiding obstacles and selecting paths of least resistance, habitat selection during this stage is minimal. Even coarse-scale habitat features such as canopy cover or substrate type are disregarded. All juvenile pond-breeding amphibians begin their departure in the away mode; however the duration of away mode may be highly dependent on individual differences and context.

Desiccation risk is likely the principal factor governing amphibian behavior in terrestrial habitats. The ontogenetic habitat shift experienced by amphibians as they metamorphose and transition into terrestrial habitats further compounds their vulnerability. With only very limited information about their terrestrial surroundings gathered while still larvae or while waiting next to the pond to depart, juveniles should benefit from moving swiftly and directly away from their natal pond. Wiens (2001) suggested that when movement is time limited (e.g. accumulation of desiccation risk over time in amphibians) linear movement may be favored. Juveniles probably continue to move in a straight path until a combination of internal state and external factors encourage more selective movements. This transition may occur very soon after departure, within a few meters of the natal wetland or just prior to settling before sunrise.

Directed Mode

After initially swiftly moving away from their natal pond in away mode, juveniles likely slow down, reorient, and attempt to select optimal movement habitat. During “directed mode”, juveniles trade speed and greater distance traveled for increased perception of coarse-scale habitat features such as forest canopy cover, substrate, topography, vegetation structure and composition, or presence of suitable refuge microhabitats. Movement paths during directed mode include more turns and stops, resulting in increased sinuosity. Individuals in directed mode are responsive to habitat quality and therefore adjust their movement rate and trajectory to match external conditions. Individuals may increase their movement rate through areas of low quality habitat until they encounter more suitable habitat. This behavior has been observed in adult amphibians (Rittenhouse and Semlitsch 2009, Semlitsch et al. 2012) as well as small mammals (see Zollner and Lima 2005) and elk (Fryell et al. 2008). Therefore, lower habitat quality may result in greater distances traveled before settling.

The existence of contrasting “away” and “directed” movement modes may explain some of the apparently conflicting findings of various studies of juvenile movement and orientation. Juveniles first departing their natal pond (away mode) may appear to be initially oriented in all directions uniformly; however if they are captured at greater distances from the pond they may appear to be clumped in more-favorable habitats (directed mode). By placing behaviors within the context of movement modes, we can begin to explain patterns that appear inconsistent or contradictory. Malmgren (2002), for example, found that recently transformed *Triturus spp*. metamorphs did not appear to orient along the movement paths of emigrating adults departing their pond, however Hayward et al. (2000) found evidence that they have this ability. This may be because in the Hayward et al. (2000) laboratory study, juvenile subjects were older and likely in a different behavioral state (directed mode) compared to the newly emerged individuals in the Malmgren (2002) study (away mode).

Re-orientation

When juveniles switch from away mode to directed mode, they no longer adhere to their initial orientation established during the pre-departure phase. During directed movement mode juvenile amphibians move adaptively, adjusting their movement trajectories toward optimal habitats such as drainages (e.g. Western Toads, *Anaxyrus boreas*; Bull 2009). Jenkins et al. (2006) observed that after initially orienting randomly, newly metamorphosed Marbled Salamanders re-oriented their movement trajectories towards areas of higher soil moisture and canopy cover. Patrick et al. (2007) observed re-orientation of Wood Frog juveniles toward a forested wetland after 5 m of movement away from an artificial natal pool. Similar adjustments in movement trajectories have been shown in juvenile Gopher Frogs (*L. capito*) moving in heterogeneous habitats. In homogenous habitats, however, juveniles maintained their initial random orientation (Roznik and Johnson 2009).

Multiple studies testing movement behavior along forest edges have documented that juvenile amphibians will redirect away from open-canopy habitats and toward forests (deMaynadier and Hunter 1999, Rothermel and Semlitsch 2002, Rittenhouse and Semlitsch 2006; S. E. Pitmann unpubl. data). Individuals that initially enter into unsuitable habitats while in away mode may abruptly change directions after they transition to directed mode. The response to unsuitable habitat in directed mode may produce a clearly discernible pattern such as a “reversal” or “habitat switching.” A reversal occurs when an individual flips its initial movement trajectory and returns to its original departure location at the natal wetland. Rothermel and Semlitsch (2002) observed this behavior in juvenile Spotted Salamanders and Small-mouthed Salamanders (*Ambystoma texanum*) emerging from artificial pools along forest-field edges; 38% of juveniles that initially moved into fields returned to their pools, in contrast with 0% reversing from forest. Rittenhouse and Semlitsch (2006) also documented significantly higher reversals among juvenile Spotted Salamanders after initially moving into open-canopy habitats (presumably unsuitable habitat). In another study using artificial pools in a field, located at varying distances to the forest edge, reversals of juvenile Spotted Salamanders increased with increasing distance from the forest edge (Rothermel 2004).

This suggests that when higher-quality habitats are unavailable, juvenile amphibians are more likely to reverse rather than risk settling in unsuitable habitat.

Habitat switching may occur when a juvenile moving in an unsuitable habitat patch transitions to directed mode and subsequently redirects their movement trajectory towards a more-suitable habitat patch. The ability to distinguish favorable from unfavorable habitats is critical for juvenile amphibians moving through novel terrestrial habitats, however their ability to perceive favorable habitats at a distance is limited by their perceptual range (Rothermel 2004). For Spotted Salamanders juveniles ~10 m may be the maximum distance which they can detect visual or olfactory cues (S. E. Pitmann unpubl. data). In a mark-recapture study, I documented switching behavior in juvenile Spotted Salamanders (Chapter 2) and Green Frogs (*Lithobates clamitans*; Chapter 3) moving from clearcuts to forests. It is unclear however, what portion of the "switches" represent directed movement toward favorable habitats and which simply reflect greater survival of individuals reaching more-favorable habitats.

Settling Mode

Following their initial movement pulse in away mode and habitat mediated movements in directed mode, pond-breeding amphibians switch to the final behavioral state of the initial juvenile movement phase. During "settling mode" juvenile amphibians cease moving along their prior trajectory and initiate searching behavior. At this point the primary objective is to locate suitable microhabitat in which to stop and use as a refuge during the coming daylight hours. Settling mode initiates when a combination of external and internal factors combine to trigger a shift to slower, more sinuous movements, and perception of fine-scale microhabitat features. This contrasts with away mode and directed mode during which suitable settling microhabitats are ignored, even when passing directly over them. Movements are slowest during this mode to allow for the detection of olfactory or visual cues. Movement paths of individuals in settling mode are often convoluted and looping as they attempt to locate refuges (M. S. Osbourn pers. observ.).

Settling mode is distinct from home range establishment in that it results in a temporary stop along a movement path, necessitated by sunrise, rather than a long-term settlement. When a juvenile selects a refuge at the end of the night they may decide to resume movement in the coming evening or wait for rainfall before resuming movement. Some individuals may locate a suitable long-term refuge after one night of movement and transition into a home range movement phase.

Multi-night initial juvenile movement

On the second night following departure, juveniles must decide whether to establish their home range at their current settling location or resume initial juvenile movement. The duration of initial juvenile movement may vary between individuals due to differences in internal state (e.g. genetic or carry-over effects) and external conditions (e.g. habitat quality or rainfall). Each time a juvenile settles it must evaluate the costs and benefits of continued movement versus stopping. Choosing to stop moving when conditions are still optimal could present as much risk as continuing to move overland. If, for example, a juvenile Wood Frog (*L. sylvatica*) settles under leaf litter in a clearcut or on an exposed ridge top on a cool rainy night and decides to remain there, it could be trapped when conditions deteriorate (see Rittenhouse et al. 2008). Individuals may choose to remain at their settling location temporarily and bolster their energetic reserves through foraging before resuming movement. They may also assume a behavioral state analogous to wait mode in the pre-departure phase, whereby they suspend surface activity until suitable weather returns. With every subsequent night of movement, juveniles gain experience and potentially sharpen their perception of habitat cues and refuge suitability. It follows that the majority of movement following the first night is likely done in directed mode, with individuals selecting optimal habitats, and avoiding or hurrying through low-quality habitats. For long-distance dispersers, however, a resumption of away mode after each stop could facilitate greater distances traveled.

End of initial juvenile movement and establishment of home range

Initial juvenile movement ends for pond-breeding amphibians when they stop moving away from their natal pond and establish a new home range. Terrestrial species, such as toads or ambystomatid salamanders, may remain at their final settling location along their initial movement path and occupy a refuge such as a small mammal burrow or underneath a rotting log. In more-aquatic species such as California Red-legged Frogs (*L. draytonii*) the first home range of juveniles may be in a small puddle or along a creek. In subsequent years, juveniles continue to grow and eventually join an adult breeding migration to a breeding pond (Semlitsch 2008). It is not unusual for juveniles of some species to arrive with adults at breeding ponds while not yet reproductively mature (M. S. Osbourn pers. observ.). In some species such as Green Frogs (*L. clamitans*), the majority of juveniles may disperse to new breeding ponds, while only a few remain in their natal population (e.g. Schroeder 1976). In many pond-breeding species such as Wood Frogs (82%; Bervan and Grudzien 1990) or Marbled Salamanders (91%; Gamble et al. 2007) however, site fidelity (philopatry) is high.

CONCLUSIONS AND IMPLICATIONS

Subdividing juvenile amphibian movement phenomena into phases associated with particular goals, achieved through multiple behavioral states, is a new and potentially useful approach to studying dispersal in pond-breeding amphibians. In recognizing different movement modes, we can begin to place patterns of juvenile movement into proper behavioral context. Continued experimentation and observation is needed to refine our understanding of each movement mode and to identify species-specific responses. This framework should enable us to reinterpret the results of prior studies and better predict juvenile movement outcomes.

By coupling fine-scale empirical studies conducted over relatively-short time periods with individual-based simulations, we can begin to predict movement over larger temporal scales (Nathan et al. 2008). Studies of individual movement behavior provide valuable information that can be used for scaling up from the individual to local population or metapopulation levels. Ultimately, this approach should help predict responses to habitat heterogeneity and aid in the conservation of populations and species (Lima and Zollner 1996, Gibbs 1998). As we continue to determine the relationship between habitat quality and movement behavior, and the factors that mediate that relationship, we will continually improve the accuracy of predictive models to aid in the maintenance of biological diversity.

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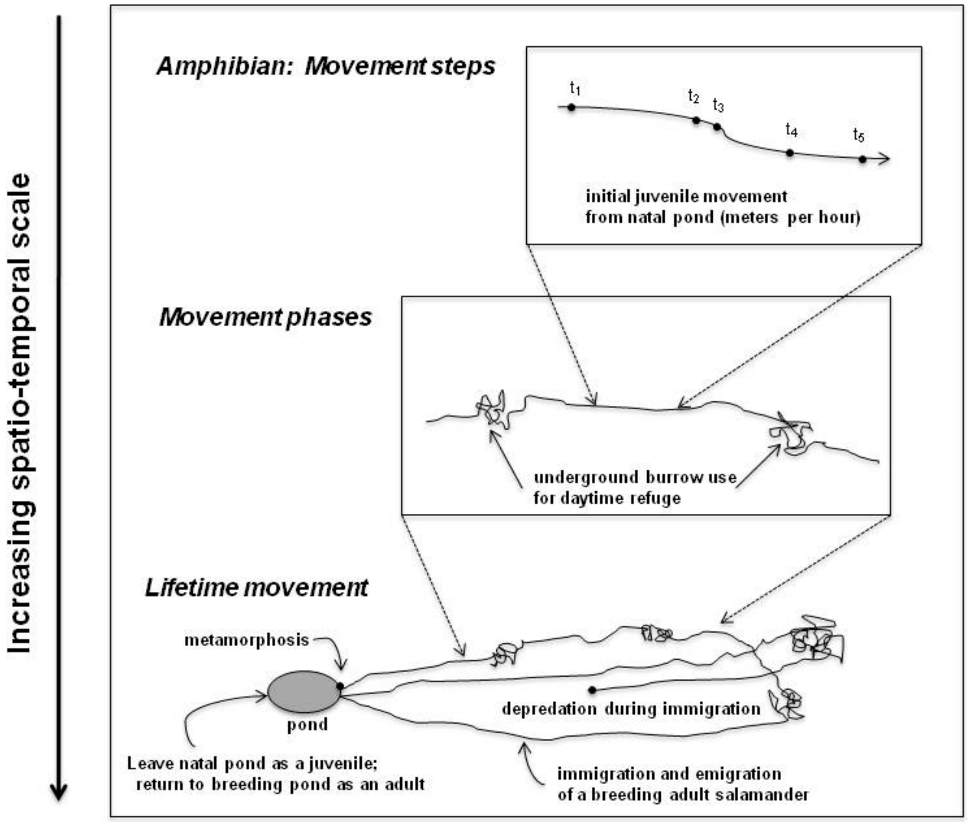
Table 1. Juvenile pond-breeding amphibian movement phases and movement modes.

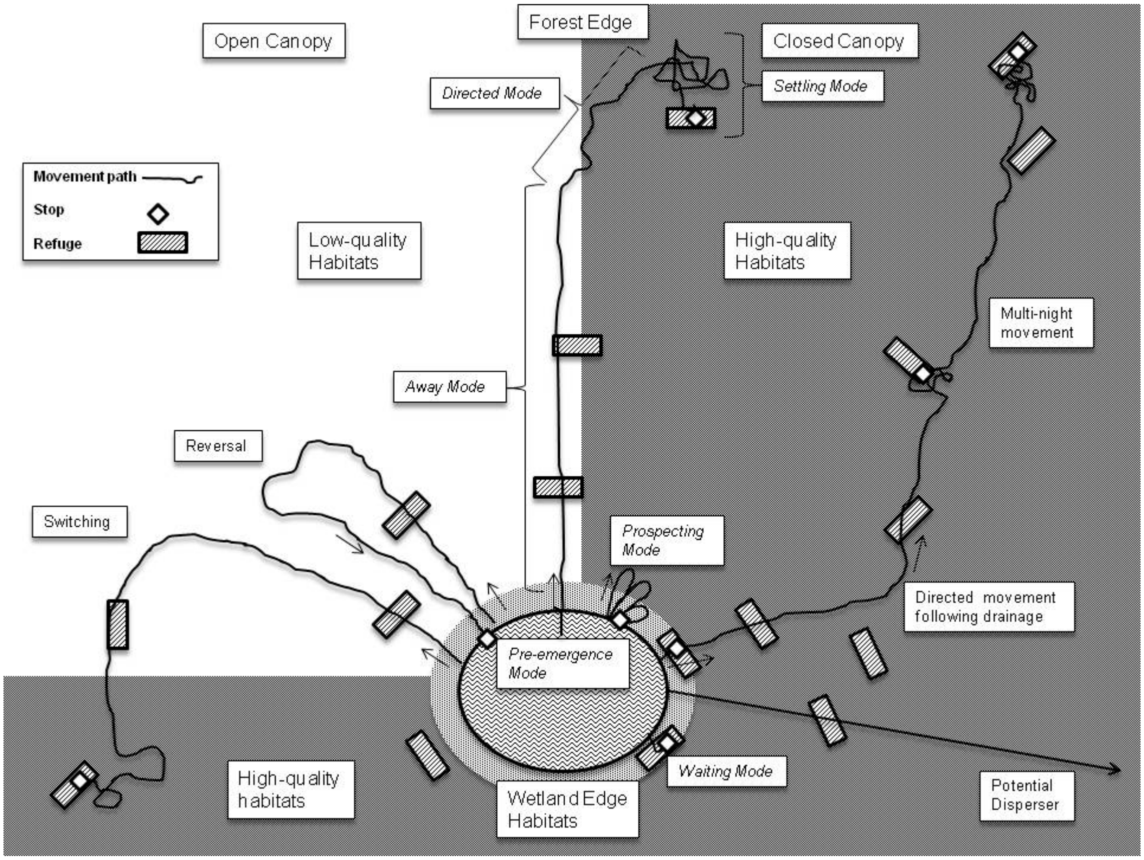
Movement Phase	Movement Mode	Decisions	Path Sinuosity	Movement Rate	Orientation	Responsive habitat
Pre-departure	Pre-emergence	*When and where to emerge?* *Where to orient?*	na	stopped	Information gathering	yes
	Waiting	*When to depart?*	na	stopped	Information gathering	probably
	Prospecting	*Where to wait?* *Where to depart?*	high	low	Information gathering	yes
Initial Juvenile Movement	Away	*Where to and how fast move?*	low	high	fixed	no
	Directed	*Where to and how fast move?*	medium	medium	adaptive	yes
	Settling (temporary)	*When and Where to stop?*	high	low	na	yes, highest
Home Range	Settling (long term)	*When and Where to end movement?*	na	stopped	na	yes

Figure 1. Life time movement tract of a pond-breeding salamander. Modified from Nathan et al. (2008).



Modified from Nathan et al. (2008)

Figure 2. Possible movement patterns of juvenile pond-breeding amphibians experiencing different movement modes.


Forest Edge
Open Canopy
Closed Canopy
Directed Mode
Settling Mode
Movement path
Stop
Refuge
Low-quality Habitats
High-quality Habitats
Multi-night movement
Away Mode
Reversal
Switching
Prospecting Mode
Directed movement following drainage
Pre-emergence Mode
Waiting Mode
High-quality habitats
Wetland Edge Habitats
Potential Disperser

CHAPTER 2

INITIAL JUVENILE MOVEMENT OF POND-BREEDING SALAMANDERS IN ALTERED FOREST HABITAT

Michael S. Osbourn

ABSTRACT

The initial juvenile movement phase represents the first stage of the multi-phase process of natal or juvenile dispersal and is particularly crucial as individuals encounter novel habitats and are highly vulnerable to mortality. For many amphibian species, juveniles represent the primary dispersal stage and therefore anything that affects their movements could greatly influence population dynamics and persistence. We conducted a mark-recapture study of recently metamorphosed spotted salamanders (*Ambystoma maculatum*) emerging from natal ponds within experimental forest arrays. To investigate how alterations in forest habitat quality impact initial juvenile movement we divided each array into four treatment quadrants containing a control, partial cut, burned clearcut, or unburned clearcut. As predicted for a forest-associated species, movement success, movement rate, and habitat fidelity of spotted salamanders were highest in forest-canopy habitats. The partial cut accounted for over half (53%) of the total recaptures in 2008, followed by the control and burned clearcut (20% each), and the unburned clearcut with the fewest (7%). Spotted salamander movement rates were 71% greater in forests than in open-canopy habitats and we observe differences in the proportion switching from one treatment to another. Of the individuals that switched treatments, we found a significantly greater proportion switching from open-canopy to forest habitats. Nearly all recaptured salamanders originally released into partial cuts were recaptured there (97% treatment fidelity) and only 3 % switched to other habitats, whereas in unburned clearcuts 61 % switched habitats. Initial juvenile movement success is likely mediated by condition-dependent factors; for example we found that greater juvenile body size in 2007 coincided with 43% higher overall recapture rates, despite less-favorable conditions. By increasing our understanding of individual-level movement responses to habitat quality we are providing valuable insights needed for better predicting patterns of dispersal at larger scales.

INTRODUCTION

Movement of individual organisms is a vital component of many ecological and evolutionary processes. In addition to fulfilling basic necessities at the individual level (e.g., habitat selection, foraging, establishing home-range), movement is integral to the maintenance of local populations, metapopulations, communities, and ecosystems (Clobert et al. 2001, Dingle and Drake 2007, Nathan et al. 2008, Revilla and Wiegand 2008). Movement of individuals not only affects the arrangement of organisms in space and time but also the distribution of genes and evolutionary diversification of species (Nosil and Crespi 2004). The major conservation problems associated with habitat fragmentation, biological invasions, emerging disease epidemics, and responses to climate change are all tied to animal movement (Kokko and López-Sepulcre 2006, Nathan et al. 2008).

Nathan et al. (2008) proposed a conceptual framework for depicting lifetime movements of individuals as a series of phases associated with fulfillment of particular goals. The goal of a movement phase could, for example, be foraging, breeding migration, or long-distance dispersal. Each movement phase involves trade-offs in terms of fitness and has specific behavioral modes which produce discernible patterns measured at varying spatiotemporal scales throughout the lifetime of an individual (Holyoak et al. 2008, Nathan et al. 2008).

The initial juvenile movement phase represents the first stage of the multi-phase process of natal or juvenile dispersal. The first movements of individuals away from their natal site are particularly crucial as they encounter novel habitats and are highly vulnerable to mortality (Lucas et al. 1994, Alberts and Altmann 1995, Delgado et al. 2009). Unlike adults, juveniles lack experience with resource patches or migration paths and have more limited perceptual ranges (Zollner and Lima 2005). Examples of initial juvenile movement include: post-fledging movements of juvenile birds (e.g., Walls and Kenward 1998, White and Faaborg 2008, Delgado et al. 2009), hatchling turtles moving away from their natal nest (e.g., Pappas et al. 2009), post-weaning juvenile hares leaving their natal burrow (e.g., Devillard and Bray 2009), and salmon fry moving into the water column after emerging from their redd in the streambed (e.g., De Garcia Leaniz et al. 2000, Bujold et al. 2004). In some species the challenges of initial juvenile movement can be compounded by an ontogenetic habitat shift, such as occurs with juvenile pelagic seabirds (Huyvaert and Anderson 2004), sea turtles (Janzen 1993, Adam et al. 2007), or amphibians (Semlitsch 2008). For many species, initial juvenile movement represents an ecological bottleneck in which the majority of juveniles suffer high mortality before establishing individual home ranges or dispersing to a new breeding population.

By manipulating factors predicted to affect movement, we can elucidate the basic determinants of movement patterns and their fitness consequences. Further, such spatiotemporally fine-scale empirical studies are needed for parameterization of spatially explicit population models. This will enable us to begin to predict movement over larger scales and under differing land-use contexts and its effect on population persistence (Lima and Zollner 1996, Zollner and Lima 2005, Nathan et al. 2008).

Pond-breeding amphibians are an ideal system for studying juvenile movements. Because of their complex life cycle (aquatic larval phase and terrestrial adult/juvenile phase) pond-breeding amphibians are often spatiotemporally concentrated at breeding sites. The susceptibility of amphibians to water loss requires them to time movements to coincide with humid or rainy and cool nights to avoid desiccation (Semlitsch 2008). For many species, hundreds or thousands of recently metamorphosed individuals will emerge in multiple bouts over the summer on wet nights. They provide a source of subjects for testing movement behavior hypotheses, at smaller spatial scales than would be possible for most other vertebrate taxa. Also, the acute susceptibility of amphibians to desiccation (Jørgensen 1997) and limited energetic reserves of recent metamorphs (Scott et al. 2007) make them a particularly sensitive group for examining the effects of land use on initial juvenile movement (Rothermel and Luhring 2005, Todd and Rothermel 2006, Rittenhouse et al. 2008).

As metamorphosing amphibians move from aquatic to terrestrial habitats they incur high mortality rates due to desiccation and predation (Jameson 1956, Shoop 1974, Wassersug and Sperry 1977, Rothermel and Semlitsch 2002). Survival of metamorphosing salamanders during this period may be as low as 17% and is strongly affected by land use (Rothermel and Semlitsch 2002, 2006). Of the individuals surviving the initial juvenile movement phase, the majority will settle and return at reproductive maturity to breed in their natal pond and a small portion will disperse to new breeding sites. Dispersal of juveniles as opposed to experienced breeders (adult dispersal) is likely the primary dispersal mode in amphibians (Semlitsch 2008). In a 7 year study of a marbled salamander (*Ambystoma opacum*) metapopulation in Massachusetts, Gamble et al. (2007) found that 91% of first-time breeders returned to breed at their natal pond while 9% dispersed to non-natal ponds. Though philopatry is high in many amphibian species, the small proportion that disperse are vitally important for local and metapopulation dynamics and regulation, and long-term persistence of species (Semlitsch 2008). The proportion of individuals available for recruitment into natal or neighboring populations may be dramatically reduced within the first days of initial juvenile movement. Habitat heterogeneity and quality have been shown to be important drivers of dispersal (e.g. Ferreras et al. 1992, Revilla and Wiegand 2008). By experimentally manipulating the configuration and quality of amphibian habitat we can begin to assess the sensitivity of juveniles during the initial movement phase.

We conducted a mark-recapture study of recently metamorphosed amphibians emigrating from natal ponds in experimental forest arrays. Our objective was to determine how alterations in forest habitat quality impact initial orientation, movement success, movement rate, and movement behavior. We also examined condition-dependent factors that may mediate the effects of habitat quality on initial juvenile movement including rainfall, conspecific density, and individual body size. Ultimately we want to better understand how land-use changes in forest habitat impact a key life stage in local population and metapopulation persistence. We expected that initial orientation would be more dependent on fine-scale habitat cues, but that movement success, movement rate, and potentially behaviors such as habitat fidelity would be greater in unaltered forest habitat.

METHODS

Study site

We implemented our experiment at Daniel Boone Conservation Area (DBCA; 1,424.5 ha) in the upper Ozark Plateau in Warren County, Missouri (Semlitsch et al. 2009). The habitat at DBCA is characterized by mature second-growth forest (80-100 years old) dominated by oak (*Quercus* spp.) and hickory (*Carya* spp.), with sugar maple (*Acer saccharum*) in the understory. Ponds in DBCA were constructed ~30 years ago along ridge tops for deer and turkeys and have been naturally colonized by up 16 amphibian species (Hocking et al. 2008).

Experimental design and delineation of treatments

We established two replicate experimental forest arrays centered on small breeding ponds (160-330 m^2 high-water surface areas; Semlitsch et al. 2009). The size of experimental arrays encompassed 95% of the core terrestrial habitat required by locally occurring salamander breeding populations (164 m radius from pond edge; Semlitsch 1998). To delineate treatments, we divided each array into four wedge-shaped quadrants of equal size (~2.11 ha each) and manipulated forest habitat within each quadrant in an attempt to affect amphibian habitat quality while emulating typical regional forestry practices (Figure 1). Our treatments included a burned clearcut, unburned clearcut, a partial cut, and an unharvested forest control. We randomly assigned the control with the two clearcut treatments assigned to two adjacent quadrants and the partial-cut treatment placed opposite the control. All timber extraction occurred between March 2004 and January 2005 with burns occurring just prior to the experiment in March 2007. The partial-cut treatment was thinned by girdling or felling locally invasive species (primarily sugar maple and red cedar) to a basal area of 13.8 m^2 per ha or approximately 60% stocking level.

Capture techniques

We completely encircled breeding ponds with drift fences, allowing us to census juvenile amphibians as they emerged. Drift fences consisted of aluminum flashing buried 30 cm in ground and extending 60 cm above ground (Gibbons and Semlitsch 1982) with paired pitfall traps (23 cm in diameter, 45 cm deep plastic plant pots) on both sides of the fence, buried to ground level at 3 m intervals. At each trap we provided a wooden board suspended on rebar stakes 4 cm above for shelter and protection from predation, along with moist sponges to reduce desiccation. In each treatment quadrant, within terrestrial habitat surrounding the ponds, we installed drift fences at distances of 20 m (two 7 m sections) and 50 m (three 11-15.4 m sections) from the pond fence (0 m). We constructed terrestrial drift fences from plastic-weave silt fencing with similar dimensions as the aluminum pond fences and evenly spaced to cover 40% of the circumference at that respective distance.

Mark-recapture procedure

To test the effects of habitat quality on initial juvenile movement, we chose spotted salamanders (*Ambystoma maculatum*), a pond-breeding, forest-associated species common in our region. Spotted salamanders are an appropriate focal species because their sensitivity to forest habitat alteration is well documented (e.g. deMaynadier and Hunter 1998, Patrick et al. 2008). Upon their initial capture at pond drift fences (0 m), we measured each juvenile's snout-vent length (SVL; mm) and mass (g; Acculab Pocket Pro electronic balance) and recorded initial orientation.

We individually marked all salamanders with Visible Implant Alphanumeric tags (VIAlpha tags; Northwest Marine Technology Inc., USA). This marking system allowed us to compare a salamander's origin with its recapture location and thereby discern coarse-scale changes in movement trajectory. We were able to discern if individuals moved from one treatment to another (habitat switching) and test for differences in movement rate and body size. The marking procedure involved anesthetizing salamanders with 500 mg/L of Tricaine Methanesulfonate (MS-222; Peterman and Semlitsch 2006). The VIAlpha tag injection procedure followed Osbourn et al. (2011). After a 6 - 12 hour recovery period and following sunset, we released marked juveniles into their natal pond treatment quadrants (at 0 m) and checked pitfall traps for recaptures every morning for the duration of juvenile emergence (June- October, 2007-2008). Upon recapture we recorded the individual's tag ID and trap number and re-released them on the opposite side of the drift fence under moist leaf litter. We used subsequent recaptures to determine movement success, movement rates, movement behaviors, and potential mediating factors.

Habitat measurements

To more fully characterize differences among forest treatments, we collected detailed measurements of variables thought to affect amphibian habitat quality, including percentage of bare ground and ground covered by leaf litter, downed wood, and herbaceous plants, as well as daily rainfall data for our region. Detailed methods and findings are in Appendix A.

STATISTICAL ANALYSES

Effects of habitat quality on initial orientation

We used initial capture locations of emerging juveniles at pond drift fences (0 m) to test for effects of forest treatments on initial orientation. Captures at pond fences were summed by forest treatment and array, and tested for random effects in initial orientation with a goodness of fit log-likelihood G-test (Zar 1999). We first examined initial orientation with individual ponds used as replicates to distinguish orientation toward forest treatment from orientation toward cardinal direction. Second, we tested each pond independently to see if directional biases were site specific.

Effects of habitat quality on movement success

To examine movement success, we used proportion recaptured as our response variable, arcsine square-root transformed to achieve a normal data distribution. We tested for differences in proportion recaptured among years, arrays, forest treatments, and recapture distances using a two-way analysis of variance (ANOVA). We also tested canopy-type effects in our model by designating control and partial-cut treatments as forest canopy and the clearcut treatments as open canopy.

Effects of habitat quality on movement rate

For movement rate, our response variable was the treatment quadrant mean of meters per night (m/night) moved by recaptured individuals. To standardize distance traveled, we limited our analysis of movement rate to individuals recaptured at 20 m within their original treatment. We tested for differences in log-transformed movement rates with AVOVA, using the same factors as the movement success analysis.

Effects of habitat quality on movement behavior

Habitat switching may represent an important behavioral response to variations in habitat quality. To assess the effects of forest treatments (or canopy types) on the proportion of individuals redirecting their movements into adjacent treatments or canopy types (proportion switching) we conducted ANOVA using year, array, treatment (or canopy type), and recapture distance as fixed effects.

Factors mediating the effects of habitat quality on movement

Rainfall is thought to mitigate to effects of habitat quality on juvenile amphibian movement because of their high susceptibility to evaporative water-loss (Jørgensen 1997). Amphibians usually time their movements to correspond with rainfall events (e.g. Semlitsch 1981, Todd and Winne 2006). For example, we know that ~75% of juvenile spotted salamander movement occurs within the first three days following rainfall (S. Pittman, unpubl. data). To assess the relationship between rainfall and movement, we preformed ANOVA on the treatment quadrant mean of the number of days between rainfall and recapture for individuals (“days since rainfall”; DSR). We log-transformed DSR means to achieve a normal distribution and tested year, array, distance, and treatment (or canopy) as factors in our model.

We also examined the potential for body length (SVL) and body condition (mg/mm) to mediate the effects of altered habitat quality on initial juvenile movement. For our ANOVAs of body size we used treatment quadrant means of log-transformed individual size measurements. We tested for body size differences between recaptures versus non-recaptures, between recaptures at 20 m versus 50 m, among recaptures from different forest treatments or canopy types, and between individuals demonstrating habitat switching versus fidelity. When ANOVA revealed significant effects, we used Tukey’s post-hoc tests for pairwise comparisons between treatments. We used SAS (PROC GLM, SAS version 9.1) for all statistical procedures and determined significance at a level of $\alpha = 0.05$.

RESULTS

Effects of habitat quality on initial orientation

Initial orientations of newly metamorphosed salamanders exiting natal ponds were predominantly nonrandom. Orientations across both ponds were non-random in 2008 (G_3= 31.57, P<0.001), but not in 2007 (G_3= 4.49, P=0.21). Analyzed separately by year, orientation in all combinations of year and array were nonrandom except for in 2007 at Pond 1 (Pond 1 2007 G_3=3.34, P=0.34; Pond 1 2008 G_3=52.577, P<0.001; Pond 5 2007 G_3=8.133, P=0.043; Pond 5 2008 G_3=65.249, P<0.001; Table B1). In 2008, initial orientations at Pond 1 were primarily West toward the partial cut (37 %). Pond 5 initial orientations were consistently North toward the burned clearcut both years (36 % and 50 % in 2007 and 2008, respectively; Table B1).

Effects of habitat quality on movement success

Of the 358 spotted salamanders released in 2007 and 703 released in 2008, we recaptured 13.73% (n=46) and 7.80% (n=55) respectively, at terrestrial drift fences (Figure 2A). The proportion recaptured at distances of 20 m compared to 50 m varied between years ($F_{1,15}$=4.71, P= 0.046; for complete ANOVA tables refer to Appendix D). Also, the effect of treatment on recapture distance differed with year (year × treatment × distance; $F_{3,15}$=3.42, P= 0.045), therefore we chose to analyze each year independently. We recaptured more individuals 20 m from their natal pond than at 50 m in both 2007 (78%) and 2008 (76%; $F_{1,7}$=35.62, P<0.001 and $F_{1,7}$=5.75, P=0.048 respectively; Figures 2B and 2C).

Although recapture distances were similar, the responses to forest treatments showed greater variation between years (Table B2). In 2007, there were significant interactions between forest treatment and distance ($F_{3,7}$=5.86, P= 0.025). This effect is attributable to the partial-cut treatment alone, where a high proportion of recaptures occurred at 50 m, roughly equaling recaptures at 20 m, whereas recaptures declined with distance in the other treatments and the control (Figure 2B). When not considering distance, we found no significant effects of forest treatment or canopy type on movement success in 2007 (P=0.363 and P=0.276 respectively).

The proportion of juveniles recaptured in 2008 differed significantly among the forest treatments ($F_{3,7}$=4.90, P=0.038), but not between canopy types (P=0.098). Although not significantly different from the control or burned clearcut, the partial cut had significantly more recaptures at both distances than the unburned clearcut in 2008 (Figure 2C). There were also significantly more juveniles recaptured in burned clearcuts compared to unburned clearcuts (Tukey's post-hoc test, P<0.05). The partial cut accounted for over half (53%) of the total recaptures in 2008, followed by the control and burned clearcut (20% each), and the unburned clearcut with the fewest (7%).

Effects of habitat quality on movement rate

The effects of forest treatment on movement rates (m/night) differed between years (year × treatment $F_{1,3}$=8.98, P=0.058) as did the effects of canopy (year × canopy $F_{1,9}$=5.31, P=0.047; Figure 3). In 2007, movement rate did not differ between canopy types or among treatments (P>0.05). In 2008 however, there was a 71% higher movement rate in forest canopy compared to open canopy ($F_{1,3}$=25.36, P=0.015). Movement rates also differed among treatments in 2008 ($F_{3,2}$=21.36, P=0.045). Tukey post-hoc analysis of 2008 forest treatments indicated greater movement rates in the partial cut (18.07±0.57 m/night) than the unburned clearcut (3.39±0.62 m/night), however the control (15.56±4.44 m/night) and burned clearcut (8.00±0 m/night) did not differ significantly from other treatments (P<0.05).

In general, movement rates in 2008 were more than double those of 2007 (11.72±2.52 m/night and 5.64±1.08 m/night, respectively). This increase was driven by a >300% increase in movement rates in forest canopy from 2007 to 2008, however there was no change in open-canopy movement rates. Among treatments, movement rates in clearcuts did not vary between years, but there was a 13% and 9% increase in movement rates for the control and partial cut from 2007 to 2008, respectively.

Effects of habitat quality on movement behavior

We documented two types of changes in movement trajectory: reversals and habitat switching. Following release into the forest treatments, a portion of juveniles that were initially moving away from their natal pond reversed direction and were recaptured back at 0 m. The percent reversing did not differ between years (2007: 9% and 2008: 7%; P=0.35), nor among treatments (2007: P=0.582 and 2008: P=0.094).

Analyses of switching behavior revealed no significant differences between years (P=0.68), allowing us to pool them together to increase statistical power. Although there was no difference in switching behavior between canopy types (P=0.11), the responses to forest treatment were significantly different ($F_{3,8}$=5.38, P=0.026; Figure 4). Nearly all salamander juveniles released into the partial cut that were recaptured, were recaptured there (97% treatment fidelity) and only 3 % switched to other treatments. Although Tukey's post-hoc test did not indicate a significant difference in switching behavior among partial cut, burned clearcut (26 %) and control (44 %), the partial cut had significantly lower switching than the unburned clearcut (61%; $P<0.05$). The unburned clearcut was the only habitat in which the majority of recaptured individuals were recaptured in other treatments.

We next tested for differences in movement direction among individuals which switched habitats. As with our analysis of switching behavior, our analysis of switching direction did not reveal differences between years (P=0.20), allowing us to pool years. Switching direction did not differ among forest treatments (P=0.197), however a significantly higher proportion of juveniles switched from open to forest-canopy habitats (71 %; $F_{1,4}$=10.18, P=0.033; Figure C1).

Factors mediating the effects of habitat quality on movement

Rainfall amounts contrasted sharply between years with 2007 17.27 cm below average, while 2008 was a record wet year, 52.30 cm above average (National Weather Service archives for the St. Louis area). During the active months for spotted salamander initial juvenile movement (May-October), there was 53% less rainfall in 2007 (39.37 cm) than in 2008 (83.31 cm). Our analysis of days since rainfall (DSR) revealed differences between the wet and dry years (year × canopy × distance; $F_{1,18}$=7.50, P=0.014). In 2007, we found an interaction between canopy type and distance ($F_{1,7}$=5.50, P=0.052). In the drier conditions of 2007 there was little difference in DSR between individuals recaptured at 20 m (mean 1.1 DSR) versus 50 m (2.0 DSR), in forest canopy. In open canopy, however, recaptures at 20 m occurred on average 2.1 days after rainfall compared to 50 m recaptures which occurred immediately following rainfall (0 DSR).

In addition to rainfall amounts conspecific density and mean body size also varied greatly between years. In the wet conditions of 2008, 49% more juveniles emerged from natal ponds in our arrays than in

2007. Juveniles emerging from ponds in 2007 were 10% longer (SVL) with 17% greater body condition (BCON) than in 2008 ($F_{1,24}$=67.00, P<0.001 and $F_{1,24}$=73.62, P<0.001, respectively). We also found a significant interaction between year and body length and body condition of recaptures versus non-recaptures ($F_{1,24}$=13.04, P=0.001 and $F_{1,24}$=6.61, P=0.02, respectively). When we analyzed years independently, we found that 2007 recaptures were 2% shorter (SVL) with 3% lower body condition than non-recaptures ($F_{1,7}$=11.09, P=0.01 and P=0.08, respectively). Individuals in 2008 showed the opposite trend, with recaptures being 6% longer and having 6% greater body condition compared to non-recaptures ($F_{1,7}$=7.38, P=0.03 and P=0.22, respectively).

When we tested for canopy type and forest treatment interactions with size of recaptures versus non-recaptures, we found significant differences in body length among forest treatments in 2007 (SVL; $F_{3,7}$=8.04, P=0.01; Figure C2). Lengths of recaptures were shorter than non-recaptures in all treatments accept in unburned clearcuts. Recaptures in burned clearcuts were significantly shorter than recaptures in unburned clearcuts (Tukey's post-hoc test, P<0.05). We did not find significant differences among forest treatments with body condition in 2007 (P=0.44), nor were there interactions with canopy type (SVL: P=0.84, BCON: P=0.43). Also, in 2008, there were no interactions between canopy type (SVL: P=0.51, BCON: P=0.49) or among treatments (SVL: P=0.75, BCON: P=0.73) with recaptures versus non-recaptures.

When we examined body sizes of individuals recaptured at different distances, we found a strong trend in 2008, with 50 m recaptures having 8% greater body condition than those recaptured at 20 m (P=0.056), however there were no significant interactions with canopy type (P=0.197) or forest treatment (P=0.83). Individuals that switched from forest canopy to open canopy in 2007 were 5% shorter with 18% lower body condition than individuals that remained in forests. Conversely, individuals switching from open to forest canopy were 3% longer with 8% greater body condition (Figure 5; $F_{1,10}$=4.78, P=0.05 and $F_{1,10}$=11.49, P=0.007 respectively). Individuals in 2008 showed a similar pattern, however the interactions were not significant with canopy (P=0.188) and lacked sufficient power to test forest treatment.

DISCUSSION

Our study provides experimental evidence that initial juvenile movement is affected by habitat quality. As predicted, movement success, movement rate, and habitat fidelity of juvenile spotted salamanders were highest in habitats with forest canopy. We documented greater habitat switching behavior by individuals leaving clearcuts, suggesting active habitat selection. Factors that may mediate behavioral responses to habitat quality include rainfall, individual body size, and conspecific density.

Effects of habitat quality on initial orientation

The initial orientation of recently metamorphosed amphibians, when first moving away from their natal pond, may play an important role in initial movement success. We observed primarily nonrandom initial orientation of salamanders at both ponds. Though in one prior study juvenile amphibians oriented in the direction of greatest forest cover (Walston and Mullin 2008), our study and others suggested that factors determining initial orientation are more complex. Initial orientations were consistent at each pond regardless of year, with the greatest numbers orienting west to the partial cut at Pond 1 and north to the burned clearcut at Pond 5. Interestingly, our spotted salamander initial orientations were identical to those of a congeneric species studied concurrently at these ponds (*A. annulatum*; M. S. Osbourn unpubl. data). Other studies showing nonrandom initial orientation in amphibians revealed varying orientations among multiple sites or shifting among years at the same site (Jenkins et al. 2006, Timm et al. 2007, Homan et al. 2010). Given the limited perceptual ranges of juvenile salamanders (5-10 m, S. E. Pittman unpubl. data), it is most likely that they are orienting towards near-pond, fine-scale microhabitat features rather than larger-scale habitat features. The consistency of orientation at each pond suggests that fine-scale microhabitat features such as moisture gradients, herbaceous vegetation structure and composition, and microtopography at the pond edge may funnel juveniles disproportionately, rather than active selection of larger-scale habitat.

Effects of habitat quality on movement success

In 2008 we found lower movement success by juveniles in clearcut treatments compared to unharvested control and partial-cut habitats. Our findings are consistent with previous studies of amphibian terrestrial habitat use, which demonstrated high sensitivity to forest-canopy removal (deMaynadier and Hunter 1998, Rothermel and Semlitsch 2002, Rittenhouse and Semlitsch 2006, Patrick et al. 2008). Removal of forest canopy fundamentally alters the forest environment by exposing the forest floor to increased sunlight and wind, creating a drier, warmer microclimate (Keenan and Kimmins 1993, Chen et al. 1999, Zheng et al. 2000). The process of timber extraction can further degrade habitat quality through reduction in leaf litter and soil compaction. Lower movement success in clearcuts is likely due to increased mortalities (e.g. Rothermel and Semlitsch 2006, Harper and Semlitsch 2007, Rittenhouse et al. 2008), evacuation (Semlitsch et al. 2008), and/or avoidance of open-canopy habitats (Rothermel and Semlitsch 2002, Rittenhouse and Semlitsch 2006).

The 2008 treatment effects were largely driven by considerably greater salamander recaptures in the partial cut compared to other treatments. In 2007, the partial cut was the only treatment in which recaptures did not taper off with increasing distance from natal ponds. We also observed the lowest proportions of individuals switching to other treatments from the partial cut, suggesting favorable conditions for movement and settling. Semlitsch et al. (2009) reported that the partial cut had the smallest negative effects and the only positive terrestrial responses of the three forest habitat manipulations tested. Our findings contrast with those of Patrick et al. (2006, 2008) who reported decreased abundance of juvenile spotted salamanders in the partial cut. Our results may differ because in the cooler, wetter forest habitats of Maine, canopy thinning may not produce the same benefits of enhanced herbaceous growth as in drier Missouri forests.

Higher movement success in the partial cut could be the result of enhanced microclimatic properties. Forest canopy gaps created by thinning increase the amount of sunlight reaching the forest floor and encourage growth in herbaceous and shrub vegetation (Zheng et al. 2000). Ross et al. (2000) reported that reductions in tree basal area resulted in strong increases in the percentage of ground cover. The immediate negative impacts of selective timber extraction, including shorter-term increased exposure to sunlight and drying wind and longer-term effects of soil compaction, may be partially ameliorated by development of dense undergrowth. In 2007, three growing seasons after application of our forest treatments, we documented 42% higher stem densities in the partial cut compared to the control

($F_{3,24}$=42.24, P<0.001; Appendix A). The increased vegetative growth may help retain moisture longer and contribute to increases in invertebrate prey, further enhancing survival and growth of juvenile amphibians.

Burning following timber harvesting has the potential to further affect amphibian habitat quality. We recaptured more spotted salamander juveniles in burned than unburned clearcuts. This was surprising given that the 76 % post-burn reduction in leaf litter ($F_{3,32}$=26.80, P<0.001; Appendix A) should have decreased the availability of suitable microhabitat. Roznik and Johnson (2009) found that recently metamorphosed gopher frogs (*Lithobates capito*) directed their movements toward fire-managed areas. Spotted salamanders may similarly benefit from burning. For example, increased abundance of small-mammal burrows in fire-managed areas (Roznik and Johnson 2009) could increase the number of refuges for juvenile salamanders and contribute to our observed higher recaptures in burned clearcuts. Also, dense growth of herbaceous plants following burning may improve habitat quality by maintaining a more favorable surface microclimate (lower temperature, higher humidity) or increasing prey availability. Conversely, burning may lower overall habitat quality, and higher recapture rates in burned clearcuts are the result of increased movement and decreased settling in inhospitable habitat. This latter scenario has been observed for spotted salamander juveniles when soil is compacted or cover objects are less abundant (Chapter 4).

Effects of habitat quality on movement rate

In a telemetry study of adult wood frog movements, Rittenhouse and Semlitsch (2009) documented increased rates of travel following timber harvesting. However, the spotted salamander juveniles in our study are much smaller and likely less capable of traversing clearcuts. Here we documented 71% lower movement rates in open-canopy habitats compared to partial cut or unaltered forests in 2008, suggesting that the need to select optimal routes and locate moist refuges to avoid desiccation may hinder more rapid movement. These effects are likely exacerbated by reduced moisture availability in the dryer year, 2007, where mean movement rates were overall 52% slower.

Effects of habitat quality on movement behavior

Habitat switching represents a clear behavioral response to habitat quality. Not only did we observe differences in the proportion of individuals switching among forest treatments, but of those that switched, more moved from open-canopy to forest habitats. There are several potential explanations for this pattern. First, individuals entering open-canopy habitats may be immediately reversing and moving directly toward the forest. Reversals of juvenile spotted salamanders encountering open-canopy habitats have been documented along forest edges (Rothermel and Semlitsch 2002, Rittenhouse and Semlitsch 2006), however we found no differences in proportions reversing between forests and clearcut treatments. Although we recaptured significantly fewer spotted salamander juveniles in clearcuts, their presence at 20 m and 50 m demonstrates that they are not all avoiding open-canopy habitats and likely move through them readily during their initial movement pulse. It is more likely that the pattern of individuals switching from open-canopy to forest habitats occurs after they have initially proceeded into the clearcut.

Jenkins et al. (2006) found that juvenile marbled salamander (*A. opacum*) movement routes coincided with higher canopy cover and soil moisture. Studies that placed forest-associated pond-breeding amphibians along forest edges found that they moved disproportionately into forested areas (deMaynaider and Hunter 1998, Rothermel and Semlitsch 2002), however it is unlikely that they can perceive forest edges at greater distances (e.g. 5-10 m, S. E. Pittman unpubl. data). Rothermel (2004) observed that spotted salamander juveniles emigrating from artificial pools in pastures showed no orientation toward forest edges, even when as close as 5 m. It is more likely that juvenile salamanders use fine-scale olfactory cues to orient their movements. Experiments testing juvenile spotted salamander substrate choice demonstrated significant preferences for forest litter and soils over grassland substrates (Rittenhouse et al. 2004; M. S. Osbourn unpubl. data). Juveniles switching from open-canopy to forested habitats would need to be moving along routes close enough to forest edges to detect olfactory cues indicative of high-quality habitat to redirect their movements.

It also is possible that patterns of initial juvenile movement in amphibians are the result of a series of distinct movement modes or behavioral states. The movement ecology framework put forward by Nathan et al. (2008) proposes that animals alternate among various movement modes which are influenced by a complex interaction of internal state, motion capacity, navigation capacity, and external factors (e.g. habitat characteristics). Movement modes have been described in other taxa (e.g. elk; Fryxell et al. 2008 and owls; Delgado and Penteriani 2008) and we propose that they likely also occur in amphibians. Juveniles must decide for example, when to move or where to stop. Each of these decision points should theoretically be accompanied by a switch in behavioral state or mode. Newly metamorphosed amphibians are often densely packed and highly vulnerable to predation at the margins of their natal pond (e.g., Wassersug and Sperry 1977; Osbourn and Semlitsch pers. obs.). Spending time conspicuously searching for suitable habitat near the pond could be costly. Timing movements on wet or humid nights and moving swiftly and straight away would be advantageous for movement success. The fact that we recapture juvenile forest-associated amphibians in open-canopy habitats (although significantly less) suggests that they are not initially orienting toward terrestrial habitat, but rather away from their natal pond. Juveniles may first leave the pond with the goal of moving away as quickly as possible while conditions are optimal. After an unknown duration the “away” movement mode may switch into a “directed” movement mode where juveniles move more slowly, use habitat cues (e.g., forest leaf litter), and re-orient their trajectories toward optimal habitat. Previous studies have presented evidence of juveniles adjusting their movement orientations after traveling away from their natal pond (Jenkins et al. 2006, Patrick et al. 2007). Eventually the “settle” movement mode initiates and juveniles begin searching for suitable microhabitats in which to stop moving and seek refuge before sunrise. Patrick et al. (2008) proposed that juvenile wood frogs respond differently to habitat heterogeneity depending on their behavioral phase. The consideration of movement modes for amphibians may aid in explaining some observed inconsistencies in movement outcomes at varying times after metamorphosis and help us better understand the links between individual behavior, habitat, and demographic effects.

Factors mediating the effects of habitat quality on movement

Initial juvenile movement is likely influenced by multiple spatiotemporally dynamic factors, which are often confounded or produce complex interactions acting at different scales. Habitat quality and structure may affect movement success of juveniles differently at different times, depending on other external conditions (e.g. weather patterns or population dynamics) or internal conditions (e.g. body size or energy reserves; Ims and Hjermann 2001). Condition-dependent dispersal is a well-documented phenomenon in other taxa (e.g. Bowler and Benton 2009, Clobert et al. 2009), and the concept is likely applicable to the initial juvenile movement phase of amphibians. Apparent inconsistencies in initial juvenile movement responses between years may reflect the influence of variation in external and internal conditions. The two years of our study contrasted sharply in rainfall totals, number of metamorphosing juveniles, and mean juvenile body size, all of which logically could have contributed to different responses to forest-habitat manipulations and movement distances between years.

The 2007 field season was comparably dry with below average rainfall amounts during the active season (May-October) and contrasted sharply with 2008, which was extremely wet with record high rainfall totals. Given the importance of rainfall for amphibian movement we would predict that movement propensity and success is greatly influenced by fluctuations in rainfall.

Although we recaptured significantly fewer juveniles at 50 m than 20 m in both years, this effect was most pronounced in the dry year. Dry conditions likely exacerbate the higher desiccation risk involved in moving farther or through open-canopy habitats. Our analysis of days between rainfall and recapture indicated that the majority of 50 m open-canopy recaptures occurred immediately following rainfall in the dry year. Lower movement rates in 2007 suggest that juveniles may respond behaviorally to drier conditions by shortening their movement durations and locating moist refuges closer to their natal pond. During extended dry periods, suitable moist, cool microhabitats should become more limited, resulting in aggregations of individuals competing for increasingly smaller isolated patches. This uneven clumping of individuals may have contributed to lowered movement success in clearcuts due to density-dependent mortality (e.g. Patrick et al. 2008). It is possible that the only individuals to survive movement beyond 20 m in open-canopy habitats were individuals that moved all 50 m immediately following the rainfall that triggered their first movements.

Although we anticipated that increased rainfall would act to mitigate the negative effects of lower habitat quality, we recorded the greatest differences between forests and clearcuts in the wet year. Also, despite having drier, less favorable conditions for movement, the proportion of juveniles recaptured in 2007 was twice that of the much wetter 2008 field season. These somewhat counter intuitive results lead us to suspect that factors other than rainfall are contributing more to the observed differences.

The 2008 spotted salamander cohort contained over twice as many juveniles as 2007, so even though movement conditions should have been much more ideal in 2008, there was increased competition for resources. Density-dependent effects may play an important role in movement success in years with large juvenile recruitment (e.g. Berven 2009). The lower fitness of individuals experiencing high terrestrial densities (decreased growth and smaller body size) may have exacerbated the negative effects of forest canopy removal in 2008 (Harper and Semlitsch 2007). Further, if the high number of metamorphosing juveniles in 2008 also indicates higher larval densities then lowered fitness or altered movement propensity may be a carry-over effect from the aquatic habitat (Scott 1994, Benard and McCauley 2008). High larval densities are known to contribute to lowered growth rates and earlier metamorphosis, leading to smaller juvenile body sizes (Semlitsch et al. 1988). This is consistent with our findings showing smaller mean body sizes, along with a 24-day earlier first metamorphosis, in 2008 compared to 2007.

Larger body sizes have been shown to be important factors influencing movement success and propensity in various taxa including reptiles (Léna et al. 1998), birds (Barbraud et al. 2003), mammals (O'Riain et al. 1996), and amphibians (Chelgren et al. 2008). Also, larger body size at metamorphosis is associated with higher juvenile salamander survival in terrestrial habitats (Rothermel and Semlitsch 2006). The higher recapture rate in 2007 may reflect higher movement success and/or propensity by larger individuals. Not only were 2008 juveniles shorter in length, but their body condition indicated that they were thinner with higher surface area to volume ratios, suggesting increased desiccation risk and lower energy reserves.

Mean body lengths of recaptured individuals in 2007 were smaller than non-recaptures in all treatments except the burned clearcut. This pattern may reflex competition for limited moist refuges during dry periods. Larger individuals are generally believed to be competitively superior, and when resources are limited such as in the dry conditions of 2007, smaller, competitively inferior individuals may be forced to move farther from their natal pond. Hanski et al. (1991) reported a similar pattern in a comparison of dispersers to resident common shrews (*Sorax araneus*). The exception in 2007 was the burned clearcut, where lack of leaf litter post burn may have limited settling options thereby forcing larger individuals to move farther as well.

The strong negative relationship between body size and desiccation risk has been shown to affect movement behavior in other amphibians, with larger individuals having a higher propensity to enter clearcuts (Chan-McLeod 2003) and greater robustness to environmental variability (Chelgren et al. 2008). It is possible that the lowered desiccation risk and increased energetic reserves produced the pattern of switching behavior we observed, explaining greater movement of larger individuals from open-canopy to more-favorable forest-canopy habitats. Rather than any one factor alone, initial juvenile movement is likely mediated by complex interactions among multiple condition-dependent factors. Though our study design does not allow us to separate potential mediating effects from one another, they should provide ample opportunities for future research on initial juvenile movement.

Our study addresses the paucity of knowledge on individual level movement decisions by juveniles leaving their natal site, while testing the effects of habitat quality on movement success. By releasing hundreds of individually marked juvenile salamanders, we were able to record previously undescribed habitat switching behavior, movement rates, and body size effects on movement success under varying conditions. Because of the comparably small scale of initial juvenile movement in pond-breeding amphibians, we were able to characterize movement phenomena which are very difficult to obtain for other vertebrate taxa. Information gained here is applicable to other systems and broadens our general understanding of initial juvenile movement.

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Figure 1. Experimental forest array centered on amphibian natal pond completely surrounded by a drift fence (0 m). Two drift fences at 20 m and three drift fences at 50 m cover 40% of the circumference at their respective distances. Our study used two replicate arrays referred to as Pond 1 and Pond 5.

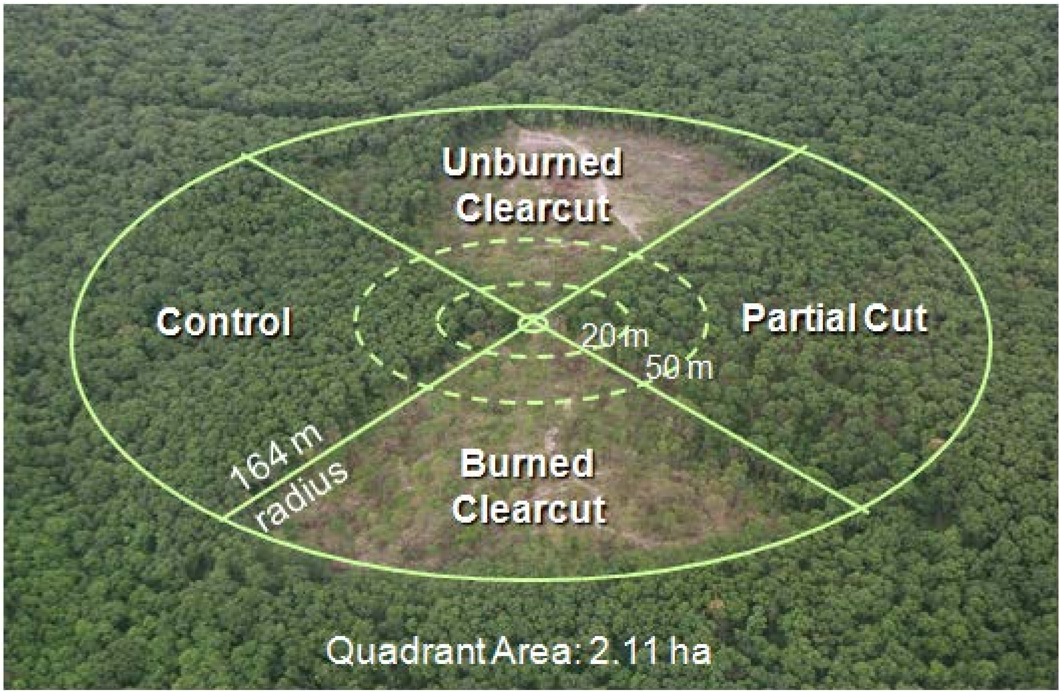

Unburned Clearcut
Control
Partial Cut
20 m
50 m
164 m radius
Burned Clearcut
Quadrant Area: 2.11 ha

Figure 2. The effects of distance and treatment on movement success. (A) Number of juvenile spotted salamanders released at 0 m each year and recaptured with increasing distance from natal pond†. (B & C) Mean percent recaptured in forest treatments at 20 m and 50 m from natal ponds. In both years significantly more juveniles were recaptured at 20 m compared to 50 m. In 2007 (B), there was a significant treatment × distance interaction and in 2008 (C) treatments differed significantly. †Our analyses were based on drift fences at 20 m and 50 m covering 40% of the circumference at their respective distances. For Figure 2A, we adjusted our recapture numbers to show predicted recaptures if 100% of circumference at 20 m and 50 m were covered.

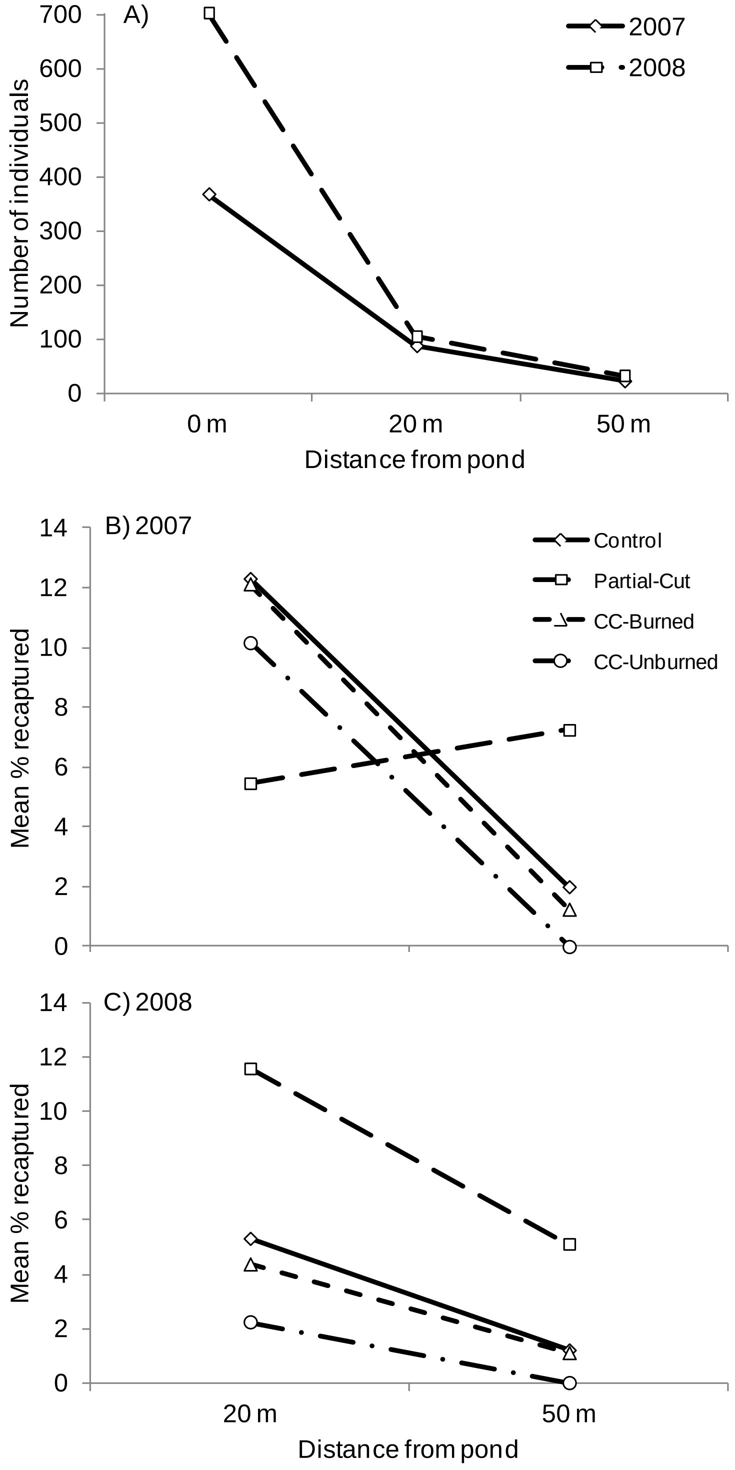

A)
2007
2008
Number of individuals
0
100
200
300
400
500
600
700
0 m
20 m
50 m
Distance from pond
B) 2007
Control
Partial-Cut
CC-Burned
CC-Unburned
Mean % recaptured
0
2
4
6
8
10
12
14
C) 2008
Mean % recaptured
0
2
4
6
8
10
12
14
20 m
50 m
Distance from pond

Figure 3. Yearly differences in mean (±SE) movement rates (m/night) of salamanders recaptured in forest versus open canopy types.

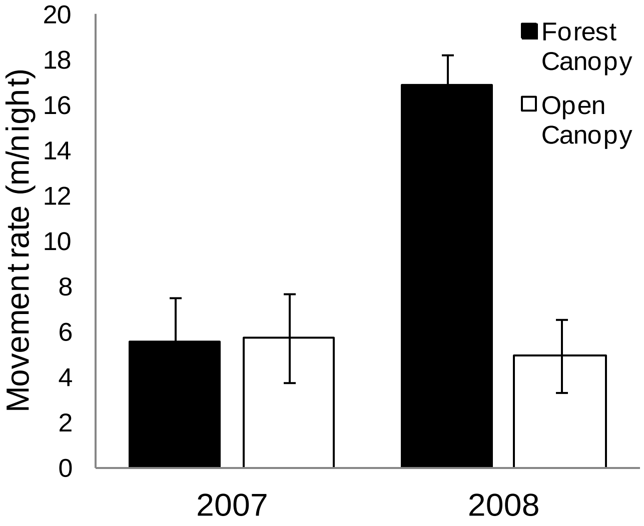

Movement rate (m/night)
20
18
16
14
12
10
8
6
4
2
0
■ Forest Canopy
□ Open Canopy
2007
2008

Figure 4. Habitat switching behavior in spotted salamanders showing the proportion that remained in their initial forest treatment (fidelity; indicated within a black rectangle) and the proportion that moved to other habitats (switching).

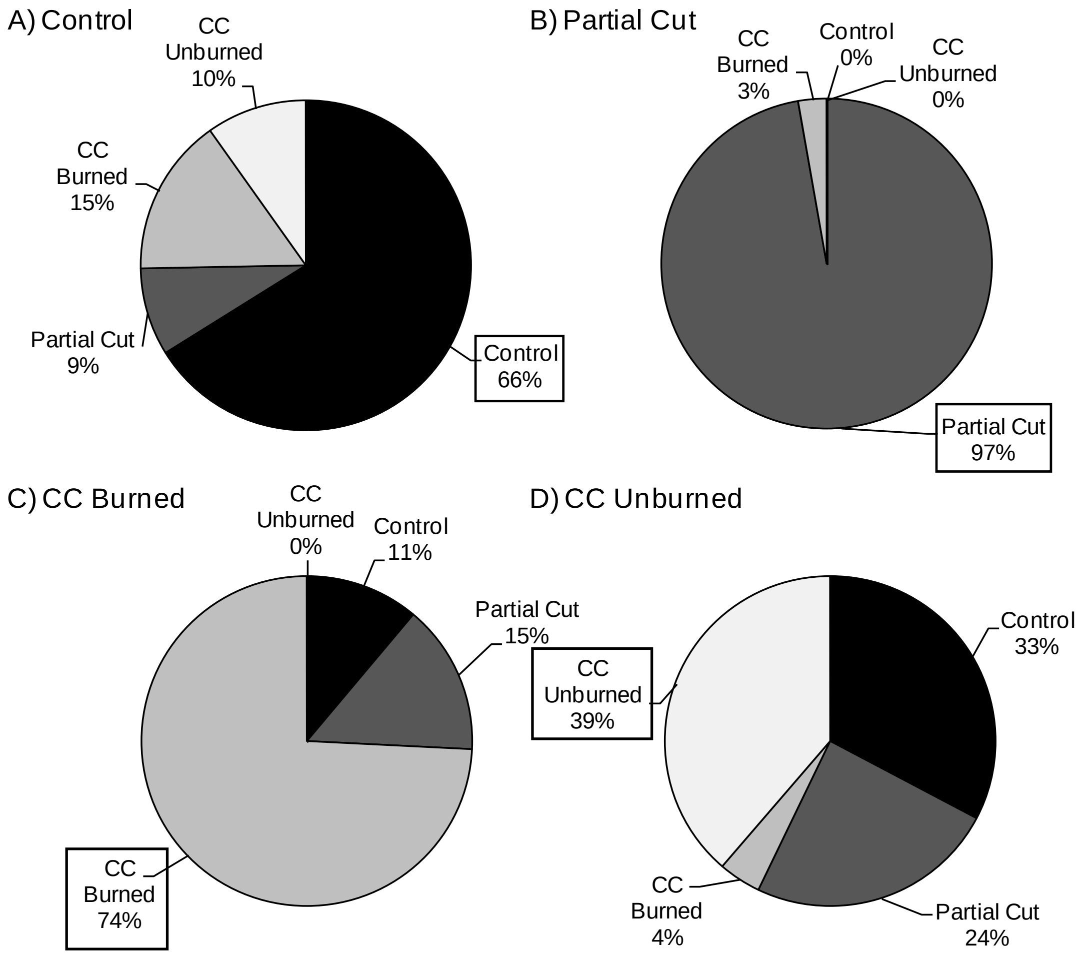
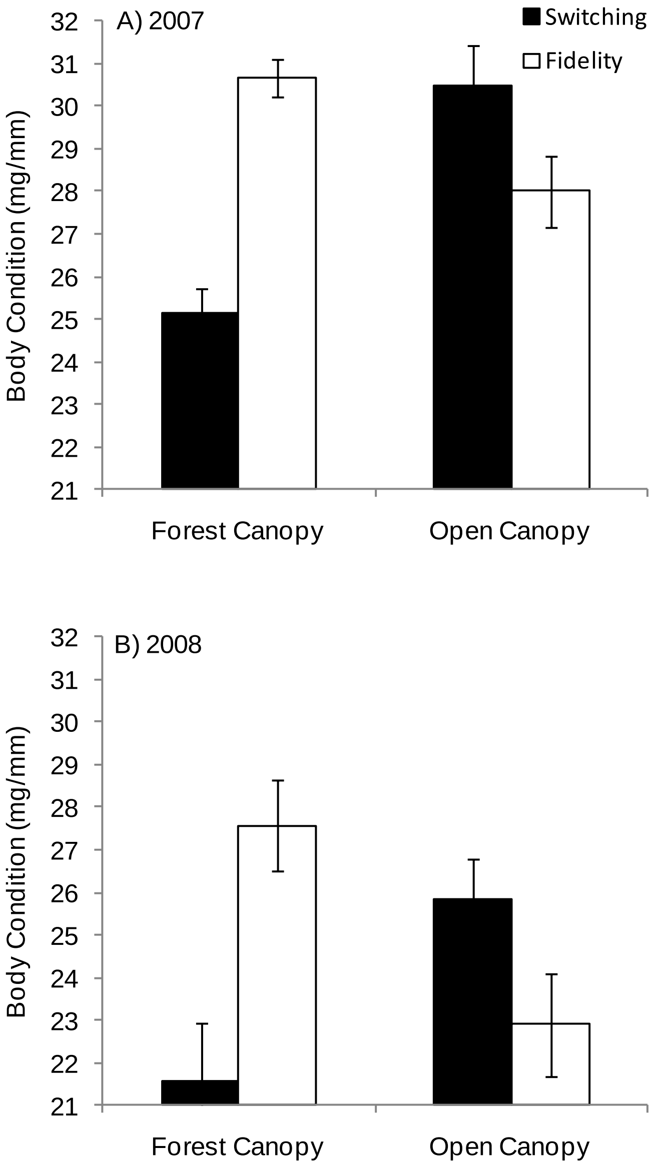

A) Control
CC Unburned 10%
CC Burned 15%
Partial Cut 9%
Control 66%
B) Partial Cut
CC Burned 3%
Control 0%
CC Unburned 0%
Partial Cut 97%
C) CC Burned
CC Unburned 0%
Control 11%
Partial Cut 15%
CC Burned 74%
D) CC Unburned
Control 33%
CC Unburned 39%
CC Burned 4%
Partial Cut 24%

Figure 5. Differences in mean (±SE) body condition (mg/mm) between individuals that showed habitat fidelity and those which switched canopy types (switching).


A) 2007
■ Switching
□ Fidelity
Body Condition (mg/mm)
32
31
30
29
28
27
26
25
24
23
22
21
Forest Canopy
Open Canopy
B) 2008
Body Condition (mg/mm)
32
31
30
29
28
27
26
25
24
23
22
21
Forest Canopy
Open Canopy

CHAPTER 3

BEHAVIORAL RESPONSES TO HABITAT QUALITY AND STRUCTURE DURING INITIAL TERRESTRIAL MOVEMENTS OF JUVENILE GREEN FROGS (*LITHOBATES* [*RANA*] *CLAMITANS*)

Michael S. Osbourn

ABSTRACT

The interplay of animal behavior and habitat configuration drives movement between populations and determines functional connectivity. As a consequence of this relationship, animal movement paths are strongly affected by landscape structure. By examining fine-scale movements and behavioral responses of individual animals encountering habitat patches of varying quality, we can begin to predict patterns at larger ecological and spatial scales such as local population and metapopulation dynamics. We implemented a mark-recapture study of recently-metamorphosed Green Frogs (*Lithobates* [*Rana*] *clamitans*) experiencing their first movements into terrestrial habitats. Our objective was to determine how alterations in forest habitat quality and structure affect initial orientation, movement success, and movement behavior. We established two replicate experimental forest arrays centered on small breeding ponds, divided into four wedge-shaped quadrants of equal size (~2.11 ha each). Within each quadrant we manipulated forest habitat to create a burned clearcut, unburned clearcut, and partial-cut treatments, along with an unharvested forest control. We recaptured individually marked frogs using drift fences surrounding natal ponds (0 m), as well as in the terrestrial habitat within each treatment quadrant, at distances of 20 m and 50 m. We installed additional edge drift fences 2 m within control boundaries of the two clearcut treatments. Initial orientation of juvenile Green Frogs exiting their natal pond was nonrandom, with the greatest proportion moving toward the partial cut. Of the 1,354 Green Frog juveniles marked and released, we recaptured 13.8% (n=187) at terrestrial fences and an additional 7.3% (n=99) at edge fences on the border of control forests and clearcut treatments. Movement success was greatest in the control (32.4±7.39%; mean percent ± SE) followed by the partial cut (15.1±1.92%). By comparison, juvenile movement success through clearcut treatments was greatly reduced (burned clearcut: 3.7±1.27%; unburned clearcut 2.2±1.13%). Habitat switching was also far more prevalent in the two clearcut treatments than in the control and partial cut. In the burned clearcut and unburned clearcut 77.9±11.26% and 94.4±5.56%, respectively, of the frogs originating there switched to other treatments before being recaptured. Most striking was the percentages of individuals from clearcuts that switched to the control forest (burned clearcut: 57.7±9.01% and unburned clearcut: 65.4±24.63 %). Edge fences bordering the unburned clearcut treatment accounted for 89.9% (n=89) of the total edge recaptures, compared to only 10.1% (n=10) at the burned clearcut edge. This suggests that the unburned clearcut-control forest edge served as a movement corridor, providing both ease of movement in the open control forest floor and a nearby, easily accessible refuge in the dense successional clearcut. The findings of this study provide empirical support for the assertion that behavioral mechanisms contribute to the distribution and abundance of amphibians in heterogeneous habitats. The important movement parameters provided by this study will aid in the development of simulation models and ultimately strengthen predictions of the effects of habitat alteration on amphibian populations.

INTRODUCTION

How an animal’s movement behavior interacts with variations in habitat quality can determine a habitat’s permeability and, consequentially, the spatial distribution of individuals (Ricketts 2001, Mazerolle and Desrochers 2005, Figueira and Crowder 2006). This interplay of behavior and habitat configuration drives movement between populations and determines functional connectivity (Baguette and Van Dyck

2007, Rizkalla and Swiharts 2007). Inter-patch distance and habitat patch quality interact with predation and metabolic risks to either impede or facilitate animal movement through the landscape (Sjögren-Gulve 1994, Larsen and Boutin 1994, Rothermel and Semlitsch 2002, Turcotte and Desrochers 2003). Some animals can change their movement behavior in response to the habitats they encounter. Many species, for example, demonstrate reluctance to traverse certain habitat boundaries (e.g. butterflies: Haddad 1999; salamanders: Rittenhouse and Semlitsch 2006, squirrels: Larsen and Boutin 1994). As a consequence of this relationship between behavior and habitat, animal movement paths are strongly affected by landscape structure (Stamps et al. 1997, Haddad 1999). By examining fine-scale movements and behavioral responses of individual animals encountering habitat patches of varying quality, we can begin to predict patterns at larger ecological and spatial scales such as local population and metapopulation dynamics (Haddad 1999, Morales and Ellner 2002, Morales et al. 2010). Unfortunately, fine-scale individual-level empirical movement data is often difficult to obtain for many vertebrate species (Bowler and Benton 2005) and complexity and condition-dependence make isolating individual mechanisms challenging (Massot et al. 2002, Clobert et al. 2009).

Various authors have attempted to conceptualize the complexity of animal movement by proposing theoretical frameworks which subdivide movement phenomena into distinct units (e.g. Bowler and Benton 2005, Nathan et al. 2008, Clobert et al. 2009, Bonte et al. 2012). A "movement phase" as described Nathan et al. (2008) involves movements associated with the fulfillment of a particular goal (e.g. foraging or predator evasion). Each movement phase involves trade-offs in terms of fitness and has specific behavioral modes which produce discernible patterns when measured at varying spatiotemporal scales throughout the lifetime of an individual (Holyoak et al. 2008, Nathan et al. 2008).

Natal dispersal involves the movement of individuals from their natal site to a new site for breeding and has consequences for individual fitness, population dynamics and genetics, and species distributions (Hanski 1999, Clobert et al. 2001). Despite its importance to ecological and evolutionary processes, natal dispersal persists as a significant gap in our understanding of ecology (Ronce 2007). By subdividing this movement phenomenon into distinct movement phases we can begin to identify processes and relate them to patterns at larger scales. The first movements of individuals as they venture beyond their natal site, with the goal of reaching their new home range, comprise the initial juvenile movement phase. For many animals, such as in fledging birds or sea turtle hatchlings emerging from their nest, initial juvenile movement is a highly vulnerable time during which the majority of individuals may die within a brief period.

Pond-breeding amphibians provide an excellent study system for examining the interplay of habitat quality and movement behavior during initial juvenile movement. They can be studied at smaller spatial scales than most other vertebrate taxa and are characterized by complex life cycles (aquatic larval phase and terrestrial adult/juvenile phase) that result in spatiotemporal concentrations of recently-metamorphosed juveniles at their natal ponds following emergence. Their acute susceptibility to evaporative water loss in terrestrial habitats (Jørgensen 1997) and limited energetic reserves following metamorphosis (Scott et al. 2007) make them a particularly responsive system for studying the effects of land use on initial juvenile movement (Rothermel and Semlitsch 2002, Rothermel and Luhring 2005, Todd and Rothermel 2006, Rittenhouse et al. 2008). These vulnerabilities translate into high mortalities due to desiccation and predation as juveniles move from aquatic to terrestrial habitats (Jameson 1956, Shoop 1974, Wassersug and Sperry 1977, Rothermel and Semlitsch 2002).

Examining behavioral responses to habitat quality in this system is particularly pertinent given that habitat loss and alteration have been implicated as a major contributor in global amphibian declines (Stuart et al. 2004, Gardner et al. 2007). Here we experimentally manipulated natural habitat features in order to reveal behavioral mechanisms underlying patterns of initial juvenile movement, and thereby better predict movement over larger scales and under differing land-use contexts (Wiens 1993, Gibbs 1998). Because of the challenges inherent in predicting movement behavior, fine-scale empirical studies are needed for the parameterization of simulation models and to aid in conservation planning (Knowlton and Graham 2010, Pe’er et al. 2011).

We implemented a mark-recapture study of recently metamorphosed Green Frogs (*Lithobates* [*Rana*] *clamitans*) experiencing their first movements into terrestrial habitats, within experimental forest arrays. Our objective was to determine how alterations in forest habitat quality and structure affect initial orientation, movement success, and movement behavior. We expected that initial orientation would be less associated with course-scale habitat quality and more dependent on fine-scale habitat features, but that movement success would be greater in unaltered forest habitat. We further predicted that the high mobility of Green Frogs would allow them to avoid and behaviorally mitigate low quality habitats.

METHODS

Study site and species

We conducted our experiment at Daniel Boone Conservation Area (DBCA; 1,424.5 ha) in the upper Ozark Plateau in Warren County, Missouri. The habitat at DBCA is characterized by mature second-growth forest (80-100 years old) dominated by oak (*Quercus* spp.) and hickory (*Carya* spp.), with sugar maple (*Acer saccharum*) in the understory. Ponds in DBCA were constructed 20-40 years ago along ridge tops for deer and turkeys and have been naturally colonized by up to 16 amphibian species (Hocking et al. 2008, Semlitsch et al. 2009).

To investigate how variations in forest habitat quality affect initial juvenile movement success we selected Green Frogs, Lithobates clamitans as our focal species. Green Frogs are considered habitat generalists and are therefore assumed to be less sensitive to forest canopy removal than forest-associated species. Green Frogs are an interesting study species because their near-ubiquity in a wide range of Missouri habitats (Shulse et al. 2010) suggests they possess behavioral mechanisms for adapting to habitat heterogeneity. Furthermore, various authors have reported a high degree of vagility and relatively far juvenile dispersal distance in Green Frogs (Martof 1953, Oldham 1967, Schroeder 1976).

Experimental design and delineation of treatments

We established two replicate experimental forest arrays centered on small breeding ponds (160-330 m2 high-water surface areas; Semlitsch et al. 2009). The size of experimental arrays encompassed 95% of the core terrestrial habitat required by locally-occurring amphibian populations (164 m radius from pond edge; Semlitsch 1998). We divided each array into four wedge-shaped quadrants of equal size (~2.11 ha each) and manipulated forest habitat within each quadrant in a manner which emulates typical regional forestry practices (see Chapter 2, Fig. 1): a burned clearcut, an unburned clearcut, a partial cut, and an unharvested forest control. All timber extraction occurred between March 2004 and January 2005, with burns occurring just prior to the experiment in March 2007. The partial-cut treatment was thinned by girdling or felling trees to a basal area of 13.8 m2 per ha or approximately 60% stocking level. To more fully characterize differences among forest treatments, we collected detailed measurements of variables thought to affect amphibian habitat quality, including: percentage of bare ground and ground covered by leaf litter, downed wood, and herbaceous plants, as well as daily rainfall data for our region (Detailed methods and findings can be found in Appendix A).

Capture techniques

We completely encircled breeding ponds with drift fences, allowing us to census juvenile Green Frogs as they emerged. Drift fences consisted of aluminum flashing buried 30 cm in ground and extending 60 cm above ground (Gibbons and Semlitsch 1982) with paired pitfall traps (23 cm in diameter, 45 cm deep plastic plant pots) on both sides of the fence, buried to ground level at 3 m intervals. At each trap we provided a wooden board suspended on rebar stakes 4 cm above for shelter and protection from predation, along with moist sponges to reduce desiccation. In each treatment quadrant, within terrestrial habitat surrounding the ponds, we installed drift fences at distances of 20 m (two 7 m sections) and 50 m (three 11-15.4 m sections) from the pond fence (0 m; see Chapter 2, Figure 1). Terrestrial fences were evenly spaced to cover 40% of the circumference at each respective distance. We also installed drift fences (three 15.4 m sections) 2 m within control treatment quadrants at the boundaries of the two clearcut treatments (“edge fences”), which allowed us to monitor frogs’ two-way lateral movement between the clearcuts and unmanipulated control forests (Semlitsch et al. 2008). We constructed terrestrial drift fences from plastic-weave silt fencing with dimensions similar to the aluminum pond fences.

Mark-recapture procedure

We initially captured recently-metamorphosed Green Frogs at their natal pond drift fence (0 m), and measured snout-urostyle length (SUL; 0.1 mm) and mass (0.01 g; using Pesola spring scales) for each individual. After measuring, we individually marked frogs with Visible Implant Elastomers tags (VIEs; Northwest Marine Technology) and cohort marked additional frogs according to release treatment by clipping two adjacent toes. Toe clipping (Donnelly et al. 1994) and VIEs (Nauwelaerts et al. 2000) are both widely used in amphibian research and have been shown to be both safe and effective.

After sunset, we released each marked frog outside its natal pond drift fence (0 m) into the forest treatment corresponding with its initial orientation. On the following morning and all subsequent mornings during the juvenile emergence period (June through September) we checked all pitfall traps within our experimental arrays for recaptures. Upon recapture, we recorded the individual's tag ID and trap number and re-released them on the opposite side of the drift fence under moist leaf litter. We used subsequent recaptures to determine movement success in different habitats. Identification of individuals allowed us to match a juvenile frog's location of origin with its recapture location and thereby discern specific behavioral responses to variations in habitat quality.

STATISTICAL ANALYSES

Effects of habitat quality on initial orientation

We used initial capture locations of emerging juvenile frogs at pond drift fences (0 m) to test for effects of forest treatments on initial orientation. Captures at pond fences were pooled by forest treatment and array, and tested for random effects in initial orientation with a goodness of fit log-likelihood G-test (Zar 1999). We first examined mean initial orientations with individual ponds used as replicates to distinguish orientation toward forest treatment from orientation toward cardinal direction. Second, we tested each pond independently to see if directional biases were site specific.

Effects of habitat quality on movement success

To examine movement success, we used the proportion of frogs recaptured as our response variable, arcsine square-root transformed to achieve a normal data distribution. We tested for differences in the proportion of frogs recaptured between experimental arrays, among terrestrial drift fence locations (distances of 0 m, 20 m, and 50 m), and among forest treatments, using a two-way analysis of variance (ANOVA).

Effects of habitat quality on movement behavior

Habitat switching may represent an important behavioral response to variations in habitat quality. To assess the effects of forest treatments (or canopy types) on the proportion of individual frogs redirecting their movements into adjacent treatments or canopy types ('proportion switching') we conducted two-way ANOVA using array, treatment (or canopy type), and recapture distance as fixed effects. When ANOVA revealed significant effects, we used Tukey's post-hoc tests for pairwise comparisons between treatments. We used SAS (PROC GLM, SAS version 9.1) for all statistical procedures and determined significance at a level of $\alpha = 0.05$.

RESULTS

Effects of habitat quality on initial orientation

Newly metamorphosed Green Frogs exiting their natal pond initially oriented nonrandomly (experimental unit = array; $G_3 = 12.08$, $P<0.01$). When we analyzed initial orientations at each array separately, orientations at Pond 5 differed significantly from random ($G_3=21.31$, $P<0.0001$). Pond 1 showed a similar, but not strong, trend ($G_3=5.68$, $P=0.128$). The largest percentages of frogs oriented toward the partial cut treatment at both ponds (Pond 1: 28.5%; Pond 5: 31.3%; Table 1).

Effects of habitat quality on movement success

Of the 1,354 Green Frog juveniles marked and released (Pond 1: n=453; Pond 5: n=901), we recaptured 13.8% (n=187) at terrestrial drift fences and an additional 7.3% (n=99) at edge drift fences on the border of control forests and clearcut treatments. The proportion of juveniles recaptured differed significantly among forest treatments ($F_{3,7}=16.10$, $P=0.002$). Movement success was greatest in the control (32.4±7.39%; mean percent ± SE) followed by the partial cut (15.1±1.92%). By comparison, juvenile movement success through clearcut treatments was greatly reduced (burned clearcut: 3.7±1.27%; unburned clearcut 2.2±1.13%; Table 2). Tukey's post-hoc test revealed that the proportion recaptured was significantly greater in the control than either clearcut treatment ($P<0.05$). The partial-cut treatment did not differ significantly from the control or the burned clearcut, but was different from the unburned clearcut

(*P*<0.05; Figure 1). There were no differences between the proportion of individuals recaptured at distances of 20 m compared to 50 m ($F_{1,7}$=0.34, *P*= 0.578). Also, there was no interaction between treatment and recapture distance (treatment × distance; $F_{3,7}$=0.24, *P*= 0.864; for complete ANOVA tables refer to Appendix D).

Effects of habitat quality on movement behavior

Our marking scheme enabled us to track movements of individual juvenile Green Frogs from their origin to their recapture location, and thereby identify patterns of movement. We documented two distinct behavioral responses to the variations in habitat quality and structure of our experimental treatments. Following their initial capture at the pond fence (0 m) and release into the forest treatment quadrants, a portion of individuals altered their initial movement trajectory and were recaptured at a drift fence in an adjacent treatment (habitat switching). The propensity to switch habitats during movement away from the pond differed among forest treatments ($F_{3,3}$=12.35, *P*=0.034; Figure 2), being far more prevalent in the two clearcut treatments than in the control and partial cut. In the burned and unburned clearcut 77.9±11.26% and 94.4±5.56%, respectively, of frogs originating there switched to other treatments before being recaptured at terrestrial drift fences. Most striking was the percentage of individuals from clearcuts that switched to the unaltered forest; 57.7±9.01% and 65.4±24.63 % moved to the control from the burned and unburned clearcuts, respectively. Tukey's post-hoc test confirmed that significantly more Green Frogs switched treatments after originating in the burned clearcut than the control (*P*<0.05). In contrast, very few individuals switched out of the control (4.4±4.41% switching or 95.6±4.41% treatment fidelity). No individuals originating in the control switched to either clearcut treatment. Similar to the control, the majority of Green Frogs moving through the partial cut remained there as well (31.9±12.85% switching or 68.1±12.85% treatment fidelity), though 24% did switch to the control (Figure 2).

The second pattern of movement we observed was movement along the control-clearcut edges. We recaptured 99 individuals at edge fences along the border of the control and clearcut treatments in our two arrays (Pond 1: n=47; Pond 5: n=52). The percentage of individuals moving into the control (51.5%) did not differ from those moving toward clearcut treatments (48.5%; $F_{1,3}$=0.73, *P*=0.456; Figure 3a). There was, however, a dramatic difference in the percentage of recaptures between the two edges. Edge fences bordering the unburned clearcut treatment accounted for 89.9% (n=89) of the total edge recaptures, compared to only 10.1% (n=10) at the burned clearcut edge ($F_{1,3}$=109.21, P=0.002; Figure 3b). Roughly, one third of captures along edges of the control (33.7%) were individuals that originally departed their natal pond at the control quadrant. Of the remaining edge captures 23.2% originated in the partial cut, 22.1% in the burned clearcut, and 21.1% in the unburned clearcut.

DISCUSSION

The findings of this study provide empirical support for the assertion that behavioral mechanisms contribute to the distribution and abundance of amphibians in heterogeneous habitats. In our Green Frogs, initial juvenile movement success and behavior are greatly influenced by terrestrial habitats surrounding natal ponds. By individually marking >1300 juvenile Green Frogs we were able to observe previously undocumented movement behaviors and relate them to overall habitat quality and structure. The results support our prediction that juvenile Green Frogs experience greater movement success and habitat fidelity in unaltered forest habitats compared to habitat that has been anthropogenically altered by clearcutting.

Effects of habitat quality on initial orientation

The initial orientation of recently metamorphosed amphibians likely contributes to their movement success after departing their natal pond. Because of the high vulnerability of juvenile amphibians to desiccation (Schmid 1965, Todd and Rothermel 2006, Rothermel and Semlitsch 2002, 2006) and predation (Wassersug and Sperry 1977, Arnold and Wassersug 1978), the decision of “where to go” in novel terrestrial habitats could be critical. We observed nonrandom initial orientation of juvenile Green Frogs, with the majority moving towards partial-cut treatments. It is not clear, however, if they are selecting habitat at the scale of our forest treatment quadrants. Watson and Mullin (2008) documented juvenile Wood Frogs (*L. sylvatica*) and Small-mouthed Salamanders (*A. texanum*) initially orientating toward areas of greater forest habitat. Others studies of initial orientation in amphibians suggest greater complexity, with orientations varying among multiple sites or shifting among years at the same site, depending on conditions (Jenkins et al. 2006, Timm et al. 2007, Homan et al. 2010). Some studies have further suggested that initial orientation may be less important than the selection of a new movement trajectory once an individual has experienced the terrestrial habitat (Jenkins et al. 2006, Patrick et al. 2007, Roznik and Johnson 2009). While the initial orientations of juvenile Green Frogs in our study appear to indicate a preference for the partial-cut treatment, we are reluctant to attribute it to coarse-scale habitat features. It seems more plausible that fine-scale habitat features within the perceptual ranges of juvenile frogs, such as microtopography or vegetation structure, would be responsible for this pattern.

Effects of habitat quality on movement success

Juvenile Green Frog's initial movement success differed strongly among the four treatment quadrants, with more individuals successfully moving through the control and partial-cut forests than either clearcut treatment. Our findings are consistent with previous studies of amphibian terrestrial habitat use, which demonstrated high sensitivity to forest-canopy removal (deMaynadier and Hunter 1998, Rothermel and Semlitsch 2002, Rittenhouse and Semlitsch 2006, Patrick et al. 2008). Removal of forest canopy fundamentally alters the forest environment by exposing the forest floor to increased sunlight and wind, creating a drier, warmer microclimate (Keenan and Kimmins 1993, Chen et al. 1999, Zheng et al. 2000). The process of timber extraction can further degrade habitat quality through reduction in leaf litter and soil compaction. For many species, particularly those strongly associated with closed canopy forest habitats such as Wood Frogs (*L. sylvatica*) or Spotted Salamanders (*Ambystoma maculatum*), lowered movement success in clearcuts is likely due to increased mortalities resulting from increased desiccation (e.g. Rothermel and Semlitsch 2006, Harper and Semlitsch 2007, Rittenhouse et al. 2008). Green Frogs, however, are considered habitat generalists with a broad geographic distribution and are commonly found in habitats representing a wide range of anthropogenic disturbance, from pristine wetlands and riparian areas to more-degraded habitats such as agricultural ponds, road-side ditches, and urban wetlands (Birdsall et al. 1986, Hecnar and M'Closkey 1997, Pauley and Lanoo 2005). Although we recorded lowered juvenile Green Frog movement success in clearcuts, this is not necessarily in alignment with results reported elsewhere. In a mark-recapture experiment in the coastal plain of South Carolina, Russell et al. (2002) reported increased immigration of adults and unchanged numbers of emerging juveniles, following timber harvesting. Several other studies also reported increased numbers of Green Frogs in clearcuts (Pais et al. 1988, Clawson et al. 1997, Perison et al. 1997). On the surface our findings appear to contradict these previous studies, however the differences may be attributable to the successional stage of the timber cut being examined and subsequent changes in vegetation structure, hydrology, and microclimatic properties. The clearcuts in our study were relatively older by comparison (approximately 3 years since timber extraction). In the younger clearcuts, Green Frogs may be attracted to the increased amount of saturated soil and standing water in ruts created by tree removal and skidding (Shepard 1994, Perison et al. 1997). Similarly, in a study prior to ours within the same experimental arrays, Semlitsch et al. (2008) described increased movements of Green Frogs into clearcuts during the summer immediately following timber extraction. Through succession and vegetative growth, the water table within these clearcuts lowered in subsequent years, decreasing the number of pools of standing water, likely making them less attractive to Green Frogs for habitation (M. S. Osbourn pers. observ.).

Another key consideration when examining habitat use by amphibians is an individual's movement phase (Nathan et al. 2008). Our study focused on the initial juvenile movement phase and therefore should theoretically show very different responses to habitat quality and structure than would a study focused on migrating adults. For Green Frogs, juveniles are the primary dispersal stage, with the majority departing their natal pond following metamorphosis and dispersing to other breeding populations (Martof 1953, Schroeder 1976). Because Green Frogs are closely associated with water for the majority of their life, the goal of the initial juvenile movement phase should be to escape the competition and predation pressures of their natal pond, move swiftly through terrestrial habitats, and locate a small, often temporary wetland or drainage to occupy until suitable conditions permit them to resume overland dispersive movements. Despite their association with aquatic habitats, Green Frogs juveniles are known to travel relatively long distances while dispersing overland (e.g. 4.8 km: Schroeder 1976).

For juvenile frogs engaged in overland movements, open-canopy habitats present potential tradeoffs between increased desiccation risk (Schwarzkopf and Alford 1996), ease of movement (Birchfield and Deters 2005, Mazerolle and Dessrochers 2005), and (if recently harvested) increased settling options in temporary pools (Shepard 1994, Perison et al. 1997). The balance of these three factors should determine whether the best behavioral response to a habitat is movement through or settling in. Clearcuts that lack standing water should present more risks than benefits for juvenile frogs, unless they are relatively small and free of obstructions, and therefore can be traversed quickly.

Effects of habitat quality on movement behavior

Green Frogs demonstrate substantial phenotypic plasticity (Schalk et al. 2002), which may also contribute to the behavioral flexibility of the species. The relatively high vagility of Green Frogs compared to other amphibians, implicates behavioral mechanisms as underlying their patterns of abundance and distribution in heterogeneous landscapes (Pauley and Lannoo 2005). Various authors have documented behavioral responses by pond-breeding amphibians to low-quality habitats, such as evacuation following timber harvesting (Semlitsch et al. 2008) and avoidance of open-canopy habitats (Rothermel and Semlitsch 2002, Mazerolla and Desrochers 2005, Rittenhouse and Semlitsch 2006).

Before conclusions about the effects habitat quality can be formulated, it is important that individual-level responses be placed within the context of the individual's behavioral state (i.e. movement mode; Nathan et al. 2008). A recently-metamorphosed frog, for example, may initially depart their natal pond in a movement mode focused on rapid dispersive movements away from the competitive and predation pressures of the pond and therefore be unresponsive to habitat quality (e.g. "away mode"; see chapter 1). At some point, perhaps within only a few meters from where they initially departed, a juvenile frog transitions to a movement mode characterized by adaptive, directed movements, sensitive to variations in habitat quality (e.g. "directed mode"; chapter 1). For juvenile amphibians, this is a critical transition, because movement too far into unsuitable habitats could be lethal if they are unable to locate adequate cover by sunrise. We documented evidence of two different behavioral responses by juvenile Green Frogs within our experimental arrays: habitat switching and edge movements.

The high prevalence of juvenile Green Frogs subsequently captured outside of their treatment of origin demonstrates that habitat switching is likely an important behavioral response to variations in habitat quality and structure. Ranid frogs, in general, are highly mobile juvenile dispersers (e.g. Schroeder 1968, Dole 1971, Funk et al. 2005) and their ability to select not just settling habitat, but also optimal movement pathways facilitates rapid rates of movement and long distances traveled. The greater vagility of frogs (Rittenhouse and Semlitsch 2007a; Graeter et al. 2008), along with differences in body morphology (Thorso and Svihla 1943) and physiology (Duellman and Trueb 1986) may be why they appear to show greater flexibility than do forest-dependent salamanders when encountering open-canopy habitats (deMaynader and Hunter 1995; although see chapter 2). Ranid frogs can, for example, choose not only to avoid hostile environments, but also reasonably attempt to rapidly move across them within a single night (e.g. Rittenhouse and Semlitsch 2007b). Accordingly, the wedge-shape of the 2.11 ha treatment quadrants ensured that the boundaries of adjacent treatments were likely to be easily accessible to juvenile frogs after departing their natal pond, regardless of forest treatment. This ability to sample multiple habitat types during initial juvenile movement, and choose the one with the greatest perceived potential for successful movement, could be critical for vulnerable juveniles in novel terrestrial habitats. Habitat switching in our experiment was far more prevalent in the two clearcut treatments than in the control and partial cut treatment. Specifically, individuals that initially moved into clearcuts dramatically changed course, and redirected their movements toward adjacent forest habitats; however, individuals departing the pond in the control overwhelmingly remained there (Figure 4). This behavior is in alignment with the conclusions of other authors that amphibian patterns of abundance in disturbed habitats reflect behavioral avoidance, we assume is driven by desiccation risk (Gibbs 1998, deMaynader and Hunter 1999, Rothermel and Semlitsch 2002). For ranid frogs, the quality of movement habitat may largely be a function of its structure. Habitat structure resulting from the composition of ground-level vegetation, downed woody debris, and leaf litter, likely determines the balance of risk versus ease of movement evaluated by frogs during overland movements. Various authors have reported that adult ranid frogs are more likely to occupy locations with more complex ground structure and avoid barren surfaces (L. clamitans; Mazerolle and Desrochers 2005; *L. pipiens*: Blomquist and Hunter 2010). Mazerolle and Desrochers (2005) further established that vegetative cover greatly reduced evaporative water loss in Green Frogs on dry soil substrates, compared to those lacking cover. It therefore seems plausible that the nearly complete switching by small-bodied juveniles originating in clearcuts to forested habitats represents a behavioral response to increased risk in those habitats.

An alternate, although not mutually exclusive interpretation of the striking differences in habitat switching between clearcuts and forests, is that clearcuts are less conducive to rapid movements. Ranid frogs in general appear to prefer open habitats within or adjacent to forests that facilitate unimpeded movement (e.g. Green Frogs: Birchfield and Deters 2005; Southern Leopard Frogs, *L. sphenocephala*: Graeter et al. 2008, Owens et al. 2008; Wood Frogs, *L. sylvatica*: Patrick et al. 2006). Within our experimental arrays control forests were characterized by comparably open forest floors with sparse undergrowth and significantly less stem density (see Appendix A). The combination of lower desiccation risk in closed forest canopy and fewer obstructions to impede movement, likely contributed to overall higher permeability (i.e. lower resistance) of control habitats. While tracking the movements of displaced adult Green Frogs on a golf course, Birchfield and Deters (2005) found that frogs selected the maintained short grass of the fairway for movement over nearby forest or unmaintained tall grass. Their findings suggest that Green Frogs select the path of least resistance, however a closer examination of their movement paths revealed that frogs were attempting to balance ease and speed of movement with the need to easily access refuges. The authors observed a tendency of displaced frogs to travel on short grass within two meters of the edge of tall grass and to jump into taller vegetation when threatened. In another displacement experiment with adult Edible Frogs (*Rana klepton*), Mazerolle and Vos (2006) observed that when given a choice between a shorter, but more risky path across a mined peat bog or a longer safer route along a hedge row, they chose the safer route. In our mark-recapture experiment the clearcut treatments appear to contain both higher desiccation risk and more impediments to movement, resulting in both decreased movement success and increased habitat switching there.

The pattern of recaptures at edge fences along control forest borders is more difficult to interpret. We found that an equal number of individuals on the boundaries of clearcuts were moving into and out of the control. On the surface, this seems to contradict to our habitat switching results which show large numbers of juvenile frogs moving into, but not out of control forests. The complete lack of any individuals originating in the control being subsequently recaptured in a clearcut, suggests that edge-captured individuals moving in the direction of clearcuts likely altered their trajectory once they reached the clearcut boundary. Also of interest were the overwhelmingly greater numbers of recaptures at the boundaries of the unburned clearcuts compared to the burned clearcuts. This disparity may have been the result of changes in habitat structure within successional clearcuts following burning. The unburned clearcuts were characterized by significantly greater stem density of herbaceous plants and woody saplings. In contrast, the burned clearcuts where more open with fewer impediments to movement, but lacked leaf litter and suitable cover (see Appendix A). These structural differences likely greatly influenced the movement paths of juvenile frogs. The burned clearcut edge was more exposed with very few refuges, and therefore not a suitable movement corridor for juvenile frogs attempting to both move efficiently and seek shelter when necessary. The unburned clearcut edge may have served a similar function as the tall grass edge in the Birchfield and Deters (2005) study by providing both ease of movement in the open control forest floor and a nearby, easily accessible refuge in the dense successional clearcut.

The origin of frogs moving along the unburned clearcut-control edge was nearly evenly divided among treatments, suggesting a degree of funneling of individuals into this movement corridor. The use of movement corridors along edge habitats has been shown in other taxa as well (e.g. butterflies: Haddad 1999; salamanders: Rosenberg et al. 1998). Previous studies have also demonstrated that ranid frogs tend to concentrate their movement paths along favorable habitats such as creek drainages (Martof 1943, Funk et al. 2005) and adult Green Frogs displaced into unfamiliar habitats tended to move down hill, presumably to locate moist habitats (Oldham 1967).

Conclusions and Implications

These findings provide new insights into juvenile amphibian movement behavior, especially habitat switching, and should also contribute to our understanding of natal dispersal across taxa. The results of this study are highly valuable because they go beyond comparing recapture counts and identify the behavioral mechanisms driving the patterns of abundance observed at larger scales. Understanding these mechanisms is crucial because they have direct implications for connectivity and the persistence of amphibians in the landscape. Furthermore, these findings yield important movement parameters (e.g. orientation and probability of successful movement in specific habitat types) to aid simulation models and will strengthen predictions of the effects of habitat alteration on amphibian populations (e.g. spatially explicit models: Dunning et al. 1995, South 1999, Collingham and Huntley 2000).

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Table 1. Initial orientation of recently metamorphosed Green Frogs (*Lithobates clamitans*), as indicated by initial capture point along natal pond drift fences. We performed goodness of fit G-tests using counts from individual arrays and means.

		Experimental forest treatments % (n)				
Analysis	Array	Control	Partial Cut	CC Burned	CC Unburned	*P*<0.05
Individual array	P1	23.0 (104)	28.5 (129)	26.9 (122)	21.6 (98)	No
	P5	20.4 (186)	**31.3 (282)**	24.4 (220)	23.6 (213)	Yes
Means (±SE)	P1 & P5	21.8±1.16	**29.9±1.41**	25.7±1.26	22.6±1.00	Yes

Notes: For analyses differing significantly from random the treatments with the highest percentage of initial captures are indicated in bold.

Table 2. Number of juvenile Green Frogs (*Lithobates clamitans*) marked and released (n) and mean percent recaptured (±SE) in each experimental forest treatment at 20 m and 50 m from natal ponds. Means are calculated from replicate arrays.

	Experimental forest treatment			
	Control	Partial Cut	CC Burned	CC Unburned
Released (n)	290	411	342	311
Recaptured (20 m)	17.2±1.07	6.6±1.93	1.9±0.55	1.2±1.17
Recaptured (50 m)	14.7±8.94	8.1±0.38	1.8±1.81	0.5±0.47
Recaptured (Total)	32.4±7.39	15.1±1.92	3.7±1.27	2.2±1.13

Figure 1. The effects of experimental forest treatments on juvenile Green Frog (*Lithobates clamitans*) movement success. Pair-wise comparisons are of mean percent (±SE) of individuals recaptured in each treatment (Tukey's post-hoc test; $P<0.05$).

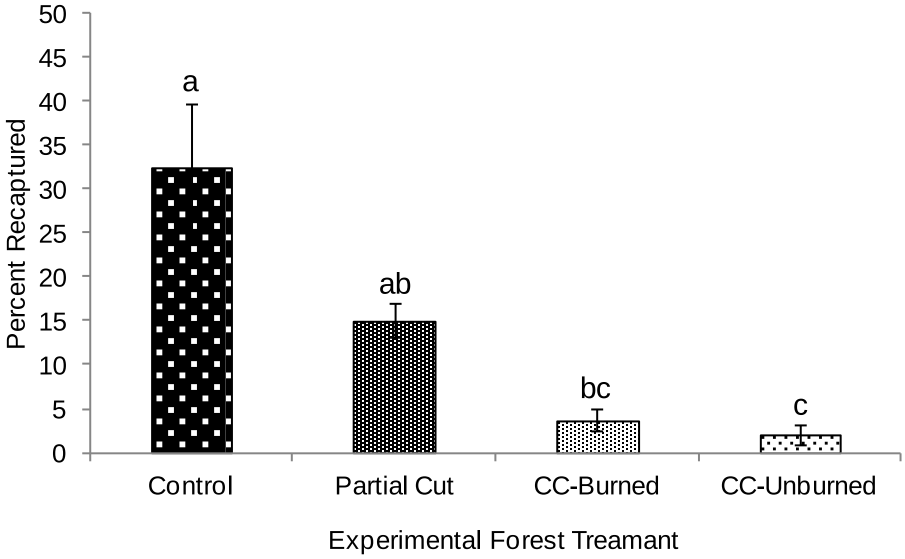

50
45
40
35
30
25
20
15
10
5
0
Percent Recaptured
a
ab
bc
c
Control
Partial Cut
CC-Burned
CC-Unburned
Experimental Forest Treamant

Figure 2. Habitat switching behavior in juvenile Green Frogs (*Lithobates clamitans*) showing the proportion that remained in their initial forest treatment (fidelity; indicated within a black rectangle) and the proportion that moved to other habitats (switching).

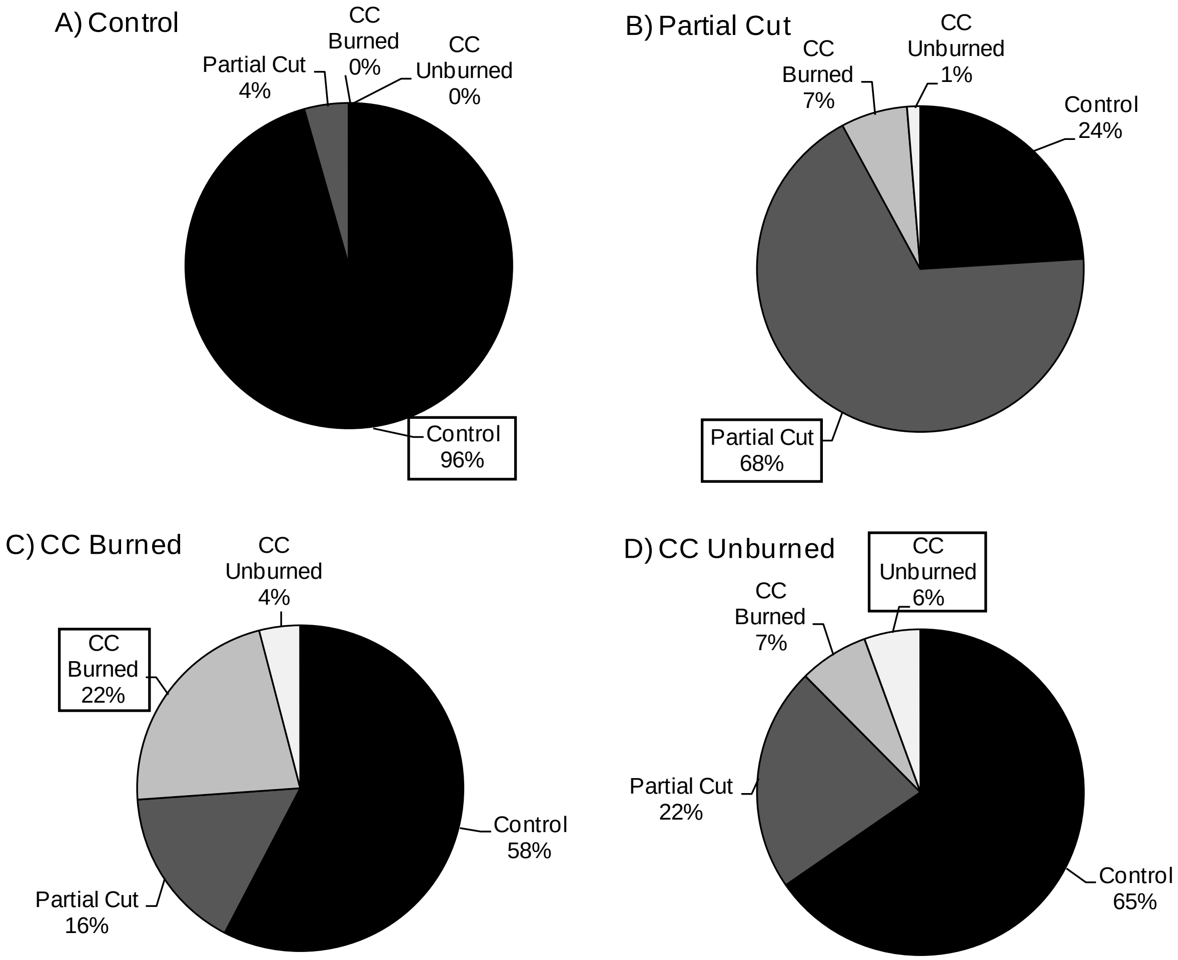

A) Control
Partial Cut 4%
CC Burned 0%
CC Unburned 0%
Control 96%
B) Partial Cut
CC Burned 7%
CC Unburned 1%
Control 24%
Partial Cut 68%
C) CC Burned
CC Unburned 4%
CC Burned 22%
Control 58%
Partial Cut 16%
D) CC Unburned
CC Unburned 6%
CC Burned 7%
Partial Cut 22%
Control 65%

Figure 3. Edge movements along boundary of control forest and clearcut treatments. A) Movement direction of juvenile Green Frogs either into (In) or out of (Out) of the control forest as determined by the side of the edge fence where they were captured. B) Percentage of edge recaptures from the burned clearcut (CC-burn) and unburned clearcut (CC-unburned). All values are percent of total edge recaptures.

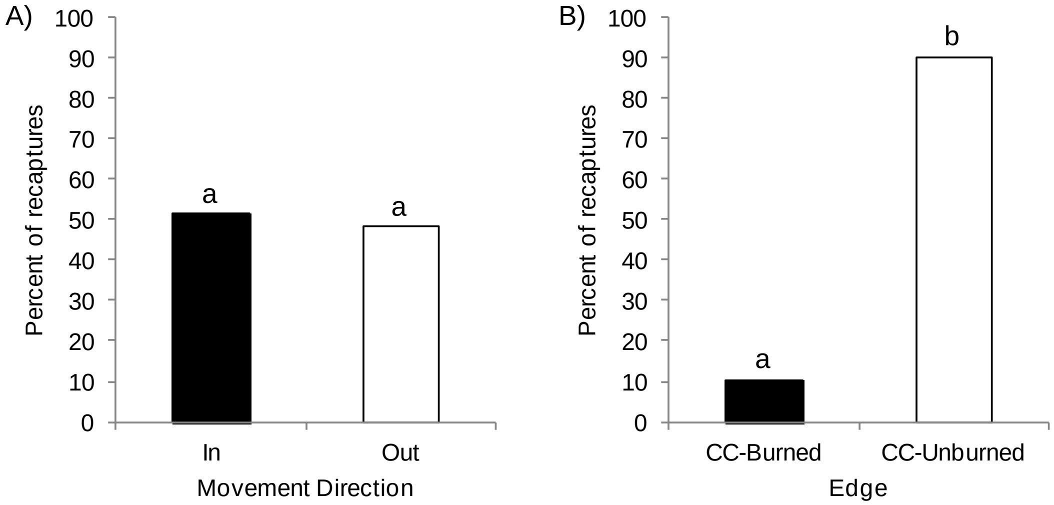
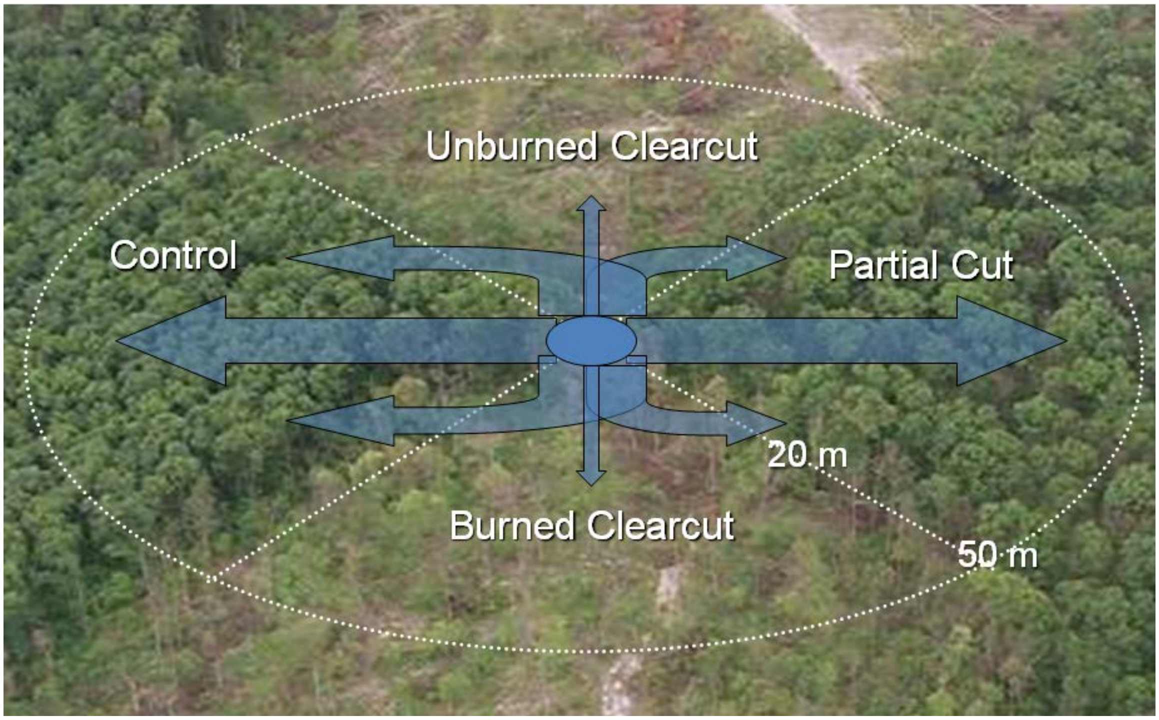

A)
100
90
80
70
60
50
40
30
20
10
0
Percent of recaptures
a
a
In
Out
Movement Direction
B)
100
90
80
70
60
50
40
30
20
10
0
Percent of recaptures
b
a
CC-Burned
CC-Unburned
Edge

Figure 4. Representation of switching behavior by juvenile Green Frogs (*Lithobates clamitans*) in experimental forest array.


Unburned Clearcut
Control
Partial Cut
20 m
Burned Clearcut
50 m

CHAPTER 4

EFFECTS OF FINE-SCALE FOREST HABITAT QUALITY ON MOVEMENT BEHAVIOR AND SETTLING DECISIONS IN JUVENILE POND-BREEDING SALAMANDERS

Michael S. Osbourn

ABSTRACT

How individuals respond to variation in habitat quality, while moving through heterogeneous habitats, remains a key question necessary for better predicting phenomena at larger ecological scales, such as local population and metapopulation dynamics. We examined this question in the context of juvenile pond-breeding salamanders (*Ambystoma maculatum*, Spotted Salamanders and *A. annulatum*, Ringed Salamanders) departing their natal ponds and moving into terrestrial forest habitats. We sought to identify how fine-scale habitat quality affected juveniles’ decisions to cease moving away from their natal pond, select a refuge, and settle. We used replicated experimental field enclosures to isolate the effects of forest canopy and microhabitat manipulations on salamander settling decisions relative to unmanipulated forest controls. We employed generalized linear mixed models to examine the effects of canopy cover (closed or open), microhabitat (control, compacted soils, high coarse woody debris, high burrow density), temperature (weekly mean ˚C), weekly total rainfall amount (cm), and body size (mass; g) on the probability of settling.

Our models for both species revealed strong effects of habitat quality on this key decision. Specifically, in the open canopy control, *A. maculatum* and *A. annulatum* had 10% and 30% decreased probability of settling, respectively, compared to the closed canopy control. *Ambystoma annulatum* were 24% less likely to settle in compacted soil. The responses to the increased refuge density appear to be species-specific. While habitat quality did not impact the settling probability of *A. annulatum*, for *A. maculatum*, the probability of settling increased 18% and 25%, respectively, under conditions of high burrow density and high coarse woody debris. These findings go beyond previous studies of amphibian movement in that they reveal how the interplay of external factors and individual behavior produce observed patterns of movement and habitat selection. A better understanding of the fine-scale behavioral mechanisms underlying the distribution of juvenile amphibians should allow for better predictions of demographic patterns at larger scales. These findings should also broaden our general understanding of transitions between movement modes with implications across taxa.

INTRODUCTION

A long-standing goal of ecologists is to understand the mechanisms driving ecological phenomena. Proponents of hierarchy theory advocate that such mechanisms originate at lower levels of hierarchical scale, such as at the level of individual responses (O'Neill 1989). The mechanistic roots of many ecological phenomena lie in two individual behaviors: movement and habitat selection (Wiens et al. 1993). By examining fine-scale movements and habitat selection of individual animals within habitat patches of varying quality, we can begin to predict larger ecological patterns such as local population and metapopulation dynamics (Morales and Ellner 2002). Unfortunately, fine-scale individual-level empirical movement data is often difficult to obtain for many vertebrate species (Bowler and Benton 2005) and complexity and condition-dependence make isolating mechanisms challenging (Massot et al. 2002, Clobert et al. 2009).

Various authors have attempted to stimulate research efforts by proposing conceptual frameworks that address our lack of understanding of movement ecology (Nathan et al. 2008) and particularly animal dispersal (Bowler and Benton 2005, Clobert et al. 2009). Traditionally movement phenomena have been described simplistically, with dispersal, for example, often treated as a linear movement between patches of suitable habitat. Recently proposed frameworks attempt to conceptualize the complexity of individual animal movements by identifying distinct movement phases associated with specific goals and behaviors. The goal of a movement phase could for example be foraging or predator evasion (Nathan et al. 2008). Also fundamental to these approaches is the influence of external factors (e.g. microclimate, conspecific interactions) and internal state (e.g. energy reserves, body size) on individual-level decisions and movement success.

Resolving to an even finer scale, within each phase can be observed discrete behavioral states or "movement modes" which produce their own discernible patterns of movement (Nathan et al. 2008, Getz and Saltz 2008). Shifts between movement modes are thought to be initiated by changes in an individual's internal state and/or external factors (Nathan et al. 2008). Mutiple movement modes should be advantageous in heterogeneous landscapes, allowing individuals to respond adaptively to variations in habitat quality. Theoretically, within high quality patches with abundant resources slower, more sinuous movement should increase the probability of locating resources. Conversely, in low-quality habitats moving more quickly and straighter should be advantageous. Fryxell et al. (2008) observed this pattern in elk as they encountered patches of either dense or sparse food resources. Movement modes therefore provide a behavioral means to optimize movement success while balancing trade-offs between movement rate, searching, or vigilance with energy reserves, predation risk, or desiccation risk (Zollner and Lima 2005, Wiens 2001).

The importance of natal dispersal (the movement of individuals from their natal site to a new site for breeding) to ecological and evolutionary processes is well documented; however it persists as a significant gap in our understanding of ecology (Ronce 2007). By subdividing this movement phenomenon into distinct movement phases we can begin to identify processes and relate them to patterns at larger scales. The first movements of individuals as they venture beyond their natal site with the goal of reaching their eventual new home range, comprise the initial juvenile movement phase. Within this movement phase are multiple behaviorally distinct movement modes (Chapter 1). The critical decision of when to stop moving and where to select a refuge, represents an essential transition between movement modes (Wiens 2001). This decision point is likely integral in determining whether a juvenile settles within either their natal population (philopatry) or continues moving until they reach a new breeding population (natal or juvenile dispersal).

With no prior knowledge of resource patches or optimal movement paths, juveniles are highly vulnerable to mortality during their first movements into novel habitats (Lucas et al. 1994, Alberts and Altmann 1995, Delgado et al. 2009). Furthermore, their perceptual ranges are limited compared to adults, making them less able to detect suitable habitats from greater distances (Zollner and Lima 2005). Within heterogeneous landscapes the ability to recognize suitable habitat is essential for individual fitness. Therefore, juveniles must be able to perceive differences in habitat quality and where reliable cues exist, there should be selection for individuals that recognize and chose optimal available habitat (e.g. Delgado et al. 2010). These cues may serve as triggers initiating changes in movement mode. Some birds, for example, stop dispersing and initiate settling behavior when they encounter conspecifics (Nicholaus et al. 2012).

Ambystomatid salamanders are an excellent study system for examining initial juvenile movement. They can be studied at smaller spatial scales than would be possible for most other vertebrate taxa and their complex life cycle (aquatic larval phase and terrestrial adult/juvenile phase) results in spatiotemporal concentration of recently-metamorphosed juveniles as they emerge from natal ponds and move into terrestrial habitats. Forest-associated ambystomatid salamanders are also known to be responsive to cues indicating habitat quality (see Rittenhouse et al. 2004; M. S. Osbourn unpubl. data) and have been shown to alter their behavior in low-quality clearcut forests (Rothermel and Semlitsch 2002, Rittenhouse and Semlitsch 2006; see Chapter 2). Furthermore, amphibians' high susceptibility to evaporative water loss in terrestrial habitats is exacerbated by the high surface area to volume ratios of juveniles (Jørgensen 1997). As amphibians metamorphose and move from aquatic to terrestrial habitats they incur high mortality rates due to desiccation and predation (Jameson 1956, Shoop 1974, Wassersug and Sperry 1977, Rothermel and Semlitsch 2002). It is critical that they are able to locate moist, cool, sheltered refuges in which to retreat during hot, dry daylight hours and extended dry periods. Due to their high sensitivity, survival during this period is often very low and is strongly affected by land use alterations to forest habitat (Harper 2007, Rothermel and Semlitsch 2002, 2006, Rittenhouse et al. 2008). The prominence of habitat loss and alteration as leading contributors to global amphibian declines (Stuart et al. 2004, Gardner et al. 2007) further makes examining the affects of habitat quality on amphibian movement behavior pertinent.

Although philopatry is often very high in pond-breeding salamanders (e.g. 91%-Gamble et al. 2007), juveniles are likely the primary dispersal stage (Semlitsch 2008). The small proportion of individuals that disperse to new breeding sites are vitally important for local population and metapopulation dynamics and regulation, as well as long-term persistence of species (Semlitsch 2008). It follows, therefore that changes in habitat quality which affect the success of initial juvenile movement could have a disproportionate effect on the population as a whole and represent an underlying mechanism for changes at larger ecological scales.

Using experimental forest arrays, we demonstrated that coarse-scale forest manipulations could produce differences in juvenile movement success and behavior in *Ambystoma maculatum* (Spotted Salamanders; Chapter 2). Juvenile movement success in this study was significantly lower in open-canopy clearcuts compared to closed-canopy forests and recaptures declined sharply with increasing distance from natal ponds. Considering the well-documented high mortality rates following juvenile dispersal (e.g. Rothermel and Semlitsch 2006), a logical assumption is that the majority of non-recaptures represent mortalities. However, if we consider the existence of multiple movement modes, the observed patterns of movement success could be partly shaped by a behavioral shift from a dispersive movement mode to a settling movement mode (see Chapter 1).

Here, we present results from a field experiment examining fine-scale movement and habitat selection of juvenile salamanders. By manipulating microhabitat features within terrestrial habitat encountered initially by newly-metamorphosed juveniles, we sought to determine specific behavioral responses to fine-scale habitat quality. Our goal was to identify the existence of multiple movement modes in juvenile salamanders and isolate the specific mechanisms responsible for triggering the transition between them. Specifically, we wanted to reveal whether habitat quality affected the decision of when to stop moving away from the natal pond, select a refuge, and settle. We predicted that juveniles in lower-quality habitats would either move less and settle sooner or conversely, exhibit greater movement compared to settling.

METHODS

Study site and species

We conducted our experiment at Daniel Boone Conservation Area (DBCA; 1,424.5 ha) in the upper Ozark Plateau in Warren County, Missouri (Semlitsch et al. 2009). The habitat at DBCA is characterized by mature second-growth forest (80-100 years old) dominated by oak (*Quercus* spp.) and hickory (*Carya* spp.). Wildlife ponds in DBCA were constructed >30 years ago along ridge tops for deer and turkeys and were naturally colonized by up 16 amphibian species (Hocking et al. 2008). The presence of large populations of forest-associated species of pond-breeding salamanders, combined with ongoing timber management make DBCA an ideal site for examining the effects of land use on amphibian movement. We chose *A. maculatum* (Spotted Salamanders) and *A. annulatum* (Ringed Salamanders) as our focal species, because the sensitivity of A. maculatum to forest habitat alteration is well documented (e.g. deMaynadier and Hunter 1998; Patrick et al. 2008) and there is currently very little known about *A. annulatum*.

Experimental enclosures

We used replicated experimental field enclosures to isolate the effects of specific habitat features on settling decisions during initial juvenile movement. Long rectangular enclosures, referred to as “runs” have been used effectively in previous movement studies (see Rosenberg et al. 1998, Rothermel and Semlitsch 2002). We constructed each run (n=16, 2 m x 20 m) with plastic-weave silt fencing walls (~90 cm high) supported by wooden stakes and buried 12 cm into the ground. After observing salamander climbing behavior in 2009 (see Osbourn et al. 2012), we added inward facing lips by folding down the top 10 cm of the walls and securing them with cable ties and duct tape to form 45-90˚angles. To capture individuals reversing back to the release point (0 m) or moving the full length of the run (20 m), we installed pitfall traps (plastic plant pots - 23 cm diameter, 45 cm deep) level with the ground at each inside corner (4 per run). A wooden board suspended on rebar stakes 4 cm above each trap, provided shelter from sunlight and protection from predation. We placed a moist sponge at the bottom of each trap, to prevent desiccation. To simulate a natal pool, we placed a plastic wading pool (1.5 m in diameter by 36 cm deep) at the release point (0 m) of each run (as in Rothermel and Semlitsch 2002; Figure 1). We inoculated each pool with 40 liters of filtered pond water, added 1.0 kg of forest leaf litter, and allowed them to fill with rainwater.

Experimental design and habitat manipulations

We employed a two-by-four factorial design to test the effects of canopy cover and microhabitaton settling behavior, for a total of eight treatment combinations at two different sites at DBCA. We manipulated three microhabitat features thought to impact salamander movement and survival, including: downed coarse woody debris (CWD; deMaynadier and Hunter 1999, Harper 2007), burrow densities (Loredo et al. 1996, Rothermel and Luhring 2005), and soil compaction. We placed our compacted soil run along a former log skidder road (last used 3-5 years prior to experiment), then randomly assigned treatments to three adjacent runs: unmanipulated control, high course woody debris, or high burrow density (see Figure 1). Of our three microhabitat manipulations, the compacted soil treatment was intended to test a potentially enduring and previously unexamined negative impact of timber extraction. The remaining two microhabitat manipulations (high course woody debris and high burrow density) were intended to enhance habitat quality by increasing the number of suitable refuges.

Following Harper (2007), we standardized all runs with ~9 m (0.22 m of CWD per m^2) of decaying logs (decay class 3; Maser et al. 1979) to represent a typical amount of downed wood found on a forest floor in Missouri (Shifley and Brookshire 2000). We added an additional 40 m (1 m of CWD per m^2) of newly cut white oak (*Quercus alba*) logs to high CWD treatments (Harper 2007). To simulate high burrow density, we installed artificial burrows at a density of one per m^2. Our burrows consisted of a plastic mesh cylinder (15 cm long, 2.5 mm diameter) closed at the bottom inserted into a slightly larger mesh cylinder tightly packed into the soil. This designed allowed us to easily remove the inner cylinder, inspect it, extract salamanders, and replace it in the ground without repeatedly disturbing the soil (See Osbourn et al. in review). The diameter of our burrow openings was selected to closely emulate the burrow entrances of short-tailed shrews (*Blarina* sp.), a common *A. maculatum* refuge (Madison 1997, Faccio 2003). Osbourn et al. (in review) found that when given the choice between the retractable-mesh artificial burrows we used in this study and packed-soil holes of equal dimensions, juvenile *A. maculatum* burrow choice did not differ significantly from random and juvenile *A. annulatum* may have shown a preference for them. We inserted burrows at 30˚ angles with entrance facing the direction of the natal pool and arranged them in four rows of 10 at distance of 2 m, 5 m, 10 m, and 15 m from the release point.

At both replicate experimental arrays, we placed a group of four runs, containing the three microhabitat manipulations along with an unmanipulated control, within two canopy types, including a successional clearcut (open-canopy) and a forest (closed-canopy). Our successional clearcuts were harvested between March 2004 and January 2005, approximately four years prior to installation of our experimental enclosures. To reverse successional changes in vegetation composition and height, we mechanically removed all tree saplings from within and immediately adjacent (2 m) to our clearcut enclosures.

Experimental salamanders

Because of the disparate timing of metamorphosis among individuals, it was necessary for us to acquire juvenile salamanders by multiple means from the same population. In May-June, we collected *A. maculatum* (2008 and 2009) and *A. annulatum* (2009 and 2010) eggs and larvae with dip nets at breeding ponds near our arrays, and raised them until metamorphosis in cattle watering tanks (1000 liters, 1.52 m diameter), located on site. We further supplemented these individuals with recently metamorphosed salamanders captured at drift fences surrounding adjacent ponds (see Chapter 2). Following metamorphosis, we held juvenile salamanders in plastic shoe boxes (31 cm long x 19 cm wide x 11 cm deep) filled with moist leaf litter until release and housed them in a temperature controlled (24˚ C) animal care facility at the University of Missouri. We ensured salamander well-being through regularly misting of containers and initiated bi-weekly feeding with earthworms or crickets if individuals were held for over one week.

For each salamander, we measured snout-vent length (SVL; mm) with a ruler and mass (g) with an electronic balance (Acculab Pocket Pro). We individually marked each salamander with a permanent Visible Implant Alphanumeric tag (VIAlpha tag; Northwest Marine Technology Inc., USA; Osbourn et al. 2011). The recovery of all individuals was monitored for 6 - 12 hours prior to release. Once we accumulated enough salamanders to release ≥10 individuals into each enclosure at one of our replicate arrays, we then waited for rainy conditions before conducting a nighttime release.

Experimental procedure

Just prior to the release, we allowed salamanders two to three hours to acclimate and orient themselves along the edge of the artificial pool at their enclosure. Our intention was to expose individuals to the pond cue, thereby aiding them in establishing a reference point for orientation. We released a total of nine groups (5 at array 1 and 4 at array 2) of 12-18 *A. maculatum* (n= 1053) from July-October 2008-2009, and ten groups (5 at each array) of 10-18 *A. annulatum* (n= 1150) from June-July 2009-2010. We did not release both species simultaneously in the same trials.

For the duration of the study period, both within and between trials, we inspected pitfall traps in the morning and recorded individuals recaptured in the 0 m pitfall traps near the release location as “reversers” and individuals recaptured at the far end in 20 m pitfall traps as “movers.” We measured (0.01 cm; SVL) and weighed (0.01 g) individuals recaptured after the first day of the experiment. After the eighth night we conducted thorough searches of all enclosures, with an approximate search effort of three person hours per enclosure. During searches we carefully sifted through leaf litter and vegetation, and inspected under cover objects and within burrows. When we encountered a salamander within a refuge (“settler”), we recorded its distance from the natal pool and the refuge type.

Habitat and environmental measurements

We collected detailed habitat measurements and used analysis of variance to confirm that our habitat manipulations resulted in quantifiable differences in habitat structure (ANOVA; Proc GLM, SAS version 9.1). We also counted burrow entrances encountered during enclosure searches to use as a measure of small mammal burrowing activity and refuge availability. Complete habitat sampling procedures and results are located in Appendix A.

In addition to measurements of habitat quality, we documented changes in external conditions by recording environmental variables throughout the experiment. We monitored daily rainfall amounts with a rain gauge (Tru-Check) located at each array and soil moisture within each run by collecting and drying soil samples, then using the difference between the wet and dry weights to estimate percent water content (see Appendix A for details). Within each canopy treatment, at each array, we measured relative humidity with HOBO data loggers (15 min intervals; OnSet Computer Co., Bourne Massachusetts, USA). We measured ground-level air temperature within each run with HOBO data loggers (1 hr intervals). In our four high burrow density runs, we measured subsurface temperatures within artificial burrows, with iButton data loggers set to record at five minute intervals (three per run; ~ 4 cm below surface).

STATISTICAL ANALYSES

Our analyses sought to identify factors which influence the settling probability of salamanders during their initial juvenile movement phase. We used settling probability as a binary response variable representing whether each individual settled in (recaptured in microhabitat refuges during enclosure searches) or moved through their enclosure (recaptured in pitfall traps at 20 m). We employed generalized linear mixed models (GLMMs) to examine the effects of canopy cover (closed or open), microhabitat (control, CWD, burrow, compacted), temperature (weekly mean ˚C), weekly total rainfall amount (cm), and body size (mass; g) on settling probability. Based on these explanatory variables, we built a small set of *a priori* models and used Akaike's Information Criterion for model selection (AIC, Burnham and Anderson 2002). Each model represented a plausible biological explanation for observed settlement behavior (Tables 1 and 2). To account for the potential correlation of individual responses within runs, all models included a random effects term for run. We fitted models using the “lme4" package in program R and used the Laplace approximation for maximum likelihood estimation of parameters (Bates et al. 2011; R Development Core Team, 2012).

To characterize the effects of canopy cover and microhabitat manipulations, we back-transformed settling probabilities for each manipulation based on parameter estimates from our best-supported model for each species. In our 4 x 2 factorial experiment, the unmanipulated microhabitat treatment in the closed-canopy forest represented our true control. For simplicity, we report changes in settling probabilities due to microhabitat manipulations as the percent change relative to this control level. Similarly, when discussing differences in settling probabilities due to canopy manipulations, we report the percent change between the unmanipulated microhabitat treatments in open and closed-canopy.

RESULTS

Of the 1053 *A. maculatum* and 1150 *A. annulatum* released into our runs, we recaptured 62% (n= 655) and 38% (n= 441) respectively. Of the recaptured *A. maculatum*, we classified 22% (n=228) reversers, 25% (n=267) movers, and 15% (n=159) settlers. For *A. annulatum* there were 17% (n= 197) reversers, 18% (n=203) movers, and 4% (n=41) settlers. To examine the effects of external factors on the transition between dispersive and settling movement modes, we focused our analysis solely on individuals which either chose to move or settle (*A. maculatum* n= 426; *A. annulatum* n=244). Our models for both species revealed strong effects of habitat quality on this key decision. In both *A. maculatum* and *A. annulatum*, the model selection procedure (AICc) ranked the global models highest and they were the only models with Δi< 2.0 (Table 1), indicating substantial evidence that these are the best-supported models from our *a priori* model set (Burnham and Anderson 2002). For both species, this model (global model) included body mass, total rainfall and mean nightly temperature for each release period, along with canopy and microhabitat manipulations as explanatory variables (Tables 1 and 2). While we cannot ignore that including body mass and temperature improves our model, their influence on settling is minimal or without consistent direction.

For both species the probability of settling appears to decrease with decreased habitat quality. Specifically, in the open canopy control *A. maculatum* and *A. annulatum* had 10% (GLMM; *Z*= -2.120, *P*= 0.034) and 30% (*Z*= -3.96, *P*< 0.001) decreased probability of settling compared to the closed canopy control, respectively. Microhabitat manipulations also affected the probability of settling in both species. *Ambystoma annulatum* were 24% less likely to settle in the compacted soil microhabitat (*Z*= -1.989, *P*= 0.047). Although not significant, *A. maculatum* showed a similar trend with individuals having a 10% lower settling probability in compacted soil treatments (*Z*= -1.410, *P*= 0.159). There appear to be species-specific responses to our two refuge enhancement manipulations. The high coarse woody debris and high burrow density treatments did not significantly affect the probability of settling by *A. annulatum* juveniles (*Z*= -0.476, *P*= 0.634 and *Z*= -0.816, *P*= 0.415, respectively). In *A. maculatum*, however, increased refuge density did increase the probability of settling. Juvenile *A. maculatum* have an 18% and 25% increased probability of settling in the high burrow density (*Z*= 2.340, *P*= 0.019) and high coarse woody debris (*Z*= 3.159, *P*= 0.002) treatments, respectively. Also notable is the apparent compensatory effect of increased refuge density in open canopy habitats. Juvenile *A. maculatum* in open-canopy clearcuts have a 6% and

13% increased probability of settling in high burrow density (Z= 2.340, P= 0.019) and high coarse woody debris treatments relative to forest controls (Z= 3.159, P= 0.002), respectively. While weekly total rainfall amount did not appear to affect *A. annulatum* juveniles (Z= 0.657, P= 0.511), increased rainfall did appear to decrease the likelihood of settling by *A. maculatum* juveniles (Z= -2.122, P= 0.034; Figures 2 and 3).

Habitat and environmental measurements

We confirmed that runs within clearcuts had significantly less canopy cover ($F_{1,47}$ = 329.94, P<0.0001) and leaf litter depth compared to forest runs ($F_{1,56}$ =20.47, P<0.0001). In addition to lower leaf litter depth, there were significantly fewer small mammal burrows in clearcuts ($F_{1,145}$ =53.54, P<0.0001). This combination of increased solar exposure and decrease in moist leaf litter for refuges exacerbates desiccation risk for amphibians moving through clearcuts. Using a penetrometer, we verified significantly greater soil compaction (kg/cm2) within the compacted soil treatments ($F_{3,48}$ =39.26, P<0.0001). Also, ANOVA revealed significantly fewer burrows within the compacted soil treatments ($F_{3,145}$ =136.04, P<0.0001). A third habitat feature differentiating compacted soil treatments was the presence of significantly less leaf litter ($F_{3,56}$ =11.5, P<0.0001). When we combined our counts of small mammal burrows with the installed artificial burrows, the high burrow density treatment had significantly more burrows than other treatments ($F_{3,145}$ =136.04, P<0.0001). Also, as assumed, the high course woody debris treatments contained significantly more downed wood than the other treatments ($F_{3,41}$ =26.93, P<0.0001).

DISCUSSION

This study provides empirical evidence that transitions between juvenile salamander movement modes are influenced by external factors. Specifically, we found that in lower-quality habitats the probability of settling decreased and more individuals choose instead to continue moving. Our analysis further indicates that in addition to our microhabitat and forest canopy manipulations of habitat quality, other external factors (temperature and rainfall amount), along with internal state (body mass) potentially contribute to the observed pattern of movement and settling behavior. These findings indicate that initial juvenile movement in pond-breeding amphibians is not random diffusion into the landscape, but suggest the presence of adaptive behavior, with information about external conditions interacting with internal state to influence changes in behavior and produce multiple distinctive movement modes.

Effects of habitat manipulations

Because of the acute risk of desiccation, selecting a refuge may be the single most important decision made by a juvenile amphibian in its first night of movement through terrestrial habitats. This high risk of mortality likely results in intense selection pressure for juvenile amphibians to recognize both direct and indirect cues of habitat favorability. Laboratory substrate choice experiments have demonstrated that juvenile *A. maculatum*, for example, will select not only moist over dry substrates (direct cue), but also the olfactory cue for forest over grassland substrate (indirect cue; Rittenhouse et al. 2004; M. S. Osbourn unpubl. data). This is vital because juvenile amphibians typically depart their natal pond on wet, rainy nights when terrestrial habitats may be uniformly moist. The ability to recognize not only which habitats are currently suitable, but also which habitats will tend to be suitable after stopping is critical. This evidence of cue use also suggests that juvenile amphibians moving through heterogeneous habitats should be able to detect and respond to variations in habitat quality. Our findings in this study further demonstrate that the availability of suitable refuges for settling serves as an external trigger, initiating transitions among movement modes. Generally within our experimental runs, when habitat quality was higher (e.g. forest canopy and high refuge density) the probability of settling was also highest.

In the context of habitat alteration, the importance of refuge selection could be magnified. The negative effects of canopy removal on forest-associated amphibians are well documented (Petranka et al. 1994, deMaynadier and Hunter 1995, Semlitsch et al. 2009). Timber harvesting and resulting canopy removal is known to affect amphibian survival (deMaynadier and Hunter 1999, Rothermel and Semlitsch 2002, Harper and Semlitsch 2007), individual vital rates (Todd and Rothermel 2006), and adult movement behavior (Chan-McLeod 2003, Rittenhouse and Semlitsch 2006, Semlitsch et al. 2008). Osbourn (Chapter 2) reported negative effects of canopy removal on initial juvenile movement success and behavior in *A. maculatum*. Similarly, our forest canopy manipulation in this study produced strong responses in *A. maculatum* and *A. annulatum*. The decreased probability of settling in open-canopy habitat is consistent with the prediction that juvenile forest-associated salamanders will choose continued movement, in an attempt to pass through areas of low habitat quality, rather than risk settling in unsuitable habitats.

In addition to the removal of forest canopy, timber harvesting may produce more-subtle impacts such as the reduction of leaf litter and compaction of soil. While we did not directly manipulate leaf litter within our experimental enclosures, reduced leaf litter was strongly associated with our compacted soil treatment. This was surprising because the log-skidder roads, where we located our enclosures, had been inactive for more than four years. In the compacted soil enclosures within the forest, leaf litter tended to accumulate within the deeper road ruts and to be bare elsewhere. In the clearcuts, the lack of sapling growth and predominance of dense herbaceous plant growth may have contributed to the lack of leaf litter. Leaf litter is a vital component of salamander terrestrial habitat because it can serve as a temporary refuge during moist conditions, insulates the surface of the soil from temperature extremes and drying, and is habitat for numerous invertebrate prey species. Moseley et al. (2004) found that when pine litter was removed from experimental enclosures, Mole Salamanders (*Ambystoma talpoideum*) moved more and for longer durations. A similar response to litter removal has been observed in terrestrial plethodontid salamanders (see Rosenberg et al. 1998, Semlitsch et al. 2012). In these studies, as well as ours, the principle motivation for increased movement and decreased settling in habitats with low or absent leaf litter, is most likely higher risk of desiccation and predation.

Very little is known about the effects of soil compaction on animal movement and habitat selection and the strong responses we observed by *A. annulatum*, as well as the weaker responses in *A. maculatum*, suggest that it represents an overlooked, but potentially important impact of timber extraction. The scant literature on the subject is concerned mainly with effects on fossorial organisms' ability to burrow tunnels. Gans (1974) found that Worm Lizards require increased energy expenditure when digging in compacted soils and Ducey et al. (1993) revealed that caecilians would not enter and construct burrows in areas with high soil compaction. Increased surveying behavior in an attempt to locate areas of lower compaction was also observed in caecilians (Ducey et al. 1993), as well as in mole rats (Lovegrove 1989) and pocket gophers (Vleck 1979). Presumably, this is a behavioral tradeoff to limit energetic costs of digging in compacted soils. While most ambsytomatid species (e.g. *A. maculatum*) do not exhibit burrowing behavior, their reliance on preexisting burrows for refuges (Semlitsch 1983), means that a decrease in the number of in small mammal burrows would limit a critical refuge for juvenile salamanders. Probably the greatest effect of soil compaction on salamander settling is the lowered number of small mammal burrows available for use as refuges. Despite our attempts to exclude small mammals, burrowing continued virtually unabated within our enclosures, although significantly less in the compacted soil treatments.

The abundance of small mammal burrows in terrestrial habitats is likely an important factor governing both the survival of individuals and population densities of ambystomatid salamanders (e.g. Loredo et al. 1996). The presence of burrows also allows juvenile salamanders to behaviorally mitigate some of the negative effects of canopy removal by providing access to more-favorable microclimates (Rothermel and Luhring 2005). Our findings reveal that for *A. maculatum* the addition of both artificial burrows and coarse woody debris result in an increased probability of settling. The increased probability of settling in open-canopy high burrow density and high coarse woody debris treatments, relative to forest controls, indicates that the addition of refuges more than compensated for the 10 % decrease in settling probability due to canopy removal. These findings are in alignment with previous studies demonstrating that the retention of downed wood following timber harvesting may increase the overall suitability of those habitats (deMaynadier and Hunter1995, Moseley et al. 2004, Rittenhouse et al. 2008).

The propensity of *A. maculatum* juveniles to settle within open-canopy habitats when refuge density is high could be interpreted in multiple ways. On the surface, increased settling in clearcuts with high amounts of downed course woody debris would seem to suggest that increased refuge density can mitigate the negative effects of canopy removal. While increased refuge density certainly would aid juveniles by providing temporary short-term refuges, allowing them to cross open canopy habitats over multiple nights (e.g. Rittenhouse and Semlitsch 2009), the long-term success of individuals electing to remain there is doubtful (see Harper 2007). Because our study documented settling decisions a week after release into our enclosures, it leaves open the possibility that a portion of the settled individuals we documented may have established long-term home ranges there, rather than just stopping temporarily. It is therefore plausible that for some individuals the enticement to stop moving through open-canopy habitats because of the presence of abundant refuges, may serve as an ecological trap, contributing to decreased fitness and higher mortalities over longer time scales.

Small-mammal burrows are often associated with downed wood and may be more important refuges than the wood itself (deMaynadier and Houlahan 2008). The number of individuals using small-mammal burrows in our experiment is likely much higher than we were able to observe. We detected many more salamanders in our artificial burrows (n= 25) than in natural burrows (n= 2), validating them as an effective monitoring technique, while reinforcing the presumption that burrows are critical refuges for juvenile salamanders. While surface microhabitats such as leaf litter and downed wood are known to be important for increasing survival of amphibians immediately following metamorphosis (see Rittenhouse et al. 2008), burrows may provide more-stable long-term refuges. Surface refuges experience wider fluctuations in temperature and more-rapid drying compared to subsurface microhabitats.

The overall suitability of refuge microhabitats likely fluctuates temporally with changes in local weather conditions. Steady rainfall on the night of the initial movement pulse may create uniform moisture throughout terrestrial habitats and therefore result in a more-diffuse distribution of juveniles. As conditions begin to dry out, however, lower-quality habitats may become unsuitable. Individuals experiencing elevated rates of water loss are likely motivated to move from their refuge once surface conditions become optimal for movement. Therefore, the inverse relationship between weekly rainfall amount and *A. maculatum* settling suggests that juveniles are using refuges largely as temporary stopping locations during initial juvenile movement and choosing to resume movement during wet conditions. Previous phenological studies have focused on the relationship between the timing of rainfall and arrival and departure of amphibians at breeding ponds. Our findings are novel in that they cast light on how the amount of rainfall can affect the transition between moving and settling during initial juvenile movement. Furthermore, the influence of temperature and rainfall in our model, along with body size, suggests that the external conditions may be interacting with the internal state (physiology) of individuals. Desiccation risk likely plays a key role in recalibrating the behavioral state of juvenile salamanders.

While rainfall amount negatively affected settling behavior in *A. maculatum*, it did not appear to produce the same effects among *A. annulatum* juveniles. Also increased refuge density increased the probability of settling in *A. maculatum* juveniles, while not showing an effect in *A. annulatum*. This possibly reflects the greater vagility of *A. annulatum* juveniles. Our observations of *A. annulatum* juvenile movements suggest that they generally move at a faster rate and exhibit overall higher activity compared to

A. maculatum (M. S. Osbourn and S. E. Pittman pers. observ.). Therefore, while the 20 m length of our experimental runs was sufficient to encompass the transition from a dispersive movement mode to a settling movement mode in *A. maculatum*, it may have been insufficient for *A. annulatum*. It is conceivable that future experiments using longer enclosures could reveal a response in *A. annulatum* juveniles which mirrors that of *A. maculatum*. Another possibility is that the disparate responses are more attributable to mean body sizes between species (*A. annulatum* are generally larger), rather than differences in behavior or movement capacity. This seems less likely, however, given the lack significance for body mass in our analysis. Differences in sample size limit us, however, in our ability to make reliable species comparisons (there were roughly four times as many *A. maculatum* settlers as *A. annulatum*).

Behavioral mechanisms

When an animal encounters a potential refuge its response is likely dependent on their current behavioral state. Movement mode may dictate whether an individual crosses through unsuitable habitat or moves around it. Movement mode may also determine an individual's level of responsiveness to external factors within its habitat. Therefore, juvenile amphibians first departing their natal pond in a movement mode focused on rapid linear movements and may disregard potential settling locations. Once they have escaped the immediate competition and predation pressures adjacent to their natal pond, adaptive movement, which is responsive to variation in habitat quality, should be favored. At this point, external factors such as habitat quality and environmental conditions likely shape juvenile amphibians' movement paths and serve as triggers, initiating the transition to a settling movement mode.

There are several potential behavioral explanations for the observed pattern of decreased settling and increased movement within low-quality habitats. This pattern could be caused by a delay in the behavioral shift from a dispersive movement mode focused on rapid displacement away from the natal pond (e.g. "away mode" or "directed mode"; see Chapter 1), to a settling movement mode focused on selecting refuge microhabitat. It is plausible that the presence of suitable refuges or cues indicating high-quality habitat serve as a trigger to initiate the shift between these movement modes. In patches with sparsely distributed refuges, individuals likely have to move farther before encountering suitable settling microhabitat, delaying the switch in movement mode.

Alternatively, juvenile salamanders may not be responding to cues for high-quality habitat, but instead the trigger may come from cues indicating low habitat quality. Accordingly, individuals encountering low-quality habitat may shift to an entirely different “gap-crossing” movement mode. It is likely that forest-associated juvenile salamanders view closed-canopy habitats as high quality, while open-canopy habitats, with elevated desiccation risk, are low quality and generally unsuitable for long-term settlement. When juvenile salamanders encounter low-quality habitats, they may respond with comparably swift, straight movements as though they are attempting to cross unsuitable gaps in their habitat (e.g., in *Plethodon*- Semlitsch et al. 2012). Similar shifts in movement mode by individuals crossing between patches of suitable habitat have be observed in butterflies (Delattre et al. 2010), woodpeckers (Kesler et al. 2010), and pelagic birds (Barraquand and Benhamou 2008). Gap-crossing movement behavior may also be indicative of long-distance dispersers attempting to depart unsuitable conditions. It is important to recognize, however, that our study placed salamanders within habitat patches without the option of switching to higher-quality habitats. Previous behavioral studies show that both juvenile and adult pond-breeding amphibians will often avoid entering clearcuts when given a choice (Rittenhouse and Semlitsch 2006, Patrick et al. 2008, Todd et al. 2009; but see Graeter et al. 2008).

It is also plausible that there is neither a change nor a delay in movement mode transition, but rather the decreased probability of settling simply reflects the lack of suitable settling sites in low-quality habitats. Following this line of reasoning, individuals in both low-quality and high-quality habitats would transition into a settling movement mode concurrently, however individuals in low-quality habitats would be required to search a wider area and for a longer duration to locate a refuge. The observed differences in settling probability between treatments, therefore, would reflect differences in area required to locate a suitable refuge. Potential ramifications of increased search time in low-quality habitats could include increased predation and desiccation risk, and further depletion of limited energy reserves. Unfortunately our experimental design does not allow us to distinguish increased searching movement from dispersive movement.

The “increased searching” hypothesis seems less likely, however, than the prior two hypotheses involving external triggers affecting either the timing of a shift in movement mode or the initiation of an alternate gap-crossing movement mode. Given the influence of environmental variables along with habitat quality in our model, it appears unlikely that increased searching for refuges could produce the observed pattern alone. Most likely there is a combination of external triggers interacting with internal physiological thresholds to prompt the decision of when to stop moving away from the natal site and where to select a refuge before sunrise. Identifying the precise movement path of individuals is beyond the scope of this study, but what is clear is that a the pattern of settling in these juvenile salamanders is affected by habitat quality and weekly mean rainfall amount (*A. maculatum* only), with weekly mean air temperature and individual body mass potentially contributing to this response.

Conclusions and implications

The behavioral responses of juvenile forest-associated salamanders to variations in habitat quality should have evolved in the context of continuous forests with isolated, small patches of open-canopy, resulting from stochastic events such as a tree fall. Within continuous forest habitat, heterogeneity in habitat quality, resulting from an uneven distribution of suitable refuges and suitable microclimates, likely drove selection for movement and settling behaviors. In this context, the consequences of movement through unsuitable habitats would have been comparably lower than in the context of land-use altered forests today, because of the greater scale of the disturbance. Specifically, increased movement in open-canopy habitats may have evolved when low-quality patches within forests were typically traversable within a single night of movement. In the context of land-use altered habitats, this behavior may be maladaptive because recently metamorphosed amphibians entering open-canopy habitats are likely only to successfully reach suitable forest patches when conditions are ideal.

In the context of habitat loss and alteration there is an even greater need to understand and predict the causes, mechanism, patterns, and consequences of animal movement (Kokko and López-Sepulcre 2006, Nathan et al. 2008). Understanding individual movement responses is particularly valuable for scaling up to the population level and has the potential to aid in better predicting the effects of land use on species habitat use (Lima and Zollner 1996, Gibbs 1998, Haddad 1999, Wiens et al. 1993). Ultimately, this fine-scale empirical data can be coupled with individual-based modeling to predict movement over larger scales (Nathan et al. 2008). Because of the inherent difficulty of parameterizing predictive models, unrealistic assumptions about animal movement are often incorporated, in turn yielding inaccurate predictions and costly management errors (Morales and Ellner 2002). Here, we have identified potential mechanisms at the level of fine-scale individual behavior, which likely play an important role in the distribution of individuals and dynamics of populations. These findings go beyond previous studies of amphibian movement in that they reveal how the interplay of external factors and individual behavior produce the observed patterns of movement and habitat selection. Also, these findings further underscore the importance of accounting for multiple movement modes in studies of juvenile amphibians and contributes to our understanding of the critical initial juvenile movement phase.

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Table 1. Generalized linear mixed models explaining settlement behavior of *A. maculatum* during the initial juvenile movement phase.[a]

	Explanatory Variables								
Model	Microhabitat	Canopy	Mass	Rain	Temperature	K	AICc	ΔAICc	ω_i
Global	+	+	+	+	+	9	457.54	0.00	1.00
Internal State			+			2	469.49	11.94	0.00
External Factors	+	+		+	+	8	542.27	84.73	0.00
Habitat Quality	+	+				6	549.05	91.50	0.00
Intercept Only						2	551.34	93.80	0.00
Environment				+	+	3	555.48	97.93	0.00

[a] + indicates that an explanatory variable was included in the model. ΔAICc represents the difference in AICc values between each model and the best model. ω_i gives the Akaike weight for each model.

Table 2. Generalized linear mixed models explaining settlement behavior of *A. annulatum* during the initial juvenile movement phase.[a]

	Explanatory Variables								
Model	Microhabitat	Canopy	Mass	Rain	Temperature	K	AICc	ΔAICc	ω_i
Global	+	+	+	+	+	9	186.79	0.00	1.00
Internal State			+			2	198.95	12.17	0.00
External Factors	+	+		+	+	8	210.50	23.71	0.00
Habitat Quality	+	+				6	213.95	27.16	0.00
Intercept Only						2	220.61	33.82	0.00
Environment				+	+	3	226.56	39.77	0.00

[a] + indicates that an explanatory variable was included in the model. ΔAICc represents the difference in AICc values between each model and the best model. ω_i gives the Akaike weight for each model.

Figure 1. Experimental enclosure arrays containing two groups of four enclosures (“runs”), with one group in closed-canopy forest habitat and one in open-canopy clearcut habitat at each site. Within each group there are three microhabitat manipulations (compacted soil, high woody debris, and high burrow density) and one unaltered control. Salamanders are released at the end adjacent to the pool and recaptured in pitfall traps in the corners at 0 m and 20 m or discovered in refuges during searches.

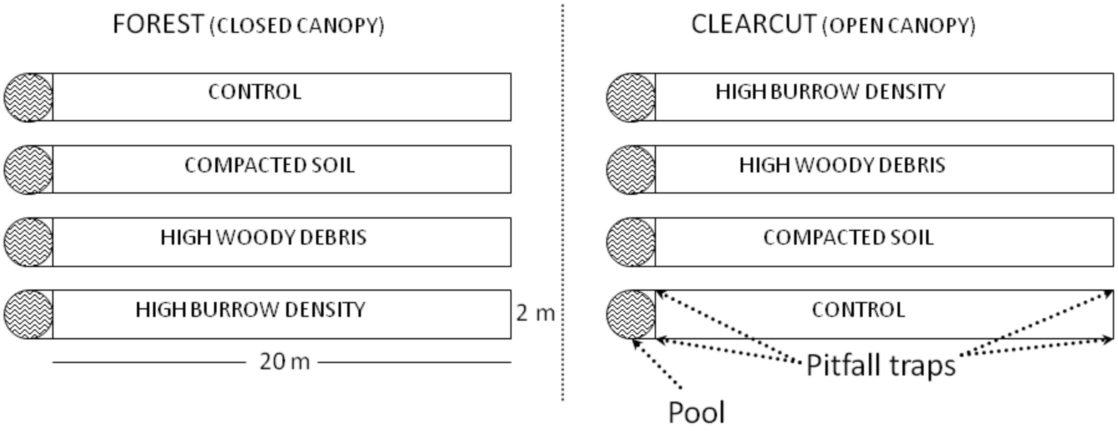

FOREST (CLOSED CANOPY)
CONTROL
COMPACTED SOIL
HIGH WOODY DEBRIS
HIGH BURROW DENSITY
2 m
20 m
CLEARCUT (OPEN CANOPY)
HIGH BURROW DENSITY
HIGH WOODY DEBRIS
COMPACTED SOIL
CONTROL
Pitfall traps
Pool

Figure 2. Estimated effects of microhabitat and rainfall on the probability of settling in A. maculatum. Probabilities give the fitted values from the global model, evaluated under closed canopy at the mean temperature and body size for this study.

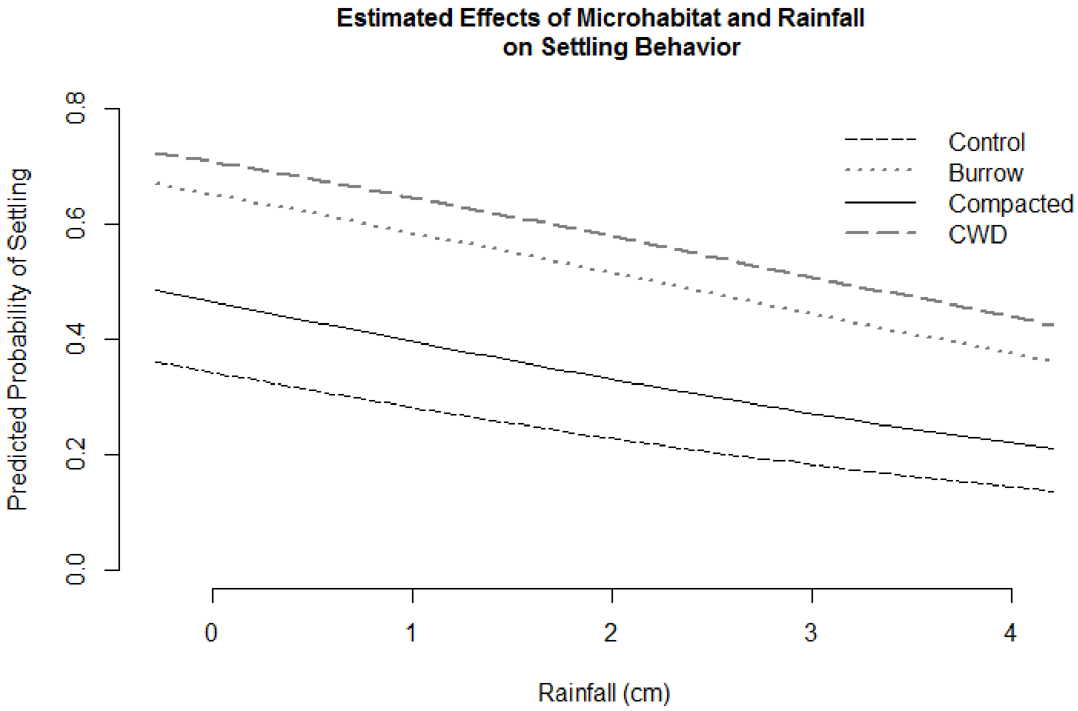
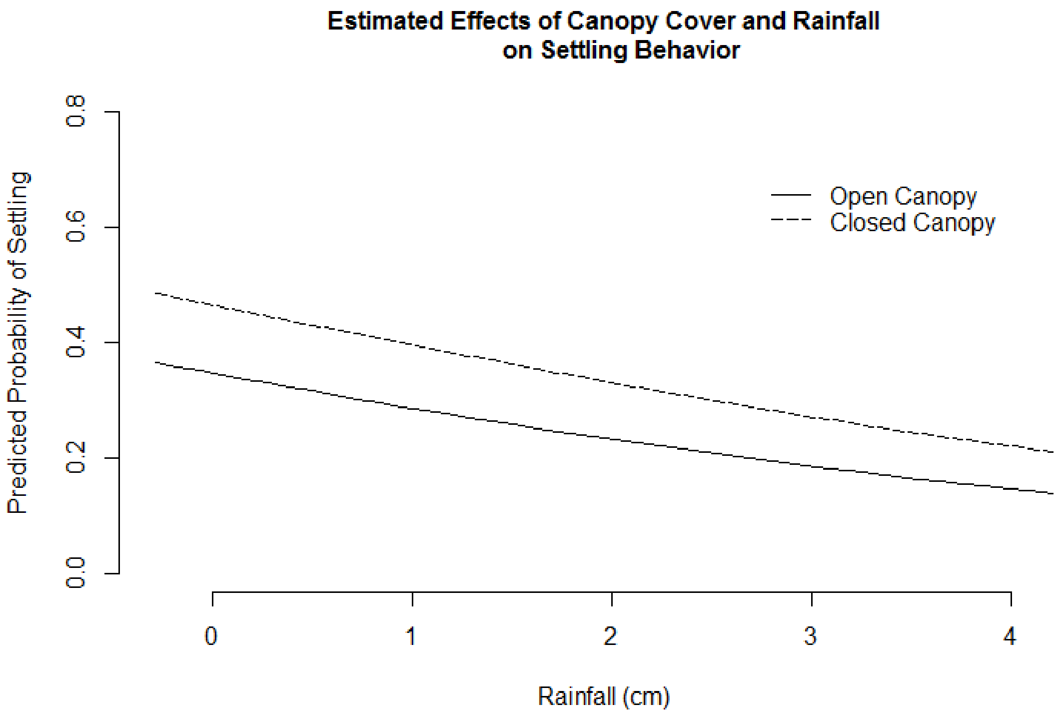

Estimated Effects of Microhabitat and Rainfall
on Settling Behavior
Predicted Probability of Settling
0.0
0.2
0.4
0.6
0.8
0
1
2
3
4
Rainfall (cm)
Control
Burrow
Compacted
CWD

Figure 3. Estimated effects of canopy cover and rainfall on the probability of settling in A. maculatum. Probabilities give the fitted values from the global model, evaluated under the control microhabitat condition and at the mean temperature and body size for this study.Figure 1. Hypothesized pathway for orientations toward teaching science to impact the implementation and outcome of outreach activities conducted in K-12 classrooms that are designed to model effective teaching for the classroom teacher.


Estimated Effects of Canopy Cover and Rainfall
on Settling Behavior
Predicted Probability of Settling
0.0
0.2
0.4
0.6
0.8
Open Canopy
Closed Canopy
0
1
2
3
4
Rainfall (cm)

CHAPTER 5

SUMMARY AND IMPLICATIONS FOR AMPHIBIAN CONSERVATION AND FUTURE RESEARCH

Michael S. Osbourn

For many pond-breeding amphibian species, juveniles are the primary dispersal stage and are vital for maintaining connectivity within metapopulations (Gill 1978, Berven and Grudzien 1990, Gamble et al. 2007, Semlitsch 2008). Pond-breeding amphibian populations are often centered around small, shallow, fishless wetlands which may only hold water for part of the year. These habitats are often ephemeral and experience periodic local extinctions. In this dynamic system, interpond dispersal of juveniles is essential for the maintenance of metapopulations, as juveniles recolonized breeding sites following local extinctions or rescue populations in decline (Brown and Kodric-Brown 1977, Harrison 1991, Hanski 1999).

Despite their vital role, juveniles are particularly sensitive to the effects of land use (e.g. (Rothermel and Semlitsch 2002). Land use fundamentally alters the overall quality, structure, and configuration of habitat patches within the landscape and thereby has the potential to exacerbate the risks associated with overland movement by amphibians. As a result, population viability in pond-breeding amphibians is closely associated with terrestrial habitat quality. Numerous studies have demonstrated how land-use practices that affect amphibian terrestrial habitat quality (e.g. timber harvesting, row crop agriculture, urbanization) can reduce the size and persistence of local populations (Semlitsch et al. 2009). Driving the population-level effects of land use are increased mortalities and sub-lethal affects on individuals occupying or moving through unsuitable altered habitats. As a result, habitat loss and alteration have been implicated as the leading contributor to amphibian declines globally (Stuart et al. 2004, Gardner et al. 2007).

A longstanding goal of conservation biologists and ecologists is to identify the specific mechanisms underlying the observed patterns of distribution and abundance of animals in heterogeneous habitats. Many of the mechanistic roots of population-level patterns lie at the level of individual responses (O'Neill et al. 1989, Wiens et al. 1993). Specifically, if we can predict how an individual will behave in response to specific habitats features, then we will be much closer to understanding land-use effects on populations and therefore better able to plan for and mitigate negative effects.

In this dissertation, I have attempted to fill some of the gaps in our knowledge of juvenile movement and habitat selection within altered forest habitats. Although various authors in recent decades have also empirically examined the effects of land use and habitat alteration on amphibians, my work is different in that I have adapted and applied a movement ecology conceptual framework to this topic. The movement ecology framework proposed by Nathan et al. (2008) along with dispersal-specific frameworks of others (Bowler and Benton 2005, Clobert et al. 2009, Bonte et al. 2012) have the potential to greatly inform our understanding of animal movement when combined with empirical studies. This approach attempts to capture the complexity of individual animal movements by identifying distinct movement phases associated with specific goals and behaviors. Furthermore, accounting for condition-dependent behavioral responses (Massot et al. 2002, Clobert et al. 2009) as well as the interplay of external factors (e.g. microclimate, conspecific interactions), internal state (e.g. energy reserves, body size), and movement and navigation capacities, provides a more-complete view of the intricacies of animal movement (Nathan et al. 2008). This marks a true departure from overly simplistic studies that do not place movement phenomena within a multi-stage, condition-dependent context.

In addition to the new conceptual approach, this study is important because thorough studies of juvenile dispersal and movement behavior have been lacking in the literature (Ronce 2007). As a result, knowledge of juvenile movement has persisted as a significant gap in our understanding of animal movement. This lack of information is largely attributable to the difficulties inherit in studying the movements of small animals. High juvenile mortality rates in many species make acquiring adequate sample sizes difficult. Furthermore, many marking and tracking techniques are not suitable for small individuals, such as a two-gram salamander juvenile. Because of these technical challenges and the time and effort involved in marking the large numbers of small juveniles these data are exceedingly rare and valuable for inferring responses across multiple taxa. For amphibians in particular, the number of studies focused entirely on this important life stage are very few in comparison those focused on adults. This dissertation is unique in the depth at which it explores juvenile amphibian movement. By individually marking over five thousand juveniles and testing their behavioral responses in experimentally altered habitat, I was able to identify previously unobserved movement and settling behaviors.

SUMMARY OF FINDINGS AND POTENTIAL IMPLICATIONS

Initial orientation in altered forest habitats

I documented nonrandom initial orientations in forest-associated Spotted Salamanders (*Ambystoma maculatum*) and Ringed Salamanders (*A. annulatum*), as well as habitat generalist Green Frogs (*Lithobates* [*Rana*] *clamitans*; see Chapters 2 and 3). The initial orientations of recently metamorphosed amphibians may contribute to the movement success of individuals first departing their natal wetland and moving into novel terrestrial habitats. Although I observed consistent directional orientations across species at individual sites, juveniles selected different forest treatments at different sites. Therefore, it seems unlikely that juvenile pond-breeding amphibians in this study are selecting coarse-scale habitat. It seems more likely that they are choosing their initial orientation based on fine-scale microhabitat features such as moisture gradients, microtopography, or available refuges, within their limited perceptual ranges. Furthermore, initial orientation may be less important than the selection of a new movement trajectory once an individual has experienced the terrestrial habitat. The existence of adaptive habitat switching behavior, identified in this study, lends further credence to this view. This also underscores the necessity of studies of juvenile movement in pond-breeding amphibians that go beyond near-pond habitats. Conservation managers trying to infer the direction of juvenile movements with initial orientation data collected at drift fences, immediately surrounding natal ponds, may draw inaccurate conclusions about their terrestrial habitat selection.

Effects of canopy removal on initial juvenile movement success

The results of this study are consistent with previous studies of amphibian habitat use, which demonstrated high sensitivity to forest-canopy removal (deMaynadier and Hunter 1998, Rothermel and Semlitsch 2002, Patrick et al. 2008, Semlitsch et al. 2009). Initial juvenile movement success was low for both Spotted Salamanders and Green Frogs in open-canopy clearcut habitats. This is important because it demonstrates the vulnerability of amphibians to changes in terrestrial habitat quality. Although some adult amphibians may cross directly through open-canopy habitats during breeding migrations, juveniles are unlikely to be able to reach higher quality habitats in adjacent forests if distances are too great. This illustrates how in the context of land use, productive amphibian breeding sites (i.e. sources) can become ecological traps (i.e. sinks).

Effects of forest thinning on initial juvenile movement success

For juvenile Spotted Salamanders, forest thinning may enhance habitat quality and facilitate greater movement success (Chapter 2). I observed the highest recapture rates in the partial cut treatment. This was consistent with other studies conducted at LEAP sites which reported that the partial cut had the smallest negative effects and only positive responses of the three forest habitat manipulations tested (Land-use effects on amphibian populations collaborative research project; Semlitsch et al. 2009). Higher movement success in the partial cut may be the result of enhanced microclimatic properties. Forest canopy gaps created by thinning increase the amount of sunlight reaching the forest floor, which encourages growth of herbaceous and shrub vegetation (Zheng et al. 2000). This increased vegetation may decrease an amphibian’s exposure to direct sunlight and desiccating winds, and thereby create a more-favorable microclimate for movement and settling. Before thinning can be recommended as a forest management practice for enhancing juvenile amphibian habitat, more long-term studies are needed. Thinning and subsequent timber extraction evolves disturbance of the leaf litter and compaction of the soil. The effects of soil compaction reported in Chapter 4 suggest that it may have a much greater effect on juvenile movement and settling decisions than previously assumed.

The effects of clearcut burning on initial juvenile movement success

Future research efforts need to examine how fire used as a management tool affects amphibian habitat quality. Here, I examined how it affected the suitability of successional clearcuts for juvenile movement. Green Frogs strongly preferred to move along the edges of unburned clearcuts over the edges of burned clearcuts (Chapter 3). This preference is likely only indirectly related to burning, in that the unburned edge provided more cover and therefore provided a lower-risk movement corridor. Spotted Salamander juveniles experienced greater movement success through burned clearcuts than unburned clearcuts, despite a 76% decrease in leaf litter following the burn (Chapters 2). This was an unexpected and not easily interpreted result. Dense growth of herbaceous plants following burning may have created a more-favorability surface microclimate. This is speculative however, and further studies are needed to identify the mechanisms behind the observed pattern. Future studies should investigate how the application of fire and subsequent changes in forest floor microhabitat structure and communities affect amphibian population dynamics and individual behavior.

Habitat switching behavior

Habitat switching is a previously undescribed behavioral response to variations in habitat quality, where an individual departing their natal pond in one habitat (treatment quadrant) alters their initial trajectory and move into an adjacent more-suitable habitat. I observed this behavior frequently in both Spotted Salamander and Green Frog juveniles. Spotted Salamanders in the partial cut exhibited the least switching behavior (3%), providing further evidence of the favorability of those habitats. This contrasted with the unburned clearcut, where 61% of recaptured individuals originating there, switched to other habitats (Chapter 2). For Green Frogs, juveniles in the unharvested control forest switched habitats the least (4%) followed by the partial cut (32%). The majority of recaptured individuals from the burned (78%) and unburned clearcuts (94%) switched to adjacent forest habitats (most switched to control forests; Chapter 3). This is important because we are beginning to see more-clearly how juveniles move through terrestrial habitats in the landscape. It suggests the existence of directed movement with individuals responding to habitat quality and structure, and actively selecting optimal habitat. This knowledge will greatly aid the development of predictive models.

Edge corridor behavior

Recaptures at edge fences along the boundaries of control forests and clearcuts provide possible evidence of corridor movement by Green Frogs (Chapter 3). The control forest edge bordering the unburned clearcut accounted for 90% of all edge captures. Green Frog juveniles may select the unburned edge because it provides both the ease of movement offered by the open control forest floor and the easily accessible refuge habitat in the successional clearcut.

Complexity and mediating factors affecting initial juvenile movement

This dissertation provides evidence of the complex and condition-dependent nature of initial juvenile movement in pond-breeding amphibians and the influence of multiple spatiotemporally dynamic factors. In the two years of the Spotted Salamander mark-recapture study, I observed contrasting differences in rainfall totals, conspecific densities, and mean juvenile body size and condition (Chapter 2). As a result, habitat quality may have affected juvenile movement success differently at different times, depending on the interaction between external (days since last rainfall) and internal conditions (body size). An example of this complexity was the 300% greater movement rate of individuals in forest canopy treatments in the wet conditions of 2008, despite being smaller than 2007 juveniles. Also, in my enclosure study, increased mean weekly rainfall resulted in increased movement and decreased settling in Spotted Salamanders (Chapter 4).

Effects of canopy removal on settling decisions

Forest canopy removal not only affects movement success of juvenile amphibians, but the decision of where to stop moving, select a refuge, and settle. In open-canopy clearcuts, juvenile Spotted and Ringed Salamanders showed decreased probabilities of settling compared to closed-canopy forest controls (Chapter 4).

Effects of soil compaction on settling decisions

Soil compaction often occurs during timber extraction, however, very little is known about its effects on forest floor communities. The strong responses I observed in Ringed Salamanders and trend in Spotted Salamanders suggests that it represents an overlooked and potentially important impact of land use. In Ringed Salamanders soil compaction reduces the probability of settling, likely due to decrease refuge density and quality. Future studies of the impacts of land use on amphibians need to consider soil compaction.

Effects of fine-scale microhabitat quality on settling decisions

In general, increased habitat quality and refuge density increased settling in Spotted and Ringed Salamanders. For Spotted Salamanders increased refuge density, either through increased burrows or downed wood, increased the probability of settling. Increased refuges also appeared to have a compensatory effect, with salamanders having higher probability of setting in clearcuts with high refuge densities than forest controls. This apparent mitigation may only be short term and future studies need to determine the quality of open-canopy refuges and their long-term effects on individual growth and survival.

The implications of movement modes in juvenile amphibians

In Chapter 1, I outlined potential movement phases of juvenile pond-breeding amphibians and their accompanying movement modes. I proposed a pre-departure phase for individuals just prior to and immediately following metamorphosis and included three potential movement modes (pre-emergence, prospecting, and waiting modes). The initial juvenile movement phase encompasses the first movements of juveniles through terrestrial habitats after departing their natal wetland. The three movement modes of initial juvenile movement include away, directed, and settling modes. This is a new concept for studies of amphibians and I have provided empirical evidence of the existence of multiple movement modes in juvenile pond-breeding amphibians. Switching behavior in Spotted Salamanders and Green Frogs, as well as edge corridor movement in Green Frogs is an example of directed movement (Chapters 2 and 3). I also documented how external factors such as habitat quality can affect the timing of the transition between movement modes (Chapter 4). Consideration of movement modes will inform future studies by placing observed patterns within an appropriate behavioral context. Future studies should continue to empirically test the concept of multiple movement modes in juvenile amphibians and identify the specific movement paths associated with each.

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APPENDIX A. HABITAT MEASUREMENTS

EXPERIMENTAL FOREST ARRAYS

To more fully characterize differences among forest treatments, I collected detailed measurements of variables thought to affect amphibian habitat quality. In September 2007, I randomly assigned three 1 m^2 quadrats adjacent to each drift fence within each experimental array (15 per treatment quadrant, 120 total). Within each sampling quadrat I estimated the percentage of ground covered by leaf litter, downed wood, herbaceous plants, and bare ground. To determine stem density we counted all plant stems at 20 cm height. At four locations, within the quadrat, we measured litter depth (0.5 cm) with a ruler and percent canopy cover with a spherical densitometer.

EXPERIMENTAL RUNS

In September 2008, I collected data on habitat variables important to forest-associated amphibians. Using a reel measuring tape, I divided each 20 m run into four sections (0-5m, 6-10m, 11-15m, 16-20m), and placed one 1 m^2 quadrat at a randomly determine location within each section. For each quadrat, I collected percent canopy cover (n=3, spherical densitometer), leaf litter depth (0.5 cm; ruler), percent ground cover (visual estimate), percent vegetative cover (visual estimate), stem density (count), and recorded predominant tree species present. I collected standard canopy cover measurements at chest height and attempted to measure the shading effect of the shrub layer, by collecting second set of canopy cover measurements at 20 cm above the ground surface. I collected soil samples adjacent to each enclosure at 3 locations on 3 occasions during each release week.

Table A1. Mean (±SE) habitat variables measured within forest treatments. Significance determined at $\alpha=0.05$ (ANOVA).

	Control	Partial cut	CC Burned	CC Unburned	*P*<0.05
Stem density (per m^2)	15.07 (±2.01)	26.03 (±3.07)	96.40 (±11.47)	106.03 (±19.93)	yes
Leaf litter (%)	71.68 (±5.89)	65.08 (±5.30)	10.50 (±1.36)	31.00 (±4.90)	yes
Bare ground (%)	1.67 (±0.63)	3.58 (±1.79)	17.17 (±2.72)	0.17 (±0.12)	yes
Downed wood (%)	1.50 (±0.80)	3.00 (±1.14)	8.50 (±2.09)	5.50 (±1.66)	yes
Herbaceous cover (%)	0.73 (±0.40)	5.20 (±1.70)	6.00 (±1.40)	12.25 (±2.49)	yes
Litter depth (cm)	3.65 (±0.46)	2.93 (±0.27)	0.61 (±0.10)	2.53 (±0.12)	yes
Canopy cover (%)	83.22 (±1.04)	71.38 (±1.85)	21.27 (±2.55)	21.98 (±3.15)	yes

APPENDIX B. SUPPLEMENTAL TABLES

Table B1. Initial orientations of recently metamorphosed spotted salamanders, as indicated by initial capture point at 0 m drift fence. We preformed goodness of fit G-tests using counts from individual arrays and means.

			Experimental forest treatments (%)				
Analysis	Array	Year	Control	Partial Cut	CC Burned	CC Unburned	P<0.05
Individual array	P1	2007	23.98	27.64	27.64	20.73	no
		2008	10.14	**37.16**	22.64	30.07	yes
	P5	2007	22.32	25	**35.71**	16.96	yes
		2008	14.49	19.16	**50.47**	15.89	yes
Means	P1 & P5	2007	23.46	26.82	30.17	19.55	no
		2008	11.96	29.61	**34.31**	24.12	yes

Notes: For analyses differing from random the treatments with the highest percentage of initial captures are indicated in bold.

Table B2. Number of juvenile spotted salamanders released (n) and mean percent recaptured (±SE) in each experimental forest treatment at 20 m and 50 m from natal ponds. Means are calculated from replicate arrays

Year		Experimental forest treatment				
		Control	Partial Cut	CC Burned	CC Unburned	Total
2007	Released (n)	167	176	181	179	358
	Recaptured (% 20 m)	12.31±3.69	5.46±1.89	12.13±0.37	10.17±0.36	10.48±1.13
	Recaptured (% 50 m)	2.00±2.00	7.25±0.11	1.25±1.25	0	3.25±1.22
	Recaptured (% Total)	16.23±7.76	12.71±2.00	14.63±2.87	10.17±0.36	13.73±2.35
2008	Released (n)	84	96	108	70	703
	Recaptured (% 20 m)	5.31±1.07	11.56±2.87	4.37±2.29	2.24±0.04	5.96±0.71
	Recaptured (% 50 m)	1.20±0.05	5.10±0.07	1.11±0.01	0	1.85±0.10
	Recaptured (% Total)	6.51±1.45	16.67±4.17	5.47±3.22	2.24±0.06	7.80±0.81

APPENDIX C. ADDITIONAL FIGURES

Figure C1. Percent of juvenile spotted salamanders switching canopy types moving to forest versus open-canopy habitats.

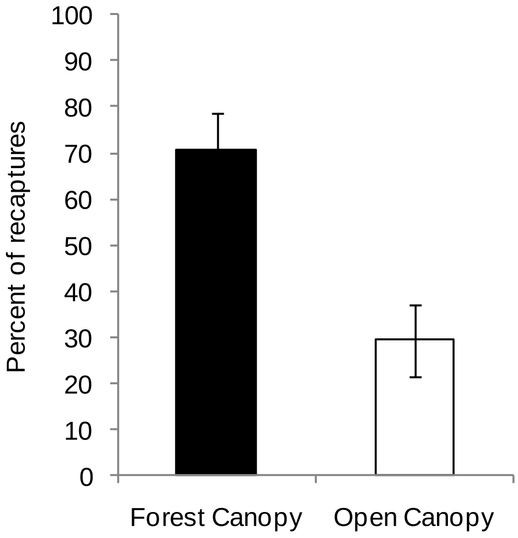
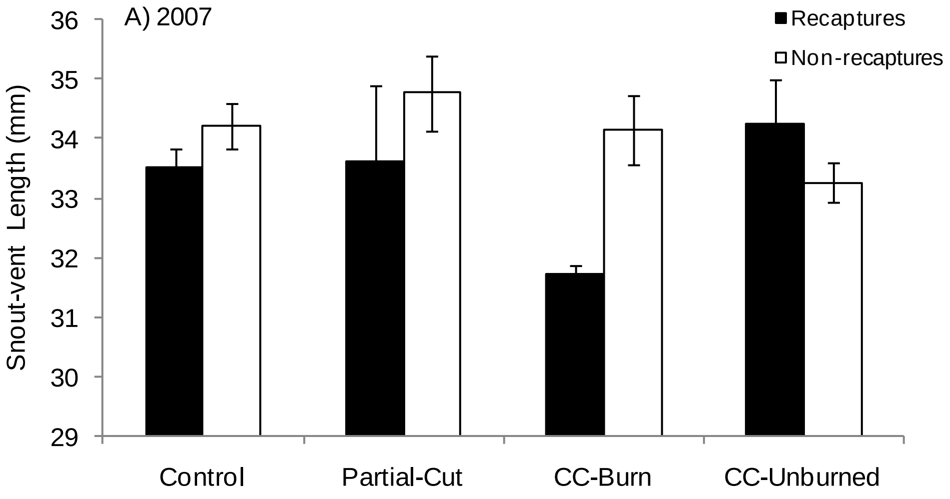
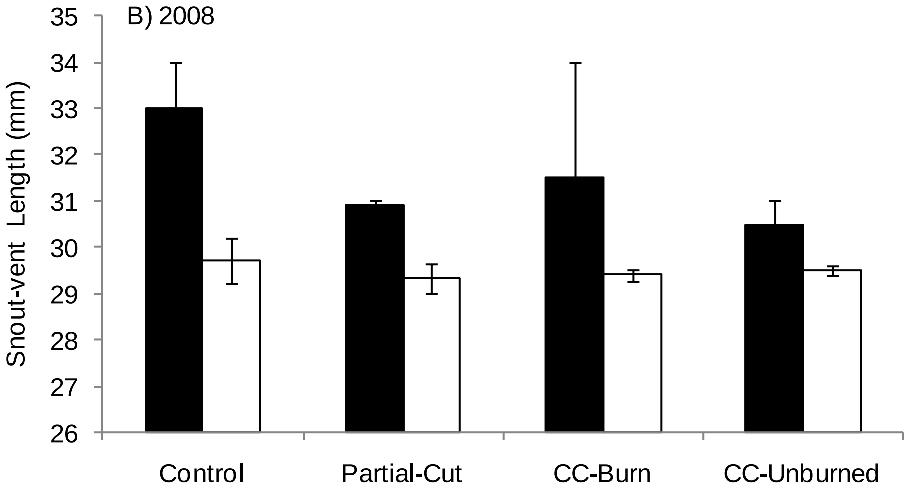

100
90
80
70
60
50
40
30
20
10
0
Percent of recaptures
Forest Canopy
Open Canopy

Figure C2. Differences among forest treatments in mean body length (SVL) of recaptured versus non-recaptured juvenile spotted salamanders, in 2007 (A) and 2008 (B).


A) 2007
■ Recaptures
☐ Non-recaptures
Snout-vent Length (mm)
36
35
34
33
32
31
30
29
Control
Partial-Cut
CC-Burn
CC-Unburned


B) 2008
Snout-vent Length (mm)
35
34
33
32
31
30
29
28
27
26
Control
Partial-Cut
CC-Burn
CC-Unburned

APPENDIX D. ANOVA TABLES

Table D1. ANOVA testing the effects of forest treatment and distance on proportion of juvenile spotted salamanders recaptured (movement success) in both years combined.

Source	DF	Type III SS	F value	Prob > F
Year	1	0.0087	1.70	0.2122
Array	1	0.0103	2.01	0.1766
Treatment	3	0.0911	5.91	0.0072
Distance	1	0.1767	34.37	<0.0001
Year*Treatment	3	0.0160	1.04	0.4040
Year*Distance	1	0.0242	4.71	0.0464
Treatment*Distance	3	0.0441	2.86	0.0720
Year*Treatment*Distance	3	0.0528	3.42	0.0447
Error	15	0.0771		

Table D2. ANOVA testing the effects of forest treatment and distance on proportion of juvenile spotted salamanders recaptured (movement success) in 2007.

Source	DF	Type III SS	F value	Prob > F
Array	1	0.0104	2.24	0.1781
Treatment	3	0.0174	1.25	0.3632
Distance	1	0.1659	35.62	0.0006
Treatment*Distance	3	0.0819	5.86	0.0253
Error	7	0.0326		

Table D3. ANOVA testing the effects of forest treatment and distance on proportion of juvenile spotted salamanders recaptured (movement success) in 2008.

Source	DF	Type III SS	F value	Prob > F
Array	1	0.0017	0.28	0.6104
Treatment	3	0.0897	4.90	0.0383
Distance	1	0.0350	5.75	0.0477
Treatment*Distance	3	0.0150	0.82	0.5219
Error	7	0.0427		

Table D4. ANOVA testing the effects of canopy and distance on proportion of juvenile spotted salamanders recaptured (movement success) in 2007.

Source	DF	Type III SS	F value	Prob > F
Array	1	0.0104	1.36	0.2682
Canopy	1	0.0101	1.31	0.2762
Distance	1	0.1659	21.62	0.0007
Canopy*Distance	1	0.0374	4.88	0.0494
Error	11	0.0844		

Table D5. ANOVA testing the effects of canopy on juvenile spotted salamander movement rate (m/night) in both years.

Source	DF	Type III SS	F value	Prob > F
Year	1	1.1510	3.09	0.1127
Array	1	0.0061	0.02	0.9014
Canopy	1	1.1909	3.20	0.1074
Year*Canopy	1	1.9779	5.31	0.0467
Array*Canopy	1	0.0000	0.00	0.9990
Error	9	3.3526		

Table D6. ANOVA testing the effects of canopy on juvenile spotted salamander movement rate (m/night) in 2008.

Source	DF	Type III SS	F value	Prob > F
Array	1	0.8027	3.19	0.0853
Canopy	1	7.3173	29.08	<0.0001
Array*Canopy	1	0.3285	1.31	0.2632
Error	27	6.7934		

Table D7. ANOVA testing the effects of forest treatment on juvenile spotted salamander movement rate (m/night) in 2008.

Source	DF	Type III SS	F value	Prob > F
Array	1	0.1329	2.43	0.2596
Treatment	3	3.5142	21.40	0.0450
Error	2	0.1095		

Table D8. ANOVA testing the effects of forest treatment on the proportion switching habitats in both years.

Source	DF	Type III SS	F value	Prob > F
Year	1	0.0159	0.18	0.6801
Treatment	3	1.4047	5.38	0.0255
Year*Treatment	3	0.1086	0.42	0.7465
Error	8	0.6966		

Table D9. ANOVA testing the effects of canopy on switching direction in both years.

Source	DF	Type III SS	F value	Prob > F
Year	1	0.0000	0.00	1.0000
Canopy	1	0.3956	10.18	0.0332
Year*Canopy	1	0.0302	0.78	0.4275
Error	4	0.1554		

Table D10. ANOVA testing the effects of forest treatment and distance on proportion of juvenile green frogs (*L. clamitans*) recaptured (movement success).

Source	DF	Type III SS	F value	Prob > F
Array	1	0.0335	5.70	0.0484
Treatment	3	0.2838	16.10	0.0016
Distance	1	0.0020	0.34	0.5781
Treatment*Distance	3	0.0043	0.24	0.8640
Error	7	0.0411		

Table D11. ANOVA testing the effects of forest treatment on the proportion of juvenile green frogs (*L. clamitans*) switching habitats.

Source	DF	Type III SS	F value	Prob > F
Array	1	0.0342	0.70	0.4658
Treatment	3	1.8255	12.35	0.0340
Error	3	2.0075		

Table D12. ANOVA testing for differences in edge movements by juvenile green frogs (*L. clamitans*) along the boundary of control forests and two clearcut treatments (burned and unburned). We compared the proportion of individuals captured along each edge and whether individuals were moving in or out of control (direction).

Source	DF	Type III SS	F value	Prob > F
Array	1	0.0016	0.32	0.6096
Edge	1	0.5292	109.21	0.0019
Direction	1	0.0035	0.73	0.4561
Edge*Direction	1	0.0049	1.01	0.3893
Error	7	0.5537		

VITA

Michael Osbourn was born on June 13, 1973 in Knoxville, Tennessee. His experiences as a young child catching salamanders and exploring the forests and cool mossy streams of the Great Smoky Mountains solidified his life-long love of the natural world. He received his B.S. from Emory in May 1996, majoring in Biological Anthropology and Human and Natural Ecology. Following graduation, Michael spent the summer in an Ecuadorian cloud forest, studying epiphytic orchids and bromeliads. For the next four years, Michael worked as an environmental educator or national park ranger in Georgia, Montana, California, and Washington.

In response to a growing awareness of global amphibian declines, Michael rededicated his efforts to their conservation in 2000. He monitored threatened frog species in the high Sierra Nevada Mountains in California, as well as responses of stream salamanders in the Appalachian Mountains to land use and pollution. In May 2005, he received his M.S. in Biological Sciences from Marshall University, in West Virginia, where he focused on the natural history of cave-dwelling salamanders. While at Marshall, Michael learned a great deal about the natural history of amphibians, reptiles, and birds from his mentor Dr. Tom Pauley. In 2007, he enrolled as a Ph.D. student at the University of Missouri to study under the guidance of amphibian conservation biologist Dr. Ray Semlitsch. Michael received his Ph.D. in December 2012 from the University of Missouri in Biological Sciences, with an emphasis in Ecology, Evolution, and Behavior. He is currently living in Boone, North Carolina, where he works as a biology instructor at

Appalachian State University. In the future, Michael plans to continue research in amphibian conservation and ecology.