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Habitat type and distance to edge affect movement behavior of juvenile pond-breeding salamanders

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Abstract

Behavioral strategies of natal dispersers in response to human-altered habitat have far-reaching implications for functional connectivity and local population dynamics. Spotted salamanders *Ambystoma maculatum* are forest-dependent, pond-breeding amphibians which metamorphose and disperse out of aquatic habitat with limited knowledge of the terrestrial habitat. We quantified the fine-scale movement behavior and search strategies of recently metamorphosed spotted salamanders in three different habitat types (field, early successional forest and forest) and at varying distances from both hard (field and forest) and soft (early successional forest and forest) edges using fluorescent powder tracking. We found that salamanders moved straighter and with fewer turns through field habitat compared with both forest and early successional habitat. Salamanders significantly oriented movement toward forest when released in the field and when released on the edge between the forest and field. We found that salamander movement in the forest and early successional forest was approximated by a correlated random walk. Based on these results, dispersing spotted salamanders exhibit strong edge-mediated behavior when differences between habitats are stark (forest and field) and can perceive forest habitat from distances of at least 10 m. These results indicate that dispersing juvenile salamanders exhibit reasonable behavioral rules when moving through habitat types of differing quality. Knowledge of these behavioral rules will improve predictions of the effects of habitat type and configuration on amphibian survival and dispersion in altered landscapes.

Introduction

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

Natal dispersal is an important mechanism by which species mitigate the effects of unpredictable variation in the spatial distribution of resources and is critical to many species' spatial dynamics (Clobert *et al.*, 2001). Habitat alteration impacts the spatial patterning of resources and the risks associated with movement. Simulations have shown that certain search strategies employed by dispersers yield higher probabilities of encountering resources than others (Zollner & Lima, 1999). The impacts of habitat alteration on dispersal may be especially strong in species with complex life cycles, as individuals have no previous experience of the habitat into which they are dispersing and may employ standardized search strategies to maximize the probability of encountering suitable habitat. Search strategies employed by species with complex life cycles may therefore not always be optimal in relation to the spatial structure of habitat in altered landscapes (Fahrig, 2007).

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

Semlitsch, 2007), and juveniles are often the primary interpopulational dispersers (Gill, 1978; Gamble, McGarigal & Compton, 2007). Habitat loss and fragmentation increase the influence of movement strategies on juvenile survival by truncating the breath of behavioral variation that yields the highest likelihood of finding habitat. Despite its importance, movement behavior employed by juvenile amphibians during initial movement out of ponds remains poorly understood.

Spotted salamanders *Ambystoma maculatum* are pond-breeding, forest-dependent amphibians in which juveniles are primary dispersers between populations (Gamble *et al.*, 2007). Recently metamorphosed spotted salamanders make initial movements out of natal wetlands on the scale of 20–50 m (Osbourn, 2012). Mortality during this initial movement phase is considerable; *c.* 17% of spotted salamanders may survive 1 year after metamorphosis (Rothermel & Semlitsch, 2002, 2006). Documented causes of mortality during this initial movement phase include desiccation (Rothermel & Luhring, 2005), predation (Rittenhouse, Semlitsch & Thompson, 2009), depletion of energy (Scott *et al.*, 2007) and density effects (Harper & Semlitsch, 2007). Spotted salamanders have lower survival in open as opposed to close-canopy habitats (Rothermel & Semlitsch, 2002), and population persistence is highly dependent on the amount of forested habitat surrounding breeding ponds (Porej, Micacchion & Hetherington, 2004; Skidds *et al.*, 2007). While it is clear that habitat strongly affects the survival and distribution of spotted salamanders, the behavioral mechanisms underlying the observed patterns are currently unknown.

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

Methods

Study area

This study was conducted at Daniel Boone Conservation Area (DBCA, 1424 ha) in Warren County, MO. DBCA is characterized by mature second-growth forest dominated by oak and hickory tree species (*Quercus* sp., *Cary* sp.) in the canopy and sugar maple *Acer saccharum* in the understory. Small grassland clearings (~5 ha) are maintained within DBCA through biannual mowing and consist of native warm season grasses such as big bluestem *Andropogon gerardii* and Indian grass *Sorghastrum nutans*.

We conducted this study at two pond locations within DBCA, situated ~500 m apart. Each pond was located within *c.* 200 m of two land use types: early successional forest (5 years post clear-cutting, hereafter referred to as ‘early successional’) and open grassland habitat (hereafter referred to as ‘field’). The early successional patches were ~2.11 ha in size, and the field patches were *c.* 1 ha in size (Semlitsch *et al.*, 2009). Both habitat types were bordered by mature second-growth forest. Clear-cutting of the early successional areas took place in March 2004. We considered the borders between early successional and mature forest ‘soft edges’ and the borders between field and mature forest ‘hard edges’ for this study. Ground cover in the field habitat consisted of grass vegetation with no downed wood or leaf litter. Ground cover in the early successional habitat consisted of a mixture of leaf litter, herbaceous cover and downed wood (Osbourn, 2012). Ground cover in the mature forest was dominated by leaf litter and some downed wood (Osbourn, 2012).

Salamander collection and release design

We collected 200 metamorphosed salamanders from traps surrounding two ponds and from cattle tanks stocked with egg masses collected from pools within 100 m of the ponds. Salamanders were held in containers with damp moss until conditions were ideal for release, which were defined as within 24 h of, but not concurrent with, a rain event and within 2 weeks of metamorphosis. We released salamanders no later than 1 h after sunset. Fluorescent powder was used to track the continuous movement of salamanders after release (DayGlo Color Corp, Cleveland, OH, USA) and has been used successfully in previous studies to track short-term movements of small amphibians (Graeter, Rothermel & Gibbons, 2008). The pigment does not affect survival or cutaneous respiration in newts and ambystomatid salamanders (Orlofske, Grayson & Hopkins, 2009; Roe & Grayson, 2009). We covered the ventral and posterior halves of the salamanders with fluorescent pigment using a brush or eyedropper.

We released salamanders in line transects perpendicular to the edge consisting of five release points: 10 m in the field or early successional forest (−10), 5 m in the field or early successional forest (−5), directly on the edge (0), 5 m into the forest from the edge (5), and 10 m into the forest from the edge (10; Table 1). We released a maximum of 10 salamanders in a night (two transects). We placed salamanders underneath release enclosures for *c.* 10 min to allow animals to acclimate to the environment and to reduce the likelihood of observing artificial release responses (Turchin, 1998). Release enclosures consisted of an upside-down clay flowerpot (10.16 cm diameter) connected to string draped over a plastic stake which allowed lifting of the enclosure remotely (3 m minimum) to minimize the influence of observer orientation on salamander behavior.

Salamander tracking and mapping

We followed fluorescent powder trails left by the salamanders with a black light (Arachnid A14, Blacklight.com, Volo, IL, USA) 4–5 h following release. Pilot experiments found 4 h to

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

Release location	Number released	% of salamanders relocated	% paths >1 m
Hard edge			
−10	19	15.8	100
−5	23	21.7	100
0	19	63.2	84.2
5	23	52.2	87.0
10	21	71.4	76.2
Softedge			
−10	19	52.6	89.5
−5	19	68.4	78.9
0	18	44.4	77.8
5	18	64.7	94.4
10	18	72.2	72.2

be sufficient time for salamanders to move and settle (S. Pittman, unpublished data). We applied powder to a subset of 35 animals that settled in the forest or early successional habitat and tracked these animals for an additional night in order to determine whether animals maintained movement bearings for subsequent nights.

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

Data analysis

Orientation propensity

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

Estimation of movement path parameters and search strategy

Movement paths of salamanders were analyzed using the software program Fractal 5.0 (Nams, 1996). For each path with a total distance greater than 5 m and a minimum of five steps, we determined path linearity (net distance moved/total distance moved), mean step size and concentration of turning angles (k). We additionally tested each movement path used in the previous analyses for goodness of fit to a correlated random walk (CRW; Nams & Bourgeois, 2004). This test compared the net squared displacement of each movement path with predictions of net squared displacement based on a CRW model using the test statistic $\mathrm{CRW_{Diff}}$ (Kareiva & Shigesada, 1983; Benhamou, 2004). If $\mathrm{CRW_{Diff}} > 0$, the animal moved farther than predicted by a CRW, while if $\mathrm{CRW_{Diff}} < 0$, the animal moved more tortuously than a CRW. We ran the $\mathrm{CRW_{Diff}}$ test at both the species level (where errors are based on among-path variation) and at the individual level (where errors are based on within-path variation).

Comparison of movement path parameters in different habitats

We compared the mean step length and linearity (net displacement/total path length) of movement paths among individuals moving in different habitat types (forest, early successional forest and field) and at different edges using a two-way analysis of variance (ANOVA) with edge location (Edge) and habitat type (Habitat) as explanatory factors. We analyzed the first 5 m total distance of each movement path for comparisons in order to control for differences in path detection and potential changes in movement objectives as individuals moved longer distances. We performed the Shapiro–Wilk normality test for both step length and linearity, and log transformed both step length and linearity to achieve normality. When ANOVA results were significant, we used Tukey's honestly significant differences (HSD) test for pairwise comparisons between treatments. We used R (R Development Core Team, 2012) for all ANOVA and circular statistical tests and $\alpha = 0.05$ as a standard for significance.

Results

Out of the 200 salamanders in this study, three movement paths were not definitively identified and therefore were not included in analyses. The longest movement path recorded was 50.10 m net distance and a total distance of 53.44 m. Mean recorded path length was 5.67 m (SE = 0.41, $n = 50$) in the field, 10.95 m (SE = 1.70, $n = 42$) in the early successional habitat and 10.65 m (SE = 1.05, $n = 84$) in the forest (Table 2), excluding animals that settled within 1 m of the release location ($n = 21$). However, these estimates likely underestimate actual movement distances, as animals that moved farther were less likely to be relocated (Tables 1 and 2). Overall, 50% of salamanders were relocated at the end of the tracking session (98 out of 197). However, habitat type affected relocation probability (Table 1); salamanders released in field

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

	Total distance moved				Net distance moved			
	All		Relocated		All		Relocated	
Habitat	*n*	Mean	*n*	Mean	*n*	Mean	*n*	Mean
Field	50	5.88 (0.83)	10	5.35 (0.73)	50	5.67 (0.41)	10	5.14 (0.39)
Early successional	42	10.95 (1.7)	27	8.72 (1.34)	42	9.40 (2.05)	27	7.00 (1.38)
Forest	84	10.65 (1.05)	60	9.06 (0.97)	84	9.32 (1.16)	60	7.73 (1.04)

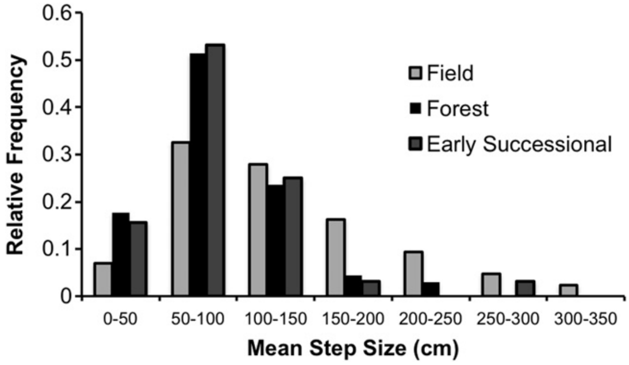


Figure 1 Histogram of mean step sizes (cm) for each salamander moving through field, forest and early successional habitat. Notice that the frequency distribution of step sizes for salamanders released within the field habitat is skewed farther to the right than salamanders released in forest and early successional habitat.

habitat were 46% less likely to be relocated at the end of the first tracking night ($t = 6.47$, d.f. = 4, $P = 0.003$), and were less likely to settle within 1 m of the release location (field: $n = 0$, early successional: $n = 6$, forest: $n = 15$). In forest and early successional habitat, 61% of salamanders were relocated (94 out of 155), and there was no difference in relocation probability between individuals released in forest and early successional habitat ($t = 0.54$, d.f. = 4, $P = 0.614$). Salamanders settled underneath leaf litter (54.6%), at the base of grass clumps (5.0%), underneath coarse woody debris (24.4%) and inside of burrows (16.0%).

Habitat-specific movement behavior

Mean step lengths and path linearity of salamanders differed significantly among habitat types [step length: $F(2, 134) = 9.683$, $P < 0.001$; path linearity: $F(2, 132) = 3.125$, $P = 0.047$; Fig. 1]. Using Tukey's HSD test, we found that salamanders in the field exhibited longer step lengths (mean = 1.32 m, SE = 0.104 m) than salamanders released in the forest (mean = 0.846 m, SE = 0.042 m, $P < 0.001$) or early successional habitat (mean = 0.90 m, SE = 0.08 m, $P = 0.008$). Although we found an overall treatment effect, we failed to detect significant pairwise differences between treatments using Tukey's HSD test for path linearity. However, pairwise differences between field and early successional and forest habitat were approaching significance (field and early successional: Tukey's HSD: $P = 0.074$; field and forest: $P = 0.076$). We did not find a difference in step lengths (Tukey's HSD: $P = 0.799$) or path linearity (Tukey's HSD: $P = 0.909$) among individuals moving in the forest and the early successional habitat.

Movement over multiple nights

A subset of 35 salamanders that settled under logs or leaf litter after the first night of tracking was tracked for a second night. Twenty-four out of 35 of these individuals did not move a net distance greater than 1 m the second night and remained in the settled habitat until a rain event. Orientations of the nine individuals that moved a second night were significantly correlated (V-test: $P < 0.001$) with orientation the first night, indicating that individuals maintained movement bearings for multiple nights.

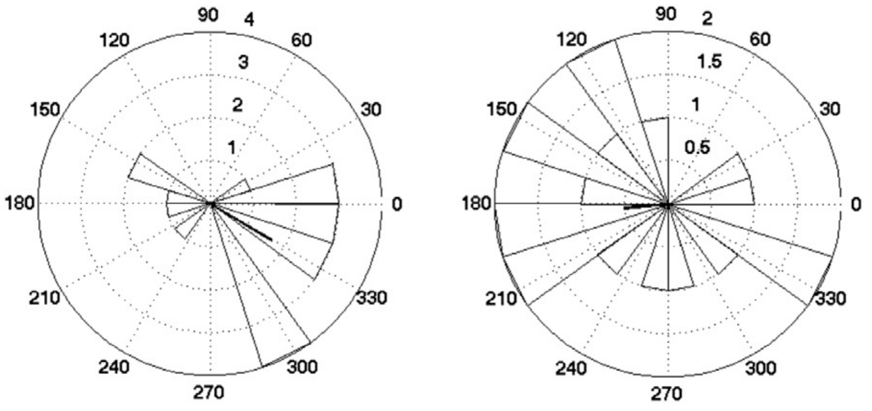
Orientation

Salamanders at 0, −5 and −10 m release locations along hard edges exhibited target-oriented movement toward forest habitat: 0 m [mean vector length (r) = 0.48, Rayleigh's test: $P = 0.004$, V-test: $P = 0.001$, $n = 19$], −5 m ($r = 0.385$, Rayleigh's test: $P = 0.03$, V-test: $P = 0.004$, $n = 23$) and −10 m ($r = 0.31$, Rayleigh's test: $P = 0.04$, V-test: $P = 0.05$, $n = 19$), with angles corrected so that 0° was toward the forest, perpendicular to the edge (Fig. 2a–c). Salamanders released within the forest at hard edges did not significantly orient away from the field habitat: 5 m ($r = 0.256$, Rayleigh's test: $P = 0.29$, V-test: $P = 0.942$, $n = 19$), 10 m ($r = 0.177$, Rayleigh's test: $P = 0.61$, V-test: $P = 0.29$, $n = 16$) (Fig. 2d–e). The orientations of salamanders released at soft edges were randomly distributed: −10 m ($r = 0.256$, Rayleigh's test: $P = 0.63$, V-test: $P = 0.492$, $n = 17$), −5 m ($r = 0.246$, Rayleigh's test: $P = 0.52$, V-test: $P = 0.774$, $n = 15$), 0 m ($r = 0.199$, Rayleigh's test: $P = 0.58$, V-test: $P = 0.795$, $n = 14$), 5 m ($r = 0.246$, Rayleigh's test: $P = 0.52$, V-test: $P = 0.774$, $n = 17$) and 10 m ($r = 0.187$, Rayleigh's test: $P = 0.63$, V-test: $P = 0.415$, $n = 13$) (Fig. 3a–e). Additionally, salamanders did not orient toward natal ponds or cattle tank locations (V-test: $P = 0.54$, $n = 197$).

Search strategy

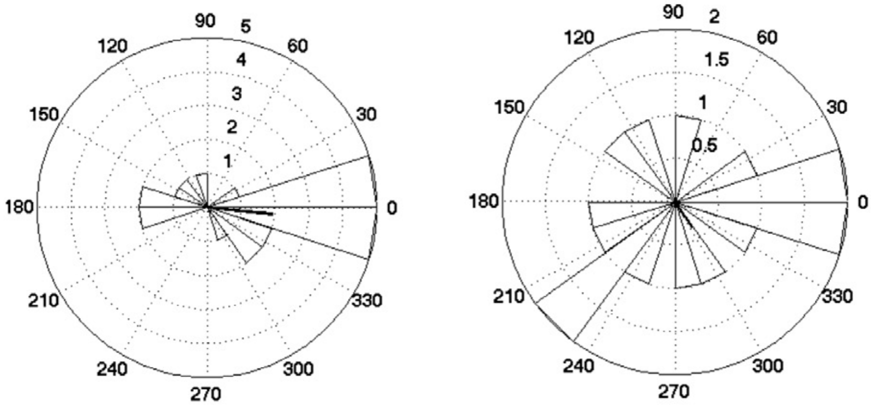
At the species level, juvenile-spotted salamanders utilized a CRW ($\mathrm{CRW}_{\mathrm{Diff}} = 0.595$, $P = 0.1617$, $n = 84$), with a mean step a 10 m - field

d 5 m - forest



b 5 m - field

e 10 m - forest



c Edge

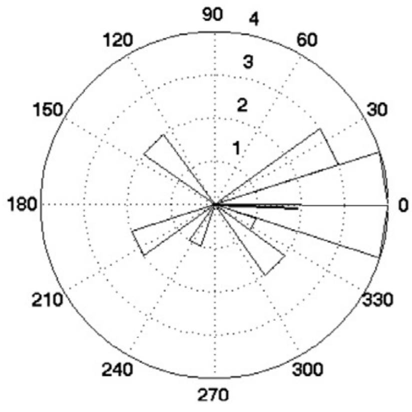
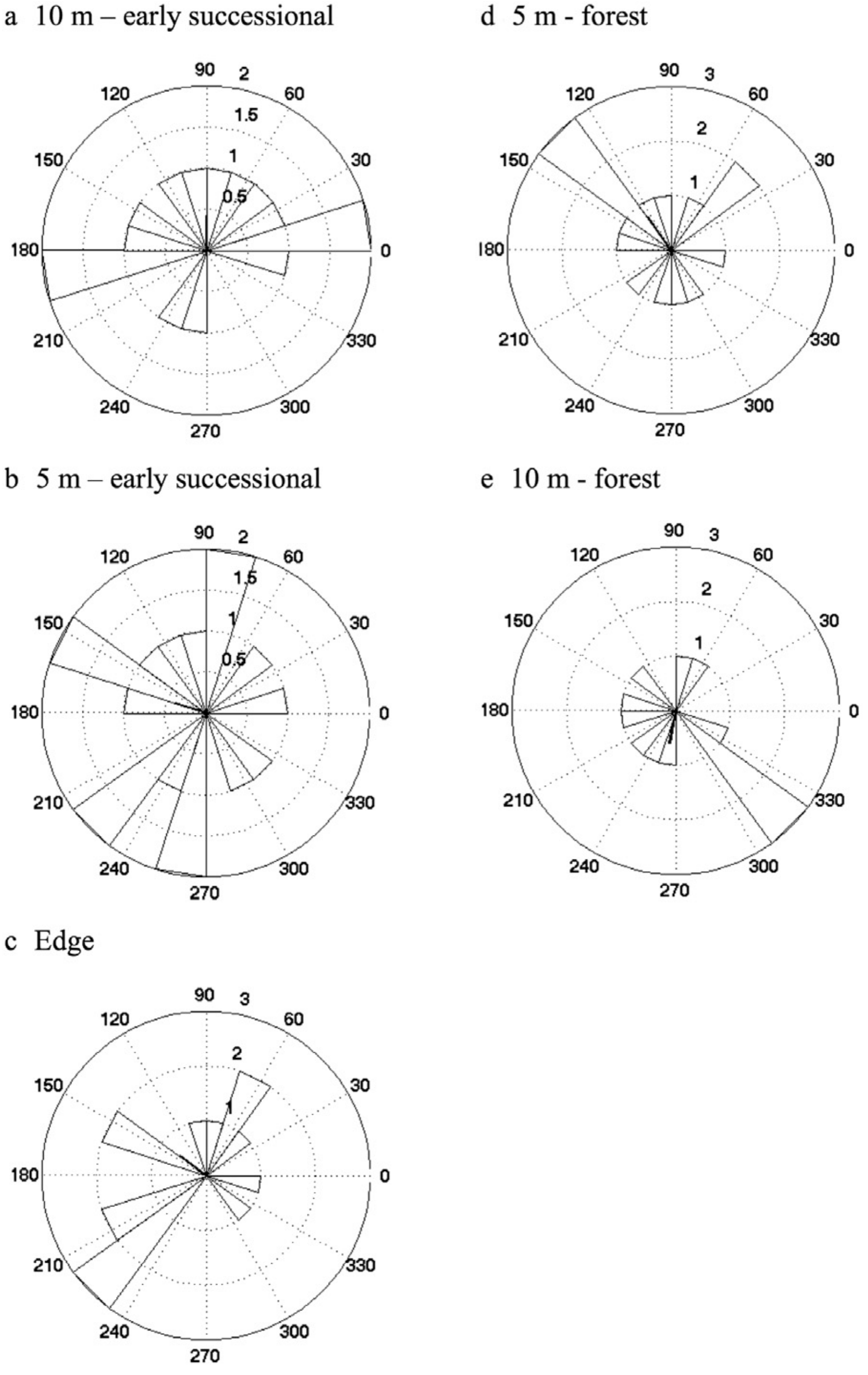


Figure 2 Orientation of juveniles released varying distances from forest/field edges: (a) 10 m away from the edge in the field, (b) 5 m away from the edge in the field, (c) at the edge, (d) 5 m away from the edge in the forest and (e) 10 m away from the edge in the forest. Bold solid lines indicate mean direction and the length of the line as a percentage of the radius of the diagram corresponds to mean vector length. Length of wedges indicates the number of animals whose orientation fell within the designated 20° bin. Orientations have been standardized so that 0° refers to the direction of the forest, perpendicular to the edge.

size of 1.20 m (SE = 0.06 m) and a mean *k* value of 0.703 (SE = 0.018) when moving through forest or early successional habitat. However, at the individual level, 23% of salamander paths did significantly deviate from CRW (19 out of 84). Of these, 95% yielded $\mathrm{CRW}_{\mathrm{Diff}} > 0$ and therefore moved farther distances than predicted by a CRW (18 out of 19). When we resampled these paths at a mean step size of 1.2 m, 68% of the paths did not deviate from a CRW, indicating that the original



a 10 m – early successional

d 5 m - forest

b 5 m – early successional

e 10 m - forest

c Edge

Figure 3 Orientation of juveniles released varying distances from forest/early successional edges: (a) 10 m away from the edge in the early successional forest, (b) 5 m away from the edge in the early successional forest, (c) at the edge, (d) 5 m away from the edge in the forest and (e) 10 m away from the edge in the forest.

mean step sizes calculated for these paths may have been smaller than the native scale of movement (Nams, 2006). Nine salamander paths through field habitat did not cross a habitat boundary and were long enough to include in this analysis. We found that salamander movement through field was not significantly different from a CRW ($CRW_{Diff} = 0.389$, $P = 0.7852$, $n = 9$), with a mean step size of 1.62 m (SE = 30 cm) and a mean k value of 0.804 (SE = 0.04).

Discussion

Elucidating behavioral rules that predict organisms' spatial ecology in altered landscapes requires species-centric, bottom-up approaches to the study of animal movement (Romero *et al.*, 2009). The fine-scale search strategies of juvenile salamanders documented in this study provide behavioral mechanisms underlying the patterns observed in previous studies (deMaynadier & Hunter Jr, 1998, 1999; Rittenhouse & Semlitsch, 2006). This study found that salamanders moved straighter through field habitat than forest or early successional habitat and biased movements strongly toward forest, indicating that recently metamorphosed amphibians exhibit reasonable movement rules during initial movement out of ponds to minimize time spent in unsuitable habitat.

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

We did not detect a significant difference in step size or path linearity between early successional and forest habitat, and juveniles moved randomly with respect to habitat boundaries when released in these habitats. These results suggest that early successional forest may not act as a dispersal barrier for spotted salamanders. However, previous studies have found that abundances of many forest-dependent amphibian species are lower in early successional habitat than mature forest habitat (Popescu *et al*., 2012; Hocking *et al*., 2013). Early successional forest may therefore act as an ecological trap if patches fail to provide the resources needed for survival.

At the species level, spotted salamander movement through field, early successional and mature forest was adequately described by a CRW, supporting the use of CRWs in amphibian movement models (Boone, Johnson & Johnson, 2006) and suggesting that juvenile amphibians may not exhibit systematic searching behavior during initial dispersal (Nams, 2006). This study additionally shows that movement models should incorporate habitat-specific movement and boundary behavior when describing amphibian dispersal (Stevens *et al*., 2006). Numerous studies have concluded that an understanding of animal behavioral rules is required to yield accurate predictions of functional connectivity or population viability in altered habitat (Hawkes, 2009; Yackulic *et al*., 2011). Previous studies have demonstrated that habitat arrangement impacts the viability of pond-breeding amphibian populations (Donoël & Ficetola, 2007); movement models incorporating edge behavior and habitat-specific movement have the ability to predict the consequence of spatial arrangement of habitat on population persistence.

Understanding the fine-scale movement responses of critical life stages to habitat alteration greatly increases the ability of models to predict species' responses to environmental change. This study suggests that juvenile salamanders are able to behaviorally mitigate some degree of habitat loss by biasing movement toward quality habitat. However, clear-cutting in close proximity to breeding ponds may negatively impact populations, as juveniles may not avoid the clear-cut habitat after succession has occurred (Semlitsch *et al*., 2009). At the landscape scale, dispersing spotted salamanders are likely to avoid open habitat from urban or agricultural development, which may limit functional connectivity but increase the survival of juveniles in existing populations. Research on juvenile amphibian movement patterns in relation to habitat type and edges over longer temporal scales will provide further insight into effects of landscape change on amphibian population distributions.

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