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Grasslands as movement barriers for a forest-associated salamander: Migration behavior of adult and juvenile salamanders at a distinct habitat edge

Tracy A.G. Rittenhouse*, Raymond D. Semlitsch¹

Division of Biological Sciences, University of Missouri, 105 Tucker Hall, Columbia, MO 65211-7400, United States

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ABSTRACT

The persistence of amphibian populations in fragmented landscapes requires dispersal and recolonization of habitat patches after local extinction. These processes entail individuals crossing habitat edges. Edge permeability integrates the behavior of individuals with the vegetative structure of the habitat edge and may influence the dispersal rates between habitat patches. We used drift fences, radio telemetry, and an experimental displacement to examine the movement behavior of juvenile and adult spotted salamanders (*Ambystoma maculatum*) at a pond located in continuous forest and a pond located on a distinct forest-grassland edge. At the pond on the habitat edge, adult salamanders migrated to and from the forested side of the pond. Resident adults with transmitters migrated to forested habitat without approaching the habitat edge. Displaced adults with transmitters halted emigration movements when they approached the habitat edge. None of the radio-tagged adults were observed more than a few meters into the grassland. Recently metamorphosed juveniles exiting the grassland side of the pond changed their direction of movement and migrated into the forested habitat. We conclude that salamanders oriented movements with respect to features in the terrestrial habitat, detected the habitat edge, and behaviorally avoided the grassland. Exploring the permeability of habitat edges will improve our understanding of dispersal within fragmented landscapes and enhance efforts to conserve regional populations of amphibians.

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1. Introduction

Human alteration of the landscape through forest fragmentation, agriculture, and development, creates habitat edges through previously continuous habitat. Habitat edges, or abrupt transitions between two habitat types (Kaplan and Meier, 1958; Allison, 1995), are often characterized by deleterious changes in abiotic and biotic factors (deMaynadier and Hunter, 1998). For example, changes in wind, light, moisture,

chemical and temperature across habitat edges (Saunders et al., 1991; Debinski and Holt, 2000) may lead to changes in species diversity and abundance (Murcia, 1995). The persistence of species within this fragmented landscape is dependent on the ability of species to recolonize isolated habitat patches after local extinctions (Fahrig and Merriam, 1994; Thomas and Hanski, 1997). Recolonization requires that individuals disperse across habitat edges, as well as, survive the time spent in matrix habitat. Edge permeability integrates

* Corresponding author. Tel.: +1 573 882 1421; fax: +1 573 882 0123.

E-mail addresses: tg9aa@mizzou.edu (T.A.G. Rittenhouse), semlitschr@missouri.edu (R.D. Semlitsch).

¹ Tel.: +1 573 884 6396; fax: +1 573 882 0123.

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the structure and vegetative composition of the habitat with the perception and movement behavior of individuals (Berggren et al., 2002), and thus altering vegetation may become a method for increasing dispersal rates. Examining edge permeability provides insight regarding the dispersal behavior of individuals, and may further our understanding of the meta-population dynamics within fragmented landscapes.

Previous studies of forest-associated amphibian species at habitat edges have identified several patterns. The relative abundance of amphibians is often highest in forest interiors and declines across a habitat edge into adjacent habitat, with edge effects in the eastern half of the United States extending 25–35 m into the forest (deMaynadier and Hunter, 1998). The type of habitat edge (e.g., forest–grassland or forest–residential) or the degree of edge contrast may influence the type of species affected or the magnitude of the effect (deMaynadier and Hunter, 1998; Gibbs, 1998a). For example, salamanders tend to be affected by high-contrast edges more than anuran species (deMaynadier and Hunter, 1998), and forest–road edges reduce amphibian abundance more than forest–residential edges (Gibbs, 1998a). However, the use of drift fences and pitfall traps in these studies identifies patterns but not mechanisms, because low capture rates may result from poor survival, low movement rates leading to reduced capture probability in traps, or behavioral avoidance of non-forested habitat (Gibbs, 1998a).

In this study, we used a combination of radio-telemetry and drift fences to examine how movement patterns and behavior may generate the previously demonstrated pattern of reduced amphibian abundance at habitat edges. Radio-telemetry has previously been effective in studying the movement behavior of ambystomatid salamanders (Madison, 1997; Madison and Farrand III, 1998). On rainy nights following breeding, ambystomatid salamanders make large migratory movements away from breeding ponds and remain underground in small mammal burrows within small home ranges during the non-breeding season (Williams, 1974; Semlitsch, 1981; Semlitsch, 1983; Madison, 1997). Emigration paths are typically straight, oriented perpendicularly to the edge of the pond (Madison, 1997), and may extend several hundred meters into terrestrial habitats (Semlitsch, 1998).

To determine whether the migratory movements of spotted salamanders in continuous habitat are similar to those in non-continuous habitat, we studied salamanders at a pond completely surrounded by forest habitat (referred to as Forest Pond; Fig. 1b) and a pond located on a distinct forest–grassland habitat edge (referred to as Edge Pond; Fig. 1a). Drift fence encircling Edge Pond allowed us to correlate the orientation of migrating salamanders to the terrestrial habitats surrounding the pond, to compare the orientation of adults to metamorphs, and another drift fence parallel to the habitat edge allowed us to detect metamorphs moving between habitat types. In addition, we performed reciprocal displacements of radio-tagged salamanders between the two ponds. The experimental manipulation allowed us to test the ability of adults to detect and respond to a habitat edge. If we only monitored the drift fence and tracked non-displaced animals at the Edge Pond and none of these salamanders moved towards the grassland, we could not conclude that the salamanders truly avoided the grassland habitat. These salamanders

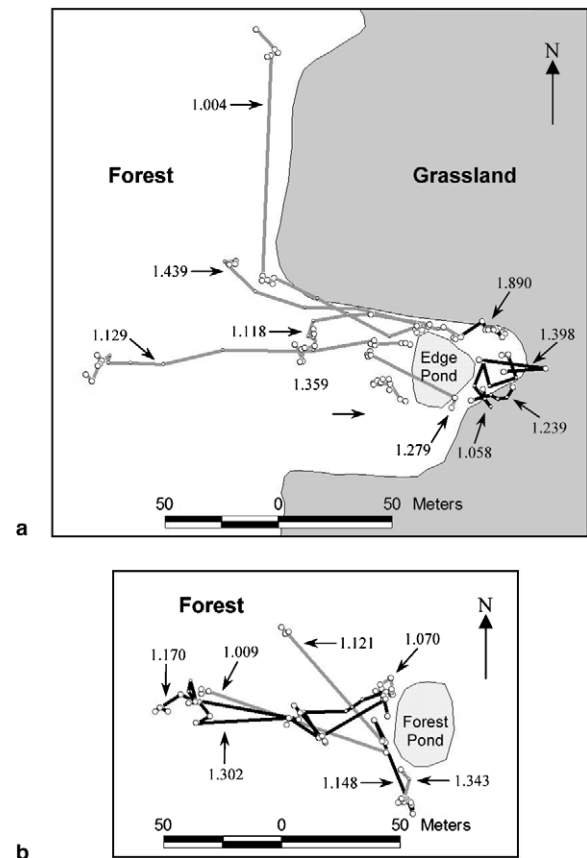


Fig. 1 – Representative movement paths of adult salamanders at Edge Pond (a) and Forest Pond (b). Gray lines are movement paths for Resident salamanders and black lines are movement paths for Displaced salamanders. Paths were constructed by drawing straight lines between both daily (i.e. large circles) and hourly (i.e. small circles) relocations. The white background represents forest habitat and the gray background represents grassland. At the Edge Pond, note the distinct habitat edge and the small forest patch on the grassland side of Edge Pond. Numbers are ID numbers for each individual. Ponds are located approximately 3 km apart.

may have been selecting forest habitat or they may have been following previously traveled migration paths, which happened to stay within the forested habitat. Because the forest–grassland edge was created more than 50 years ago, we could be witnessing the result of selection against any salamander that migrated into the grassland and suffered high mortality rates. The manipulation thus allowed us to compare how resident salamanders and salamanders with no previous knowledge of the habitat respond to a distinct forest–grassland habitat edge. The reciprocal displacement of individuals to the Forest Pond served as a control to the displacement, illustrating how displaced salamanders migrate through continuous habitat.

Our objective was to determine if salamanders behaviorally avoid the habitat edge or migrate into the grassland and experience low survival rates. We hypothesized three potential outcomes: (1) salamanders would enter but experience

high mortality in the grassland; (2) salamanders would successfully cross the grassland and enter the forested habitat approximately 100 m away; or (3) salamanders would avoid the grassland. Finally, we hypothesized that recently metamorphosed juveniles would display similar movement behavior as adults.

2. Methods

2.1. Study sites

Naturally occurring populations of spotted salamanders were found within ponds built as cattle or wildlife ponds in the 1930's. Forest Pond is located on the University of Missouri's Thomas S. Baskett Wildlife Research and Education Area. Edge Pond occurs on the USDA Forest Service Mark Twain National Forest. Both ponds are similar in size and located in Boone County, Missouri approximately 3 km apart. Forest Pond is completely surrounded by second-growth oak-hickory hardwood forest, consisting of an oak (primarily *Quercus alba* and *Quercus rubra*) and hickory (*Carya* sp.) overstory and a sugar maple (*Acer saccharinum*) understory. Edge Pond lies on a distinct forest-grassland habitat edge (see aerial photo in Rittenhouse, 2002), with forest similar to Forest Pond on the west side and grassland on the east side. The grassland consists primarily of Indian grass (*Sorghastrum nutans*) and big bluestem (*Andropogon gerardii*), with some fescue (*Festuca arundinacea*). The grassland was cultivated until 1981, left as old field, and then planted with warm season grasses about 10 years ago. The grassland is grazed by cattle for a few weeks annually.

2.2. Drift fences

Each pond was completely encircled by a drift fence with paired pitfall traps (number 10 food cans) spaced at 4.5 m (15°) intervals. Each pitfall trap contained a moist sponge and was covered with a wooden lid held 1–2 in. from the ground to minimize desiccation of amphibians and predation by raccoons. The fence at Edge Pond was completed on 6 March 2001 and male salamanders were observed in the pond at this time. In May 2001, we added two 15 m extensions of drift fence (referred to as wings) parallel to the habitat edge. Four pairs of pitfall traps were placed at 4.5 m intervals along each wing. Traps were monitored year-round from 6 March 2001 until 1 October 2002, with a checking frequency of every one to three days, depending on capture rates and time of year. In 2001, metamorphs at Edge Pond were toe-clipped according to the side of the pond from which they exited (i.e., forest or grassland). In 2002, the marking of metamorphs was modified to distinguish between individuals that clearly left from the forest or grassland side of the pond and those that exited near the wing (defined as the two traps on either side of the point where the wings intersected the circular fence), resulting in four cohort marks: forest, forest-wing, grassland-wing, or grassland.

The drift fence data were analyzed based on 18 sample populations, 9 each in 2001 and 2002: female immigration, female emigration, male immigration, male emigration, total females, total males, total adult immigration, total adult emi-

gration, and metamorph emigration. In all analyses, 0° is north, 90° is east, 180° is south, and 270° is west. Rayleigh uniformity tests were used to determine if the orientation of the 18 sample populations differed significantly from a random distribution (Batschelet, 1981). Watson-Williams tests were used to test for differences between the mean angles of migration between sample populations (Batschelet, 1981). Although significant year effects were detected in 8 of 9 comparisons (Rittenhouse, 2002), the mean angle differences were always less than 36° and did not reflect a change in the selection of terrestrial habitat types. Therefore, we combined year 2001 and 2002 and report results using 9 sample populations. A Wilcoxon matched-pairs signed-ranks test was used to compare the number of metamorph captures on the forested side of the wing drift fences to the number of captures on the grassland side of the wing drift fences (Siegel, 1956).

2.3. Telemetry

We radio-tracked resident and displaced salamanders at each pond. At the Forest Pond, we tracked resident salamanders that initially emigrated west ($n = 7$; hereafter referred to as Forest Pond Resident). Salamanders that initially emigrated east at the Forested Pond were displaced to the east side (i.e., grassland side) of Edge Pond ($n = 12$; hereafter referred to as Edge Pond Displaced). At the Edge Pond, only two salamanders large enough to implant with radio-transmitters left the pond going east, thus we tracked salamanders that initially emigrated both east ($n = 2$) and west ($n = 7$; hereafter referred to as Edge Pond Resident). Salamanders that initially emigrated west from Edge Pond were displaced to the west side of Forest Pond ($n = 11$; hereafter referred to as Forested Pond Displaced).

Adult salamanders (19 males and 20 females) weighing 18.6 ± 1.82 g and leaving the ponds in the appropriate direction were selected for radio-tracking. Four to eight individuals were selected during each rainfall event throughout the spring to ensure the sample included individuals leaving at various times. We attempted to select an equal number of resident and displaced individuals at each pond during each rainfall event.

Salamanders were brought to a laboratory at the University of Missouri, anesthetized with MS-222, and surgically implanted with 1.8 g transmitters (model BD-2G with external helix antennas, Holohil Systems Inc., Canada). Transmitters were inserted through a small cut perpendicular to the costal grooves across two costal folds and the incision was closed with 4–5 sutures (Madison, 1997; Rittenhouse, 2002). Salamanders were returned within 24 h to a damp location approximately 1 m outside of the drift fence and at the pitfall of capture.

Individuals were relocated daily for the life of the transmitters (~3 months) between 15 March and 6 June 2001. All relocation points were determined using "homing" methods (Mech, 1983; White and Garrott, 1990), marked with wire flags, and later mapped using a GPS unit with submeter accuracy (Trimble Pathfinder Pro XL). When large movements were expected (nights >5 °C with rain >4 mm), a subset of salamanders were relocated every hour from sunset until sunrise to obtain a detailed description of the movement path. During

the hourly relocations, we obtained visual sighting of the salamanders migrating above the leaf litter greater than 90% of the time. When the transmitters were close to failure, salamanders were relocated, excavated from their refuges, and transmitters were surgically removed.

All GPS locations were imported into Arcview (version 3.2; Environmental Systems Research Institute, Redlands, California, USA), but quantitative analyses were conducted only on the daily relocation points. For each movement path, we calculated the following 4 movement parameters using the Animal Movements extension (Hooge et al., 1999) to Arcview: total distance traveled (i.e., sum of the distances between each relocation), net distance (i.e., straight-line distance between release point and final location), maximum single movement (i.e., the largest movement made in a 24-h time period), and mean vector length (r ; Batschelet, 1981). The straightness of the movement path can be inferred from the value of r , which ranges between 0 and 1 (Batschelet, 1981; Claussen et al., 1997). If r is 1, then the animal moved in a perfectly straight line. We believe that the r -value did not fully represent the straightness of the migratory movement paths, because the r -value gives equal weight to each movement segment. Salamanders only make large movements during rainy nights and make small movements within an activity center the remainder of the time (Semlitsch, 1981). Small movements occurred in all directions and are likely influenced by activities not associated with migration (e.g. feeding or microhabitat selection). Therefore, we believe the large movements are more reflective of the migratory path straightness. To make larger movements weighted more than smaller movements, we calculated a 5th movement parameter by dividing the r value by the net distance.

The five movement parameters were tested for the effects of pond (Edge Pond or Forest Pond) and previous knowledge of the landscape (Resident or Displaced) using ANOVA. Number of days tracked was used as a covariate and the data were log-transformed. A Kaplan–Meier analysis was used to estimate survival probabilities and to generate survival curves for each treatment group (Kaplan and Meier, 1958; Allison, 1995). Survival curves were compared using a log-rank test (Pollock et al., 1989).

3. Results

3.1. Drift fence

A total of 1849 adult and 1931 metamorph spotted salamander captures occurred at the Edge Pond during the two years. The mean angle of migration (ϕ) for adults always occurred in the forested, northwest quadrant of the pond (means ranged from 291° to 306°) and movement was significantly oriented towards the mean angle (all P 's < 0.001). The mean angle of adult immigration ($\phi = 302^\circ$) and adult emigration ($\phi = 298^\circ$) did not differ (d.f. = 1847, $F = 0.7672$, $P > 0.05$). Therefore, adult salamanders clearly migrated to and from the forested side of the Edge Pond. The mean angle of migration for males ($\phi = 305^\circ$) and for females ($\phi = 291^\circ$) differed significantly (d.f. = 1847, $F = 11.9$, $P < 0.002$); however, the mean angles only differed by three pairs of pitfall traps, thus we conclude that

both males and females directed migratory movements with respect to forested habitat (Fig. 2). The mean angle of adult emigration ($\phi = 298^\circ$) and metamorph emigration ($\phi = 36^\circ$) significantly differed (d.f. = 2699, $F = 431.2$, $P < 0.001$). Finally, significantly more metamorphs initially leaving the pond on the grassland side were recaptured in the wing fences migrating towards the forest than were recaptured migrating towards the grassland (Fig. 3; $P < 0.01$). This result indicates that metamorphs initially migrating from the grassland side of the pond reversed direction more often than metamorphs that initially emigrated from the forested side of the pond. In 2002, most recaptured metamorphs were marked grassland-wing.

3.2. Telemetry

Resident and displaced salamanders differed significantly in the total distance, net distance, and maximum single movement ($P = 0.0385$ – 0.0797 ; Table 1). The average total distance ($59.69 \text{ m} \pm 60.21$), net distance ($44.64 \text{ m} \pm 50.57$), and maximum single movement ($37.82 \text{ m} \pm 41.71$) made by resident salamanders were longer than the average total distance ($31.11 \text{ m} \pm 41.97$), net distance ($15.73 \text{ m} \pm 23.75$), and maximum single movement ($13.57 \text{ m} \pm 14.40$) made by displaced salamanders (Fig. 4; see Rittenhouse, 2002 for distances moved by individuals). The mean vector length (r) for resident and displaced salamanders was not significantly different ($P = 0.6898$); however, the r -value divided by the net distance for resident salamanders (0.0457) was smaller than the value for displaced salamanders (0.1254; $P = 0.074$), indicating that the movement paths for resident salamanders were straighter than the movement paths of displaced salamanders. Salamanders at the Forest Pond and the Edge Pond did not differ in total distance, net distance, maximum single movement, and r -value (all P 's > 0.1; Table 1) and there were no interactions between pond (i.e., Forest Pond and Edge Pond) and previous knowledge (i.e., Resident and Displaced) (all P 's > 0.1; Table 1). However, Edge Pond Resident salamanders tended to move the greatest distances and Edge Pond Displaced salamanders tended to move the shortest distances (Fig. 4), indicating our power may have been too low to detect a biologically important interaction effect (Fig. 5).

At the Forest Pond, both resident and displaced salamanders made straight, linear movements similar to those previously described for ambystomatid salamanders (Semlitsch, 1981; Madison, 1997; Fig. 1b). At the Edge Pond, none of the salamanders, whether resident or displaced, were relocated more than a few meters into the grassland habitat (Fig. 1a). All of the Edge Pond Resident salamanders ($n = 9$; gray lines in Fig. 1a) ultimately migrated into the forest habitat, including the two individuals that initially emigrated from the pond on the grassland side. The Edge Pond Displaced salamanders ($n = 12$; black lines in Fig. 1a), initially emigrated perpendicular to the pond, as expected based on previous studies (Madison, 1997). However, when they reached the forest–grassland edge, they made short (<5 m) back and forth movements along the habitat edge, and three individuals reversed direction and moved towards the pond. Notably, the Edge Pond Displaced salamanders

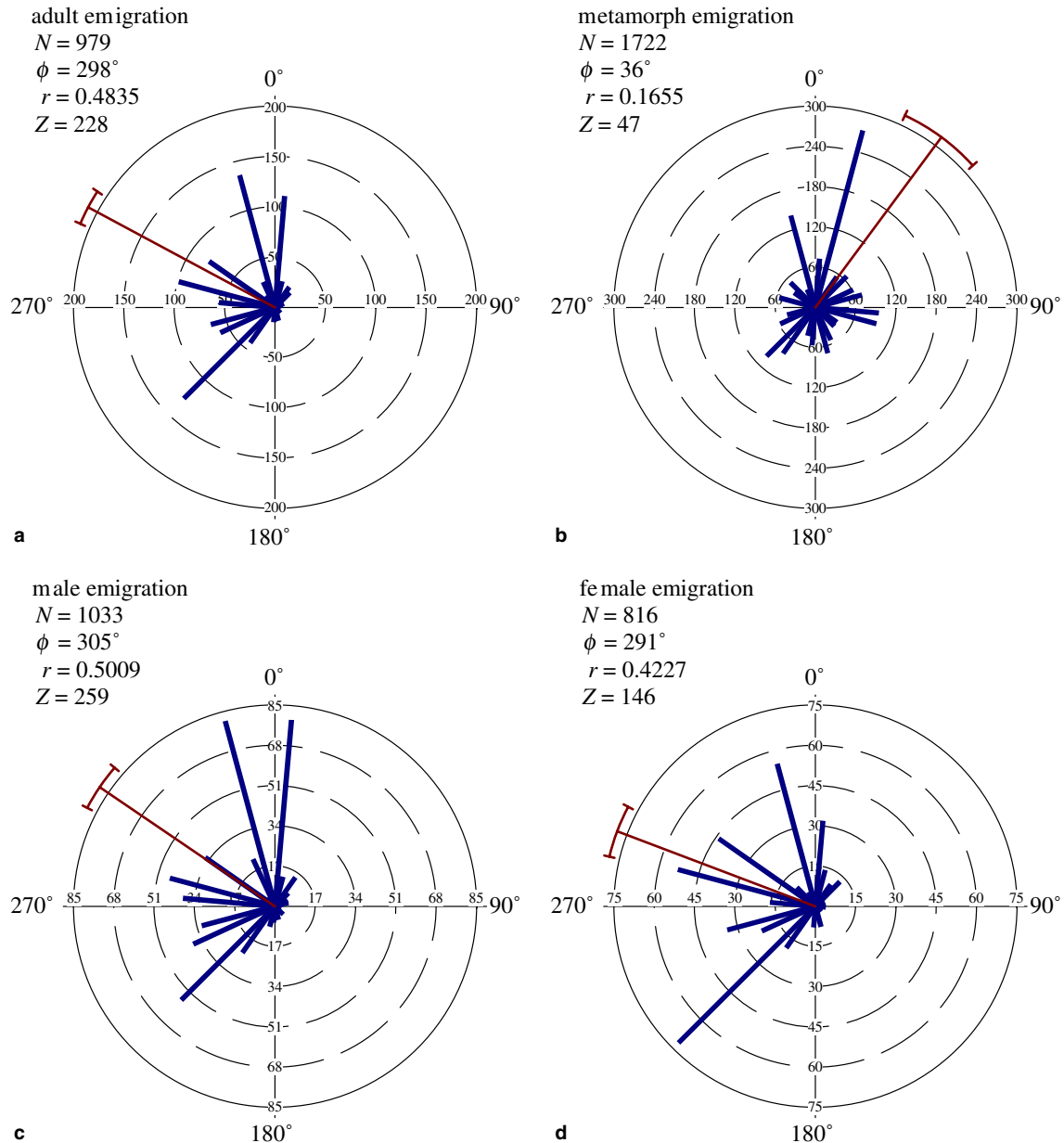


Fig. 2 – Circular histograms of drift fence data at the Edge Pond combining years 2001 and 2002. Each bar represents the number of individuals caught in the trap located in that direction of the pond. The means and 95% confidence intervals are shown. The sample size (N), mean angle (ϕ), mean vector length (r), and the Rayleigh test statistic (Z) are given for each sample population. All sample populations are directed towards the mean angle (all $P < 0.001$). 0° is north, thus 0 – 180° is towards the grassland side of the pond and 180 – 360° is the forested side of the pond.

did not move to the forested habitat on the opposite side of the pond (20–30 m away) or across the grassland (100 m away) within the duration of the study. We found no evidence of displaced individuals attempting to return to their home pond.

Survival estimates were similar across all treatment groups ($P = 0.1858$). Survival rate to the end of the study was 0.143 (SE = 0.1323) for Forest Pond Resident salamanders, 0.341 (SE = 0.1495) for Forest Pond Displaced salamanders, 0.318 (SE = 0.1799) for Edge Pond Resident salamanders, and 0.273 (SE = 0.1343) for Edge Pond Displaced salamanders.

4. Discussion

Spotted salamanders halted migratory movements when they encountered a distinct forest–grassland habitat edge. Adults captured in pitfall traps during migration demonstrated a directional bias towards the forested side of the pond. Metamorphs originally emigrating towards the grassland reversed their direction of travel and migrated towards the forest. The migratory movement paths of radio-tagged salamanders illustrate an aversion to the habitat edge and an unwillingness to cross the grassland. We conclude from drift fence,

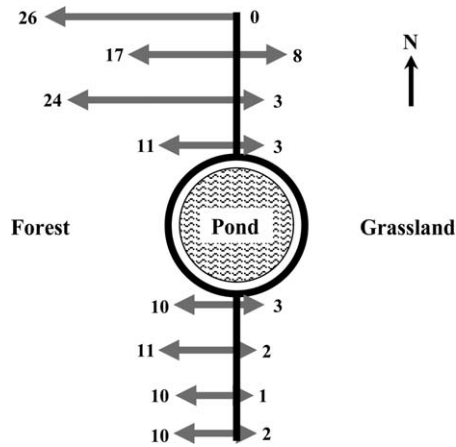


Fig. 3 – Diagram of the wing drift fences at Edge Pond. The black lines represent the drift fence circling the pond and the two wings extending 15 m north and 15 m south (i.e. parallel to habitat edge). The length of the gray arrows represents the number of metamorphs traveling in that direction and the sample size is given next to each arrow. For example in the northernmost pair of pitfall traps, 26 metamorphs were caught moving towards the forest and 0 metamorphs were caught moving towards the grassland. The size of the pond (30 m in diameter) is not drawn to scale relative to the size of the wings (15 m each).

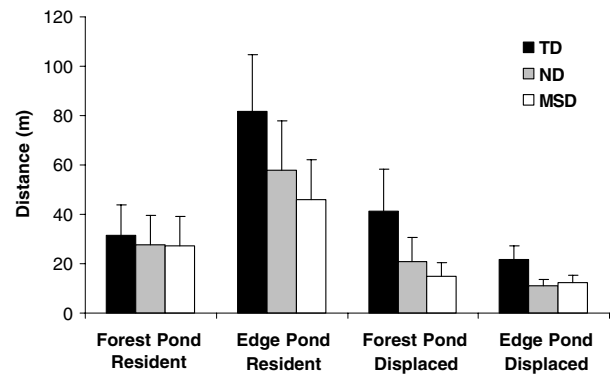


Fig. 4 – Average total distance (TD = black bars), net distance (ND = gray bars) and maximum single daily distance (MSD = white bars) with standard error bars for Forest Pond Resident (n = 7), Edge Pond Resident (n = 9), Forest Pond Displaced (n = 11), and Edge Pond Displaced (n = 12) salamanders.

telemetry, and displacement results that migrating salamanders orient with respect to features in the terrestrial habitat and that individuals behaviorally avoid the grassland. Thus, the permeability of this distinct forest–grassland edge is low. We conclude that behavioral avoidance is a mechanism driving the previously observed decreases in salamander

Table 1 – A summary of the analysis of variance for pond (forest/edge) and previous knowledge (resident/displaced) effects

Response variable	Source of variation	DF	MS	F-value	P-value
Total distance	Days tracked	1	25.036	28.19	0.0001
	Pond	1	0.517	0.58	0.4506
	Previous knowledge	1	2.898	3.26	0.0797
	Interaction	1	0.002	0.00	0.9633
	Error	34	30.193		
Net distance	Days tracked	1	20.228	20.06	0.0001
	Pond	1	0.023	0.02	0.8874
	Previous knowledge	1	4.677	4.64	0.0385
	Interaction	1	0.478	0.47	0.4957
	Error	34	34.286		
Max single movement	Days tracked	1	21.096	19.82	0.0001
	Pond	1	0.193	0.18	0.6725
	Previous knowledge	1	4.260	4.00	0.0535
	Interaction	1	1.516	1.42	0.2409
	Error	34	36.192		
r Value	Days tracked	1	0.326	7.16	0.0114
	Pond	1	0.016	0.35	0.5563
	Previous knowledge	1	0.007	0.16	0.6898
	Interaction	1	0.019	0.42	0.5232
	Error	34	2.044		
r Value/net distance	Days tracked	1	39.930	24.68	0.0001
	Pond	1	0.384	0.24	0.6293
	Previous knowledge	1	5.480	3.39	0.0744
	Interaction	1	0.083	0.05	0.8220
	Error	34	55.000		

Number of days tracked was used as a covariate in each analysis.

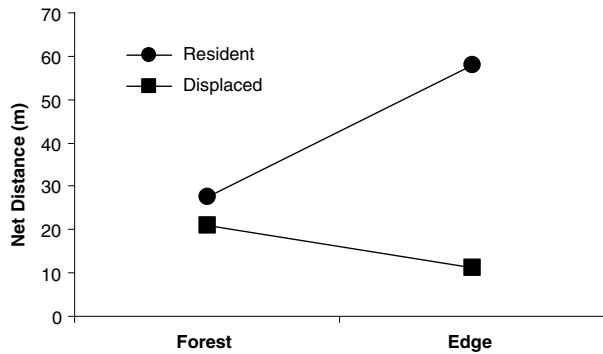


Fig. 5 – The interaction between pond (i.e. Forest and Edge) and previous knowledge (i.e. Resident and Displaced) in average net distance salamanders traveled from the pond was not statistically significant (d.f. = 1, $F = 0.47$, $P = 0.4957$). However, we suggest that the interaction visible in this figure may be biologically important. A similar pattern is visible when total distance and maximum single daily distance are graphed in this manner.

abundance at habitat edges and near clearcuts (Raymond and Hardy, 1991; Gibbs, 1998a).

The behavioral avoidance observed at the habitat edge can result from several processes that are not necessarily mutually exclusive. First, adults may use previous knowledge of the terrestrial habitat to avoid grassland. The majority of resident adults simply migrating to and from the forested side of Edge Pond suggests that the location of the forest is known. The two radio-tagged salamanders (ID 1.439 and 1.279) that initially emigrated towards the grassland were able to move around Edge Pond without approaching the grassland. These paths differed greatly from the straight movement paths described in continuously forested habitat at Forest Pond and in the study by Madison (1997). Furthermore, Edge Pond Displaced salamanders initially migrated in the same direction (i.e. east) as they started migration from Forested Pond.

Second, adults may be philopatric to the terrestrial refuges and emigration routes used successfully as a metamorph (Dodd and Cade, 1998). The metamorphs that migrate into less suitable habitat may experience low survival rates as juveniles or adults, and thus these individuals may not become part of the breeding population. Our results indicate that increased adult mortality is not a contributing factor to this process, because survival rates were comparable for radio-tagged salamanders at both Edge Pond and Forest Pond, with the lowest survival rate in Forest Pond Resident salamanders. However, metamorphs entering the grassland may not survive to maturity, because survival rates of juveniles penned in nearby old-fields was near zero compared to moderate survival rates for juveniles penned in forest (Rothermel, 2003). In addition, we may expect only a small proportion of the metamorphs that leave the grassland side of Edge Pond to happen to migrate into the forested habitat. The 12% of adults that did emigrate from the grassland side of Edge Pond may result from this small proportion of surviving metamorphs.

Finally, salamanders may avoid the grassland based on cues received from the habitat while migrating. Adult sala-

manders oriented migratory movements towards forested habitat. Other amphibian species also orient with respect to forested habitat (Dodd and Cade, 1998; Malmgren, 2002; Rothermel and Semlitsch, 2002) and recapture data for *Ambystoma talpoideum* suggest that salamanders moved away from a recent clearcut (Raymond and Hardy, 1991). Furthermore, when olfactory habitat cues are reduced by covering a pond with tarpaulin, the ability to orient migratory movements are reduced (Joly and Miaud, 1993). Edge Pond Displaced salamanders clearly demonstrate that salamanders use cues received from the habitat while migrating to behaviorally avoid habitat edges. All Edge Pond Displaced salamanders stopped migrating when they approached the habitat edge, including the movement paths of several individuals not displayed in Fig. 1 that consist of a line connecting the release point and the final point at the habitat edge (i.e. similar to ID 1.239 without the hourly points). The hourly visual relocations of an individual (ID 1.058) migrating at night during a rain began with a movement perpendicular to the pond towards the grassland (observation at 22:45 h CST, with nose pointed back towards the pond), and then moved to the pond one hour later. The salamander moved to the habitat edge for a second time by 02:45 h CST, but settled in the center of the small forest patch between the pond and the grassland. Laboratory experiments demonstrate that metamorph and adult salamanders may detect the habitat edge by changes in the substrate (McGregor and Teska, 1989; Rittenhouse et al., 2004). A variety of habitat cues may be used in addition, such as the loss of canopy cover, increase in wind and dryness, a small change in slope, or a change in vegetative structure from leaves to grass.

We found that resident salamanders migrate greater distances than displaced salamanders; however, the movement paths of resident and displaced salamanders at Forest Pond were similar (e.g. ID 1.009 compared to ID 1.170 and ID 1.302). The primary difference in the movement paths was that the resident salamanders, which may be returning to a known location, migrated to the beginning of the drainage in one night; whereas, the displaced salamanders required two evenings of rain to find the drainage. The movement distances for Forest Pond Resident and Forest Pond Displaced salamanders were always intermediate between Edge Pond Resident and Edge Pond Displaced salamanders. Edge Pond Displaced salamanders made the shortest movements due to reaching the habitat edge; whereas, Edge Pond Resident salamanders migrated the greatest observed distances. Edge Pond Resident salamanders may need to make large migrations to reach suitable terrestrial refuges due to the limited amount of forest surrounding Edge Pond.

Mortality of radio-tagged adults was higher than expected. Throughout the three months of tracking, a total of 17 individuals were found dead on top of the leaf litter with no signs of predation. Although we observed several individuals that appeared healthy migrating approximately 100 m in one night, we believe the mortality was likely related to the implanted transmitter (Rittenhouse, 2002) and thus we cannot assume that the transmitter did not impact behavior. Because mortality was equal across the four treatment groups and salamanders without implanted transmitters also avoided the grassland, we believe that comparisons between the two

ponds and between resident and displaced salamanders are valid and provide needed information regarding how salamanders select terrestrial habitats.

Adults oriented with respect to forested habitat; whereas, metamorphs tended to emigrate from Edge Pond in all directions, with 42% emigrating towards the forest and 58% emigrating towards the grassland. Adults and metamorphs may respond differently to microhabitat variables (e.g., slope, aspect, temperature gradient), competitors or predators while migrating, or they may differ in terrestrial habitat requirements. Furthermore, the small forest cue on the grassland side of the pond (i.e., 10 trees; Fig. 1a) may have been strong enough to elicit metamorph emigration towards the grassland. In addition, Edge Pond was constructed by creating a dam on the forested side, thus metamorphs climbing out of the forested side may have been hindered by the slope, as was also suggested for *Notophthalmus perstriatus* efts (Johnson, 2003). In a study that controlled for slope by placing artificial ponds on habitat edges, emigration of spotted salamander metamorphs was towards forested habitat (Rothermel and Semlitsch, 2002).

Metamorphs that initially emigrated towards the grassland ultimately reversed direction and were recaptured in the wings moving towards the forested. However, metamorphs exiting the pond near the habitat edge were more likely to reach the forested habitat than individuals that left the pond in the middle of the grassland side. Metamorphs exiting far from the forest may not detect or may experience low survival while attempting to reach the forest of the opposite side of Edge Pond. Limited abilities to detect forest edges (50–60 m) have previously been shown for metamorphs (Rothermel, 2004). Adult detection abilities may also be low, because none of the Edge Pond Displaced adults migrated to the forest on the opposite side of the pond (20–30 m) or the forest opposite the grassland (100 m).

Similar behavioral responses to habitat edges have been documented in insects and small mammals (Wolff et al., 1997; Jonsen and Taylor, 2000; Berggren et al., 2002), but how the behavioral response of individuals translates into population or metapopulation-level effects remains unclear. Computer simulations of individual movement behaviors can derive landscape-level patterns (e.g. turtles, Gibbs and Shriver, 2002; and damselflies, Jonsen and Taylor, 2000). The accuracy of these models is influenced by our understanding of individual responses that vary depending on the age or sex of the individual (Davis-Born and Wolff, 2000) or the condition of the individual (e.g. starvation; Mauremooto et al., 1995). Behavioral responses also vary with site-specific conditions, such as the amount of fragmentation in the surrounding landscape (Jonsen and Taylor, 2000), the type of disturbance causing the fragmentation (e.g., forest harvest, grazing, urban development), or the size of habitat patches. The permeability of the edge in our study was low, but spotted salamanders are known to cross open areas, such as a grassland (Shoop, 1968; Gibbs, 1998b) or small roads (T.A.G.R. & R.D.S. pers. obs.; Homan et al., 2003). The factors influencing edge permeability for salamanders are not yet evident and future work may clarify differences between edges.

Behavioral avoidance of habitat edges and philopatry to breeding sites may allow the short term persistence of local

amphibian populations in fragmented landscapes, because individuals do not risk migrating through poor quality habitat that could reduce survival (Gibbs, 1998b; Donovan and Lamberson, 2001). For example, red spotted newts (*Notophthalmus v. viridescens*), a species with an eft stage devoted to dispersal, ceased to exist in landscapes with less than 50% forest cover; whereas, spotted salamanders persisted in landscapes until forest cover dropped below 30% (Gibbs, 1998b; Porej et al., 2004; Herrmann et al., 2005). Although the mechanism in this case is unknown, behavioral avoidance of matrix habitat by spotted salamanders could prevent high mortality in fragmented landscapes and enhance the short term persistence of local populations. However, the long-term persistence of regional amphibian populations requires successful recolonization via dispersal (Semlitsch, 2000, 2002, 2003). Exploring the permeability of different habitat edges will improve our understanding of dispersal within fragmented landscapes and enhance efforts to conserve regional populations of amphibians.

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