Natural and anthropogenic substrates affect movement behavior of the Southern Graycheek Salamander (*Plethodon metcalfi*)

R.D. Semlitsch, S. Ecrement, A. Fuller, K. Hammer, J. Howard, C. Krager, J. Mozeley, J. Ogle, N. Shipman, J. Speier, M. Walker, and B. Walters

Abstract: Movement behavior is a critical process that interacts with landscape structure to affect population connectivity and persistence in fragmented or altered landscapes. The purpose of our study was to test whether different substrates (forest litter, soil, grass, gravel, and asphalt) found in fragmented forested landscapes affected the movement behavior of the Southern Graycheek Salamander (*Plethodon metcalfi* Brimley, 1912). Latency period of the salamanders was highest on grass substrate and significantly lower only on soil substrate. Sinuosity of the movement path of salamanders was lowest and contained more turns in grass and was significantly higher than only gravel and asphalt substrates. Velocity of the salamanders was highest on asphalt substrate but was not different from gravel substrate. Velocity was higher on asphalt than on grass, forest, or soil, and velocity was higher on gravel than on grass substrate. The results indicated that *P. metcalfi* reacted differently to natural and anthropogenic substrates, and we suggest that these behavioral differences could have both positive and negative implications for movement success and habitat resistance in forested landscapes fragmented by roads and development.

Key words: amphibian, connectivity, habitat resistance, movement behavior, roads, sinuosity, Southern Graycheek Salamander (*Plethodon metcalfi*), substrate, velocity.

Résumé : Le comportement de déplacement est un processus clé dont les interactions avec la structure du paysage ont une incidence sur la connectivité et la persistance des populations dans les paysages fragmentés ou modifiés. L'étude avait pour but d'évaluer si différents substrats (litière, terre, herbe, gravier et asphalte) présents dans des paysages forestiers fragmentés avaient une incidence sur le comportement de déplacement de la salamandre *Plethodon metcalfi* Brimley, 1912. La période de latence des salamandres était la plus longue sur l'herbe, mais ce paramètre n'était significativement plus faible que sur le substrat terreux. La sinuosité de la trajectoire des déplacements des salamandres était la plus faible et comptait le plus grand nombre de virages sur l'herbe, ce nombre n'étant toutefois significativement plus élevé que le nombre de virages sur substrats de gravier et d'asphalte. La vitesse des salamandres était la plus grande sur le substrat d'asphalte, bien que cette vitesse ne soit pas différente de la vitesse sur gravier. La vitesse était plus grande sur l'asphalte que sur l'herbe, la litière et la terre, et la vitesse sur gravier était plus grande que sur l'herbe. Ces résultats indiquent que les *P. metcalfi* ont réagi différemment selon que le substrat était naturel ou artificiel. Nous postulons que ces différences de comportement pourraient avoir des conséquences aussi bien positives que négatives sur le succès des déplacements et la résistance de l'habitat dans des paysages forestiers fragmentés par des routes et aménagements.

Mots-clés : amphibien, connectivité, résistance de l'habitat, comportement de déplacement, routes, sinuosité, salamandre *Plethodon metcalfi*, substrat, vitesse.

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Introduction

The movement of individuals is a critical ecological process that maintains populations through dispersal and connectivity. Successful movement is especially important in fragmented and altered landscapes for rescue of declining

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R.D. Semlitsch. University of Missouri, Columbia, MO 65211, USA.
S. Ecrement. CEMML Colorado State University, Fort Polk, LA 71459, USA.
A. Fuller, J. Mozeley, N. Shipman, and J. Speier. Western Carolina University, Cullowhee, NC 28723, USA.
K. Hammer. College of Charleston, Charleston, SC 29424, USA.
J. Howard. University of California, Davis, CA 95616, USA.
C. Krager. Finger Lakes Community College, Canandaigua, NY 14424, USA.
J. Ogle. Berry College, Mount Berry, GA 30149, USA.
M. Walker. University of Mary Washington, Fredericksburg, VA 22401, USA.
B. Walters. Michigan State University, Lansing, MI 48824, USA.

Corresponding author: Raymond D. Semlitsch (e-mail: SemlitschR@missouri.edu).

populations and re-establishment of extirpated populations (Brown and Kodric-Brown 1977; Hanski 1998, 1999), and has implications for climate change responses (Knowlton and Graham 2010). However, movement between populations or "functional connectivity" and the ability of an individual to cross a landscape depends on the interaction of landscape structure and species-specific behavior (With et al. 1999; Goodwin and Fahrig 2002; Knowlton and Graham 2010).

Because structural connectivity can be more easily measured and computed from aerial maps and GIS data layers, the number of studies analyzing landscape effects has increased sharply. Yet, the link between individual behavior and landscape structure is still missing in the majority of these studies and the real challenge for research is to understand species movement rates, habitat resistance, and sources and rates of mortality in different habitats during movement (Knowlton and Graham 2010). Supporting this need for more studies on movement behavior, small-scale movement properties are good mechanistic approximations of dispersal used for predicting population-level processes at greater scales with individual-based models (Nathan et al. 2002; Revilla et al. 2004).

One of the first experimental field studies testing movement behavior of amphibians showed that juveniles of three species varied in their response to forest and old-field matrix habitats (Rothermel and Semlitsch 2002). Two species, American Toads (*Anaxyrus americanus* (Holbrook, 1836)) and Spotted Salamanders (*Ambystoma maculatum* (Shaw, 1802)), moved significantly greater distances and survived better in forest versus old-field habitats in Missouri. However, the authors found that Smallmouth Salamanders (*Ambystoma texanum* (Matthes, 1855)) did not distinguish significantly between forest and field habitat. Furthermore, although the authors predicted no choice for American Toads, a well-known habitat generalist with a wide distribution, they found that small metamorphosing toads were highly selective, and reasoned that their small body size prevented them from entering and using old-field habitats in summer until they attained greater size as subadults or adults. A second study, conducted in the laboratory, showed that movement ability of Natterjack Toads (*Epidalea calamita* (Laurenti, 1768)) was strongly affected by land-cover substrates (Stevens et al. 2004). Vertical structure of substrates inhibited hopping movement (grass, field, forest), whereas substrates naturally selected, such as sand, actually promoted movement by increasing speed and net length of moves. Interestingly, cement promoted movement very similarly to sand. Furthermore, body size mediated some movement parameters. A more recent study has addressed the risk of water loss in agroecosystems by testing movements of juvenile Tiger Salamanders (*Ambystoma tigrinum* (Green, 1825)) in corn and soybean habitats compared with prairie and forest habitats (Cosentino et al. 2011). Water loss was greater in corn and prairie than in forest and soybean habitats, suggesting that resistance costs of dispersal are not uniformly high in all agricultural landscapes. Collectively, these studies begin to offer reliable and realistic empirical data by which to estimate landscape resistance, a huge leap beyond subjective relative estimates derived from "expert" opinion alone (e.g., Ray et al. 2002; Compton et al. 2007). Empirical studies of movement behavior on common landscape substrates are rare but vital to understanding functional connectivity in heterogeneous habitats (Knowlton and Graham 2010).

We chose to study the Southern Graycheek Salamander (*Plethodon metcalfi* Brimley, 1912), which is a member of the Jordan Salamander (*Plethodon jordani* Blatchley, 1901) complex (Petranka 1998) in the southern Appalachian Mountains. *Plethodon metcalfi* is a common, high-elevation, forest-dependent species with direct development and small home-range size. They are found almost exclusively in the leaf litter and under natural cover objects like rocks and logs during the day in mature, mesic forest, but move and feed at the surface on cool, moist nights (Petranka 1998). Although *Plethodon* salamanders are not known to have a specific migratory stage, dispersal is a necessary process for recolonization and range expansion as is true for all other vertebrates. Plethodontid salamanders are capable of homing up to 150 m when displaced (Madison 1969), and some species can readily colonize new habitats 55 m away (Marsh et al. 2004). In the southern Appalachians, *P. metcalfi* are increasingly subject to fragmentation and habitat alteration from roads and development (e.g., Price et al. 2011). The substrates we used in our experiments represent those common to natural (forest leaf litter) and anthropogenic (mown grass, bare soil, gravel roads, and asphalt roads) landscapes in the southern Appalachian Mountains.

The purpose of our study was to test whether natural and anthropogenic substrates encountered by salamanders during terrestrial movements in a fragmented landscape could alter their behavior. We hypothesized that substrates would differentially affect salamander behavior because of perceived structural differences in cover and potential for a refuge, physical microclimate factors such as moisture and temperature, or both. We recognized that each substrate under natural diel and seasonal conditions would covary with physical factors such as moisture and temperature. However, we tested salamanders under mild nighttime conditions, the normal time of surface movement, and applied moisture to substrates to minimize these inherent differences. By doing so, we believe that microclimate test conditions were near optimal for salamander movement and predicted that the majority of behavioral differences we measured would be primarily due to structure and cover or lack of cover, not temperature and moisture.

Materials and methods

Study sites and substrates

The study was conducted at the Highlands Biological Station (HBS) (35°3′16.3796″N, 83°11′24.729″W), located in the Nantahala National Forest in Macon County, North Carolina, USA. The HBS is located near a residential neighborhood, intersected with paved and gravel roads, mown fields and lawns, golf courses, and surrounded by fragmented mixed deciduous forest.

Five substrates (asphalt, gravel, grass, forest soil, forest leaf litter; Fig. 1) were chosen because they represent those commonly encountered during movement of salamanders in the region. Furthermore, these substrates allowed for comparison of movement in both natural and manmade habitat. With each substrate type we avoided slope bias by selecting relatively flat surfaces. Substrates used in trials were scouted

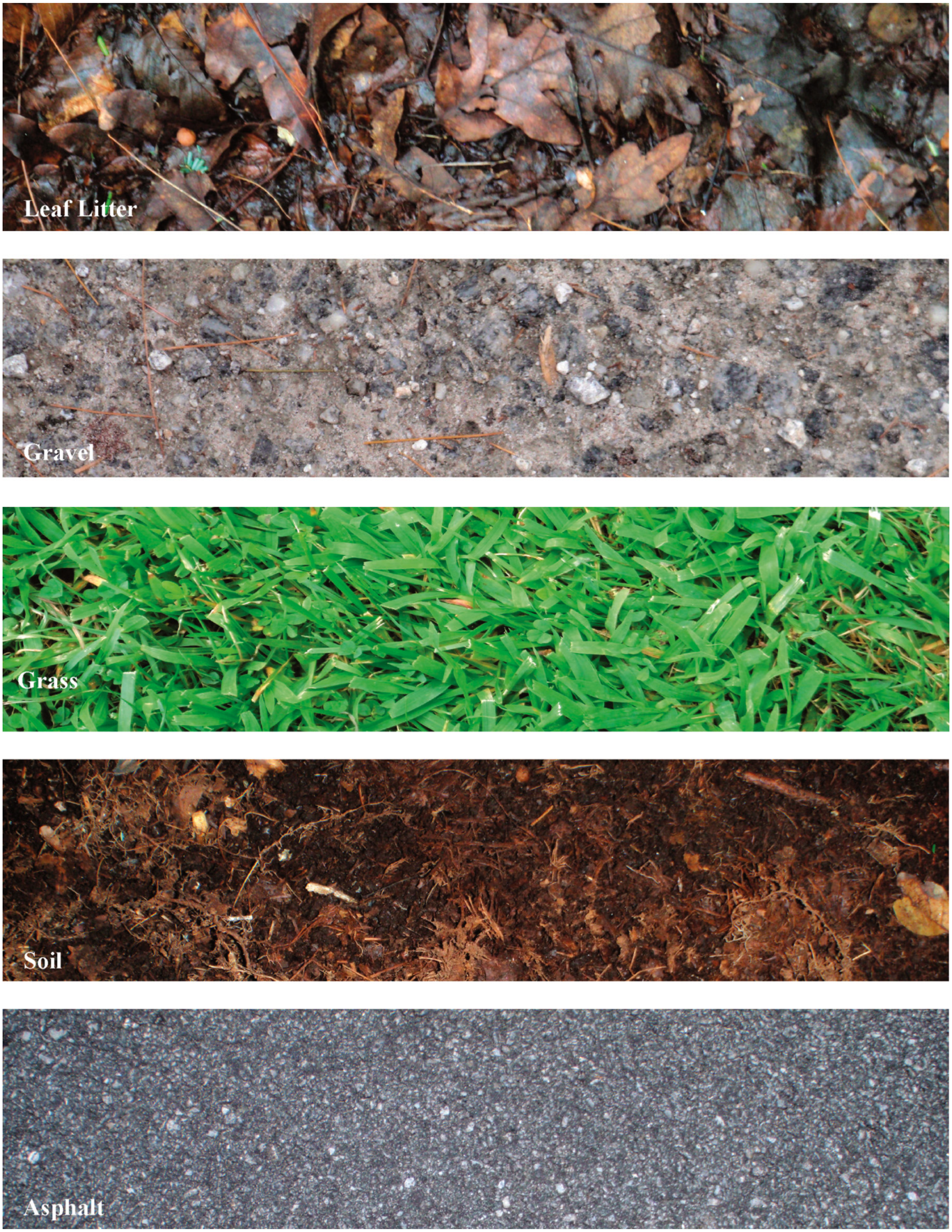


Fig. 1. Photographs of five treatment substrates (asphalt, forest leaf litter, grass, gravel, forest soil) used in behavioral observations and chosen to represent natural and anthropogenic substrates encountered during movement of salamanders in the region around Highlands, North Carolina, USA. Forest soil was the only substrate created by raking back leaf litter to expose the soil surface.

within and around HBS for uniformity and marked during daylight hours. The only substrate that we used that was not naturally present was the forest soil, so the leaf litter was raked back to expose the soil surface. No substrate location was used more than once.

Experimental trials were conducted at night, the normal time of salamander activity, on 4 days: 21, 22, 25, and 26 July 2011. Measurements during trials were recorded by five groups, each consisting of two observers, and each conducting a set of all five substrate treatments on each date to eliminate bias. The earliest trials began after dark at 21:10 EST and all trials were finished by approximately 24:00 EST.

Collection of salamanders

Plethodon metcalfi were collected from two locations. The first collection site was Yellow Mountain in Jackson County, North Carolina, USA, located approximately 12 km north of HBS, and the second collection site was on HBS property within 500 m of where trials were conducted. *Plethodon metcalfi* were collected ($n = 60$) during the day on 21 and 22 July 2011 for trials of all substrate treatments each evening. *Plethodon metcalfi* were collected ($n = 70$) on the HBS property on the evening of 23 July for sets of trials of all substrate treatments on 25 and 26 July 2011. *Plethodon metcalfi* collected were primarily adults or larger juveniles. Salamanders were stored in two large vented plastic storage containers (25 cm deep × 35 cm wide × 60 cm long) with natural moist leaf litter and bark at 20 °C in the dark until trials began. Substrate treatments were distributed equally among individuals between the two collection locations and four dates to eliminate any systematic bias. After trials, all salamanders were returned to their sites of collection.

Experimental trials

The order of treatments for each night and each replicate trial was randomly determined. Individual salamanders were haphazardly selected from a storage container and then were randomly assigned to each treatment. Each trial was performed within a 150 cm diameter circular arena of substrate delineated by a polypropylene rope (0.6 cm diameter) placed on the substrate surface. The substrate surface was wetted using a spray bottle of tap water just before each trial to eliminate differences in moisture holding capacity of substrate types, except on one night (25 July) when it had just finished raining before trials were started. Before each trial began, fluorescent powder was applied to the posterior portion of the salamander's body and tail. Fluorescent powder (Radiant Color, Richmond, California, USA) has no harmful effects on salamanders (Rittenhouse et al. 2006), and enabled us to visualize movement paths precisely. The test salamander was placed in the center of the arena under a steel can (7 cm diameter, 4.7 cm height) and allowed to rest after handling and acclimate to the substrate. After 2 min, the can was lifted slowly from outside the arena by an attached string and wooden handle. We recorded time to first movement that was designated as the latency period. After release, trials were observed using only ultraviolet or red lights. Salamanders were never touched or prodded during a trial. Once the trial ended, the salamander was collected and returned to its storage container. Most trials ended when the salamander reached the outer perimeter of the rope circle and stopped, but in approximately 10 cases when the salamander continued moving and crossed the rope, we continued to follow its path a few centimetres farther, just outside the circle. Its stopping location was marked with a wire flag. The time required for the salamander to move only to the perimeter of the rope was recorded to calculate velocity. After the trial ended, measurements were taken of the salamander's displacement (net distance = center of circle to edge of rope or stopping point just outside the circle) and total distance traveled. Total distance traveled was determined by placing a string on the salamander's exact path of fluorescent powder viewed under an ultraviolet light. Total length of the string was then measured with a tape measure to the nearest 0.5 cm. These two measurements were used to calculate the sinuosity of the path (net distance/total distance). Time spent moving and net distance measurements were used to calculate the salamander's velocity to the perimeter of the rope or stopping point (cm/s). Locations for trials were usually 1–5 m from any habitat edges. Each salamander was measured for body mass (g) and snouts–vent length (mm) after the trial was finished and individuals were only tested once. To determine the influence of the observer on salamander behavior, a compass was used to determine the salamander's direction of displacement and bearing toward or away from the observer. Temperature of substrates was recorded using an infrared thermometer at three points within the circular arena.

Each salamander and location of the trial was unique and constituted our unit of analysis. All correlations were performed with Excel using Pearson's simple correlations. Analyses of variance (ANOVA) and covariance (ANCOVA) were performed with SAS using PROC GLM (SAS Institute Inc., Cary, North Carolina, USA). Tukey's pairwise post hoc tests were used on all tests indicating a significant main effect at $P < 0.05$.

Results

We tested a total of 109 salamanders on five substrate types (Fig. 1). Body mass of the salamanders averaged 3.09 ± 0.090 g (mean ± SE) and snout–vent length averaged 55.6 ± 0.65 mm (mean ± SE). There were no differences in the body mass ($F_{[4,99]} = 0.40$, $P = 0.8058$) or snout–vent length ($F_{[4,99]} = 0.29$, $P = 0.8843$) of salamanders tested among the five substrate treatments. There was no difference in the three response variables (latency, sinuosity, velocity) among the four test dates (all $P > 0.15$). There was no difference in latency or velocity among observer groups (all $P > 0.19$), but sinuosity was different among observer groups ($F_{[4,88]} = 3.89$, $P = 0.0059$). It appeared that one group was consistently lower ($P < 0.05$) in their calculation of sinuosity than the other four groups, but did not confound results. Temperature varied significantly among the five substrates ($F_{[4,100]} = 18.56$, $P < 0.0001$) from a mean of 14.8 °C on asphalt to a mean of 12.2 °C on grass substrate. The asphalt and gravel substrates were consistently warmer ($P < 0.05$) than grass, soil, or leaf litter but only by 2–3 °C. Furthermore, direction of movement of salamanders was not correlated with ($P > 0.05$) and therefore not biased by potential homing to sites of collection or by observer position.

Latency period of the salamanders was significantly different among substrate treatments ($F_{[4,91]} = 3.13$, $P = 0.0185$;

Fig. 2. Response variables (*a*) latency, (*b*) sinuosity, and (*c*) velocity of Southern Graycheek Salamanders (*Plethodon metcalfi*) plotted by the five treatment substrates (asphalt, forest leaf litter, grass, gravel, forest soil). Bars represent means + 1 SE.

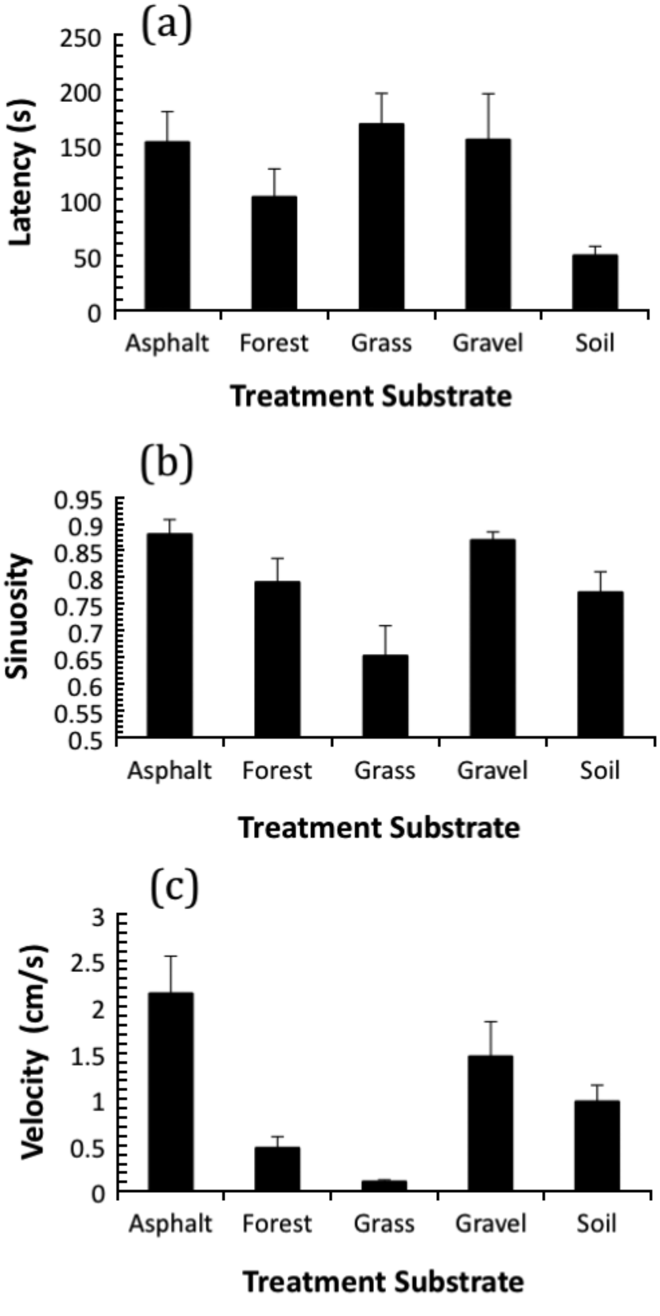


Fig. 2*a*). It was highest on grass substrate and significantly lower only on the soil substrate ($P < 0.05$). Sinuosity of the movement path of salamanders was significantly different among substrate treatments ($F_{[4,88]} = 5.29$, $P = 0.0007$; Fig. 2*b*). Sinuosity of the path was lowest and contained more turns in grass but was significantly straighter ($P < 0.05$) only on the gravel and asphalt substrates. Velocity of the salamanders was significantly different among substrate treatments ($F_{[4,81]} = 8.49$, $P < 0.0001$; Fig. 2*c*). Velocity was highest on asphalt substrate but not different from gravel substrate ($P > 0.05$). Velocity was higher on asphalt than on grass, forest, or soil ($P < 0.05$), and velocity was higher on gravel than on grass substrate ($P < 0.05$). Analysis of covariance using substrate temperature as a covariate neither indicate any contribution of temperature to salamander responses (all $P > 0.574$) nor improve fit of the simple analysis of variance models.

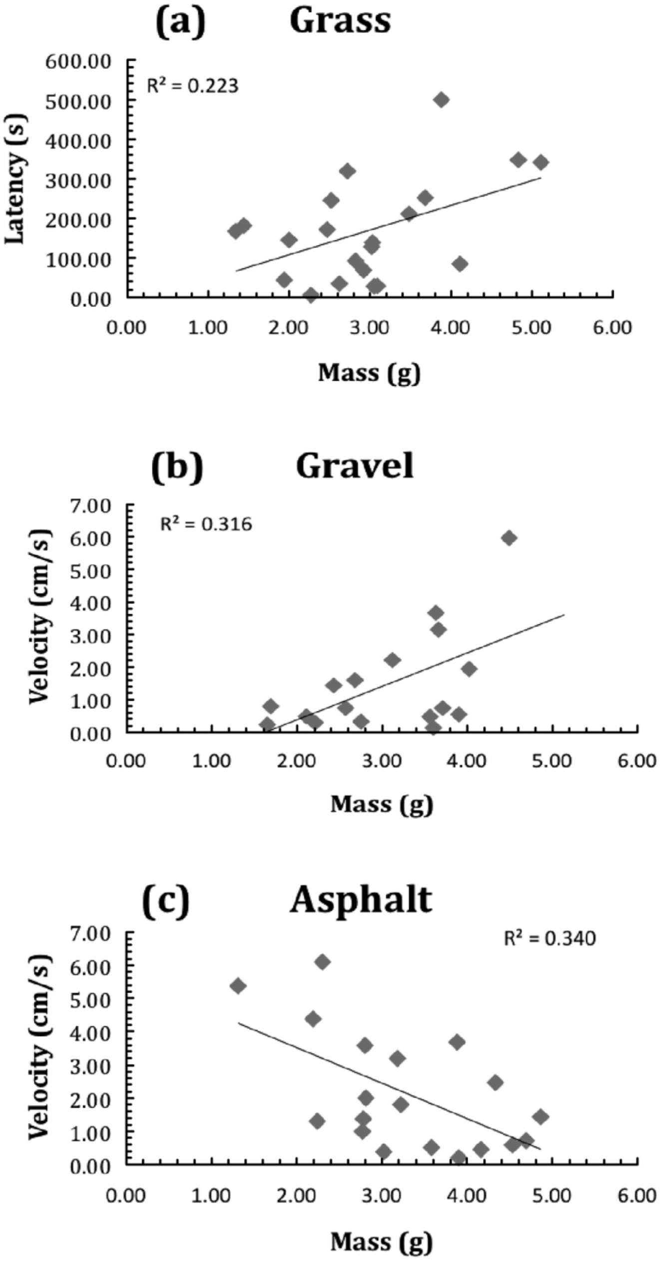
Combining all substrate treatments, none of the response variables (latency, sinuosity, or velocity of salamanders) were correlated with salamander mass ($r^2 = 0.004$, 0.014, and 0.001, respectively). Furthermore, analysis of covariance using body mass as a covariate neither reveal any significant contribution of mass to salamander response variables (all $P > 0.36$) nor improve fit of the simple analysis of variance models. However, within treatment substrates, salamander latency on grass substrate ($r^2 = 0.223$, $P < 0.05$) was positively correlated with salamander mass (Fig. 3*a*), but salamander velocity on gravel was positively and on asphalt substrate was negatively correlated with salamander mass ($r^2 = 0.316$, $P < 0.01$ and $r^2 = 0.340$, $P < 0.01$, respectively; Figs. 3*b*, 3*c*).

Discussion

The results of our experiment indicate that salamanders behave differently on natural and anthropogenic substrates, and we suggest that these behavioral differences could influence movement success in fragmented or altered landscapes. The asphalt and gravel substrates, representing the two major types of roads found in the region, had strong and consistent effects on salamander movement behavior. Salamanders initially paused longer but moved straighter to the nearest edge and faster compared with the other substrates. There was no difference between the two road substrates despite the gravel substrate being slightly cooler, by 1 °C, on average, and retaining more moisture. Our results show that when crossing a road, salamanders move quickly, perpendicular to the edge, and in a straight line off the road, which we suggest can minimize mortality. Although we do not know if the species we tested will readily cross gravel and paved roads by choice, roads appear to be partial barriers for a congeneric (Eastern Red-backed Salamander, *Plethodon cinereus* (Green, 1818)) reducing movement by 25%–75% (Gibbs 1998; deMaynadier and Hunter 2000; Marsh et al. 2005). We do occasionally see *P. metcalfi* on both road types, yet because of the high density of this and other species on the forest floor in the region (0.95–1.42/m^2 (95% CI) for the Red-legged Salamander (*Plethodon shermani* Stejneger, 1906); G. Connette and R. D. Semlitsch, unpublished data), it is actually striking that we do not see them on paved roads more often. Roads not only present a risk to crossing for woodland salamanders but also create unsuitable edge habitats that are drier and warmer for at least 20–35 m away from road edges (deGraaf and Yamasaki 2002; Marsh and Beckman 2004; Semlitsch et al. 2007). So, even if they successfully cross a road, unsuitable habitat adjacent to roads may increase mortality risk.

Our results also show that mown grass, although organic in composition, causes salamanders to pause for long periods, move in a sinuous pattern, and very slowly. Many of our test observations on grass were actually truncated because salamanders took longer than 15–20 min to reach the outer edge of the circular arena (approximately 75 cm). We suggest that their behavior reflects a response to both the structure of

Fig. 3. Correlations of the response of latency of Southern Gray-cheek Salamanders (*Plethodon metcalfi*) in relationship to salamander body mass for the treatment substrates (*a*) grass ($r^2 = 0.223$, $P < 0.05$), and the salamander response of velocity in relationship to salamander body mass for treatment substrates (*b*) gravel ($r^2 = 0.316$, $P < 0.05$) and (*c*) asphalt ($r^2 = 0.340$, $P < 0.01$).



grass and its moisture content. The grass was tall enough (4–6 cm) to provide cover to protect them from water loss and detection by predators. The grass was also cooler, by 2–3 °C at night, than all the other substrates and accumulated dew as the evening progressed, again providing protection from water loss and thermal stress. We speculate that the salamanders might sense they are safe and protected when in grass at night. However, grass represented an anthropogenic substrate associated largely with housing developments, golf courses, and possibly grazing or pasturelands with no tree canopy. If salamanders remained in the grass after sunrise, the grass would quickly heat up and dry out, leaving the salamander exposed to a very high risk of heat or desiccation mortality. So, although initially the salamanders may not perceive grass as a danger or they may even perceive it as favorable habitat, it may in fact represent an ecological trap. Forest leaf litter and soil represented a neutral or control substrates and the most natural substrates used by all woodland salamanders occurring in the region. Salamander behavioral responses to leaf litter and soil were intermediate in latency, sinuosity, and velocity to grass, asphalt, and gravel. However, salamanders on soil tended to move faster and had a shorter latency than salamanders on forest leaf litter. This may be because the soil had all the leaf litter removed, leaving little or no structure created by the leaves. The structure created by the leaves and twigs often provided places where salamanders climbed, paused, and appeared to be surveying the surroundings.

Although body size has been found to affect movement behavior of amphibians (e.g., Marsh et al. 2004; Stevens et al. 2004), we found little or no evidence that the body size of salamanders consistently affected latency, sinuosity, or velocity. We deliberately used salamanders that represented the full range of sizes found in natural populations, from juveniles near maturity to older adults (1.3–5.0 g), to test size effects. However, our results do show a possible interaction between particular behaviors on some substrates and salamander body mass. We found that velocity increased with size on gravel but decreased with size on asphalt, and that latency increased with body mass on grass. Although we can only speculate on what these relationships mean, it is possible that larger individuals perceive less risk of desiccation than small individuals on substrates like asphalt where the temperature is higher and moisture availability is lower. Smaller individuals may perceive less risk on gravel because of the presence of some moisture and slightly lower temperature relative to asphalt. Gravel size on our roads was not an issue for the size of salamanders that we used (Fig. 1), but larger gravel could impede smaller individuals or species. Variation in latency is even more difficult to interpret, but we suggest that remaining stationary for longer periods might indicate individuals perceive less risk, at least in grass. It is possible that salamanders assessed risk based largely on substrate composition and structure rather than moisture or temperature since we purposely wetted substrates before testing individuals and the analysis of covariance with temperature explained almost no variance in responses. Alternatively, salamanders could be responding to potential danger; movement studies of small metamorphosing *A. maculatum* showed less movement in the presence of scent from a known snake predator (Ring-necked Snake, *Diadophis punctatus* (L., 1766); S. Pittman and R. D. Semlitsch, unpublished data).

Although there is great interest in predicting animal movement in heterogeneous landscapes because of its functional role in population persistence and metapopulation dynamics, the few studies that have emerged suggest that caution and more research are necessary before making broad-scale generalizations about resistance of matrix habitat. Our study supports this concern. Although our experiment revealed some interesting and consistent differences in salamander behavior on natural and anthropogenic substrates, there is difficulty in accurately scaling up microbehavioral parameters to predict larger processes and associated risk. First, although roads have been reported to have negative effects on movement because of habitat fragmentation and creation of barriers, *P. metcalfi* exhibits compensatory behavior on both gravel and asphalt roads by moving quickly in a straight line off the substrate. Similar positive compensatory behavior has been found previously in another large terrestrial salamander, the Ensatina Salamander (*Ensatina eschscholtzii* Gray, 1850), in Oregon where its velocity increased when exposed to bare soil compared with natural litter substrates (Rosenberg et al. 1998). Similar findings in other taxa support the generalization that movement rates likely increase with severity of the habitat (Knowlton and Graham 2010). The opposite response was found for grass substrates in our experiments where salamanders slowed movement and remained stationary for long periods. This could be a significant danger if mown grass creates an ecological trap and leads to high mortality. Although we do not have evidence that grass is an ecological trap, we speculate that some types of land development with large areas of grass (e.g., housing development) along forest edges could inflict high mortality on salamanders, reducing population sizes and acting as strong barriers to movement, possibly greater than small forest roads. More evidence from direct monitoring of individual movements and survival across different seasons in these types of anthropogenic habitats is necessary to test this hypothesis. Furthermore, individual-based models that are parameterized with substrate-specific behavioral rules, movement rates, and probability of survival could be used to model landscape resistance. Output from such simulations could be especially critical for guiding development within protected national forests in the United States where the number of housing units has increased from 335 000 to 1 278 000 between 1940 and 2000 (Radeloff et al. 2011). Thus, we argue that understanding species-specific movement behavior, the probability of crossing habitat boundaries such as roads, and the subsequent risk of mortality among different natural and anthropogenic habitat types are necessary to develop predictive landscape models and for effective management and conservation of salamanders.

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