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Movement in the matrix: substrates and distance-to-forest edge affect postmetamorphic movements of a forest amphibian

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Abstract. Population persistence often depends on functional connectivity for animals that transit multiple vegetation types to acquire resources, particularly for dispersers navigating a landscape matrix fragmented by agriculture, forestry, or urbanization. For many pool-breeding amphibians, population viability depends on the ability of juveniles to locate and reach suitable habitat in the terrestrial matrix. Thus, identifying the scale and orientation of movements is necessary to predict the consequences of landscape configuration for populations. We conducted three experiments to evaluate if different vegetation types alter the behavior of post-metamorphic wood frogs (*Lithobates sylvaticus*). We measured the: (1) fine-scale movement (velocity, latency, path length, net displacement, path tortuosity, and orientation) of individuals ($n = 150$) released on five substrates (asphalt, corn, forest leaf litter, hay, lawn); (2) directionality of frogs ($n = 168$) released at different distances from forest in two open-cover types (lawns, hayfields); and (3) willingness of frogs ($n = 240$) to enter three land-cover types (asphalt, lawn, forest) when released within artificial refugia islands at different distances from forest. Using fluorescent powder, we mapped 318 movement paths and performance differed. Frogs demonstrated straighter paths, and greater net movements, path lengths, and velocities through treatments with lower structural complexity (asphalt > lawn > corn > forest leaf litter > hay). Frogs also exhibited forest-oriented directionality in asphalt, lawn, and corn but random orientation in forest control and hay. The willingness of individuals to leave a refugia island was lowest on asphalt (12% of released frogs), moderate on lawn (40%), and very high in forest (90%). Overall, results indicate that the quality of nonforest matrix may influence the ability of frogs to traverse open cover and orient toward forest from distances of ≥ 40 –55 m. Thus, it is inaccurate to assume movement performance is uniform across all open-matrix types, an important distinction because many landscape-population models use expert-based values that are a one-size-fits-all measure for open cover. Our study provides field-based, mechanistic approximations of juvenile movement that can be useful for predicting how matrix composition and configuration might be managed to maintain or restore functional connectivity.

Key words: amphibian; dispersal; edge permeability; functional connectivity; habitat fragmentation; habitat resistance; landscape matrix; movement behavior; orientation; sinuosity; substrate; wood frog (*Lithobates sylvaticus*).

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INTRODUCTION

Conservation strategies for many species use the patch-matrix model of landscapes (Forman 1995) with the goal of maintaining patches of

preferred habitat embedded in a matrix that allows some degree of connectivity among patches (Driscoll et al. 2013). Operationally, practitioners often focus on conserving patches but have little information on matrix quality; thus,

they can only assume that the matrix is singularly inhospitable for even temporary settlement and that the size and spatial arrangement of the surrounding matrix will allow animals to access habitat patches (Kupfer et al. 2006, Prevedello and Vieira 2010, Janin et al. 2012a). In reality, there may be a continuum of matrix conditions that vary as filters or conduits to movement, and the quality of these cover types may influence the probability of an animal entering the matrix, the efficiency of movement, and ultimate dispersal success (Kuefler et al. 2010, Cline and Hunter 2014). However, quantifying this variation in matrix quality remains a scientific and management challenge, in part because researchers need frameworks that integrate behavioral experiments with landscape-scale studies. The underpinning assumption is that successful movement depends on the characteristics of the matrix and how this interacts with species-specific behavior (Bélisle 2005, Haynes and Cronin 2006, Burgess et al. 2012). Using this lens of behavioral landscape ecology, it then becomes possible to identify: (1) the probability of an animal entering the matrix (i.e., “willingness to enter,” e.g., Popescu and Hunter 2011, Zeller et al. 2012); and (2) its subsequent (finer-scale) movement performance and orientation within each matrix type. Many modeling studies rely on expert-derived values to simulate connectivity (e.g., Hudgens et al. 2012), but these may be insufficient for adequately predicting the consequences of landscape configuration for population persistence.

It is widely understood that population viability is maintained by dispersal among breeding sites (Semlitsch 2008); thus, the ongoing conversion of natural ecosystems to human-dominated land cover (Desrochers et al. 2011) amplifies the need to consider diverse cover types that may be permeable to dispersal movements. Studies suggest that matrix type can exert a strong influence on species movements. For example, sharp edges between habitat patches and matrix may decrease dispersal (i.e., a “fence” effect; Schtickzelle and Baguette 2003, Nams 2011), due to the perceived risk of predation upon entering an open-canopy cover type. However, the risk of predation may be mitigated if individuals move rapidly once edges are crossed. While a number of studies have quantified the willingness of forest-dwelling species to enter open vegetation during dispersal

(e.g., McDonough and Paton 2006, Popescu and Hunter 2011, Cline and Hunter 2014), much remains unknown about the mechanisms by which the matrix (directly or indirectly) drives the distribution of patch-dependent species in fragmented landscapes (Driscoll et al. 2013).

Forest-dwelling amphibians are ideal taxa for this research because their movements occur at tractable scales (typically <100 m to 1–2 km although juvenile movements may be larger; Semlitsch 2008) and because many species have demonstrated sensitivity to habitat loss and fragmentation (deMaynadier and Hunter 1998). Further, many species rely on aquatic and terrestrial habitat connectivity because juveniles typically emerge into the terrestrial environment from their natal pool following metamorphosis; some will emigrate to a new breeding pool (dispersal) while others return to breed in their natal pool (philopatry; Semlitsch 2008, Clobert et al. 2009). Pittman et al. (2014) propose a unifying paradigm of juvenile amphibian movement in which dispersal is a multiphase process during which individuals adjust movement and habitat responsiveness based on internal physiological state and environmental factors. Initially, juveniles are in an “away” mode to move from the pool edge, and they are probably relatively unresponsive to external cues such as microclimate or habitat structure. As juveniles become more responsive to habitat features, they enter a “directed” or ranging mode (Dingle 1996, Barraquand and Benhamou 2008), and they are likely to exhibit exploratory behavior at large spatial scales shaped by their ability to evaluate potential habitat from a distance (Bartoń et al. 2009). Finally, individuals enter a “settlement” mode; searching for a suitable refuge, they likely respond to habitat features at very close range (Patrick et al. 2008). We hypothesize that juveniles are most likely to cross boundaries and enter open-canopy vegetation types during the exploratory, directed movement phase, since they may orient to landscape features at scales greater than their very local or immediate range.

Prior amphibian dispersal studies in agricultural or urbanizing landscapes have focused on individual orientation (Vos et al. 2007, Pittman and Semlitsch 2013), resistance of the matrix to gene flow (Van Buskirk 2012), or small-scale locomotor ability on different substrates without

regard to landscape setting or environmental heterogeneity (e.g., Baughman and Todd 2007, Semlitsch et al. 2012). Researchers have estimated the permeability of different open-canopy cover types to juvenile movements (e.g., Cline and Hunter 2014), but none have paired these with measurements of fine-scale movement once matrix boundaries are crossed and in relation to landscape configuration (e.g., orientation to the nearest forest edge).

Study species and objectives

Our goal was to test whether different substrates and open-vegetation cover typically found in fragmented forest landscapes alter the behavior of juvenile amphibians during postmetamorphic movements. For many species of pool-breeding amphibian, typical seasonal movements range from less than 100 m to 1–2 km. While conventional notions of landscapes in ecology may be orders of magnitude greater, we use the word “landscape” to invoke environmental heterogeneity rather than a particular scale. To accomplish this, we studied the wood frog (*Lithobates sylvaticus*) due to its widespread distribution in North America and its dependence on closed-canopy forest. This species avoids proximity to forest edges (deMaynadier and Hunter 1998, Semlitsch et al. 2009) and is highly sensitive to forest removal (Cushman 2006). Dispersal success (i.e., juveniles surviving to breed in new sites) is estimated at 18–20% (Berven and Grudzien 1990), with mean net dispersal distances of 1140 ± 324 m for females and 1276 ± 435 m for males and maximum distances of 2530 m (Semlitsch and Bodie 2003). By contrast, movement estimates of postbreeding adults are an order of magnitude lower: 102–340 m (Baldwin et al. 2006) and >300 m (Vasconcelos and Calhoun 2004).

We conducted three experiments to measure: (1) fine-scale movements (velocity, latency, path length, net displacement, path tortuosity, and orientation) of individuals released on five substrates (asphalt, corn, forest leaf litter, hay, lawn); hereafter, *substrate experiment*; (2) movement outcomes and directionality of individuals when released at different distances from forested corners in two open-cover types (lawns, hayfields); hereafter, *distance-to-forest experiment*; and (3) willingness of juveniles to enter three land-cover types

(asphalt, lawn, forest control) when released within artificial refugia “islands” (comprising leaf litter, duff, and mitigated microclimate conditions, 1 m in diameter) located at different distances from forest edge; hereafter, *island experiment* (Fig. 1). We undertook these experiments to extend a prior study in which permeability to wood frogs was estimated in clearcut, open-canopy, and moderate-cover lawns, row crops, and hayfields (permeability: row crop < hayfield < clearcut < open lawn < moderate-cover lawn; Cline and Hunter 2014). In this study, we refine these population-level permeability estimates with detailed measurements of fine-scale movements by individuals, and an extended measure of the willingness of juveniles to cross boundaries between forest litter and asphalt substrate (i.e., an open-cover type previously untested for willingness to enter). Our generic prediction was that movement performance and orientation to nearest forest would differ among treatments due to structural differences in cover, refuge availability, and physical impediments to locomotion. In the next section, we establish the logical framework to link this generic prediction to specific predictions of frog movement within each cover type. We further explain how each treatment (predictor) serves as an ecological surrogate for structural differences that may influence thermoregulatory stress, predation risk, or the ability of individuals to locomote across different land cover during the postmetamorphic phase.

Predictive framework for postmetamorphic movements and orientation

Prior to our experiments, we hypothesized that five environmental factors (i.e., vegetation structure, microclimate, food, conspecifics, and predators) might influence observed juvenile movement performance. Amphibians have been shown to alter movement behavior in response to habitat extent (Rothermel and Semlitsch 2002), substrate (Baughman and Todd 2007, Semlitsch et al. 2012), vegetation structure (Stevens et al. 2004), physiological factors such as stress-hormone levels (Janin et al. 2012b), microclimate (Rittenhouse et al. 2008), and predation risk (Pittman et al. 2013). We speculated that frogs in our study were largely in a directed mode: individuals had already departed

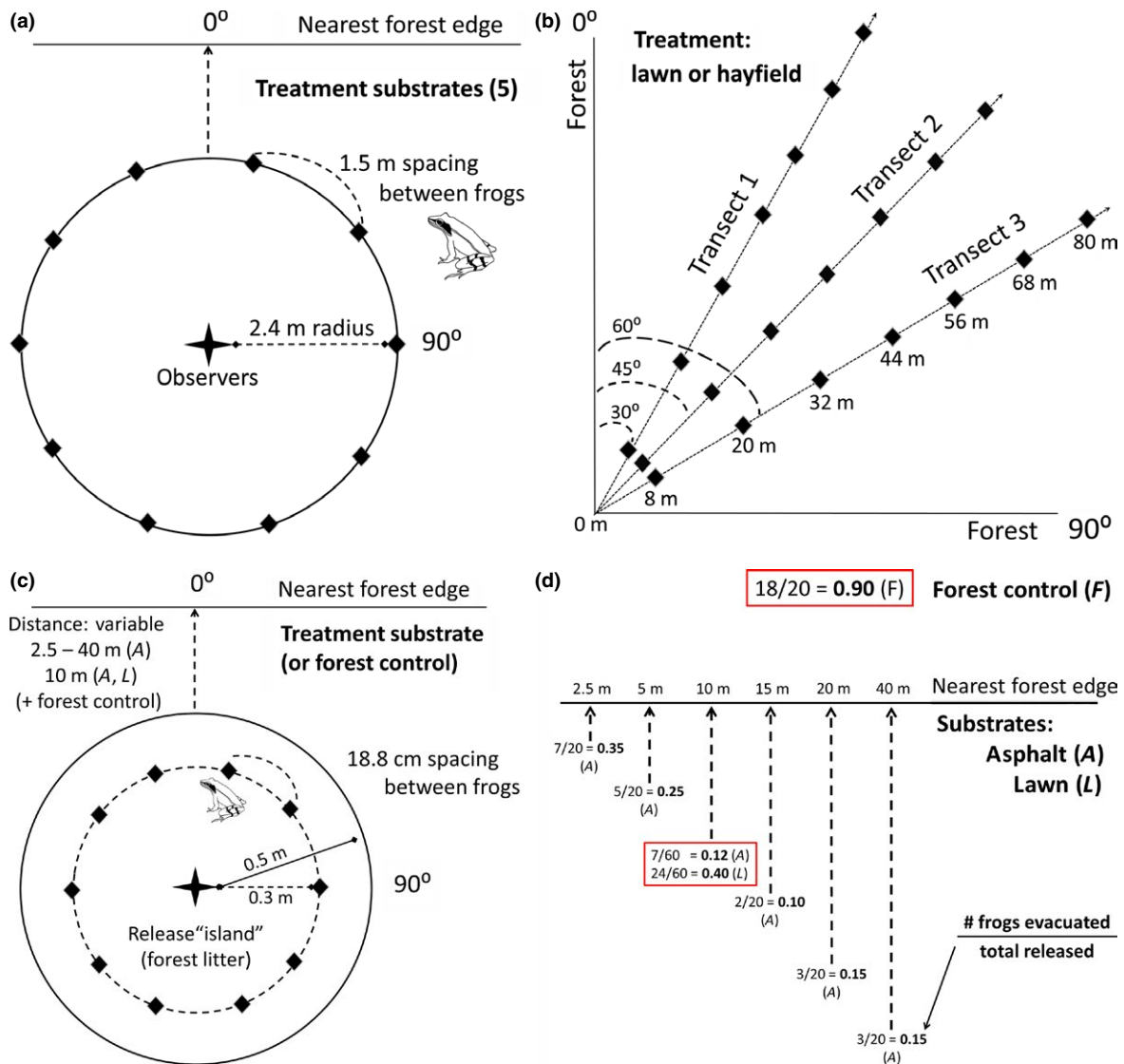


Fig. 1. Experimental design for evaluating the postmovement of juvenile *L. sylvaticus* released in: (a) five substrates (asphalt, corn, forest leaf litter, hay, lawn); (b) two open-cover vegetation types relative to distance from nearest forest edge; and (c) and (d) experimental forest-litter islands embedded in three treatments. Panel (a) depicts the substrate experiment design constituting a 2.4 m radius arena; diamonds indicate where ten frogs were simultaneously released and tracked (see embedded photo of remote release mechanism: inverted cup, fluorescent powder, and string). Panel (b) depicts the design for distance-to-forest experiment: three transects emanating (30°, 45°, and 60°, respectively) from an ~90° interface of two straight forest edges creating a corner framing lawn or hayfield. Along each 80 m, transect frogs were released at seven 12 m intervals. Panel (c) depicts the island-evacuation experiment design constituting a 1 m diameter arena (diamonds indicate where ten frogs were simultaneously released at 0.3 m radius), and panel (d) depicts the release scheme for each distance-to-forest class (in asphalt and lawn) and forest control. (Note: figure not to scale).

their natal pool and would exhibit exploratory movements in search of food, cover, ease of locomotion, and appropriate microclimate. We

assumed they were not yet in settlement mode, although we did not directly test individual motivational states.

For each of our five hypothesized environmental factors influencing juvenile movements, we established the logic of ecological surrogacy for each of our treatments (predictors). Thus, we assumed that intact control forest constituted preferred amphibian settling habitat, with ideal conditions (i.e., microclimate, vegetation structure, food availability, and presence or absence of conspecifics and predators) to maintain populations and facilitate juvenile movements. In stark contrast (and relative to the other four treatments), asphalt served as a surrogate for most extreme desiccation risk (microclimate), lowest physical impedance for movement (vegetation structure), lowest forage opportunity (food availability), lowest natural abundance of conspecifics, and moderate predation risk (for aerial rather than ground-dwelling predators). We established our lawn treatment as our most moderate surrogate across all five factors, with intermediate levels of desiccation and predation risk, physical impedance, food availability, and conspecifics. Corn presented only moderate physical impedance to movement (i.e., greater than asphalt, but much decreased relative to a thick hayfield), with moderate levels of food availability, decreased desiccation risk relative to open treatments; we further assumed that the ground predator community (e.g., garter snakes or small mammals) and consequent risk would be greater in this agricultural cover type than on asphalt or lawn. Finally, hay and corn represented the greatest physical impedance to movement due to vegetation structure, with relatively high levels of forage opportunity and decreased desiccation and predation risk due to greater structural integrity than more open treatments (asphalt and lawn).

In our substrate experiment, we predicted that velocity, path length, and net displacement of individual movements would be greater in substrates with less structural complexity (asphalt, lawn, perhaps corn) because these would directly impede locomotion less. We anticipated that path tortuosity (i.e., the sinuosity of movement) would be greater in substrates with more structural complexity (forest litter, hay, perhaps corn) and thus cool, moist microclimates or cover. We further predicted that the time to first movement following release (latency period) would be greater in substrates with more settling habitat (forest litter) and physical cover (hay, corn)

if frogs perceived these as a refuge from thermal stress or predators. By contrast, if we observe decreased latency in substrates with greater settling habitat, then frogs could be responding to perceived predation risk in open vegetation through a crouch response (i.e., suspense of motion) rather than flight. We expected that directionality would be random in forest (i.e., ample preferred habitat) and perhaps hay (where thick vegetation provides cover and may restrict the ability to see a distant forest), but that frogs would orient toward the nearest forest when the edge contrast was stark (lawn, asphalt, corn).

In the distance-to-forest experiment, we predicted that net displacement would be greater in lawns than hayfields, where thick vegetation may limit locomotion. Similarly, we predicted that frogs released far from the forest edge would not be able to detect the edge and thus would move relatively shorter distances. Finally, we expected that directionality in hayfields would be random at all but the shortest distances to forest edge (e.g., <10–15 m; Rothermel and Semlitsch 2002, Pittman and Semlitsch 2013) due to decreased visual range toward a subtler edge. By contrast, we predicted that juveniles in lawns would exhibit greater forest-oriented directionality overall; especially at greater distances (e.g., >35 m; Cline and Hunter 2014) due to wider visual range toward a stark edge.

In the island-evacuation experiment, we predicted that distance to forest would differentially affect frog behavior (i.e., willingness to enter and forest-targeted directionality) on asphalt, lawn, and in forest due to perceived differences in the ability of individuals to locate (and locomote to) the nearest edge when released from artificial islands. As with the distance-to-forest experiment, these differences may arise due to the ability of an individual to perceive the nearest edge via olfactory or visual cues. However, they may also arise due to a frog's assessment of whether it is better to seek temporary refuge in the island or venture into open cover where the potential for refuge (to avoid microclimate or predation risk) is limited. Thus, we predicted that frogs at greater distances from forest may delay departures due to greater expanses of open cover. The willingness of individuals to enter each treatment (or conversely, depart a refuge island) should be highest in the forest control, moderate in the lawn, and lowest

in the asphalt. Further, the willingness of frogs to enter asphalt and lawn should be greater close to forest edge (e.g., 2.5–20 m) and lower at longer distances. Finally, we predicted random orientation in the forest control, and forest-oriented directionality for frogs crossing asphalt and lawn <20 m from the edge (conversely, random orientation at distances >20 m).

METHODS

Study sites

Our study was conducted in Penobscot County, Maine, USA, on University of Maine lands (Demeritt Forest, Witter Farm, athletic fields, and parking lots) and the Penobscot Valley Country Club (44°51'41.87" N, 68°41'14.42" W). In the lower Penobscot River watershed (9974 km²), anthropogenic landscape fragmentation involves forestry, and to a lesser degree, residential development and agricultural practices (i.e., 78.3% of the landscape is forested, of which 20.4% has been recently cut; 3.9% is urban; 3.9% is agriculture, and the remainder comprises freshwater bodies).

We selected five treatments for the substrate experiment: asphalt, regularly cut lawn, forest leaf litter; a row crop (silage corn); and unmowed or recently mowed hay. We selected reasonably flat surfaces to avoid slope and aspect bias and used each location only once. Treatment patches averaged 3.44 ± 0.43 ha in size and were abutted by at least one forest edge ≥ 135 m long (with the exception of forest controls). Locations for all trials were 35–40 m from the nearest forest edge. For the distance-to-forest experiment, we selected locations where an $\sim 90^\circ$ interface of two straight forest edges (range of lengths: 135–295 m) created a corner framing a lawn ($n = 4$) or an uncut hayfield (2 sites, used twice; see *Experimental design* and Fig. 1b). We avoided slope bias (by using flat areas) and directional bias (by selecting corners facing different cardinal directions). For the island experiment, we selected trial locations ranging 2.5–40 m from the nearest forest edge in asphalt and lawn; treatment patches averaged 3.63 ± 0.96 ha in area; the nearest abutting forest edge was ≥ 253 m long. Our third treatment comprised forested control sites averaging 11.02 ± 0.26 ha. We selected reasonably flat surfaces for constructing forest-litter islands in all

three treatments (2 sites per treatment, used six times; see *Experimental design* and Fig. 1c).

Vegetation characteristics for all treatments were recorded in July–August 2013 for the substrate and distance-to-forest experiments and in July–August 2014 for the island experiment. Asphalt treatments consisted of 100% impervious surface with 0% canopy cover with forest along at least one edge and residential or campus land uses in other directions. Hayfields constituted a mixture of grasses and legumes, with average stem height of 1.1 m; mowing and baling occurred on 17 July but there were no differences in observed movements before or after that date (per analyses by trial date described below). Lawn treatments were exotic grasses mowed once per week to retain an average stem height of 10.3 ± 0.23 cm. Row crop treatments (hereafter *corn*) comprised feed corn sown in mid-May; inter-row distance averaged 0.95 ± 0.16 m, and the substrate underneath corn stalks consisted of bare tilled soil, interspersed with weeds. Forested controls (not recently harvested; natural regenerated with $\sim 75\%$ canopy cover) were characterized by mature mixed coniferous and deciduous forest. Ground cover was undisturbed and characterized by leaf litter interspersed with rocks, coarse woody debris, moss, and lichen, and a fairly consistent herb layer (hereafter *forest*).

Experimental design

Our substrate experiment was performed in a circular release scheme (Fig. 1a) constituting a 4.8 m diameter open area in which two observers were positioned centrally (back-to-back) to record the initial movement behavior and directionality of juveniles released at fixed-interval locations along the circle (i.e., 10 individuals spaced at 1.5 m intervals along the 15.1 m circumference). We released frogs simultaneously ~ 5 –8 min after sunset and tracked their movements using fluorescent powder and black light over the subsequent night ($n = 10$ frogs per trial in three replicates of five treatments, for a total of $n = 150$ tracked; Fig. 1A). Our substrate trials occurred on 15 dates during the height of postmetamorphic dispersal in July 2013 (replicate 1: 6–10 July; replicate 2: 13–17 July; replicate 3: 21–24 and 28 July). The substrate surface surrounding each release container was sprayed with well water just before each

trial to eliminate differences in moisture-holding capacity of the different substrates (Semlitsch et al. 2012). Thus, we intended to induce similar experimental conditions (i.e., microclimate) for the initial break of latency for each frog in each substrate.

Frog release containers consisted of an inverted opaque plastic container (SKS Bottle & Packaging, Inc., Watervliet, New York, USA; model 0610–08: 8.5 cm diameter × 6.6 cm height) with two ventilation holes, containing one of our 10 different color fluorescent powders. Powder tracking techniques have been widely applied in herpetological studies; these pigments are harmless to amphibian skin (Eggert 2002, Rittenhouse et al. 2006) and degrade when exposed to water and weather. The powders were mixed with mineral oil in a 40:1 ratio of powder to oil so that each frog would “self-coat” with the powder prior to release. We used an ECO series of powders, composed of a polymer free of carcinogens, formaldehyde, or other toxins (DayGlo Color Corp, Cleveland, Ohio, USA). Each release container was inverted on its lid and connected to string that extended to the center of the release circle and allowed observers to open all 10 containers remotely simultaneously and avoid influencing initial frog behavior.

Following a 15-min acclimation period (Turchin 1998), frogs were released and observers recorded time to first movement; after break of latency, frogs were left to traverse each substrate without interference for a period of 60–90 min (Semlitsch et al. 2012) and we observed them using only black lights (Inova X5 ultraviolet LED: 365–400 nm). We used an acclimation period to limit the risk that frog handling and transport to the study site influenced break of latency or initial movements. We further minimized observer effects on initial animal behavior using the following decision rule: if all frogs had departed release locations after the initial 60 min, two observers would approach and begin mapping two of the 10 frog paths; we would delay tracking up to an additional 30 min if latency was still unbroken for \geq two frogs to ensure a “natural” sequence of initial movements. The order of tracking was determined randomly for the first frog and observer; the second observer would begin at an interval of five release locations away (e.g., if frog three was selected at random,

the second observer would begin tracking frog eight). Researchers moved along each path slowly and quietly, extending a length of fluorescent string along the frog’s path as indicated by a trail of powder (until the frog was observed visually or path deteriorated). To safeguard against observers influencing frog behavior during mapping, we devised a decision rule for determining each frog’s final stopping location. Final locations were marked: (1) if a powder path deteriorated completely (and no frog was seen); or (2) if visual contact was attained on the marked frog. In the latter case, researchers marked the place where the frog was seen (if motionless) or where they could confidently state that the frog had not been spurred to flight due to observer activities. Each frog’s stopping location was marked with a wire flag, and the time required for it to move to its final location was recorded to calculate velocity. Our goal was to obtain five movement metrics for each frog after the break of latency: (1) net displacement (m), or the straight-line distance from start to end location; (2) total path length (m), or the length of string extended along the exact path; (3) velocity (cm/s), or the net distance/total time spent moving; (4) path tortuosity (= net displacement/total path length); and (5) directionality (azimuth from start to end location, °). We used directionality measures to derive each frog’s orientation relative to the nearest forest edge (except in the forested control, where an edge with open-cover was >125 m away and we assumed orientation would be random).

We conducted our distance-to-forest experiment using a landscape configuration of roughly a $\sim 90^\circ$ interface of two straight forest edges creating a corner framing a lawn or hayfield (Fig. 1b). At each lawn or hayfield site, we delineated three transects (30° , 45° , and 60° from one edge at each corner); each transect constituted an 80 m vector along which seven frogs were released at evenly spaced intervals (8, 20, 32, 44, 56, 68, and 80 m from corner) and subsequently tracked using powder and black light. Distance-to-forest trials occurred over four consecutive nights (31 July, 1–3 August 2013); we conducted simultaneous trials in paired lawn and hayfield sites on each date ($n = 21$ frogs per trial with two treatments and four replicates, for a total of $n = 168$ tracked). We used the same “powder” release containers described above. Following release (~ 5 – 8 min after sunset), all frogs

were permitted to transit at will until 2:00 AM, when observers would return to map frog paths using black light and obtain the following metrics: (1) net displacement (m); and (2) directionality from frog start to end location, which we later used to derive individual frog orientation relative to the nearest forest edge(s) at each site.

Our island experiment was performed in a circular release scheme (Fig. 1c), constituting a 1 m diameter “island” of forest leaf litter and duff constructed on asphalt at different distances (2.5–40 m) from the nearest forest edge and in which 10 frogs were released at 18.8 cm intervals. Forest-litter islands consisted of forest-floor substrate selected to emulate the conditions of a typical mixed coniferous-deciduous Acadian forest; temperature and relative humidity were recorded and the biomass of litter materials was kept constant among all islands and trials (~4.9 kg per island). We collected and weighed all leaf litter on the same day, storing this in slightly ventilated plastic bags in a climate-controlled lab to emulate ambient conditions until the onset of each trial. For each trial, we placed a 1-m diameter circular piece of cotton sheet on the pavement, and built each island on top of this to a 5–8 cm depth (layering leaf litter on top of forest duff,

and interspersing with rocks, a small amount of woody material, moss, ferns, and lichen). Island trials occurred over six nights (17, 18, 20, 21, 24, 25 July 2014; $n = 10$ frogs per island with four islands per trial and six replicates, for a total of $n = 240$ tracked across treatments; Fig. 1d). Islands were constructed 1–2 h before sunset on the day of each trial; we used the same “powder” release containers described above.

As with the substrate experiment, frogs were permitted a 15-min acclimation period, released ~10–12 min after sunset and permitted to roam until 3:00 AM. Then, observers returned to determine frog locations using black light and obtain the following metrics: (1) count of individuals that had evacuated islands (by inspecting the perimeter for tracks); (2) directionality from frog start to where the track crossed a circular line 3 m from the island perimeter; and (3) when possible, final location for frogs. We used prior experiments to inform our initial selection of two forest-island distances in our asphalt treatment, 10 and 40 m (see Table 1); i.e., we speculated that at 10 m most the frogs would leave the islands (i.e., evacuate toward forest) but at 40 m most would settle on the island, at least temporarily. Subsequently, we used an adaptive decision framework to test

Table 1. Movement metrics for frogs released and relocated in: (1) five substrate types across two sites and three trials per substrate (first six rows of data); and (2) distance-to-forest experiment in lawns and hayfields across six sites and four trials (final three rows). See Appendix A for the breakdown of distance-to-forest results by trial and transect.

1. Substrate	Number of released	Observed at path end	% paths >1 m	Total path length (m)†	Net displacement (m)†	Range path length (m)
				Mean ± SE	Mean ± SE	
Asphalt	30	26	100.0	39.50 ^A ± 3.81	26.10 ^A ± 2.69	5.57–106.35
Lawn	30	23	86.7	9.37 ^{AB} ± 1.87	5.12 ^{AB} ± 0.88	0.70–43.07
Forest	30	25	90.0	9.44 ^{AB} ± 2.11	5.33 ^{AB} ± 1.16	0.59–38.20
Corn	30	29	86.7	6.02 ^{AB} ± 1.25	3.60 ^{AB} ± 0.86	0.34–33.12
Hay	30	30	70.0	2.18 ^B ± 0.47	1.24 ^B ± 0.35	0.27–14.67
Total	150	133	88.0	13.30 ± 1.47	8.28 ± 0.97	0.27–106.35

2. Matrix type				Range net displacement (m)		
Lawn	84	62	34.5	...	2.18 ± 0.42‡	0.00–19.95
Hayfield	84	62	13.1	...	0.73 ± 0.20‡	0.00–14.88
Total	168	124	23.8	...	1.46 ± 0.24	0.00–19.95

† These metrics varied significantly by treatment (ANOVA; $F_{4, 145} = 38.06$; $P < 0.0001$); superscript letters indicate significant differences among groups after controlling for multiple comparisons (Tukey’s post hoc HSD at $\alpha \leq 0.01$).

‡ Net displacement varied significantly by treatment (ANOVA; $F_{1, 166} = 14.38$; $P < 0.0001$). Path length was not measured in distance-to-forest experiment.

ecologically relevant release distances at 2.5, 5, 10, 15, 20, and 40 m from nearest forest edge (Fig. 1d); we used asphalt as a benchmark since this was the only previously untested substrate in prior permeability studies (Cline and Hunter 2014). We determined that 10 m constituted a reasonable and ecologically relevant “threshold” distance for frog evacuations (Appendix D), and thus performed comparative island-release trials: (1) at 10 m from nearest forest edge in our two open treatments (asphalt, lawn); and (2) within forest controls with patch sizes of 11.62 and 19.81 ha; Fig. 1d). Before each trial, we inspected each leaf-litter island by black light to identify individuals that had temporarily settled, return them to forest, and corroborate our initial count of island departures (i.e., metric 1, above).

Juvenile amphibian rearing and release

Prior to our experiments, metamorph frogs were reared by collecting eggs from natural vernal pools, roadside ditches, and skidder ruts in Penobscot County, Maine, and larvae were raised in seminatural mesocosms (12 cattle tanks; 1500-L each) using methods described in Cline and Hunter (2014). At Gosner stages ≥ 42 , individuals were transferred into large plastic bins (200-L; moist leaf litter) for 1–2 days until metamorphosis, i.e., when tail has been fully resorbed and mouth is posterior to the eye (stage 47; Gosner 1960). This transfer limited stress from trying to leave rearing tanks before final metamorphosis. Across all experiments and trials, we never released metamorphs that maintained a tail stub; conversely, we never released frogs more than one day after metamorphosis was complete, thereby ensuring that all released animals were at the same development stage. Before each release, we measured (snout-vent length [SVL]: mm; weight: g), marked (one of 10 fluorescent powder colors in release cup), and randomly assigned frogs to one of our study sites and treatments. At the conclusion of trials, each frog was collected (if observed at path end) and returned to a forested location within 50–100 m of its natal pool.

Microclimate and habitat sampling

We collected temperature ($^{\circ}\text{C}$) and relative humidity (%) in our substrate and island experiment using iButton data loggers (Maxim,

Inc., Dallas Texas, USA). Within each substrate and cover type across all study site replicates, we measured temperature and humidity at 1-min intervals at: (1) ground level within each release circle; and (2) under thermal refugia located 15 m outside of the circle (i.e., 5–8 cm below coarse woody material in forest, under root masses in hay, etc.) to represent potential cover for a dispersing frog. For the island experiment, we measured temperature and humidity at 1-min intervals at: (1) ground level and under refugia within each island; (2) ground level within each treatment (forest, open pavement, lawn); and (3) for asphalt and lawn, at ground-level data loggers in the forest 1–2 m from the edge). We also collected microhabitat data for our substrate trials, characterizing vegetation in terms of ground cover, canopy closure (using densitometer), vegetation height, stem density, and inter-row distance (corn). We estimated ground cover as the percentage of 3×3 m plots classified as: leaf litter, moss/lichen, herbaceous, slash, bare soil, and rocks. Habitat characteristics of the hayfield, cornfield, and lawn were collected three times (July 12–13, 17–18, and 22–25) to account for vegetation growth.

Data analysis and statistical approach

Each frog was used once at one location, and thus constituted our experimental unit of analysis. In the descriptions that follow, the comparisons of movement path parameters includes the substrate, distance-to-forest, and island-evacuation experiments.

We compared the mean net displacement, latency, path tortuosity, path length, and velocity of movement paths among treatments using a one-way analysis of variance with treatment as the main effect (ANOVA, R package [*car*]; Fox and Weisberg 2011). We log transformed net displacement, latency, and velocity to achieve normality in our data distributions prior to each analysis; path tortuosity is presented on a scale of 0–1 (greater values indicate straighter paths). When ANOVA tests proved significant, we performed Tukey’s honestly significant differences (HSD) test to investigate pairwise dissimilarity between treatments while controlling for multiple comparisons. Correlations of frog size vs. movement responses were performed using Pearson’s simple correlations. To assess the number of frog

evacuations from forest-litter islands, our dependent variable was the proportion of frogs that evacuated out of the total released per treatment, distance class, island, and batch. We employed pairwise tests for proportions and Pearson's exact chi-square tests to estimate differences in proportions of recaptures at the individual and batch levels. We investigated possible additive effects of transect and frog start location in our distance-to-forest experiment using a two-way ANOVA.

For juvenile orientation, we used circular statistics to test if individuals moved toward the nearest forest edge. Orientations were standardized so that 0° represented the nearest forest edge(s) adjacent to treatments for all release sites and trials. We used Rayleigh's test of uniformity (general unimodal alternative with unknown mean direction and vector length) to determine whether orientation deviated significantly from a random distribution for each treatment, transect, or distance (Fisher 1993). To test if frog movement deviated significantly from a hypothesized mean angle (i.e., the bearing toward the nearest forest edge), we used a *V*-test and a Rayleigh test of uniformity with specified mean direction. We analyzed orientation propensity for animals that moved >0.1 m from initial release locations.

We assessed potential differences in the size of metamorphs (SVL) released among treatments, trial dates, transects, or frog start locations in each experiment separately using a one-way ANOVA. All ANOVAs and Tukey's HSD tests were conducted in Program R (version 2.15.3; R Development Core Team, 2013). Circular statistics were conducted in Program R (R packages [*CircStats*]: Jammalamadaka and SenGupta 2001, and [*circular*]: Lund and Agostinelli 2013), and Oriana (version 3: Kovach Computing Services; Anglesey, Wales, UK, 2014). Circular histograms were created using Rose.Net (version 0.10.0.0, Todd A. Thompson Software, 2012). All statistical tests were deemed significant at $P < 0.05$.

RESULTS

We quantified significant differences in the fine-scale movements of juvenile *L. sylvaticus* when released in or next to natural and anthropogenic substrates (asphalt, lawn, forest, corn, hay) and at varying distances from forest edges using six metrics (velocity, latency, path

length, net displacement, path tortuosity, and orientation).

The average SVL of juveniles in the substrate experiment was 16.59 ± 0.11 mm with no significant differences among treatments ($F_{4,145} = 0.51$, P -value = 0.74; ANOVA; Tukey's HSD), although metamorphs released later in the season (i.e., trial 3: 21–28 July 2013; 15.71 ± 0.17 mm) were significantly smaller than those released during trial one (6–10 July; 17.42 ± 0.19 mm) or two (13–17 July; 16.62 ± 0.14 mm; $F_{1,148} = 51.59$, P -value < 0.001). The overall average mass was 0.55 ± 0.02 g and tracked the same pattern observed for SVL. In the distance-to-forest experiment, the average SVL of juveniles was 14.11 ± 0.09 mm, with no differences among treatments (Welch two sample *t*-test: $t = -0.53$, $P = 0.31$) or trials ($F_{1,166} = 3.73$, $P = 0.06$). The average SVL of juveniles in the island experiment was 13.40 ± 0.13 mm, with some differences among treatments (asphalt: 13.64 ± 0.13 mm; forest: 13.20 ± 0.07 mm; lawn: 12.81 ± 0.08 mm; $F_{2,237} = 5.07$, $P = 0.007$) and trials (range: 12.48 ± 0.21 – 14.64 ± 0.14 mm; $F_{5,234} = 13.05$, $P < 0.01$), although averages remained fairly consistent by treatment. We released 150 metamorphs (30 on each substrate type) in the substrate experiment, mapped all their powder trails, and visually relocated 89% (Table 1). In the distance-to-forest experiment, we released 168 metamorphs (84 in each matrix type), mapped all their powder trails, and visually relocated 74% (Table 1 and Appendix A). For the island experiment, we released 240 metamorphs (160 on asphalt, 60 in lawn; 20 in control), mapped powder trails, determined movement status (i.e., departed vs. settled in island), and quantified directionality for evacuees (29% overall evacuation; Fig. 1c).

Substrate experiment

As hypothesized, fine-scale movement performance differed significantly among substrates: frogs demonstrated significantly greater net movements ($F_{4,145} = 38.06$, $P < 0.001$; Fig. 2a) and total path lengths ($F_{4,145} = 39.38$, $P < 0.0001$; Table 1), straighter paths (path tortuosity: $F_{4,145} = 3.23$, $P = 0.01$; Fig. 2c), and faster rates of movement (velocity: $F_{4,145} = 26.34$, $P < 0.001$; Fig. 2d) through treatments with the least structural complexity (overall trend: asphalt $>$ lawn $>$ corn $>$ forest $>$ hay; Fig. 2). We observed that frogs on pavement exhibited significantly straighter movement trajectories (0.76 ± 0.031 vs.

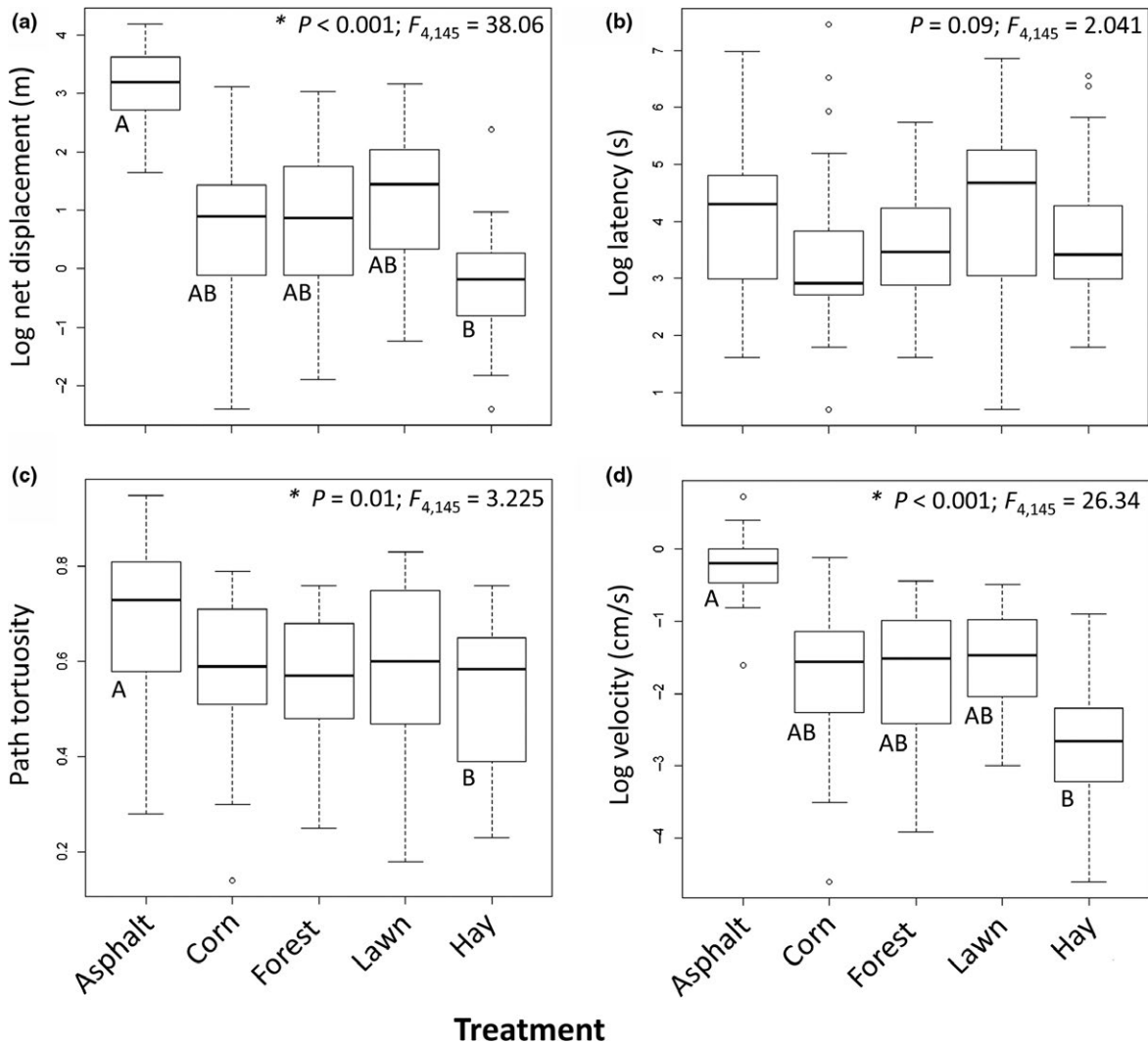


Fig. 2. The observed movement behavior of *L. sylvaticus* ($n = 150$) during releases in five types of substrate. Panels depict: (a) net distance traveled (m); (b) latency (i.e., the time from release to first movement in s); (c) path tortuosity (net distance/total path length); and (d) velocity (cm/s, based on total path length). All responses were log-transformed to achieve normality except tortuosity (scale 0–1: greater values indicate straighter paths). Reported significance values (global tests of treatment effect) are from analyses of variance (ANOVA); letters A and B indicate similarity or dissimilarity among substrates after controlling for multiple comparisons (Tukey's post hoc HSD $\alpha \leq 0.01$).

0.59 ± 0.14 ; $P = 0.007$), net displacements (26.10 ± 2.69 m vs. 1.24 ± 0.35 ; $P < 0.0001$), and velocity (0.76 ± 0.08 cm/s vs. 0.08 ± 0.01 cm/s; $P < 0.0001$, Fig. 2) than frogs on hay (Tukey's HSD test). We failed to detect significant differences in latency among substrates ($F_{4,145} = 2.04$, $P < 0.09$) due to high variability within treatments. Average latency was longest in the lawn and

asphalt (208 ± 50 s and 173 ± 51 s, respectively), intermediate in the corn (123 ± 61 s), and shortest in the hay and forest (94 ± 31 s and 61 ± 13 s; Fig. 2b). We found scant evidence of a correlation between frog size (weight or SVL) and any movement response; the strongest relationship was between latency and body length in lawn ($\rho = 391.05 \times 2.67$; $R^2 = 0.29$).

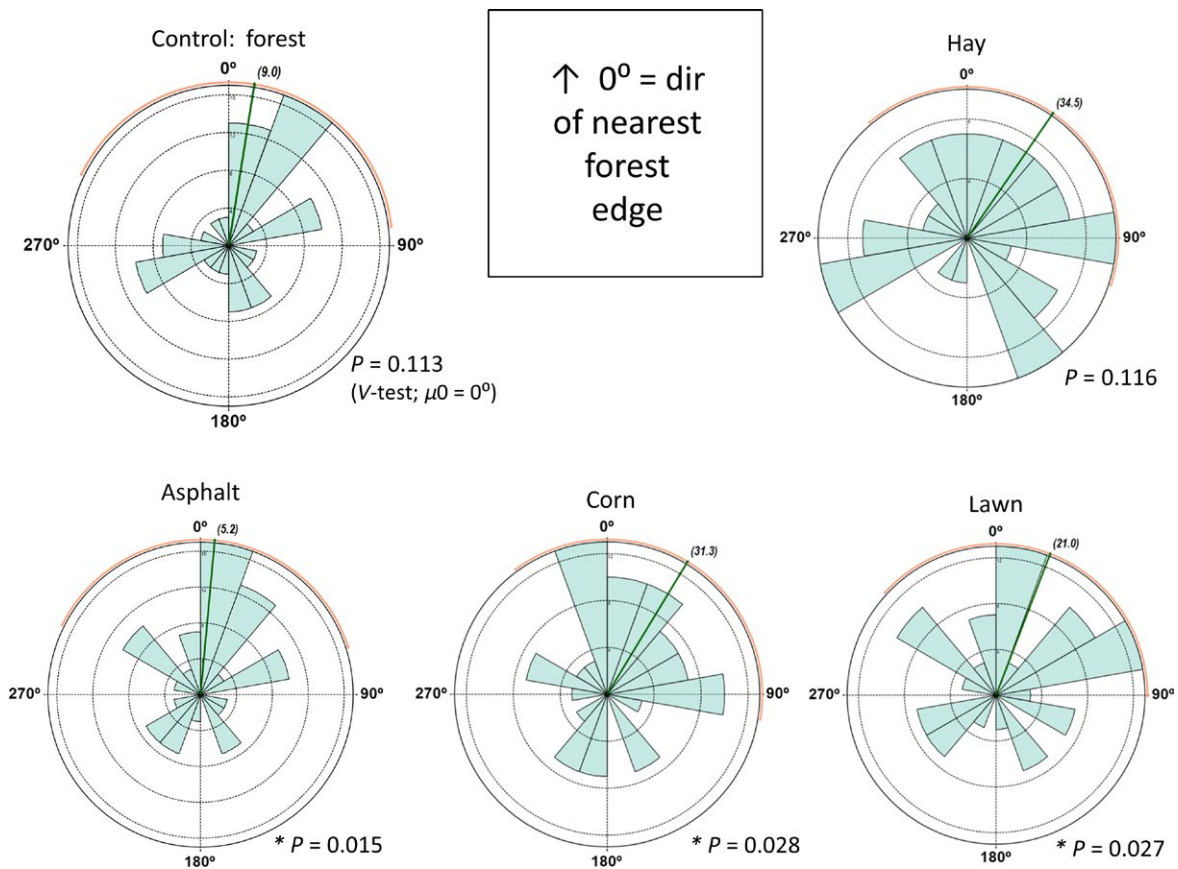


Fig. 3. Orientation of *L. sylvaticus* ($n = 150$) during experimental releases in five types of substrate. Orientations were standardized so that 0° represents the nearest forest edges (range: 35–40 m away). Bold solid lines indicate the mean direction of all frogs released in that substrate (mean direction in parentheses) and the length of the wedges represents the percentage of animals (5% increments) with orientations that fell within the designated 20° bin (standard deviations indicated by arcs external to each circular histogram). Asterisks indicate treatments in which frogs demonstrated statistically significant directionality toward the nearest forest edge(s) according to a Rayleigh test of uniformity with specified mean direction ($\mu_0 = 0^\circ$).

As predicted, we observed strong target-oriented movement toward the nearest forest edge in our most open cover types (asphalt > lawn > corn), corroborating our prediction (Fig. 3) (asphalt: Rayleigh's (R -test): $P = 0.09$; V -test: $P = 0.01$; lawn: R -test: $P = 0.12$; V -test: $P = 0.03$; corn: R -test: $P = 0.08$; V -test: $P = 0.03$). We observed random (nontarget-oriented) directionality in the control forest where there may be ample preferred settling habitat (R -test: $P = 0.47$; V -test: $P = 0.11$) as well as in the hay (R -test: $P = 0.56$; V -test: $P = 0.12$), supporting our hypothesis that greater structure may impede detection of forest at 40 m distances (Fig. 3).

During our substrate experiment, microclimates were relatively cool and moist con-

ditions at night in most substrates (e.g., 19° – 29°C and >45 – 99% relative humidity, Fig. 4), but reached potentially lethal daytime temperatures (35° and 31°C within refugia in the asphalt and lawn, respectively), after 14:00 h. Notably, during nocturnal trials (19:00–24:00 h; Fig. 4a), temperatures ranged widely in the forest ($\sim 19^\circ\text{C}$ Δ in temperature) and asphalt (almost 30°C Δ in temperature) and humidity fluctuated from 43% to 98% (Fig. 4a; also see inset for nocturnal period in Fig. 4b). In plausible frog refugia, the hay, corn, and forest treatments consistently demonstrated the most benign microclimates (15.5° – 26.8°C ; 60–99%; Fig. 4b).

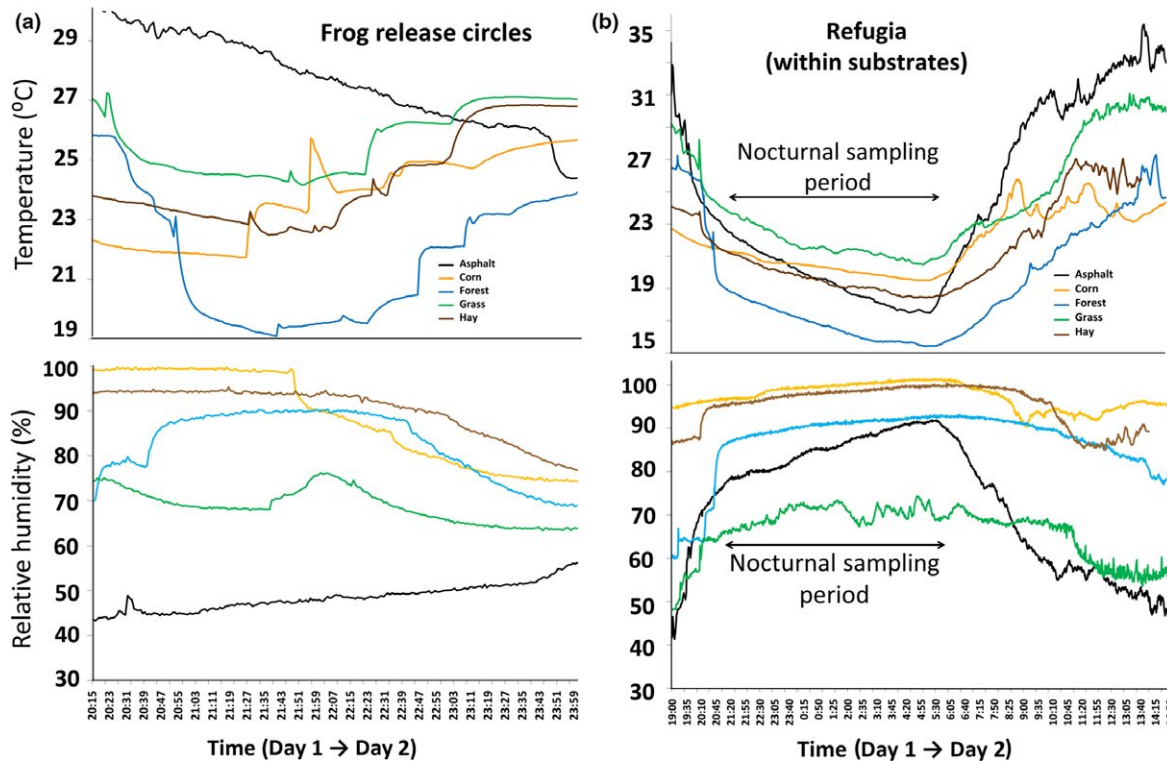


Fig. 4. Temperatures ($^{\circ}\text{C}$) and relative humidity (%) of five substrates averaged across 21 days (6–26 July) during substrate experiment. Panel (a) depicts microclimate for random surface locations within the 2.4 m radius release circle and panel (b) illustrates the microclimate at potential refugia within each substrate. Data are compiled from time of release through the conclusion of tracking on the subsequent day. Note the difference in scale for panels (a) and (b).

Distance-to-forest experiment

Frogs released in the distance-to-forest experiment exhibited differences in net displacement and directionality that could be attributed to treatment (lawn, hayfield) as well as direction and distance to the nearest forest edge (see Fig. 1b for transect design). First, patterns of net displacement corroborated the substrate experiment: average net displacement varied significantly ($F_{1, 166} = 14.38$, $P < 0.001$; Fig. 5a), with far greater movement in lawns (2.18 ± 0.42 m, comparable to 5.12 ± 0.88 m in substrate experiment) than hayfields (0.73 ± 0.20 m vs. 1.24 ± 0.35 m in substrate experiment). Net displacement ranged from 0–19.95 m and varied by treatment ($F_{1, 166} = 4.37$, $P = 0.04$), but not by transect (30° , 45° , 60° : $F_{2, 165} = 0.59$, $P = 0.56$; Appendix B). The combined effects of distance and direction to forest (i.e., transect and frog start distance) did not

significantly influence the scale of movement ($F_{8, 159} = 1.60$, $P = 0.13$), although there was a possible trend of increased displacement at greater distances (Appendix B).

As hypothesized, the orientation of juveniles toward the nearest forest edge differed by treatment and distance from the edge (Fig. 5 and Appendix C). On the lawn, frogs moved toward the forest from Transects 1 and 3 but not from the middle transect (T1: V -test: $P < 0.01$; T3: $P = 0.02$; Appendix C, Fig. 5a). By contrast, frogs exhibited random orientation on Transects 1 and 3 in the hayfield (T1: $P = 0.59$; T3: $P = 0.24$), and moderate directionality toward one of the forest edges (180° but not 270°) along the middle transect (T2: V -test[$\mu 0$] = 180° or 270° : $P = 0.03$ and 0.35 ; Table 2, Fig. 5b).

Distance to forest also influenced orientation (Appendix C), although patterns are less clear. Juveniles in the lawn demonstrated strong directionality toward forest at shorter release

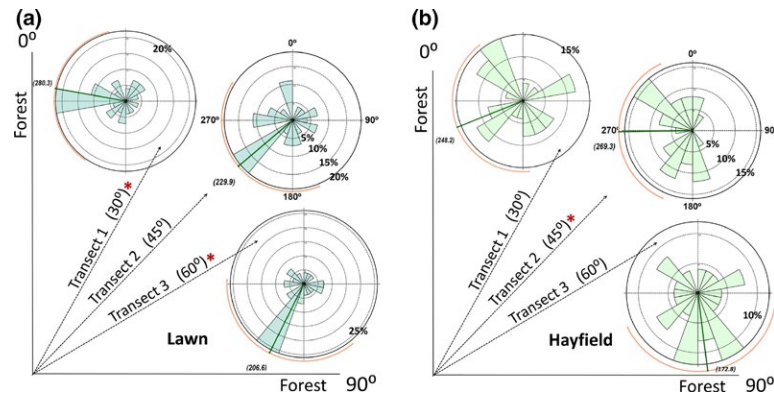


Fig. 5. Orientation of *L. sylvaticus* ($n = 168$) released along three transects emanating from forest corners (i.e., $\sim 90^\circ$ interface of contiguous forest and open-canopy vegetation) in: (a) lawns; (b) hayfields. Along each 80 m, transect frogs were released at seven 12 m intervals. Symbols, significance tests, and notation in the circular rose diagrams are parallel in structure to Figure 3 (see legend). The directions of nearest forest edge(s) are: (1) 270° for Transect 1; (2) equidistant to 180° and 270° for Transect 2; and (3) 180° for Transect 3.

distances (8–44 m) along Transects 1 and 3 (T1: V -test: $P = 0.03$; T3: V -test: $P = 0.05$; Table 2); as expected, this effect was decreased at more distant locations (56–80 m) along all three lawn transects (T1: V -test: $P = 0.067$; T2: V -test[$\mu 0$] = 180° or 270° : $P = 0.069$ and 0.84 ; T3: V -test: $P = 0.062$; Table 2, Appendix C, panel A). By contrast, hayfield frogs only exhibited strong target-oriented movement at the near stations on Transects 2 and 3 (T2: V -test[$\mu 0$] = 180° or 270° : $P = 0.02$ and 0.58 ; T3: V -test: $P = 0.01$, Table 2) and the 56–80 m distance classes on Transect 1 (T1: V -test: $P = 0.04$; Table 2, Appendix C, panel B).

Island-evacuation experiment

As predicted, juveniles released in artificial refuge islands embedded within open-cover types and a forest control exhibited behavioral differences that could be attributed to vegetation type (asphalt, lawn, forest; $\chi^2_2 = 65.97$, $P < 0.001$) and distance to the nearest forest edge (Figs 1d and 6). We observed the lowest proportion of evacuations (or greatest proportion of settling) from islands on asphalt (12% of released frogs departed island), moderate levels of evacuation in lawn (40%), and highest evacuation rates in forest control (90%; Fig. 6). Differences were also significant between all possible treatment comparisons (asphalt-forest: $\chi^2_1 = 59.65$, $P < 0.001$; asphalt-lawn: $\chi^2_1 = 15.08$, $P = 0.001$; lawn-forest: $\chi^2_1 = 19.23$, $P < 0.001$). There were no differences

in proportion of frog evacuations by batch (i.e., release night) or site in lawn ($\chi^2_2 = 1.25$, $P = 0.54$ and $\chi^2_1 = 0.82$, $P = 0.37$, respectively) and forest control ($\chi^2_1 = 2.22$, $P = 0.14$ for both batch and site effects). On asphalt, there were no differences in proportion of frogs evacuating islands by site ($\chi^2_2 = 0.18$, $P = 0.67$); however, we observed modest differences among nights ($\chi^2_3 = 10.56$, $P = 0.02$), likely attributed to higher proportion of recaptures on one outlier sampling occasion. As hypothesized, we quantified strong target-oriented movement toward the nearest forest at 10 m in lawn (Rayleigh's (R -test): $P = 0.03$; $n = 24$) and random orientation in forest control (R -test: $P = 0.06$; $n = 18$). Low numbers of frog evacuations at 10-m islands in asphalt ($n = 7$ of 60 frogs released) precluded rigorous statistical testing and inference for directionality (Fig. 7).

DISCUSSION

To predict functional connectivity for species in fragmented landscapes, many researchers reject the traditional views of the matrix as homogeneously inhospitable (Revilla et al. 2004, Eycott et al. 2012), and instead recognize that it may comprise a continuum of conditions that tend to filter or facilitate movement (Kuefler et al. 2010). If matrix vegetation influences the probability of entry and transit success, then

Table 2. Analysis of *L. sylvaticus* orientation in distance-to-forest experiment.

Treatment	Transect (°)	Distance class (m)	Sample size	Mean direction (°)	SD (°)	Vector magnitude	Consistency ratio (<i>r</i>)	Rayleigh's test (<i>R</i> -test) [†]	Test of uniformity: specified mean dir (<i>V</i> -test) [‡]
Lawn	30° (1)	All	27	280.3	66.3	8.94	0.33	0.050**	0.008**
	45° (2)	All	27	229.9	73.1	5.00	0.19	0.399	(1) 0.087; (2) 0.150
Hayfield	60° (3)	All	27	206.6	66.9	8.55	0.32	0.065*	0.0190**
	30° (1)	All	26	248.2	76.4	3.01	0.11	0.548	0.588
	45° (2)	All	25	269.3	66.0	8.42	0.34	0.057**	(1) 0.027**; (2) 0.349
	60° (3)	All	25	172.8	72.2	5.16	0.21	0.348	0.237
Lawn	1	Class 1	15	305.0	61.9	6.24	0.42	0.072*	0.031**
	1	Class 2	12	241.8	65.4	4.18	0.35	0.237	0.067*
	2	Class 1	16	255.2	76.8	1.61	0.10	0.854	(1) 0.301; (2) 0.518
	2	Class 2	11	218.9	66.4	3.61	0.33	0.312	(1) 0.069*; (2) 0.841
	3	1	15	199.4	67.3	4.65	0.31	0.240	0.055*
	3	2	12	214.9	66.3	3.97	0.33	0.274	0.062*
Hayfield	1	1	15	34.1	78.7	0.86	0.06	0.953	0.412
	1	2	11	242.3	61.2	4.72	0.43	0.132	0.037*
	2	1	15	254.0	63.5	5.78	0.39	0.107	(1) 0.024**; (2) 0.584
	2	2	10	297.4	66.7	3.23	0.32	0.362	(1) 0.268; (2) 0.193
	3	1	13	179.8	59.3	6.04	0.46	0.058**	0.008**
	3	2	12	34.3	77.2	1.11	0.09	0.906	0.664

Notes: The first six rows combine all replicates along entire transects (30°, 45°, and 60°). Distance classes comprise two categories of frog release locations along transects measured in meters from forest corner (Class 1: 8, 20, 32, and 44 m; Class 2: 56, 68, and 80 m). Circular statistics were used to test if frogs significantly oriented movements toward the bearing of the nearest forest edge(s): Transect 1: 270°; Transect 2: equidistant to 180° and 270°; Transect 3: 180°. Statistics included: mean direction (i.e., average azimuth of resultant vector); vector magnitude (i.e., *r*, or length of the mean vector); and consistency ratio (% of normalized magnitude of the resultant vector ranging from 0–1; larger *r* values indicate that observations were clustered more closely around the mean). Data included *n* = 157 frogs (of 168) that moved >0.1 m. Statistical tests were deemed significant at ***P* ≤ 0.05; marginal significance is indicated at **P* ≤ 0.08.

[†] Rayleigh's test of uniformity (*R*-test): assesses if orientation significantly deviated from a random distribution (i.e., a general unimodal distribution with unknown mean direction and vector length).

[‡] *V*-test (alternative with specified mean direction): assesses if orientation significantly deviated from a unimodal distribution with specified mean direction. We hypothesized that animals would move toward nearest forest edge(s): 270° at Transect 1; either 180° (1) or 270° (2) at Transect 2; and 180° at Transect 3.

how the matrix is managed may shape dispersal and many conservation outcomes (Driscoll et al. 2013). We studied the movement of juvenile *L. sylvaticus* released in different open-cover types and determined that matrix condition affects behavior. Prior studies have quantified either the overall permeability of open-canopy cover types to juvenile movements (e.g., Rothermel and Semlitsch 2002, Cline and Hunter 2014) or fine-scale locomotor ability on different substrates (e.g., Stevens et al. 2004, Baughman and Todd 2007). Our study bridges this previous work to provide direct estimates of fine-scale movement

once matrix edges are crossed and in relation to environmental heterogeneity and landscape configuration. In treatments with lower structural complexity, juveniles adopted straighter paths, exhibited greater overall scales and rates of movement, and oriented toward forested cover types from distances as great as 40–55 m (asphalt > lawn > corn > forest > hay; Figs 2 and 3). Further, the willingness of juveniles to cross boundaries between forest substrate and open-cover vegetation differed significantly from forest control, suggesting that the willingness of individuals to move into and across open cover

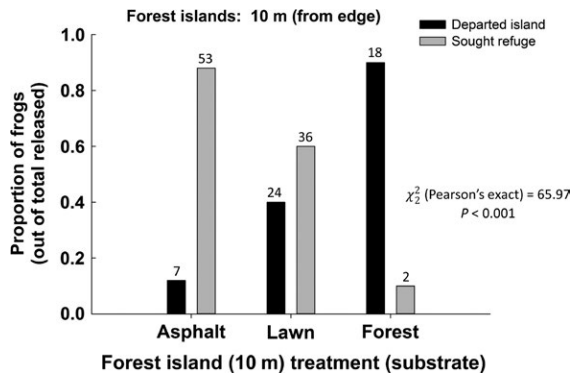


Fig. 6. Observed proportions of juvenile *L. sylvaticus* recaptured in experimental forest-litter islands (i.e., individuals temporarily settling in refuges) or tracked as departing islands and entering one of three treatments (asphalt, lawn, or forest control) at 10 m distances from the nearest forest edge (in asphalt and lawn) or within forest control in 2014. Values on y-axis are observed proportions of released individuals tracked that evacuated islands across treatments ($n = 3$ treatments), individual islands ($n = 24$), and six sites (constituting 240 frogs released during six batches in July 2014). Numbers above bars denote sample sizes of frogs released and assigned as settling or evacuating islands in each treatment. Differences in the proportion of frogs entering each treatment were significant ($\chi^2 = 65.97$, P -value < 0.001).

may depend on the structural complexity of vegetation. Structural complexity may also influence the ability of individuals to orient to forested habitat. These findings indicate that these cover types are different ecological filters to juvenile movements, and therefore it may be overly simplistic and inaccurate to assume movement performance is uniform across all matrix types.

Substrate structure and locomotion

Juveniles moved differently across different substrate types. As predicted, hay constituted the greatest physical filter, while asphalt and lawn permitted faster movement (Fig. 2d), greater overall displacement (Fig. 2a), and straighter trajectories (Fig. 2c) toward suitable habitat. Metamorphs in the forest and corn demonstrated similar and consistently moderate movement patterns for all five metrics, which could suggest that some level of

overhead cover may mitigate microclimate (Fig. 4) and decrease perceived predation risk. Previous studies have demonstrated that locomotor performance depends on the surface crossed (e.g., Eycott et al. 2012), but results vary by species, suggesting that dispersal period duration (e.g., explosive and short vs. prolonged), life history characteristics (e.g., reproductive lifespan, number and size of offspring, etc.), habitat preferences (e.g., breeding in seasonal vs. permanent water bodies, etc.), anatomical metrics (e.g., body size and shape), and mode of locomotion (e.g., fossorial or overland movements) may play a role in shaping juvenile dispersal strategies. Juveniles of three species differed in their response to old-field matrix and forest, with two species (*Anaxyrus americanus* and *Ambystoma maculatum*) moving greater distances with higher survival in the forest (Rothermel and Semlitsch 2002). In a laboratory study of natterjack toads (*Epidalea calamita*), the vertical structure of substrates inhibited hopping (grass, field, and forest), while sand and cement increased the length and speed of moves (Stevens et al. 2004). Researchers also found that movements of southern graycheek salamanders (*Plethodon metcalfi*) were greater in substrates with less structural complexity (lawn, gravel, asphalt compared to leaf litter and bare soil: Semlitsch et al. 2012). Taken together, these results support the hypothesis that simplified vegetation structure represents low impedance, but there may be other factors (e.g., desiccation and predation risk) that influence movement performance. For example, a recent study of juvenile amphibian movement in agroecosystems found that water loss was greater in corn and soybean fields compared to forest or prairie, thus suggesting resistance costs of movement due to desiccation may not be uniform in all agricultural settings (Cosentino et al. 2011). However, we found little evidence that frog weight or SVL was correlated with movement metrics. Thus, it was unlikely that larger frogs in our study perceived lower desiccation risk than small individuals on substrates like asphalt or lawn where temperature and humidity fluctuated most (Fig. 4; Peterman et al. 2013).

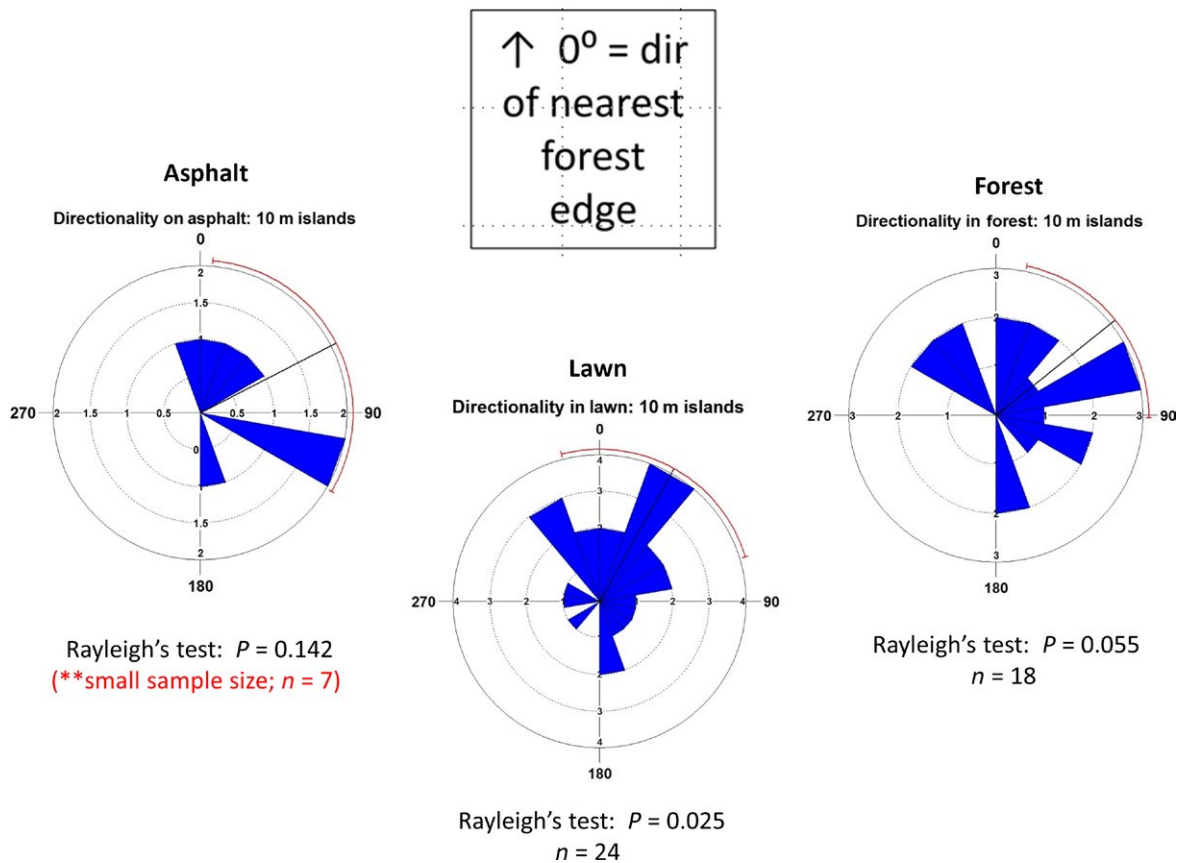


Fig. 7. Orientation of *L. sylvaticus* ($n = 49$ evacuees out of 240 total released) during experimental releases from artificial islands in three treatments. Orientations were standardized so that 0° represents the nearest forest edges (10 m away) for lawn and asphalt (random in forest control). Bold solid lines indicate the mean direction of all frogs released in that substrate (mean direction in parentheses) and the length of the wedges represents the percentage of animals (5% increments) with orientations that fell within the designated 20° bin (standard deviations indicated by arcs external to each circular histogram). Asterisks indicate treatments in which frogs demonstrated statistically significant directionality toward the nearest forest edge(s), according to a Rayleigh test of uniformity with specified mean direction ($\mu_0 = 0^\circ$).

Latency not predicted by substrates or single factors

Prior to our experiments, we predicted that latency would be longer in substrates with greater “settling” habitat (forest) and physical cover (hay, corn), assuming that frogs perceived these as a refuge from thermal stress or predators. In actuality, we observed that average latency was longest in the lawn and asphalt (208 ± 50 s and 173 ± 51 s, respectively), intermediate in the corn (123 ± 61 s), and shortest in the hay and forest (94 ± 31 s and 61 ± 13 s, respectively) although, the high within-treatment, but low between-treatment variability

(Fig. 2b) made this pattern statistically insignificant and difficult to interpret. In contrast to our prediction, results suggest that open substrates may lead frogs to crouch and cease motion in response to lack of cover. Indeed, our other metrics showcase the ability of frogs to evacuate quickly over long distances in lawn and asphalt, moving toward forest (Fig. 3). Recent studies have quantified substantial predation risks to juveniles during initial movement from ponds; e.g., 23% of ringed salamanders (*A. annulatum*) were consumed by predators during their first night in terrestrial habitat

(Pittman et al. 2013). Although we need more information (e.g., predator abundance), our latency results suggest that predation alone is not driving patterns of substrate-specific movement (e.g., Lillywhite and Brischoux 2012). For frogs deciding when to make initial movements, we posit that they were responding to an interplay of ecological pressures that reach beyond the microclimate and predation factors discussed above (e.g., to include food availability: Niecieza 2000, density-dependent behavior: Patrick et al. 2008, physiological stress: Janin et al. 2012b, etc.).

Distance-to-forest edge and orientation

Our directionality data suggest that juveniles ranging through nonforested matrix may be able to locate settling habitat at scales that are relevant to landscape configuration. Specifically, we determined that juveniles were able to orient toward the nearest forest 35–40 m away when released in asphalt, lawn, or corn, but not hay (Fig. 3 and Appendix C). This pattern was corroborated in our second experiment with greater directionality toward forest in lawn (Fig. 5a) than in hay (Fig. 5b). These findings are consistent with: (1) the “evacuation” hypothesis (Semlitsch et al. 2008), which suggests that individuals evade inhospitable conditions in open vegetation; and (2) our prediction that forest-targeted directionality would be greatest in treatments with lower structural complexity. Prior studies have demonstrated that vegetation structure and surrounding landscape configuration may affect juvenile orientation (Walston and Mullin 2008); for example, juvenile spotted salamanders (*A. maculatum*) exhibited greater forest-targeted orientation in field vs. early successional vegetation (Pittman and Semlitsch 2013). Similarly, Rothermel and Semlitsch (2002) found that juvenile American toads (*Bufo americanus*) released in old fields moved toward forest, while adult toads and small-mouthed salamanders (*A. texanum*) did not exhibit forest-targeted movement. Such results suggest that species-specific studies are necessary and that juveniles and adults may employ different movement mechanisms.

There may also be distance thresholds at which individuals no longer orient to forest due to decreased perceptual range. Frogs in lawns tend-

ed to exhibit forest directionality at greater distances compared to hayfields (i.e., up to 44–56 m and nearly significant at distances extending to 80 m; Appendix C, panel A). Amphibians have been shown to rely on a diversity of orientation mechanisms including, but not limited to, olfaction (Popescu et al. 2012), visual cues, or light polarization (Dall’Antonia and Sinsch 2001, Phillips et al. 2010), acoustic cues (Bee 2013), and magnetic reception (Landler and Gollmann 2011), although we were unable to test these mechanisms. In addition, there may be compounding factors that we were unable to measure, such as the locomotive costs of moving through dense hay. Metamorphs may balance the costs of long-distance movement decisions against assessing local resources for food and cover, and it is possible that frogs in hayfields sought temporary refuge rather than attempt a single long-distance movement to forest edge overnight (see Cline and Hunter 2014). From our observations in forest, we know that frogs in suitable habitat will move at random (Fig. 3) and initially only at moderate distances ($\sim 9.44 \pm 2.11$ mean path length) and velocities (Table 1, Fig. 2). Results support the notion that some open-cover types may afford temporary settling habitat (“retreat” hypothesis; Semlitsch et al. 2008) and that juveniles did not immediately move toward forest. This line of reasoning suggests that our hayfield orientation results may not be meaningful if frogs adopted a settling strategy at least initially.

Willingness to cross boundaries between forest and anthropogenic substrates: Island-evacuation experiments

For pool-breeding amphibians in increasingly fragmented landscapes, maintaining functional connectivity between habitats will require that individuals demonstrate willingness to enter tracts of the nonforest matrix during the post-metamorphic stage (Pittman et al. 2014). Thus, we must couple our estimates of movements through matrix with estimates of willingness to cross boundaries. Our results suggest that frogs are capable of immediate, ranging movement during the postmetamorphic period, as indicated by $\sim 90\%$ evacuation rates from our refuge islands embedded in forest controls (Fig. 6); this corroborates studies that demonstrate high permeability of mature forest to

juvenile movements (Popescu and Hunter 2011). Yet, our estimates of juveniles' willingness to enter asphalt and lawn were significantly lower (12% and 40%, respectively), and suggest that pavement is less permeable to movements than other open-vegetation types that have been examined (i.e., *asphalt* < row crop < hay-field < clear-cut < open lawn < moderate-cover lawn; Cline and Hunter 2014). Thus, open-canopy cover types may serve as differential filters to juvenile ranging movements, and numerous environmental factors (i.e., vegetation structure, microclimate, food, conspecifics, and predators) may shape an individual's willingness to enter open vegetation (e.g., Rittenhouse et al. 2008, Barbasch and Benard 2011, Eycott et al. 2012). Our willingness-to-enter estimates gain additional traction when coupled with movement estimates from our substrate experiment (Fig. 2). Specifically, individuals may move on straighter paths, at greater velocities, and demonstrate greater overall net displacements in asphalt and lawn relative to cover types with more structural complexity (Fig. 6); yet, these elevated speeds will not be realized if a perceived increase in predation or desiccation risk decreases willingness to enter (e.g., Kuefler et al. 2010, Cline and Hunter 2014). Long-term monitoring of individual movements across matrix boundaries and with respect to landscape configuration will be necessary to determine if (and at what distances across open-cover types) functional connectivity can be maintained between critical habitats, or if these open-cover types constitute sink habitats.

Potential influence of microclimate on movements: nocturnal refugia in the matrix

It is well established that microclimate influences the physiological ecology of amphibians and juveniles may be particularly vulnerable to desiccation risk in open cover due to their small size and increased surface area to volume ratios (Lillywhite 1970, Rittenhouse et al. 2008). Our microclimate data (Fig. 4) suggest that nocturnal regimes were mild and moist enough in all five substrates to allow successful transit. However, average daytime values consistently peaked at >30–35°C and <45–50% at refugia in the asphalt and lawn, suggesting that physiological stress would be greatly increased for

a frog by day and could represent an ecological trap. This was in stark contrast to patterns in the corn, forest, and hay, where humidity was consistently between 80–95% and daily temperature fluctuated least (16–30°C). Our observed high temperatures and dry microclimates in the asphalt and grass (Fig. 4) are consistent with our prediction that frogs would exhibit the straightest paths and greatest velocities to evacuate substrates with the most thermoregulatory risk.

Future studies and management implications

To predict amphibian population connectivity in fragmented landscapes, we need better field-based measurements of individual movements in a diversity of matrix types and landscape configurations (Bélisle 2005, Driscoll et al. 2013). Both types of information are necessary for parameterizing individual-based models of dispersal (e.g., Nathan et al. 2002, Hudgens et al. 2012). This study provides direct measures of fine-scale movements of a critical life stage (dispersing juveniles; Pittman et al. 2014) in five vegetation types, and quantifies orientation to the nearest forest and the willingness of individuals to enter asphalt, a previously untested open-cover type. Paired with prior estimates of frog willingness to enter other types of nonforest matrix (i.e., the degree to which matrix type either impedes or facilitates frog entry from a forest edge; Cline and Hunter 2014), our results could provide the basis for predicting how matrix composition and configuration might be managed to reduce the effective isolation of habitat patches. We also acknowledge that the ratio of habitat types in a natural setting (or at larger scales than we examined) may influence the relative importance of treatment-specific movement responses. Nonetheless, our distinctions among nonforest matrix types are important because many landscape-population models use expert-based values that are a one-size-fits-all measure for open cover (Yackulic et al. 2011).

We have demonstrated that open-canopy cover types may differ as filters or conduits to juvenile movements, and this fills a critical gap in our understanding of the behavioral mechanisms that underpin the relationship between matrix structure and the distribution of a patch-dependent

species. These distinctions may inform land-use planning; for example, how the composition and configuration of these cover types should be integrated with forest distribution to reduce the “effective” isolation of (and not just Euclidean distance between) patches of preferred habitats for dispersing amphibians. Our tracking design provides a minimally invasive way to record fine-scale movement behavior, but a more complete understanding of dispersal requires long-term monitoring of individual fitness and behavior. This will require new technology for direct tracking of small animals over long periods. In addition, our study only provides a limited assessment of the processes that could shape juvenile movements. For example, we also need to assess how seasonal land management practices such as crop-rotation, thinning, harvest, mowing, pesticide application can be best designed (including distribution in time and space) to facilitate dispersal. Research on the mechanisms that influence ranging behavior over multiple seasons and longer time scales will provide a better understanding of when juveniles switch between movement modes (i.e., away, directed, and settlement; Pittman et al. 2014), and thus how juvenile dispersal can be facilitated to maintain functional connectivity in fragmented landscapes.

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