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Clear-cutting affects habitat connectivity for a forest amphibian by decreasing permeability to juvenile movements

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Abstract. Conservation of forest amphibians is dependent on finding the right balance between management for timber production and meeting species' habitat requirements. For many pond-breeding amphibians, successful dispersal of the juvenile stage is essential for long-term population persistence. We investigated the influence of timber-harvesting practices on the movements of juvenile wood frogs (*Lithobates sylvaticus*). We used a chronosequence of stands produced by clear-cutting to evaluate how stand age affects habitat permeability to movements. We conducted experimental releases of juveniles in 2008 ($n = 350$) and 2009 ($n = 528$) in unidirectional runways in four treatments: mature forest, recent clearcut, 11-year-old, and 20-year-old regeneration. The runways were 50×2.5-m enclosures extending into each treatment, perpendicular to a distinct edge, with four tracking stations at 10, 20, 30, and 40 m from the edge. We recorded the number of animals reaching each tracking station, and the proportion of animals changing their direction of movement at each distance. We found that the mature forest was 3.1 and 3.7 times more permeable than the 11-year-old regeneration and the recent clearcut, respectively. Animals actively avoided open-canopy habitats and sharp edges; significantly more animals returned toward the closed-canopy forest at 0 m and 10 m in the less permeable treatments. There were no significant differences in habitat permeability between the mature forest and the 20-year-old regeneration. Our study is the first to directly assess habitat permeability to juvenile amphibian movement in relation to various forestry practices. We argue that habitat permeability at this scale is largely driven by the behavior of animals in relation to habitat disturbance and that caution needs to be used when using spatial modeling and expert-derived permeability values to assess connectivity of amphibian populations. The effects of clear-cutting on the migratory success of juvenile *L. sylvaticus* are long-lasting. Forestry practices that involve canopy removal and conversion of natural forest to conifer plantations may affect regional population viability by hindering successful dispersal.

Key words: connectivity; edge effects; even-aged silviculture; habitat permeability; juvenile; Lithobates sylvaticus; *migration; orientation; succession; wood frog.*

Introduction

Animals move across the landscape to gain access to various resources, and thus, understanding animal movements is often critical to conservation strategies (Semlitsch 2002). The conversion of natural land cover types to other uses disrupts movements of organisms, affecting habitat selection, and causing local declines in abundance or species richness (Cushman 2006). Because of their biphasic life cycles and generally low vagility and high sensitivity to disturbance (Semlitsch 2000), movement behavior and migratory success of amphibians are likely to be significantly altered by land-use conversion. For pond-breeding amphibians, one mechanism behind observed declines relates to decreased connectivity between breeding ponds, and between breeding and foraging or overwintering habitats (Laan

and Verboom 1990, Sjögren-Gulve 1994). Changes in land cover induced by forestry practices impact forest amphibians and the effects can be long-lasting (deMaynadier and Hunter 1995). In particular, clear-cutting and conversion of natural forests to single-species plantations are known to have detrimental effects on amphibian occupancy due to changes in habitat quality and permeability to movements (Parris and Lindenmayer 2004, Semlitsch et al. 2009). Permeability can be quantified in terms of both the costs imposed by a habitat to movement (e.g., physiological stress, risk of predation; Joly et al. 2003) and behavior (i.e., willingness to move). Thus, research aimed at investigating habitat permeability has to account for the individuals' propensity to move through a particular habitat and the effects of habitat alteration on behavior (Russell et al. 2003, Semlitsch et al. 2008). Juvenile amphibians pose a particularly interesting challenge for quantifying movements and habitat permeability because of their small size and cryptic lifestyles. Moreover, juveniles are typically the dispers-

ing life stage in many amphibian species, dispersal being defined here as the one-way trip from a natal pond to a different pond for breeding (Semlitsch 2008). Dispersers promote gene flow that maintains genetic variation among populations (Slatkin 1987) and contribute to metapopulation processes through recolonization following local extinction events (Marsh and Trenham 2001).

For juvenile forest-dwelling amphibians, permeability is assumed to decrease following timber harvesting, but empirical data on the magnitude of the decrease, as well as on how habitat alteration influences movement behavior is lacking (a notable exception is Rothermel and Semlitsch [2002]). Hence, most investigations of how landscape permeability affects amphibian movements, spatial population structure, and gene flow have been based on computer models that relied on expert opinions of the permeability of various land cover types (Ray et al. 2002, Compton et al. 2007, Zellmer and Knowles 2009). Despite the lack of empirical data on habitat permeability, this field of research is likely to become even more popular with the advent of circuit theory-based software that includes "isolation by resistance" parameters (McRae 2006).

In this study, we used an experimental approach to quantifying habitat permeability for juvenile wood frogs (*Lithobates sylvaticus*) in a forested landscape. *L. sylvaticus* are a vernal pool-breeding species, widely distributed in North American temperate and boreal forests, and the juveniles represent the only source of dispersing individuals (Berven and Grudzien 1990), critical to the persistence of regional populations (Zellmer and Knowles 2009). *L. sylvaticus* are highly sensitive to forest removal, and their local abundance is strongly affected by proximity to abrupt forest edges (deMaynadier and Hunter 1998). Habitat selection of post-metamorphic *L. sylvaticus* differs between a dispersing and a settling phase, with animals responding to coarse variation in habitat during the dispersing stage (Patrick et al. 2008).

We studied the movements of juvenile *L. sylvaticus* in a forest management context in central Maine, USA, using a chronosequence of stands resulting from even-aged silviculture (i.e., clear-cutting) as a time series proxy to evaluate how stand age affects permeability. The specific objectives of this research were: (1) to quantify the dispersal success of juveniles in various-aged stands resulting from clear-cutting; (2) to identify mechanisms that drive the movement behavior of juveniles; and (3) to evaluate the influence of forest edges on the movement patterns of juvenile amphibians.

METHODS

Study sites and experimental design

We conducted the research in Penobscot County, Maine, USA, on the University of Maine Dwight B. Demeritt Experimental Forest and Henderson Forest, and on a tract in Milford, managed by American Forest

Management. Central Maine has a long history of forest management, and as a result is a mosaic of various-aged mixed-wood stands, part of the Acadian Forest region, which covers most of northeastern United States and the Canadian Maritime Provinces (Saunders and Wagner 2008). We selected four forestry conditions that are common in the region: control *mature forest*, *recent clearcut* (2–3 years), *11-year-old regeneration* treated with herbicides, and *20-year-old natural regeneration*. We first identified a linear edge between a closed-canopy forest and each of the regeneration treatments, and then randomly selected the location of the experimental setup along the edge. The recent clearcut (hereafter clearcut) completely lacked canopy cover, as well as any tree regeneration, containing mostly herbaceous and low shrub (<50 cm) vegetation layers. The 11-year-old regeneration stand (11-yr stand) was treated with herbicide 5–6 years after clear-cutting, a silvicultural treatment known as "conifer release." The resulting stand resembled a dense conifer plantation, composed of white pine (*Pinus strobus*), red spruce (*Picea rubens*), and eastern hemlock (*Tsuga canadensis*), and the mean (±SE) tree height was 3.8 ± 0.4 m. The 20-year-old regeneration stand (20-yr stand) was left untreated after clear-cutting and resulted in a dense, mixed stand dominated by white birch (*Betula papyrifera*) and grey birch (*B. populifolia*), with sparse red maple (*Acer rubrum*), white pine, balsam fir (*Abies balsamea*), red spruce, and quaking aspen (*Populus tremuloides*), averaging 9.2 ± 0.8 m in height. The mature forest was a 70–80-year-old closed-canopy mixed stand composed of hemlock, red spruce, red maple, quaking aspen, and American beech (*Fagus grandifolia*) >15 m in height, with patchy balsam fir regeneration, and was not harvested in the past 20 years.

Experimental runways

We tested the permeability of four forestry treatments to juvenile *L. sylvaticus* movements by building terrestrial runways using a design modified from Rothermel and Semlitsch (2002). Runways consisted of 50×2.5 m silt fence enclosures (60 cm tall and buried 30 cm into the ground) oriented perpendicular to the forest edge, starting at ~3 m from the edge and extending into each treatment. The runways in the clearcut, 11-yr stand, and 20-yr stand were adjacent to closed-canopy mature stands. The runways in the mature forest were adjacent to a recent clearcut. We decided to place our runways adjacent to edges because: (1) newly metamorphosed *L. sylvaticus* tend to settle in good-quality habitat, and placing runways in interior closed-canopy conditions might not elicit movement behavior, the main focus of our experiment (Patrick et al. 2008); and (2) we wanted to investigate behavior in relation to harsh edges, which were found to alter amphibian movement (deMaynadier and Hunter 1998, Rothermel and Semlitsch 2002). We only selected one stand for each treatment because we could not identify other suitable stands that were close
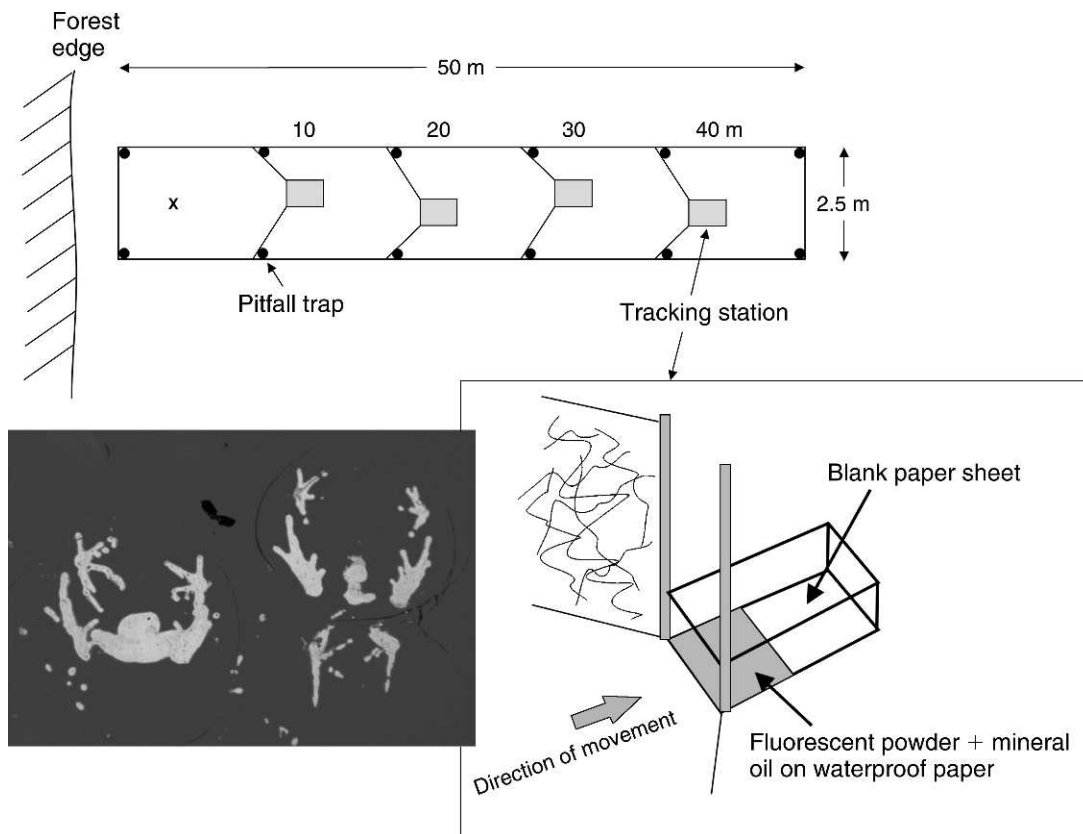
FIG. 1. Experimental setup for evaluating the permeability of four forestry treatments to movements of juvenile wood frogs, *Lithobates sylvaticus*; x marks the release location (drawing not to scale). The inset on the bottom right provides the tracking station design. The picture on the bottom left shows fluorescent powder tracks from two different individuals.

enough to allow us to implement the experiment, given our labor-intensive and time-sensitive approach. In 2008, we built six runways in mature forest, clearcut, and 11-yr stand (two per treatment). In 2009, we built another six runways: three in the 20-yr stand, and one for each of the other treatments, for a total of 12 runways. For each treatment, the runways were spaced 30–50 m apart, parallel to each other.

In each runway, we built four tracking stations (at 10, 20, 30, and 40 m from the start of the runway) to evaluate the number of animals reaching each distance (Fig. 1). The tracking stations were constructed by cutting entrance and exit openings into large plastic containers with lids ($45 \times 65 \times 20$ cm). A silt fence funnel extending from the edge toward the middle of the runway directed the experimental animals into the tracking stations. Inside the trays, we placed a mix of orange fluorescent powder (DayGlo Color Corporation, Cleveland, Ohio, USA) and mineral oil (RiteAid, Harrisburg, Pennsylvania, USA) on waterproof paper (Rite-in-the-Rain, J. L. Darling Corporation, Tacoma, Washington, USA) next to a white sheet of plain paper. Thus, individuals passing through the fluorescent powder mixture self-recorded their tracks on the white paper. The oil allowed us to accurately count tracks even

after heavy rain events. The mixture is harmless to amphibians and was used in other studies of amphibian movements (Eggert 2002). The white paper was changed daily, and the waterproof paper was recoated with powder and oil as needed.

We used pitfall traps to estimate the number of animals reaching the end of the runways, or returning toward the forest edge. Each runway contained 12 pitfall traps: two at the start and two at the end of the runway, and two at 10, 20, 30, and 40 m, in the sharp angle formed by the silt fence funnel and the runway wall (Fig. 1). Animals that changed their direction of movement at a particular distance would be captured in these traps, thus indicating a change in behavior related to the conditions in the respective treatments.

Amphibian releases

We collected egg masses in mid-April 2008 and 2009 from the University of Maine's Penobscot Experimental Forest, Maine, USA, and transported them to a site near campus where we hatched them in plastic wading pools (1 m diameter). Upon emergence, larvae at Gosner stages 21–23 (Gosner 1960) were added to 1500-L cattle tanks. Two weeks prior to larval stocking, we added plankton collected from natural vernal pools and leaf

litter to the cattle tanks to mimic a seminatural rearing environment. We maintained a density of 70 larvae per tank. The cattle tanks were located under a closed canopy and were covered by screen lids to prevent colonization by other organisms. During the emergence season (1 July–10 August in Maine), the tanks were checked daily for metamorphosed *L. sylvaticus* (stage 42 and higher). Upon capture, we added the metamorphs to large plastic bins (200 L) with moist leaf litter for up to three days until they reached the final stage of their metamorphosis. At this stage, they were measured, marked, and randomly assigned to the experimental treatments.

We released 350 juvenile *L. sylvaticus* in four batches in 2008, and 528 individuals in five batches in 2009. Between 13 and 19 animals per runway were released in each batch in 2008, and 8–10 animals were released in 2009, depending on availability, and it was consistent across runways within the same batch. The experimental animals were removed from the plastic bins during the day of release, measured (snout–vent length), marked with a single toe clip batch mark, and placed in plastic containers (one per runway). A subsequent batch was released only after no new tracks were recorded from the previous batch for at least 1 d. We released the animals 1–2 h after sunset in the center of the runway, ~3 m from the starting point (i.e., ~6 m from the forest edge). We checked the runways daily between 07:00 and 11:00 hours during 9–24 July 2008, and 11 July–6 August 2009.

Orientation arena

Due to landscape setting constraints, it was not possible to build runways with different cardinal directions in each treatment. However, we consider this not to be a limitation to our study because: (1) similar studies (Rothermel and Semlitsch 2002) did not find differences in movement patterns of juvenile amphibians among different cardinal directions, and (2) the animals used in this experiment were collected as eggs from skidder ruts and ditches along forest roads in an area (Penobscot Experimental Forest, Penobscot County, Maine) where metamorphosing *L. sylvaticus* orient randomly upon exiting the natal pools (V. D. Popescu, *unpublished data*). However, to eliminate any doubt about their initial orientation biasing the outcome of the study, we tested a subsample of the experimental animals by releasing them in a circular arena (3 m diameter) in closed-canopy conditions. The circular arena was located >50 m from the forest edge to minimize any potential edge effects that could potentially influence juvenile *L. sylvaticus* directionality (deMaynadier and Hunter 1998). Prior to release in the runways, we randomly selected three containers containing experimental animals and released them in the center of the circular arena. After placing the tray in the arena, we waited for two minutes to overcome the effect of handling (Diego-Rasilla and Luengo 2002), and

then gently lifted the lid to release them. Using a pair of night-vision binoculars (Rigel Optics, DeWitt, Iowa, UAS), we recorded the bearing for each individual when it reached the edge of the arena.

Microclimate and habitat variables

Because microclimate might affect both habitat selection and survival of juvenile *L. sylvaticus*, we recorded hourly temperatures, relative humidity, and daily precipitation at each treatment location. We used 27 iButton data loggers (Maxim, Dallas Semiconductor, Dallas, Texas, USA) to record hourly air, ground-level, and refuge (i.e., 5 cm below coarse woody debris or root channels) temperatures, as well as ground-level relative humidity, at two of the three runways in each treatment each year. Precipitation was measured daily using a rain gauge.

We characterized the vegetation cover in each 10 × 2.5-m compartment of the runways in July 2008 and 2009. We collected data on percent cover for each vegetation layer (herbaceous, shrub, canopy trees), percent leaf litter, ground cover, canopy closure (using a moosehorn densitometer, Moosehorn CoverScopes, Medford, Oregon, USA), canopy tree height (using a Recta DP10 professional prismatic clinometer; Recta, Biel-Bienne, Switzerland), and tree density.

Statistical analyses

The runways yielded three indices that characterized amphibian movements and relative habitat permeability: (1) the number of tracks at each tracking station distance, (2) the proportion of individuals captured in pitfall traps, and (3) movement rate. The first two indices directly estimated the overall migratory success of juveniles, as well as their propensity to move through each forestry treatment. Besides the number of animals returning toward the edge, as well as reaching the end of the runways, which is a direct effect of habitat permeability and weather conditions, we were also interested in the number of individuals that changed their initial direction of movement to return toward the edge, as reflected in captures at 10, 20, and 30 m. The third index, rate of movement (m/d), is indicative of how quickly the animals moved through each forest type.

We used generalized linear mixed-effects models (GLME) to investigate whether treatment, release, and individual runways had an effect on the number of tracks recorded at 10–40 m from the forest edge. GLMEs have fewer assumptions than traditional regression (Pinheiro and Bates 2000) and provide a more flexible approach to analyzing non-normal data when random effects are present (Bolker et al. 2009). In GLME, fixed effects are factors that describe experimental treatments or are sources of systematic variance; random effects are associated with particular experimental units that are selected at random from the population of interest (Pinheiro and Bates 2000). We used block random effects that apply equally to all the

individuals within a group, leading to a single level of correlation within groups (Bolker et al. 2009). Because the dependent variable was the proportion of animals that reached each tracking station following a release (inferred from the track count), we used a binomial mixed-effects regression implemented in R version 2.8.1 (R Development Core Team 2008 [package *lme4*], Bates and Maechler 2009). We only used data from batches 2–4 in 2008 and batches 2–5 in 2009, because the first release in each year was regarded as trial and did not contain equal number of animals in each treatment and runway. We ran models for each tracking station distance (10, 20, 30, and 40 m) to avoid the autocorrelation emerging from counting the same individuals in successive tracking stations. For each model, we used variables *treatment* (the four forestry treatments) and *runway* (individual runway) as fixed effects, and variable *batch* as both fixed and random effects. Due to the relatively small size of our data set, and the difficulty in interpreting regression coefficients for complex models, we only ran simple models followed by the first-order interactions of *treatment × runway* as fixed effects. We used quantile–quantile plots, residual plots, and plots of fitted vs. observed values to assess the performance of each model, and likelihood ratio tests to assess the overall effect of the fixed effects. Finally, we used the Akaike Information Criterion (AIC) to select the model that had the greatest support for each of the four tracking distances (Burnham and Anderson 2002). For all four distances, the models that had the greatest support contained *treatment* as a fixed effect and *batch* as a random effect. The interaction term *treatment × runway* was not significant for any of the four distances, suggesting that there are no differences in the number of tracks among runways within treatment, and that the microhabitat heterogeneity observed among runways was overridden by other factors.

For the second index, we investigated the differences in the proportion of animals recaptured among treatments for each distance (0–50 m) and year separately. Specifically, we evaluated what fraction of animals that reached 10, 20, and 30 m (i.e., as deduced from the total number of tracks recorded at each distance) were captured in pitfall traps at that particular distance (i.e., total number of animals captured at 10, 20, and 30 m). We pooled the number of captures at 40 and 50 m in each runway because all four traps were located in the same runway "compartment" (Fig. 1). Thus, for both 0 m and pooled 40–50 m traps, we considered the fraction of animals captured out of the total number of animals released as a measure of complete avoidance and dispersal success, respectively. We first assessed whether or not the frequency of captures and distance are associated with each other, and are independent of treatment using a three-way contingency table. If nonindependence was found, we used pairwise tests for proportions to quantify differences in proportion of captures between treatments at each distance.

We investigated whether or not there were differences in the rate of movement (m/d) between the four treatments using a Kruskal-Wallis nonparametric test implemented in R (package *coin*; Torsten et al. 2008). If the general test was significant, we performed pairwise comparisons without adjusting the significance level. For quantifying movement rates, we only used the data on individuals that were captured past the first tracking station (89 individuals in 2008, and 91 in 2009).

We tested whether or not our experimental animals exhibited some directionality that might potentially bias the outcome of the permeability experiment using omnibus tests for circular uniformity in R (package *circular*; Lund and Agostinelli 2007). Omnibus tests, such as Kuiper's and Watson's tests, are more powerful when there is little knowledge concerning the alternative hypothesis (Fisher 1993). For all statistical tests we used a significance level of $P < 0.05$.

Results

The three indices that we used to assess habitat permeability (number of track counts, proportion of captures, and rates of movement) differed significantly among treatments. The average size of the released juvenile *L. sylvaticus* was 17.19 ± 1.24 mm, and did not differ among treatments (ANOVA; $F_{3,407} = 1.23$, $P = 0.298$).

Proportion of animals reaching tracking stations

There were differences in the number of tracks recorded among the four treatments for all distances. As a general rule, the proportion of released individuals decreased with increasing distance from the edge in all treatments, but was consistently higher in the mature forest and 20-yr stand compared to the two younger stands (Fig. 2a, Appendix). More specifically, a lower proportion of animals reached the 10-m tracking station in the clearcut compared to the 11-yr stand. A higher proportion of the released animals reached the 10-m tracking station in both the mature forest and 20-yr stand compared to the other two treatments. This pattern changed at 20 m from the forest edge, and remained consistent at 30 and 40 m from the edge. At these distances, there were no differences between the clearcut and the 11-yr stand, while a significantly larger proportion of animals migrated through the mature forest and the 20-yr stand (Fig. 2b, c; Appendix). The only difference between the mature forest and the 20-yr stand occurred at the 40-m tracking station, with a moderately lower proportion of animals moving through the 20-yr stand (Fig. 2d, Appendix). Considering the differences in the proportions of juvenile *L. sylvaticus* reaching 40 m, the mature forest was 3.1–3.7 times more permeable than the clearcut and 11-yr stand, and 1.5 times more permeable than the 20-yr stand (although the latter is a consequence of behavior, rather than absolute permeability; see *Discussion*).
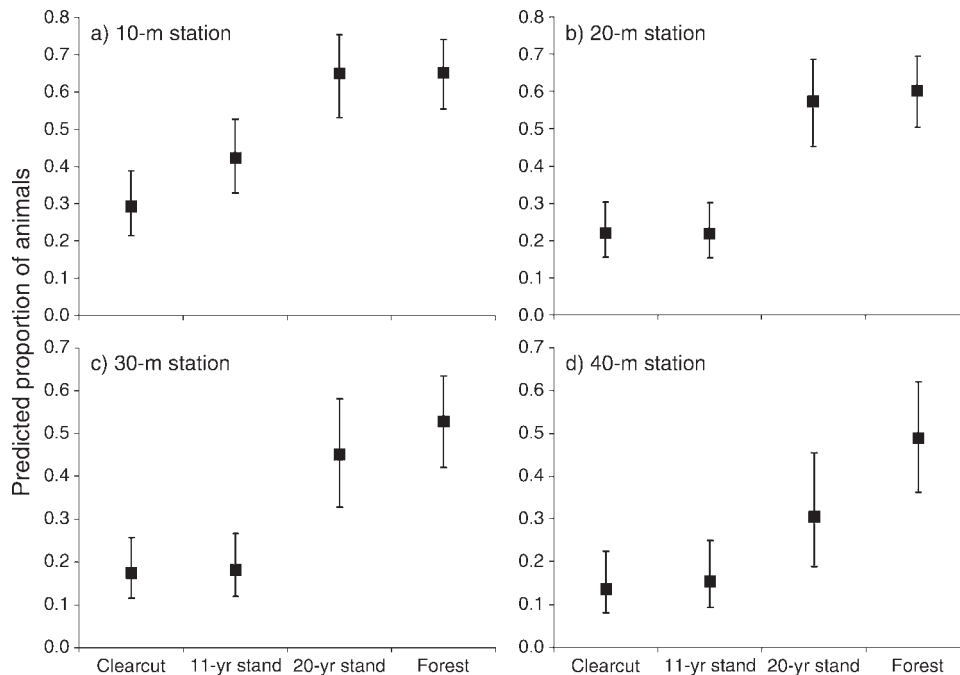
FIG. 2. Predicted 95% confidence intervals around the mean proportions of juvenile *L. sylvaticus* reaching: (a) 10-m, (b) 20-m, (c) 30-m, and (d) 40-m tracking stations (values are predicted proportions obtained by inverse logit-transforming the coefficients of the best binomial mixed-effects model fitted for each distance).

Proportion of recaptures

The pattern of pitfall captures was complementary to that of the number of tracks. We recaptured 179 individuals in 2008 (51% of the total released) and 240 individuals in 2009 (45%). For both years, the percentage of captures at each distance was dependent on forestry treatment (2008, $\chi^2_{10} = 53.7$, $P < 0.001$; 2009, $\chi^2_{15} = 116.8$, $P < 0.001$). Overall, in the clearcut and 11-yr stand most of the captures were recorded at 0 m, presumably reflecting animals trying to return toward the forest (30% and 48% in clearcut and 25% and 44% in 11-yr stand for 2008 and 2009, respectively; Table 1). Animals released in the mature forest were significantly less likely to return toward the edge, with only 19% and 18% captured at 0 m in 2008 and 2009, respectively. Individuals released in the 20-yr stand behaved similarly to those in the mature forest, with 17% captured at 0 m. In contrast, the percentage of animals traveling the entire length of the runways was significantly higher in the mature forest than in all the other treatments, with

TABLE 1. Percentage of juvenile wood frogs, *Lithobates sylvaticus*, recaptured in the runways in 2008 and 2009, by forest age.

Forest age	No. juvenile frogs released	Individuals recaptured, by distance (%)				
		0 m	10 m	20 m	30 m	40 and 50 m
2008 recapture						
Clearcut	112	30[B]	23[B]	13	10	11[B]
11-yr stand	105	25[AB]	20[B]	3	8	7[B]
20-yr-stand	. . .	. . .	. . .	. . .	. . .	. . .
Mature forest	133	19[A]	5[A]	0	1	29[A]
2009 recapture						
Clearcut	118	48[B]	24[A]	5	8	7[B]
11-yr stand	116	44[B]	18[A]	0	2	5[B]
20-yr-stand	115	17[A]		2	0	9[B]
Mature forest	117	18[A]	11[A]	0	6	31[A]

Notes: The superscript letters denote similarity or dissimilarity among treatments for each distance (within a column) and year separately, resulting from pairwise tests for proportions. The number of captures at 20 and 30 m was very low in all treatments, and data were not analyzed. Values at 10, 20, and 30 m represent the percentage recaptured relative to the number of animals that reached that particular distance. Ellipses denote that no data were collected for the 20-yr stand in 2008.

29% and 31% captured at 40 and 50 m in 2008 and 2009, respectively (Table 1).

The percentage of captures at 10 m deserves special attention. In 2008, a significantly higher percentage of animals that passed through the first tracking station were captured in the clearcut (23%) and 11-yr stand (20%) than in the mature forest (5%) (Table 1). In 2009, the same pattern was observed (24% captures in clearcut, 18% in 11-yr stand, and 11% in mature forest), but the pairwise tests for proportions did not yield statistically significant results (Table 1). The 20-yr stand had significantly lower captures at 10 m than all the other treatments (2%). This result suggests that juveniles starting to travel in the clearcut and 11-yr stand are able to assess potentially inhospitable habitat, and take the decision to return toward the forest. The number of captures at 20 and 30 m was very low (<5) for all treatments and years, and not suitable for testing differences among treatments. Thus, once juveniles started to move away from the release point, and did not turn around to be captured at 10 m, they traveled the entire length of the runways regardless of forestry treatment.

The majority of captures occurred during the first three days post-release (96% in 2008 and 86% in 2009), suggesting that juveniles try to depart and move through all treatments relatively quickly. Only 3 and 11 animals spent >4 days in the runways in 2008 and 2009, respectively.

Movement rates and timing of movements

There were differences among the four treatments with respect to the rates of movement, as well as timing of movements post-release. In all treatments, the movement rates ranged between 5 and 50 m/d, but the omnibus Kruskal-Wallis test yielded significant differences among the four treatments ($\chi_1^2 = 10.471$, $P = 0.0135$). Further, the pairwise comparisons revealed that: (1) there was no difference in the movement rate between the clearcut (median = 20 m/d) and 11-yr stand (median = 15.5 m/d) ($\chi_1^2 = 2.238$, $P = 0.138$); (2) there was no difference between clearcut and mature forest (median = 17 m/d) ($\chi_1^2 = 0.829$, $P = 0.36$), and (3) animals moved faster through mature forest and clearcut than through the 20-yr stand (median = 10 m/d) ($\chi_1^2 = 6.689$, $P = 0.008$ and $\chi_1^2 = 4.248$, $P = 0.038$, respectively) (result of juvenile behavior, rather than habitat permeability; see *Discussion*).

The timing of movements post-release reflected the choices of individuals to travel through the four treatments, and helps understanding how juvenile *L. sylvaticus* perceive differences in habitat quality. Most of the movement occurred within the first two days post-release (Fig. 3a, b). In the mature forest, >40% of the released individuals moved quickly past the second tracking station (20 m) during the first day, and 50% reached the end of the runway after four days. In the clearcut and 11-yr stand, the bulk of movement also

occurred during the first day, but only past the 10-m tracking station, and was notably lower than in the mature forest (20% and 25%, respectively; Fig. 3a). Very few animals moved through these two treatments during the third and fourth days post-release, and only 13% and 16% of the total released actually reached 40 m after four days. Animals released in the 20-yr stand exhibited a different, more constant movement pattern. Although relatively few animals reached 10 m during the first day (30%), similar to the two younger treatments, substantial movements were recorded at 20 m during the second day and at 30 and 40 m during the third day (Fig. 3b, c). On average, 40% of the animals reached 30 m during the four days post-release in this treatment.

Microhabitat and microclimate

The differences in habitat permeability among the four forestry treatments could be explained by differences in vegetation, ground cover, and microclimate. The mature forest and 20-yr stand had high canopy cover (90% and 78%, respectively), as well as extensive leaf litter ground cover (>90%; Table 2). Bare ground and moss together accounted for ~40% of ground cover in the clearcut and 11-yr stand. The herbaceous and low shrubs layers dominated the clearcut (65–70%), and to a lesser extent the 11-yr stand (≈25%; Table 2).

These differences in habitat structure were reflected in the microclimate of the four treatments. As we expected, the clearcut was warmer than the other treatments in both years (Table 3). The average daily maximum temperatures at ground level were higher (7.34°–8.57°C in 2008, and 4.46°–5.38°C in 2009) than in the older stands. In both years, the differences in average maximum temperatures between the mature forest and the 11-yr and 20-yr stands were minimal (0.9°–1.2°C), suggesting that the shade provided by regeneration alleviates the microclimate near ground. The highest temperature at ground level was 39.1°C and was recorded on 16 July 2008 at 15:00 hours in the recent clearcut. The recent clearcut was also drier than the other treatments; daily minimum relative humidity varied between 27.23% and 100% (2008) and between 62.91% and 100% (2009). The precipitation during the experimental releases was high (66 mm in 2008 and 76 mm in 2009), which places both study years above the long-term normal by 20% and 64%, respectively (data *available online*).[2] However, in 2008, one rain event accounted for two-thirds of the total rainfall (45 mm on 21 July).

Orientation of juveniles pre-release

We used a total of 87 juvenile *L. sylvaticus* to test the possibility that innate directionality might influence their propensity to move through the runways. We did not detect any departure from circular uniformity
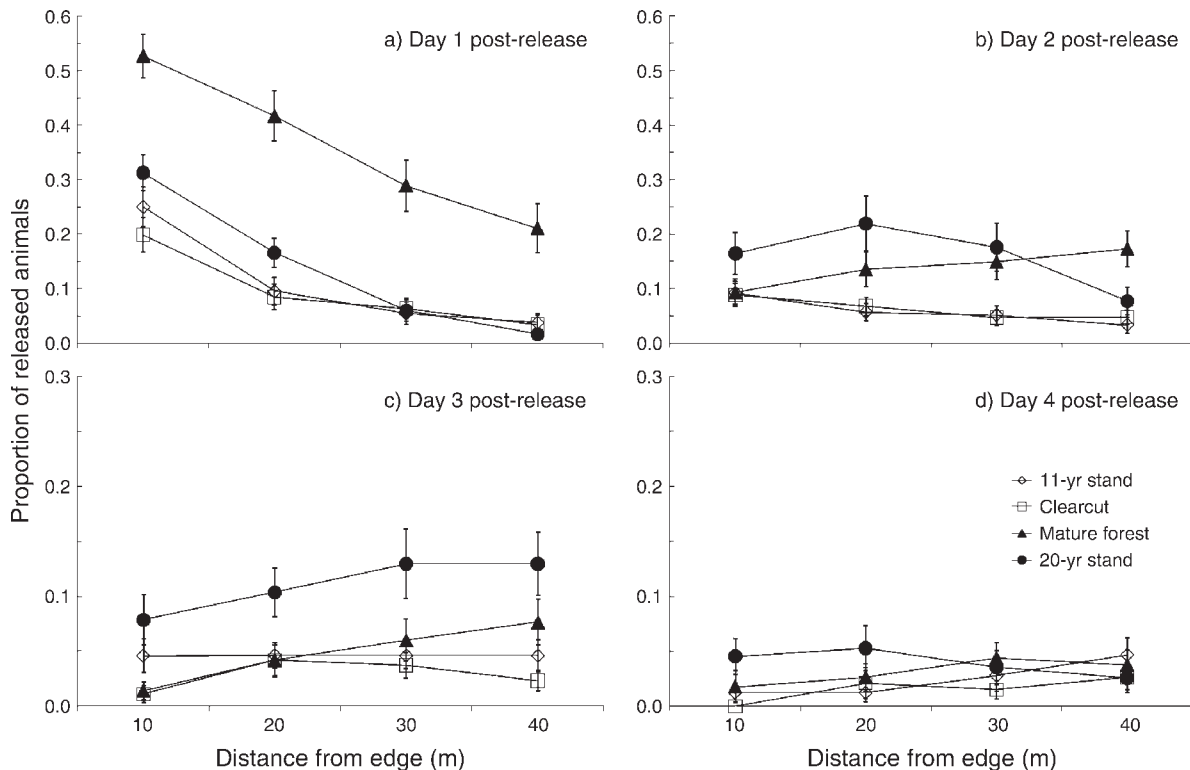
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[2] ⟨www.ncdc.noaa.gov⟩

FIG. 3. Timing of movements of juvenile *L. sylvaticus* released in four forestry treatments in 2008 and 2009. Values on the *y*-axis are the proportions of released individuals moving through the tracking stations averaged across runways and batches (mean ± SE). We show only the first four days post-release because these days accounted for most movement (note the difference in *y*-axis scale for days 1 and 2 vs. days 3 and 4).

(Kuiper $V = 1.338$, $P > 0.15$; Watson $U^2 = 0.073$, $P > 0.10$), suggesting that the juveniles oriented randomly when released at night under closed canopy at >50 m from a forest edge (Fig. 4). Hence, the direction of movement in the runways was apparently influenced by the juveniles' perception of experimental treatments only.

DISCUSSION

In this study we investigated the permeability to amphibian movements of a chronosequence of stands generated by even-aged silviculture. The greatest challenge in studying the movements of small organisms is

being able to successfully track and detect them, while interfering as little as possible with their movements. For example, mark–recapture studies employing drift fences and pitfall traps are generally used for quantifying movements, but trapping interrupts animal movements and does not provide information on fine-scale behaviors. Fluorescent powder tracking is useful for small amphibians, but its effectiveness is highly dependent on weather conditions and substrate (Roe and Grayson 2008). In this respect, we consider that our "self-tracking" approach that combines the two techniques is preferable to other methods, because it allowed an in-depth exploration of juvenile amphibian movement

TABLE 2. Habitat characteristics of the four forestry treatments (mean ± SE).

	Ground cover (%)			Cover of vegetation layers (%)			Stand density (stems/ha)	Tree height (m)
Treatment	Leaf litter†	Moss	Bare ground	Herbaceous	Shrubs	Tree canopy cover‡		
Clearcut	0	14.3 ± 3.3	25.6 ± 4.2	55.0 ± 4.5	11 ± 3.1	0	0	0
11-yr stand	37.3 ± 6.1	30.5 ± 3.6	10 ± 2.9	14.0 ± 7.7	9.5 ± 3.0	69.5 ± 4.9	5440	3.8 ± 0.4
20-yr stand	92.6 ± 1.8	6.3 ± 1.6	0.3 ± 0.3	17.6 ± 5.8	0	77.7 ± 2.6	9947	9.2 ± 0.8
Mature forest	90.0 ± 2.4	10.0 ± 2.4	0	0	0	90.0 ± 1.9	1120§	>15

† For the 11-yr stand, we measured the percentage of ground covered with coniferous duff.

‡ For the 11-yr stand, we measured the percentage of cover of conifer regeneration similar to the herbaceous and shrub layers rather than the canopy cover.

§ Canopy trees only (in addition, the mature forest contained 3573 stems/ha of balsam fir (*Abies balsamea*) seedlings and saplings in the understory).

TABLE 3. Microclimate of four forestry treatments in central Maine during experimental amphibian releases (9–24 July 2008 and 11 July–6 August 2009).

	Mean daily maximum temperature (°C)				Relative humidity (%)	
	2008		2009		2008	2009
Treatment	Ground level	Refugia	Ground level	Refugia	Ground level	
Clearcut	31.59	23.36	26.26	22.08	62.91 ± 6.33	86.33 ± 1.89
11-yr stand	24.26	19.79	21.79	17.81	76.14 ± 5.40	90.77 ± 1.75
20-yr stand	...	...	21.22	17.87	...	96.03 ± 1.17
Mature forest	23.02	18.65	20.88	17.02	78.70 ± 4.53	96.77 ± 0.99

Notes: Relative humidity was recorded at ground level only (mean ± SE). Ellipses denote no data collected for the 20-yr stand in 2008.

ecology with minimal disturbance to their fine-scale movements.

Our study suggests that clearcuts are significant barriers, altering the movements of emigrating juveniles, and that the effects are long-lasting. The clearcut and 11-yr stand had lower permeability to movement than the older treatments. In the absence of subsequent silvicultural intervention (e.g., thinning, use of herbicides), the 20-yr stand was mature enough to provide good migratory or settling habitat for juvenile *L. sylvaticus*. While the low permeability of clearcuts or other open-canopy habitats to juvenile amphibian movement has been previously demonstrated (Rothermel and Semlitsch 2002, Rothermel 2004), our findings for the 11-yr stand deserve further discussion.

During both years of the study, the 11-yr stand had the same low permeability to movements as the clearcut (~3.1–3.7 times less permeable than mature forest). Overall, a larger proportion of animals reached the 10-m tracking station compared to the clearcut, indicating that the 11-yr stand facilitated initial movements. However, the proportion of animals reaching >20 m from the forest edge dropped to a level similar to that of the clearcut. This is surprising given this treatment's microclimatic similarities to the mature forest and 20-yr stand. Despite microclimate similarities, there were striking differences in vegetation cover between this and the two older habitats, pertaining mainly to the presence of canopy cover and percent leaf litter (<30% vs. >90% in older habitats; Table 2). In southern Quebec, Canada, Aubin et al. (2008) characterized young coniferous plantation stands (of similar age and structure to our 11-yr stand) as open-canopy habitats, with understory physical and biological attributes radically different from natural-regeneration stands. Although vegetative succession mitigates for microclimate, our results suggest that other physical factors, such as canopy cover (and the correlated percent leaf litter) exert a larger influence on the movement behavior of juveniles than favorable microclimate. Hence, actions aimed at microclimate mitigation in harvested stands (i.e., by providing refugia such as burrows and coarse-woody debris) might not be successful if juveniles actively avoid such sites based on the lack of canopy

cover (Patrick et al. 2006; V. D. Popescu, *unpublished data*).

The forestry conditions studied here resulted from even-aged management. The trajectory of stand development for even-aged stands (i.e., spatial pattern, tree species mixing, and tree size differentiation) is quite predictable and yields comparable stand structures across the Acadian Forest region (Saunders and Wagner 2008). Our study sites were in stand initiation (clearcut), stem exclusion (11-yr and 20-yr stands), or understory reinitiation (mature forest) stages (sensu Oliver and Larson 1996). While there is natural site-to-site variation, these stand-level processes and disturbance regimes lead to a clear differentiation between naturally regenerated stands treated and not treated with herbicides, and conifer plantations (Newton et al. 1992, Aubin et al. 2008). Studies quantifying differences in physical and biological attributes of stands resulting from even-aged management found vegetation structure comparable to our 11-yr and 20-yr stands throughout
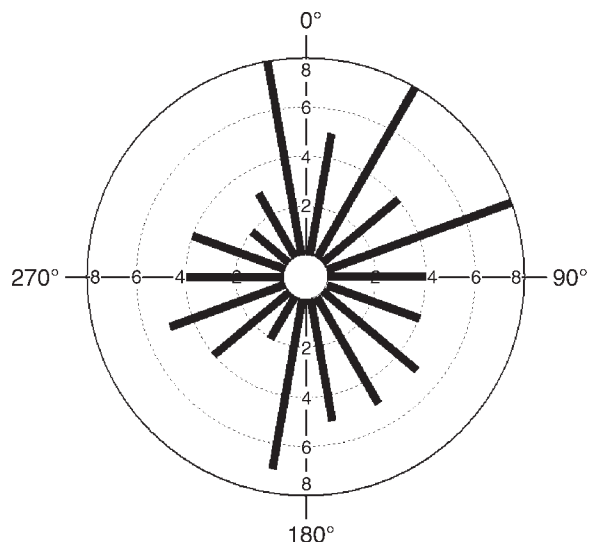

FIG. 4. Orientation of juvenile *L. sylvaticus* (*n* = 89) prior to release in experimental dispersal runways in 2009. Bars represent the number of animals reaching the edge of the circular arena; the scale is given by numbered concentric dotted circles.

the Acadian Forest region (Newton et al. 1992, Ross-Davis and Frego 2002, Ramovs and Roberts 2003). Additionally, because we studied silvicultural practices that are common throughout North America (i.e., clear-cutting), our results may be applicable elsewhere within the species' range, outside the Acadian Forest.

Abrupt changes in habitat resulting from even-aged silviculture negatively influence the abundance of amphibians, and the negative impacts of altered microclimate and microhabitat extend well into the unharvested forest (deMaynadier and Hunter 1998). The rates of movements and proportion of captures were strongly influenced by both habitat quality and proximity to edge. In the clearcut and 11-yr stand, the juveniles that chose to move away from the forest edge moved quickly, presumably in response to being exposed to poor-quality habitat, consistent with the evacuation hypothesis (Semlitsch et al. 2008). Furthermore, the difference in timing of movements between the 20-yr stand and mature forest might be due to adjacency to different quality habitats: (1) animals in the mature forest moved quickly away from the mature forest/clearcut edge, showing an active avoidance of clearcuts and edges (deMaynadier and Hunter 1998, Gibbs 1998); and (2) animals in the 20-yr stand moved away from the 20-yr stand/mature forest edge relatively slowly and tended to settle (Patrick et al. 2008). Thus, the differences in the proportion of animals captured at 40–50 m (i.e., successful dispersers) between these two treatments are probably not due to permeability per se, but to edge-related movement decisions. Settling behavior was also observed in the mature forest (lower number of individuals passing through the 40-m compared to the 20- and 30-m tracking stations). No settling behavior was observed in the clearcut and 11-yr stand. Released animals that were not recaptured either settled in the mature forest and the 20-yr stand or died due to predation or desiccation. Predation is likely to be higher in the open-canopy habitats, and we recorded garter snakes (Thamnophis sirtalis) in runways in both the clearcut and 11-yr stand. Notably, some juvenile L. sylvaticus traveled 50 m per night through all four treatments, sometimes in no-rain conditions, suggesting that the vegetation and substrate of our experimental treatments did not represent physical resistance to locomotion.

Permeability of clearcuts to amphibian movements has been found to be highly dependent on climate parameters such as rainfall or high temperatures (Chan-McLeod 2003, Graeter et al. 2008, Veysey et al. 2009). During our study, the maximum temperatures at ground level rarely reached the critical thermal maximum for L. sylvaticus of 34.8°C (Brattstrom 1963), and the existing refugia provided a cool, moist microclimate throughout the study period (Table 3). However, we found that the study clearcut and 11-year-old coniferous regeneration have limited permeability to juvenile L. sylvaticus even in wet conditions. In both years, we released animals in

both "wet" (rain during the first two days post release) and "dry" conditions, but the rainfall did not have a large impact on the movement patterns. For example, in 2009, the third release (22 July) coincided with two heavy rain events ($\geq$30 mm on 22 July and 25 July), but juveniles in the clearcut and 11-yr stand did not show a higher propensity to move in these treatments compared to the other releases. Only two animals (7%) reached 40 m in the 11-yr stand and three (10%) in the clearcut during this release, which was similar to batches that completely lacked rain: four (13%) and two (7%) animals, respectively, during the fifth release (2 August).

Dispersal plays a critical role in the ecology and biology of many species of amphibians. Dispersers are able to colonize new breeding habitats, recolonize pools following extinction, and affect gene flow. For L. sylvaticus, contemporary metapopulation processes drive population dynamics and maintain high genetic diversity in fragmented landscapes (Zellmer and Knowles 2009). Predicting the process of animal movement and its implications for population or metapopulation dynamics cannot rely solely on assessing habitat cover and landscape configuration (Winfree et al. 2005), although this overly simplified approach has been applied in previous studies of amphibians (see, for example, Stevens et al. 2005). Dispersal in heterogeneous landscapes involves an interaction between habitat structure and configuration (such as various-aged clearcuts in an industrial forest landscape), and behavioral responses of individuals to these structures (Ricketts 2001). Our results suggest that decision behavior (in our case, willingness to travel and avoidance of clearcuts, which dispersers perceive as inhospitable habitat), is more important than the effect of the physical structure on locomotion.

Pond-breeding amphibians are able to recognize and preferentially use suitable habitat, and avoid less optimal habitat at all life stages. In large-scale experiments on the effects of forestry practices on amphibian communities, adult ambystomatid salamanders (Ambystoma maculatum, A. opacum), frogs (Lithobates spp., Pseudacris ornata, Scaphiopus holbrooki), and southern toads (Anaxyrus terrestris) preferentially used closed-canopy habitats (uncut forest and light partial cuts) during their post-breeding migrations (Patrick et al. 2006, Semlitsch et al. 2009, Todd et al. 2009). Similarly, adult European common frogs (Rana temporaria) actively avoided agricultural lands and moved preferentially through hedgerows and meadows (Vos et al. 2007). Juveniles of spotted salamanders (A. maculatum) and American toads (Anaxyrus americanus) are able to recognize and preferentially use suitable habitat, and avoid less optimal old-field habitat (Rothermel and Semlitsch 2002). Our observations on the behavioral response of juvenile L. sylvaticus add to this body of evidence. Almost 30% of the juveniles released in the clearcut and 11-yr stand in 2008, and 50% in 2009, actively avoided these habitats by immediately returning

toward the adjacent forest. Moreover, of the individuals that decided to move away from the forest in these two treatments, a large percentage was captured at 10 m from the release point (20–25%). However, this pattern was not observed at 20 and 30 m from the release point, suggesting that juveniles that decided to move traveled the entire length of the runway. Juvenile amphibians are likely to use proximate orientation cues, such as olfactory or visual cues, and presumably have a limited range of perception given the interaction between understory vegetation and weather conditions (i.e., rainy nights) that usually characterize amphibian migrations (Semlitsch 1985). Support for this idea comes from the study of Rothermel (2004), who found that juvenile salamanders and anurans failed to orient toward the nearest forest when placed 50 m from the forest edge in an open field.

The concept of habitat permeability offers a practical way to predict population dynamics and set conservation priorities across broad spatial scales using Geographic Information Systems (GIS; Compton et al. 2007, Baldwin and deMaynadier 2009). In a recent study, Janin et al. (2009) introduced a new method for assessing landscape permeability for the natterjack toad (*Bufo calamita*) using a calibration/validation method that yielded improved permeability measures that did not require much biological data (compared to the expert-based values). While such exercises have the potential to offer valuable results for conservation planning, our simple forestry-oriented experiment suggests a cautious approach to assigning expert-based permeability (resistance) values to various habitat types. Differing silvicultural management practices lead to different outcomes in terms of vegetative succession, which may affect habitat permeability in the long term. This poses problems for modeling exercises that rely on land cover or habitat maps derived from aerial or satellite imagery. First, the identification of forest successional stages using satellite imagery is difficult (Liu et al. 2008). Second, given the dynamic nature of forest succession, it is necessary to minimize the time lag between acquisition of spatial data and its analysis (Popescu and Gibbs 2009). Moreover, the type of management subsequent to harvesting cannot be extracted from land cover or habitat maps. Without such information, the permeability values assigned to forests are likely to be overestimated.

Our research was limited by the fact that we had no stands with natural regeneration of intermediate age (the 11-yr stand had been sprayed with herbicides to favor conifers and resembled a coniferous plantation). We do have evidence that the avoidance behavior observed in the clearcut and 11-yr stand persisted up to six years after clear-cutting, even when natural vegetative succession was allowed (V. D. Popescu, *unpublished data*). The second limitation is the scale at which we conducted the study. Given that animals reached the end of the runways in one night, we underestimated the true

dispersal abilities of juvenile *L. sylvaticus* by constraining their maximum movements to 50 m. Also, permeability of clearcuts might be slightly overestimated due to the shade provided by the enclosure walls (Patrick et al. 2008).

Our finding of active avoidance of open-canopy habitat, as well as habitats where the successional vegetation mitigates for microclimate effects, but lacks canopy closure, suggest that silvicultural practices that retain greater canopy cover (i.e., partial harvests) are less likely to inhibit juvenile dispersal than clear-cutting. Evidence from large-scale experiments on the effects of various forestry practices on amphibian movements, replicated across three ecoregions support this finding, and partial harvests that retain at least 50% of canopy cover are as permeable to migrating amphibians as uncut forests (Semlitsch et al. 2009). Coniferous plantations have been found to negatively affect amphibian abundance and species richness (Pough et al. 1987, Waldick et al. 1999, Parris and Lindenmayer 2004) and the strong avoidance of the 11-yr coniferous stand during two successive years in our study corroborates these results. Whether or not amphibians exhibit metapopulation dynamics (Smith and Green 2005), extinction and recolonization are landscape-level processes common to many amphibians. Because recolonization of a breeding site is in part the realization of dispersal processes, highly fragmented habitats that have low permeability to movements may hinder recolonization success (Richter-Boix et al. 2007).

The lack of directionality and the preference for closed-canopy habitats observed in this study suggest that in heavily forested landscapes activities that lead to habitat alteration or loss (e.g., timber harvesting, development) need to pay attention to the spatial arrangement of potential breeding sites. Thus, movements of dispersing amphibians might be directed by retaining a certain level of canopy cover between identified high-quality breeding sites (Baldwin and deMaynadier 2009). This management strategy would also be beneficial for the local populations that generally require high-quality habitat for foraging and overwintering in the immediate vicinity of the breeding pool.

Movement ecology of amphibians is taxon specific owing to differences in vagility, vulnerability to desiccation, and habitat preferences. Thus, empirical investigations of habitat permeability for other forest-associated species are warranted. Focusing on the dispersal life stage of various species is likely to give a better understanding of regional population or metapopulation dynamics (Smith and Green 2005). Investigations on the amount of canopy cover retained during partial cuts that will allow for successful amphibian dispersal could also be fruitful. Because we only used recently metamorphosed animals for our experiments, we are uncertain how movement behavior might change during ontogenetic development, and testing habitat permeability for older/larger individuals

should be a priority. Furthermore, a better grasp on the cues that dispersing amphibians rely on for orienting in natural forested landscapes would aid our understanding of movement behavior in fragmented urbanizing landscapes and better inform land-use planning.

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APPENDIX

Proportion of released juvenile Lithobates sylvaticus reaching 10-, 20-, 30-, and 40-m distance from the forest edge in four forestry treatments in 2008 and 2009 (Ecological Archives A021-059-A1).