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Initial Movements of a Dispersing Amphibian in Response to Partial Harvesting in the Acadian Forest of Maine, USA

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Abstract

Maintaining amphibian populations in managed forests requires a balance between timber extraction and retaining functional connectivity for animals that use multiple vegetation types to satisfy habitat requirements, particularly where extensive harvesting may increase fragmentation. Quantifying dispersal patterns in response to harvest, especially across high-contrast edges adjacent to unlogged forest, is critical for evaluating the effects of harvest configuration on amphibians. We tested the initial post-metamorphic orientation of juvenile wood frogs (*Lithobates sylvaticus*) at edges in harvests (31– 60% retention standwide) in the Acadian forest of Maine, USA, during the period when juveniles emigrate from breeding pools. We released juveniles (*n* = 621) in 10-m diameter arena enclosures spanning edges. Frog movement in uncut controls (~70 –75% canopy) was contrasted with movement in the following: harvester trails (0% retention) running parallel to edges of uncut forest; perpendicular harvester trails; or residual strips of partially cut matrix-forest (~30% retention) between trails. We observed a nonsignificant trend for higher proportions of individuals entering control forests versus harvests (x_1^2 = 2.504, *P* = 0.113) and a stronger trend for movements into control forests versus perpendicular-oriented trails (52:35 for forest versus treatment; x_1^2 = 3.322, *P* = 0.068). The biological relevance of such patterns warrants further consideration. Juveniles may enter partial harvests at rates similar to those for intact forest, but quantifying the effects of harvest configuration on movement patterns, residency times, and ultimately survival is necessary to determine whether these harvests represent sink habitats.

Introduction

Integrating timber management goals with biodiversity conservation often involves linking management of unlogged areas with forest practices on adjacent harvested areas, especially for relatively mobile animals that navigate multiple vegetation types to meet habitat needs (Hunter and Schmiegelow 2011, Driscoll *et al.* 2013). For amphibians in managed-forest landscapes, quantifying the tendency of post-metamorphic juveniles to enter harvests across high-contrast edges adjacent to unlogged forest remains a critical challenge in predicting population responses to forest harvesting due to the vital link between successful juvenile dispersal and population regulation (e.g., Semlitsch 2008). In northeastern North America, this issue gains additional traction as silvicultural methods shift away from intensive clearcutting toward partial harvesting, because the cumulative effects of multiple entries implemented over large areas may only increase the effects of fragmentation (e.g., Vanderwel *et al.* 2009, Hocking *et al.* 2013a). Successful dispersal may depend on the characteristics of the matrix that intervenes between suitable habitats (Kuefler *et al.* 2010, Burgess *et al.* 2012). Thus, quantifying the movement patterns of individuals as they encounter logging-induced edges could have important implications for maintaining connectivity as harvest practices trend away from even-aged management.

In recent decades, understanding the effects of forest management on amphibian populations has been of particular concern because of their demonstrated sensitivity to habitat loss or fragmentation (deMaynadier and Hunter 1995), biphasic life histories linking terrestrial and aquatic systems (Davic and Welsh 2004, Tilghman *et al.* 2012), and potential keystone roles in forest ecosystems as abundant apex predators in detrital food webs (Walton 2005, Best and Welsh 2014, Semlitsch *et al.* 2014). Many studies have documented long-term negative impacts of complete canopy removal (i.e., clearcutting) on amphibian distribution and abundance (Karraker and Welsh 2006, Semlitsch *et al.* 2009, Popescu *et al.* 2012). Similarly, high-contrast edges between recently cut and mature forests have exhibited low permeability to movements (Stamps *et al.* 1987, Popescu and Hunter 2011), probably because of higher levels of sunlight, wind speeds, and greater variation in humidity and temperature found at the edge relative to those in the interior forest (Harper *et al.* 2005, Olson *et al.* 2007). Yet, there remains a critical need to assess amphibian movement across landscapes that may be fragmented by logging (e.g., Graeter *et al.* 2008) because long-term population viability may depend on dispersal vis-a`-vis unidirectional movement of some juveniles from natal areas to new breeding locations (Pilliod *et al.* 2002, Semlitsch 2008). In contrast to assumptions of patch-matrix models that oversimplify the nonforested matrix as inhospitable, recent evidence suggests that some frogs may transit various vegetation types (including open cover) during the dispersal period, even if they are unsuitable for settling (Mazerolle 2004, Cline and Hunter 2014). Further behavioral studies may elucidate factors influencing juvenile amphibian movements in forests fragmented by logging and, specifically, may quantify their movements relative to various harvested and nonharvested vegetation types within the matrix (Franklin and Lindenmayer 2009, Van Buskirk 2012).

The need to assess amphibian dispersal behavior in forestry settings is particularly pressing in northeastern North America, where harvesting practices have shifted from a heavy reliance on intensive clearcutting in distinct patches to more extensive partial harvesting where stands are naturally regenerated. Typically, partial harvests in the Acadian region are implemented in herring-bone patterns of parallel harvester machine trails (3–4 m wide) spaced 15–20 m apart; often 30–60% of the matrix stand between the trails is removed (Bataineh *et al.* 2013) (Figure 1). We define harvests that remove 40–60% of the stand basal area as “heavy partial harvests.” Partial harvesting is currently the predominant form of timber extraction in Maine, USA, accounting for 95% of the total 186,703 ha harvested during 2012 (Maine Forest Service 2013). This trend has been attributed to changes in forest policy, market conditions, equipment technology, silvicultural knowledge, and landownership including large quasi-industrial landbases where logging contractors can balance investments for extensive operations that often result in strong geometric harvest arrays (Sader *et al.* 2003). Multiple entries using a diversity of cut-to-length result in variable stocking, stand structure, and fragmentation patterns.

However defined, there is a limited understanding of how heavy partial harvesting implemented in a herringbone pattern affects regeneration, future stand structure, or landscape-level composition (Bataineh *et al.* 2013). The dearth of information hinders our ability to devise silvicultural prescriptions, project future wood supplies, and assess biodiversity impacts (Driscoll *et al.* 2013). For example, in a review of wildlife responses to partial harvesting (sensu lato), researchers found that 38 of 65 vertebrate species associated with mature or old boreal forest decreased in abundance after high-intensity harvesting (30% retention) (Vanderwel *et al.* 2009, also see Rosenvald and Lõhmus 2008), a result corroborated by other studies that documented a negative relationship between harvest intensity and amphibian habitat use (e.g., Homyack and Haas 2009) and survival (Todd *et al.* 2014). However, few studies provide a mechanistic link of vegetation structure to faunal response (e.g., Vanderwel *et al.* 2011), and there is a need to investigate species responses through field studies of wildlife responses to treatments, including studies of movement patterns. Throughout the Acadian region, partial harvesting is increasing fine-scale spatial heterogeneity (depicted in Figure 1) at widely varying harvesting intensities, which raises concerns about the effects of this form of management on a diversity of biota including amphibians.

Study Species

We studied the wood frog (*Lithobates sylvaticus*) because of its widespread distribution in North America and its dependence on closed-canopy forest. This species has demonstrated high sensitivity to forest removal and avoids forest edges (deMaynadier and Hunter 1998, Semlitsch *et al.* 2008). After emergence from natal pools, juveniles inhabit moist terrestrial landscapes, foraging on invertebrates and hibernating within refugia (e.g., burrows, tree root channels, leaf litter, and coarse woody material) (Cushman 2006). Although some juveniles will return to natal sites to breed (i.e., philopatry), ultimate dispersal success (i.e., juveniles surviving to breed in new sites) is estimated to be 18–20% (Berven and Grudzien 1990). Dispersal distances have been recorded at >1,000 m (females: 1,140 ± 324 m; males: 1,276 ± 435 m), with a maximum of 2,530 m (Semlitsch and Bodie 2003). Postbreeding movements of adults have been estimated to be 102–340 m (Baldwin *et al.* 2006) and >300 m (Vasconcelos and Calhoun 2004). The scale of overland movements may make this species vulnerable to upland habitat disturbances that result in alterations of movement patterns and dispersal success.

Study Goal and Predictive Framework for Post-metamorphic Movements

Our goal was to document the short-term behavioral responses of juvenile wood frogs to habitat condition during the post-metamorphic period. Within each arena, juvenile frog movements in uncut control forest were contrasted with one of three conditions in the adjacent partially harvested stand immediately next to the arena: harvester trails running parallel to the edge of the uncut forest; harvester trails running perpendicular to the edge; or residual strips of partially cut matrix forest between trails (Figure 1).

We hypothesized that five environmental factors (i.e., vegetation structure, microclimate, food, conspecifics, and predators) might influence observed juvenile movement behavior at the edge between the control and partially harvested forest. Previous studies have documented that amphibians may 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.* 2012), microclimate (Rittenhouse *et al.* 2008), and predation risk (Pittman *et al.* 2013). We conjectured that the frogs in our study were largely in a directed mode and were using a variety of cues (e.g., visual, chemosensory, and others) to explore in search of food, cover, and appropriate microclimate, often influenced by habitat and landscape features beyond the boundaries of our experimental arenas.

Given that partial harvesting reduces overstory cover and eliminates cover completely in the harvester trails (cumulatively comprising >20% of the managed stand), our guiding hypothesis was that juveniles would move toward vegetation that provided greater cover from thermal stress and predators. We further hypothesized that movement timing would be more protracted in the control if some frogs were able to occupy suitable microhabitats in the experimental area. Finally, we speculated that harvester trail orientation might influence responses. Specifically, we conjectured that parallel trails would be more permeable to movements than perpendicular trails.

Methods

Study Sites

Our experiment was conducted in Penobscot County, Maine, on harvests prescribed by American Forest Management (AFM), a private timber company that conducts harvests representative of current regional practices. AFM's Northeast Region currently manages greater than 400,000 ha in Maine and New Hampshire (T. Massey, pers. comm., American Forest Management, Inc., Nov. 21, 2013). We used two study sites in Titcomb Pond and Great Pond Townships, Maine (44.94°N, 68.43°W and 44.99°N, 68.31°W, respectively) that had similar prescriptions, and where edges were oriented in different cardinal directions relative to trails (Figure 1) to eliminate any possible directional bias. Multiple harvest entries had occurred on our sites; intensive clearcutting was conducted in the late 1980s, but more recent harvests were broadly categorized as second or third stage shelterwoods with harvesting traffic concentrated in parallel strips (Figure 1). The most recent timber removal occurred in 2008 or 2009. All harvests were performed using whole-tree removal (Timbco 425 track harvester and grapple skidder; Timbco LLC, Morrisville, NC) with delimbing off-site; trails were devoid of canopy and diminished in cover objects that might serve as amphibian refugia.

The prescription goal was to maintain 80% forested conditions, with 20% occupied in trails and a standwide nominal goal of 31–60% crown closure (with 0% closure in the center of harvester trails, this would mean 39–75% in residual strips). We documented 27.4– 30.4% average canopy cover across residual strips, suggesting standwide closure of 23%. The width of harvester trails ranged from 4.9 to 5.5 m, depending on sizes of equipment and trees. The distance between harvester trails (center-to-center, not edge-to-edge) was 22.8–27.4 m. Our closest experimental arenas were 124 m apart, and the farthest were 12.7 km apart.

Our study region is characterized by a humid continental climate (Köppen Dfb) (Peel *et al.* 2007), with warm-hot, humid summers and cold-severely cold winters, and is part of the Acadian region (Seymour 1995), a transitional zone between temperate forest and boreal forests. Partial disturbances from insect, wind, and natural senescence and small-scale gap dynamics probably characterized the presettlement natural disturbance regime (Seymour *et al.* 2002, Fraver *et al.* 2009). However, extensive forest management has generated a mosaic of mixed-wood stands of various age classes (e.g., Arseneault *et al.* 2011). Our sites were composed of a mixture of northern conifers and tolerant hardwoods: red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), eastern hemlock (*Tsuga canadensis*), eastern white pine (*Pinus strobus*), northern white cedar (*Thuja occidentalis*), red maple (*Acer rubrum*), bigtooth aspen (*Populus grandidentata*), paper birch (*Betula papyrifera*), and American beech (*Fagus grandifolia*). Stand composition indicated a successional shift toward hardwood dominance (30–70% basal area).

Experimental Design and Arenas

We constructed nine experimental arenas at the edge of intact forest and partially harvested stands representing three harvest treatments always paired with a control (Figure 1). We built nine 10-m diameter arenas (3 treatments X 3 replicates) using partially opaque polyethylene silt-fence 40–50 cm in height plus 10–15 cm buried in the ground. Arenas of 10 m are small relative to the general distribution patterns of amphibians near edges (deMaynadier and Hunter 1998), but detailed studies of the movements of juvenile wood frogs indicate that they are responsive to edges at such fine scales. Recent studies (e.g., Popescu and Hunter 2011, Pittman and Semlitsch 2013, Pittman *et al.* 2014) use direct tracking methods to follow individual movement and indicate that dispersing juvenile amphibians are able to perceive proximate conditions and make movement decisions at quite small spatial scales (5–10 m) during the post-metamorphic period in managed forest settings. In particular, two studies (Popescu and Hunter 2011, Cline and Hunter 2014) determined that juvenile wood frogs actively avoided open-canopy habitats and sharp edges and returned toward closed-canopy forest at 0 and 10 m distances in recent clearcuts and other open-canopy habitats. Thus, we designed 10-m diameter experimental arenas to document the juvenile amphibian movement decisions (relative to each silvicultural edge) at a fine and immediate spatiotemporal scale. Within each arena, we buried two pitfall traps along the inner perimeter of fence walls, one in the middle of the control forest portion of the fence and another directly opposite. Arena walls were 60 cm in height and buried 15–20 cm into the ground to minimize metamorph trespass or escape from arenas during trials. Pitfalls consisted of two 10-cm aluminum cans taped together and buried 24-cm in the ground, with a 10-cm deep funnel extending into buckets (Figure 1).

Juvenile Amphibian Rearing and Release

Before the experiment, we collected 12 *L. sylvaticus* egg masses from diverse breeding locations (e.g., natural vernal pools, roadside ditches, and skidder ruts) at the University of Maine's Dwight B. Demeritt Experimental Forest, Maine (44.92°N, 68.67°W) during the spring egg-laying season (April–May 2011). Larvae and metamorph frogs were reared communally in seminatural mescosms (12 cattle tanks; 1,500 liters each) at a forested site using methods described in Cline and Hunter (2014). At Gosner stages 242, individuals were transferred into large plastic bins (200 liters; moist leaf litter) for 1–2 days until metamorphosis (stage 47) (Gosner 1960). Because of this mixing of individuals at the larval stage (i.e., egg masses from different sources were distributed among multiple tanks), a genetic effect of clutch was unlikely.

Frogs were released in five batches of individuals from mixed clutches over 20 days: one batch each on July 6, 12, 15, 18, and 26, 2011. Before each release, we measured (snout-vent length), marked (single different toe clip per batch), and randomly assigned frogs to one of our two study sites, three treatments, and nine arenas. We released 7–18 frogs per batch (621 frogs across five batches). Frogs were placed at the forest edge and in the arena center 1–2 hours after sunset and then traps were monitored daily between 6:30 and 11:00 am from July 6 and August 10. Because each pitfall trap was placed in the center of each 180° treatment "arc" of silt-fence framing each arena, an individual frog that elected to move toward the center of one treatment would ultimately fall in the pitfall trap associated with that treatment if it continued to move in the same direction of its initial orientation when it encountered the fence. If an individual frog continued to orient in the direction that it selected immediately after release, it would be "guided" (by the silt fence) to the pitfall trap associated with the directionality of its initial movement decision. Changes in initial movement orientation and directionality have been documented for juvenile wood frogs during the post-metamorphic period (e.g., Popescu and Hunter 2011, Cline and Hunter 2014) and might even be common during the exploratory phase of juvenile dispersal if immediate cues (or experimental treatments in our study) do not act strongly on individual movement decisions. We released subsequent batches only after recapture rates were >40% of the total number released in the prior batch. By waiting 3–8 days between batches, most frogs from the prior releases had been recaptured (minimizing density-dependent effects). Recaptured frogs were returned to forest near their pools of natal origin.

Microclimate and Habitat Sampling

We characterized microclimate, microhabitat, and stand-scale vegetation within arenas and adjacent control and partially cut forests. We recorded hourly temperatures (° C) and relative humidity (%) using 36 iButton hygrochron dataloggers (Maxim, Inc., Dallas, TX) for the duration of the experiment. Temperatures were measured at the center of each arena at (1) ground level, (2) under refugia (i.e., 5–8 cm under coarse woody material or slash), and (3) 120 cm aboveground in shade; we also measured ground-level relative humidity (4). We sampled hourly temperature in the control and partial-harvested treatment 15 m from the edge.

We characterized vegetation and microhabitat in terms of ground cover, canopy closure, vegetation height, dominant-species composition, leaf-litter depth, and soil moisture. Sampling occurred in 54 3 X 3-m (9 m^2) plots positioned within each arena (2 plots per arena; 1 in the control and 1 in the partial-harvest treatment semicircle) and outside of each arena, 10 m into each control or treatment (4 plots per arena). We measured percent vegetation cover in four height classes (0–0.5, 0.5–1, 1–2, and >2 m) and dominant composition at the tree, shrub, and herb level. We estimated percent canopy cover using a densiometer (Moosehorn CoverScopes, Medford, OR). We estimated ground cover as the percentage of 3 X 3-m plots classified as leaf litter, moss/lichen, herbaceous, slash, bare soil, and rocks. We collected leaf-litter depths and soil moisture (Field-Scout TDR 100 soil moisture meter; Spectrum Technologies, Aurora, IL) at 8 cm belowground at 3 randomly determined locations per plot.

Analytical Approach

To assess the initial orientation of each frog relative to the forest edge and recapture outcomes, our dependent variable was the proportion of frogs that were recaptured in the control versus treatments out of the total released per treatment, arena, and batch. We used pairwise tests for proportions and X^2 tests to estimate differences in proportions of recaptures at the individual and batch levels.

We also evaluated potential differences in movement timing (1–25 days after release). For each recaptured frog, we calculated the number of days that had passed between the date of initial release and final recapture and evaluated differences using a nonparametric (X^2) Kruskall-Wallis test for proportions (R package [coin]) (Ho-thorn *et al.* 2008), selected because it is well suited for data that comprise proportions and does not assume a normal distribution of the residuals. We examined the goodness of fit of our observed movement timing data (i.e., the number of individuals recaptured on days 1–25 post-release, pooled by treatment) relative to predicted values using a nonlinear mixed-effects model, allowing for nested random effects and assuming a nonlinear exponential decay function (R package [nlme]) (Lindstrom and Bates 1990, Pinheiro and Bates 2000). We assessed potential differences in the size of metamorphs (SVL) released among treatments and arenas using a one-way analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) single-step test for multiple comparisons. In the strictest sense, statistical tests were deemed significant at $P < 0.05$ and marginally significant at $P<0.07$. However, we also acknowledged that field studies in behavioral landscape ecology may be suggestive of biologically relevant patterns at slightly elevated αlevels (i.e., $P≤0.10$) relative to tightly controlled studies of animal behavior in laboratory settings where single causation factors are more easily isolated (e.g., Okland 2007, Garamszegi et al. 2009). All statistical tests were conducted in R, version 3.0.2 (R Development Core Team, Vienna, Austria 2013).

Results

Our experimental design generated three simple metrics to quantify the initial post-metamorphosis orientation of juvenile *L. sylvaticus* released at partially harvested forest edges: movement direction of recaptured individuals; percentage of released animals that were recaptured; and movement timing and latency (described below). The average size of juveniles was 15.4±0.1 mm (snout-vent length [SVL]), with no significant differences among batches 2–5 (i.e., 12, 15, 18, and 26 July, 2011); batch 1 individuals (July 6) were significantly smaller (13.9 ± 0.1 mm; $F_{1,243} = 4.27$, $P < 0.001$; ANOVA, Tukey's HSD).

Movement Behavior at the Harvest Edge: Initial Post-metamorphosis Orientation and Proportion of Recaptures

Across all trials, we recaptured a greater proportion (54.8%) of frogs in the control forest portions of enclosures than in the partial harvest areas (45.2%, based on the distribution of 270 recaptured individuals out of 621 released) (Figure 2). A test for global significance (i.e., forest captures versus treatment captures summed across sites, arenas, and batches) was not strictly significant ($x_1^2=2.504$, $P=0.113$), but the trend may have biological relevance. Analysis by treatment revealed a trend for avoiding the edges that were oriented perpendicular to trails (captures=52:35 for forest versus treatment; $x_1^2 = 3.322$, *P* = 0.068) (Figure 2), but no trend in arenas located adjacent to parallel trails (57:53 for control forest and treatment, respectively; $x_1^2 = 0.146$, *P* = 0.703) or at the confluence with residual strips (39:34 for control versus treatment; $x_1^2 = 0.343$, *P*= 0.558).

Departures from the Harvest Edge: Percentage of Frogs Recaptured in Experimental Arenas

Across all arenas, 43.2% of released frogs were recaptured (270/621) (Table 1). We observed the least proportion of recaptures in the control versus residual strip arenas (30.4–36.2% across replicates); in contrast, we observed the highest recaptures within arenas located at the edge of harvester trails (mean percent recaptures_ 42.0% for perpendicular trails and 53.2% for parallel; x_8^2= 19.20, *P* = 0.013) (Table 1). Among batches, the percentage of recaptures tended to be greater earlier in the emergence season (43.1–51.0% between July 6 and 18 versus 27.8% for those released on July 26), although these differences were insignificant ($x_4^2 = 0.7.51$, *P* = 0.111).

Latency at the Edge: Movement Timing and Potential Short-Term Residency

Most movements (92.5%) occurred within the first 8–10 days after a release, and the timing of recaptures did not differ significantly between the control and partial-harvest portions of arenas (*P* = 0.693 for comparison of generalized linear mixed models) (Figure 3). However, it is noteworthy that individuals could persist along the forest edge (presumably in temporary settling mode or latency) for up to 25 days postrelease (*n* = 17 from initial batch releases on July 6 and 12). Finally, treatment-side captures occurred earlier (59.2% by day 2 versus 46.6% for control side) (Figure 3), although differences were insignificant ($x_1^2 = 1.501$, *P* = 0.221).

Harvested and Forested Edge: Microclimate and Microhabitat Features

As expected, we observed a >10° C difference in average daily maximum temperatures between control and partially cut forest at points 10 m from the edge (23.7° C versus 33.9° C, respectively) (Table 2). Within arenas, we observed the lowest daily maximum air, ground, and refugia temperatures in the residual strip arenas (31.8°, 33.9°, and 30.7°, respectively) and the highest average daily maximum at ground level in arenas abutting harvester trails (40.4° and 38.8° in parallel and perpendicular, respectively). On average, treatment edges maintained similar levels of ground-level humidity (84.3– 88.6%), although mean daily minimums showcase the wide range of possible moisture levels (driest in parallel trail treatments: 37.8%) (Table 2).

By design, the control had high canopy cover within and outside of arenas (68 and 73%, respectively) (Table 3). Tree canopy cover was moderate in the residual strips (27 and 30% within and outside arenas), which was below prescribed targets (31–60% closure). In contrast, low-vegetation layers (0.5–2 m) dominated harvester trails; herbaceous and shrub layers constituted 24–35% of cover (tree canopy cover: 19.6 and 6.4% within and outside of arenas, respectively). For ground cover, leaf litter and moss together accounted for >70–89% in the control, whereas herbaceous vegetation and slash comprised high coverage in trails (31 and 21%, respectively, within arenas; 21 and 40% outside arenas). Soil moisture was highly variable among sites (9.1–23.2%) and greatest in control forest outside of arenas. The greatest average soil moisture was in harvester trails (21%), presumably due to reduced transpiration. Leaf-litter depth ranged from 1.4 to 2.5 cm but was deepest in control and partial cuts (e.g., 2.4 and 2.5 cm within arenas, respectively) and 1.8 cm in all trails (Table 3).

Discussion

Despite the well-established body of knowledge on the effects of even-aged silviculture on amphibians (e.g., deMaynadier and Hunter 1999, Semlitsch *et al.* 2009, Todd *et al.* 2014), there is still much to learn about effects on movements (and ultimately natal dispersal), particularly in the context of the heavy partial-harvesting practices that have become prevalent in the Acadian region (Thorpe and Thomas 2007, Turner *et al.* 2013). In this study, we tested the initial and short-term orientation of juvenile frogs at the edge of heavy partial harvests (average, 30.4% retention; nominal goal, 31–60%) (Table 3) to evaluate whether pool emigrants might respond differently to harvests by altered movement patterns. Contrary to our prediction, we observed no statistically significant difference in the proportions of individuals entering the control forest versus harvests, although P =0.11 may be suggestive of a biologically relevant pattern for field studies in behavioral ecology (e.g., Garamszegi *et al.* 2009). The only difference that approached strict statistical significance was for selection of forest versus perpendicular-oriented trail (52:35 for forest versus treatment; P =0.068). This pattern suggests that the vegetative structure and microclimatic regime of partially harvested stands is not as likely to be avoided by emigrating juveniles as clearcuts (e.g., Semlitsch *et al.* 2008).

Comparisons with Prior Studies of Partial Canopy Removal and Juvenile Amphibians

A recent meta-analysis on the effects of timber harvest on terrestrial amphibians highlights considerable variation: Tilghman *et al.* (2012) found that short-term population declines (of fully terrestrial species) ranged from 29% in partial harvests (95% confidence interval [CI] =-2 to 51% for 108 species and 24 studies) to 62% for clearcutting (95% CI =29-80%). In particular, patterns of amphibian response to partial cutting are confounded by wide variations in harvest intensities (when reported: retention of 30–70% canopy and 4–59 m2/ha basal area). In accord with some past studies of partial harvests and amphibians (e.g., Perkins and Hunter 2006, Popescu *et al.* 2012, Todd *et al.* 2014), our experimental animals showed little difference in the use of control and partial-cut treatments (Figure 2). For example, similar abundances of western slimy salamanders (*Plethodon albagula*) occurred in uncut control and partially harvested forest with 60% stocking density retained (Hocking *et al.* 2013b). Yet, some prior studies suggest a contrary pattern, instead detecting decreases in species abundances after high-intensity (30% retention) partial harvesting (Morneault *et al.* 2004, Vanderwel *et al.* 2009, Tilghman *et al.* 2012). Our study occurred in heavy harvests with low canopy retention (average of 30.4%) (Table 3), and our focus was on initial dispersal decision-making. Studies of individual movements across a range of harvest intensities will be critical for elucidating dispersal success and survival. For example, in a study of the effects of partial canopy removal (~75% retention) on survival of ambystomatid salamanders in North America, Todd et al (2014) found that adults survived as well as or better in partially harvested stands as in controls, but juvenile survival in harvests was significantly less. Low juvenile survival in partially cut stands could mean that these harvests constitute habitat sinks if individuals are willing to enter harvests but then have high mortality during the critical post-metamorphic or dispersal period.

It is not surprising that by retaining some structural features of more mature forests, partial harvests may exhibit weaker effects on populations than intensive clearcutting (e.g., Steventon et al. 1998, Semlitsch et al. 2009, Titus et al. 2014). However, evidence suggests that there may be cumulative negative impacts of partial harvesting due to repeated-stand entries (Reichenbach and Sattler 2007, Homyack and Haas 2013). If populations cannot recover quickly, multiple harvests may depress abundances on decadal scales (e.g., Petranka et al. 1993, Harper and Guynn 1999, Karraker and Welsh 2006).

Effects of Partial-Harvest Landscape Configuration on Juvenile Orientation

Consistent with predictions, our results suggest that the perpendicular trail orientation may represent a partial filter to movements (captures = 52:35 for forest versus treatment; *P* = 0.068) (Figure 2). Studies indicate that amphibians modify movements in response to ground substrate (Semlitsch et al. 2012), habitat extent (Walston and Mullin 2008), vegetation structure, microclimate (Rittenhouse et al. 2008), and physiology (Janin et al. 2012). Pool-exiting juvenile salamanders (*Ambystoma texanum*) and wood frogs have also been shown to exhibit nonrandom orientation influenced by the width and shape of the surrounding forest (Walston and Mullin 2008). At our sites, the harvest pattern resulted in a high perimeter/area ratio for strips within stands (<6-m-wide skid trails; <28-m-wide residual strips) and two different edge configurations: where trails were perpendicular about 20% of the edge would be trail-to-forest and for parallel trails 100% of the edge would be trail-to-forest. If frogs rely on visual orientation cues, animals may have perceived an increase in predation or desiccation risk when facing a perpendicular trail; this is consistent with prior evidence that pool-exiting amphibians can perceive forest from at least 10 m (Rosenberg et al. 1998, Pittman and Semlitsch 2013) and with a recent study of our target species suggesting that juveniles in open cover orient toward forest 40–55 m away (Cline and Hunter 2016).

Potential Effect of Microclimate and Microhabitat on Edge Effects and Forest Influence

It is well established that timber harvesting temporarily modifies microclimatic regimes for amphibians (Feder 1983, Karraker and Welsh 2006) and thus may affect orientation and habitat selection for dispersers (e.g., Baker et al. 2013). Given that partial harvesting reduces canopy cover overall and eliminates it completely in trails, we hypothesized that juveniles would avoid our treatments. Overall, our results suggest only limited links between humidity, temperature, and the ecophysiology associated with frog behavior because the microclimate regime of our treatments did not deter a significant portion of frogs from entering (with the possible exception of the perpendicular-oriented trails). However, limited evidence suggests a possible link between microclimate and frog behavior. Notably, more frogs in the treatment side of arenas were captured early (59.2% by day 2 versus 46.6% for the control side captures) (Figure 3) perhaps because they moved quickly due to risk of desiccation. We also observed lower mean daily maximum temperatures at all levels in residual strip arenas (range, 30.7–33.9°) relative to trails. Although microclimate appeared to play a limited role in frog behavior during our study, we should note that the relative influence of these factors on amphibian movements may differ markedly by region; for example, between Maine and Missouri (Semlitsch et al. 2008) where the climate is hotter and drier.

Implications for Future Research and Forest Management

In our experiment, we focused on a short-term behavioral response—the initial movement direction of pool-exiting juveniles— because post-metamorphic movements and eventual dispersal potentially involve large-scale travel. During this post-metamorphic period, unexperienced or naive frogs may be willing to enter open trails or strips even if they differ from preferred conditions for settlement. Given our short time frame, we urge caution in extrapolating to adult stages or other seasons when the behavioral context may involve prior experience, site fidelity, or nonrandom directionality. Indeed, the use of partial harvests and subsequent survival may differ between adults and juveniles (Popescu *et al.* 2012), and juveniles have also been shown to make forays of >30 m into open-canopy vegetation before changing direction toward forest (Cline and Hunter 2014). In our study, we constrained movement within 10 m and thus could not evaluate the ability of individuals to enter treatments, assess habitat, and change directionality. We did not construct arenas solely in control forest (rather, our arenas straddled uncut control forest), a feature that could be useful for future studies in partial harvest settings, although it is well documented that juvenile amphibians demonstrate more meandering paths, random directionality, and prolonged latency when transiting through intact forest (i.e., >20 years post-harvest) (Popescu and Hunter 2011, Cline and Hunter 2016). Longer-term tracking of individual movements (e.g., using fluorescent powder or another tracking mechanism) is needed to elucidate behavior (e.g., search mechanisms, velocities, and path tortuosity) and to determine scales over which movement decisions are made.

Current forest practices in the Acadian forest are creating unprecedented harvest configurations (i.e., extensive strips of trails and logged matrix), and the effects of this spatial structure on wildlife populations remains relatively unknown (Fuller *et al.* 2004, Reichenbach and Sattler 2007, Graham-Sauvé *et al.* 2013). Partial harvesting may result in (1) increased forest edge and fragmentation, (2) expanded harvester-trail coverage, (3) greater variability in harvest intensity, and (4) more frequent stand entry, all of which may affect habitat connectivity and biodiversity patterns. Our study is among the first to empirically test individual amphibian behavior in partial harvests as currently implemented in the Acadian region. However, we need more studies to assess the ability of individuals to survive within harvests (Todd *et al.* 2014) or recolonize regenerating partial harvests between entries (Homyack and Haas 2009). Ultimately, the habitat value of partially harvested forests for amphibians will depend on whether populations are capable of persisting and across a complete cycle of harvests, and this will require some dispersal among breeding sites.

Predicting these responses to partial harvesting is hindered by the dearth of direct, long-term studies of stand composition and structural changes over time (Bataineh *et al.* 2013), which underscores the need to develop a scheme to better describe harvest intensity, stand reentry, and landscape configuration. In summary, to conserve amphibian population connectivity in landscapes where partial-harvest silviculture is predominant, we need to integrate more refined descriptions of harvest practices with studies of individual behavior across a range of approaches to harvesting.

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Figures

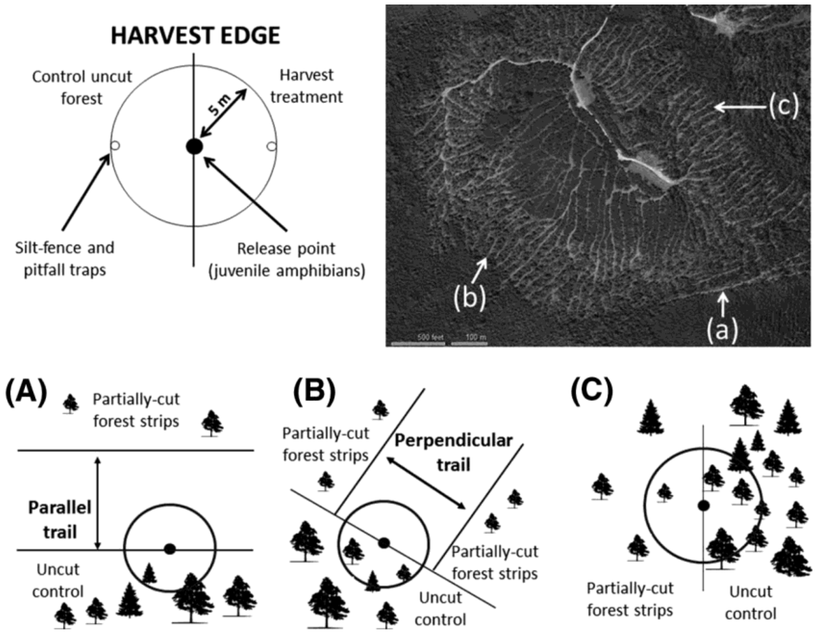


Figure 1 Experimental design for evaluating the initial dispersal orientation of juvenile wood frogs (*L. sylvaticus*) in 2011 along three types of linear edges between partial harvest treatments and intact forest (i.e., closed-canopy mixed-wood stands directly adjacent to heavy partial harvests). Silvicultural edge treatments included tracts of uncut control forest located (A) parallel to harvester trail (trail within cut; 100% canopy removal), (B) perpendicular to harvester trail (trail within cut; 100% canopy removal), and (C) adjacent to residual strips of partially cut forest (off-trail). Each experimental arena (two replicates of each edge treatment, for a total of *n* = 9 arenas in two study landscapes) consisted of a 10-m diameter circular silt-fence enclosure (40–50 cm height), extending 10–15 cm in the ground. Two pitfall traps (indicated by open circles, above) were buried on the fence interior of each arena, located in opposite cardinal directions and extending into each edge treatment to test initial frog orientation following experimental release (mark-recapture).

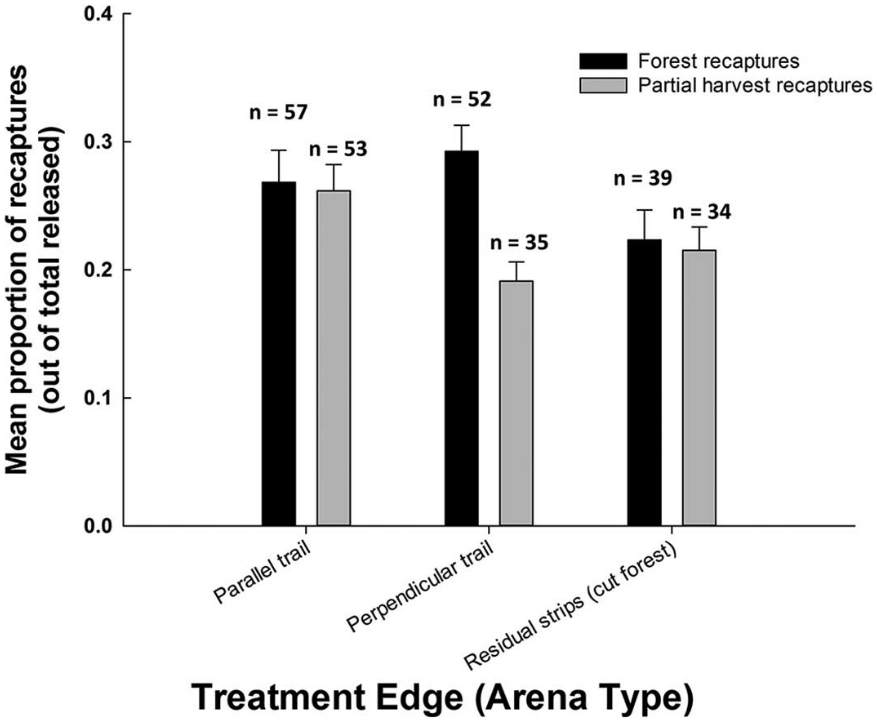


Figure 2 Observed proportions of juvenile *L. sylvaticus* recaptured in forest or partial harvest treatments, after experimental releases along three types of silvicultural edges between contiguous control forest and heavy partial-harvested stands in 2011 (means ±SE). Silvicultural edge treatments included tracts of uncut control forest located parallel to harvester trail (trail within cut; 100% canopy removal), perpendicular to harvester trail (trail within cut; 100% canopy removal), and adjacent to residual strips of partially cut forest (without harvester traffic) within the harvested stand. Values on the *y*-axis are observed proportions of released individuals recaptured in pitfall traps averaged across treatments (*n* = 3 arena types), individual arenas (*n* = 9 arenas), and experimental batches (constituting 621 individual frogs released during 5 batches between July 7 and Aug. 2, 2011). Differences in the orientation of recaptured juvenile frogs approached significance in the edge treatment with perpendicular trail configuration (middle bars in above graph; X^2 =3.322; *P* = 0.068).

Table 1 Numbers of juvenile wood frogs (*L. sylvaticus*) recaptured in experimental arenas after releases located along three types of silvicultural edges between control forest and three partial-harvest treatments (parallel harvest trail, perpendicular harvest trail, and residual strips of partially cut forest between trails) in 2011.

	Treatment/release date	Arena (no.)	No. juveniles released	Individuals recaptured by site, treatment, arena or batch (date of experimental release)	
				No. juveniles recaptured	Proportion of recaptures
Site					
Titcomb	CF, parallel	1	69	46	0.667
	CF, perpendicular	2	69	31	0.449
	CF, residual strips (cut)	3	69	25	0.362
Great Pond	CF, parallel 1	4	69	32	0.464
	CF, parallel 2	5	69	32	0.464
	CF, perpendicular 1	6	69	30	0.435
	CF, perpendicular 2	7	69	26	0.377
	CF, residual strips (cut)	8	69	27	0.391
	CF, residual strips (cut)	9	69	21	0.304
	Totals	9	621	270	
Batch (no.)					
1	July 6, 2011		65	33	0.508
2	July 12, 2011		144	67	0.465
3	July 15, 2011		153	66	0.431
4	July 18, 2011		162	77	0.475
5	July 26, 2011		97	27	0.278
Totals			621	270	
Mean recapture proportion					0.432

Harvest trails have complete overstory removal; residual strips are off-trail (~30% retention). Data are proportion of recaptures in either the forested or partially harvested treatment out of the total released, further categorized by individual arena and batch. CF, control forest.

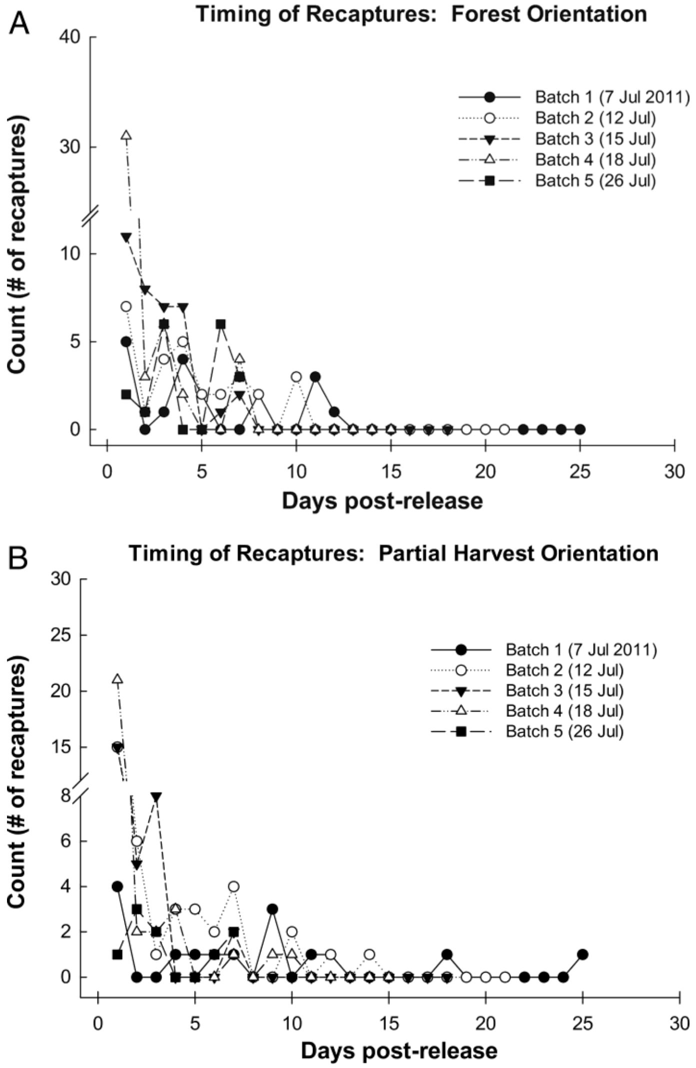
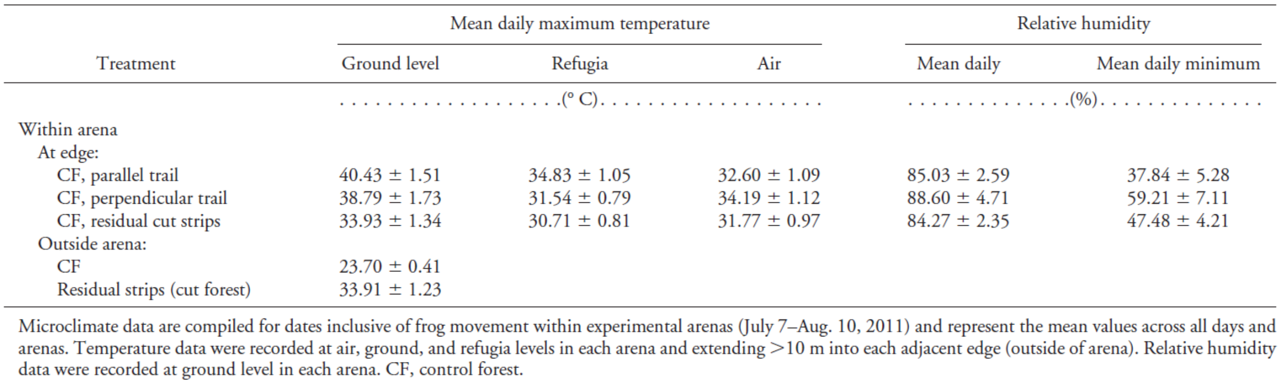


Figure 3 Timing of movements of juvenile *L. sylvaticus* experimentally released in three treatments in enclosed arenas along silvicultural edges between control forest and partially harvested stands. The number of recaptured individuals (*y*-axis) denotes the number recaptured in either the forested (A) or partially harvested (B) semicircle of each experimental arena out of the total released for that treatment and arena (means ± SE). Each line of the response designates one of five experimental release dates or batches (constituting 621 individual frogs released during 5 batches on July 6, 12, 15, 18, and 26, 2011). The first 8–10 days accounted for the majority of movements as detected by recaptures (however, note the scale bar difference for the response variable between graphs). Individuals not recaptured by the conclusion of the experiment (Aug. 2, 2011) may have suffered direct mortality or settled in the arena.

Table 2 Mean daily maximum temperature and relative humidity of control forest and three partial-harvest treatments during experimental juvenile amphibian releases along silvicultural edges.



Treatment	Mean daily maximum temperature			Relative humidity	
	Ground level	Refugia	Air	Mean daily	Mean daily minimum
	. . . .(° C).			. . . .(%).	
Within arena					
At edge:					
CF, parallel trail	40.43 ± 1.51	34.83 ± 1.05	32.60 ± 1.09	85.03 ± 2.59	37.84 ± 5.28
CF, perpendicular trail	38.79 ± 1.73	31.54 ± 0.79	34.19 ± 1.12	88.60 ± 4.71	59.21 ± 7.11
CF, residual cut strips	33.93 ± 1.34	30.71 ± 0.81	31.77 ± 0.97	84.27 ± 2.35	47.48 ± 4.21
Outside arena:					
CF	23.70 ± 0.41				
Residual strips (cut forest)	33.91 ± 1.23				

Microclimate data are compiled for dates inclusive of frog movement within experimental arenas (July 7–Aug. 10, 2011) and represent the mean values across all days and arenas. Temperature data were recorded at air, ground, and refugia levels in each arena and extending >10 m into each adjacent edge (outside of arena). Relative humidity data were recorded at ground level in each arena. CF, control forest.

Table 3 Habitat characteristics (means ±SE) of control forest and three partial-harvest forestry treatments in central Maine during experimental juvenile amphibian releases along silvicultural edges in 2011 (July 6–August 10).

	Cover of vegetation layers				Ground cover							
Treatment	≤0.5 m	0.5–1 m	1–2 m	Tree canopy	Leaf litter	Moss/lichen	Herbaceous	Slash	Bare ground	Rocks	Leaf litter depth (cm)	Soil moisture (%)
	(%)											
Within arena												
Control forest	23.3 ± 8.1	22.3 ± 6.4	19.4 ± 5.0	67.9 ± 7.6	48.1 ± 10.8	28.0 ± 9.1	9.8 ± 1.5	7.0 ± 1.5	6.7 ± 6.3	0.4 ± 0.3	2.4 ± 0.5	15.9 ± 1.7
Residual cut forest	3.7 ± 1.3	6.3 ± 2.7	7.0 ± 4.2	30.4 ± 10.4	45.0 ± 18.9	26.7 ± 2.9	7.7 ± 2.8	19.7 ± 5.2	0.7 ± 0.6	0.3 ± 0.3	2.5 ± 0.6	13.9 ± 1.6
Harvester trail	32.5 ± 7.7	24.2 ± 7.9	12.8 ± 4.0	19.6 ± 7.9[a]	22.2 ± 6.9	14.5 ± 6.0	30.5 ± 7.2	21.2 ± 6.7	9.2 ± 4.4	0.8 ± 0.7	1.4 ± 0.3	20.8 ± 3.2
Outside arena												
Control forest	10.8 ± 2.9	17.7 ± 5.0	21.9 ± 5.4	72.9 ± 4.6	45.1 ± 7.9	43.6 ± 7.8	6.2 ± 0.9	4.3 ± 1.0	0.3 ± 0.2	0.6 ± 0.6	2.1 ± 0.3	23.2 ± 3.3
Residual cut forest	6.8 ± 1.9	5.3 ± 2.1	6.8 ± 3.5	27.4 ± 6.9	27.5 ± 5.4	22.8 ± 11.4	18.0 ± 9.7	13.8 ± 4.1	17.8 ± 1.0	0.2 ± 0.3	1.8 ± 0.3	9.1 ± 1.4
Harvester trail	34.8 ± 9.4	29.8 ± 10.4	14.6 ± 7.1	6.4 ± 3.8[a]	26.1 ± 4.5	5.6 ± 1.8	21.3 ± 5.3	40.0 ± 10.4	5.3 ± 1.8	1.7 ± 0.9	1.7 ± 0.4	18.3 ± 3.3

[a] Tree canopy in harvester trails constitutes average cover estimates across the entire width of trails (i.e., estimates are derived from data in randomly located plots within trails to incorporate the forest edge influence, despite 0% harvest retention in the center of harvester trails).