

## TERRESTRIAL HABITAT SELECTION AND STRONG DENSITY-DEPENDENT MORTALITY IN RECENTLY METAMORPHOSED AMPHIBIANS

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**Abstract.** To predict the effects of terrestrial habitat change on amphibian populations, we need to know how amphibians respond to habitat heterogeneity, and whether habitat choice remains consistent throughout the life-history cycle. We conducted four experiments to evaluate how the spatial distribution of juvenile wood frogs, *Rana sylvatica* (including both overall abundance and localized density), was influenced by habitat choice and habitat structure, and how this relationship changed with spatial scale and behavioral phase. The four experiments included (1) habitat manipulation on replicated 10-ha landscapes surrounding breeding pools; (2) short-term experiments with individual frogs emigrating through a manipulated landscape of 1 m wide hexagonal patches; and habitat manipulations in (3) small (4-m<sup>2</sup>); and (4) large (100-m<sup>2</sup>) enclosures with multiple individuals to compare behavior both during and following emigration. The spatial distribution of juvenile wood frogs following emigration resulted from differences in the scale at which juvenile amphibians responded to habitat heterogeneity during active vs. settled behavioral phases. During emigration, juvenile wood frogs responded to coarse-scale variation in habitat (selection between 2.2-ha forest treatments) but not to fine-scale variation. After settling, however, animals showed habitat selection at much smaller scales (2–4 m<sup>2</sup>). This resulted in high densities of animals in small patches of suitable habitat where they experienced rapid mortality. No evidence of density-dependent habitat selection was seen, with juveniles typically choosing to remain at extremely high densities in high-quality habitat, rather than occupying low-quality habitat. These experiments demonstrate how prediction of the terrestrial distribution of juvenile amphibians requires understanding of the complex behavioral responses to habitat heterogeneity. Understanding these patterns is important, given that human alterations to amphibian habitats may generate extremely high densities of animals, resulting in high density-dependent mortality.

**Key words:** behavioral phase; density dependence; habitat choice; *Rana sylvatica*; spatial distribution; spatial scale; terrestrial enclosure; terrestrial habitat selection; wood frog.

### INTRODUCTION

Improving our understanding of habitat selection requires examination of how animal behavior, environmental structure, and variation in habitat quality interact to determine the spatial distribution of organisms (Figueira and Crowder 2006). These relationships can determine density-dependent mortality through competition (Hixon and Jones 2005), predation (Johnson 2006), and disease (Bradshaw and Brook 2005). Spatial distribution can also influence the probability of dispersal between populations, in turn determining rescue effects (Hanski et al. 1994, Trenham et al. 2001), genetic variation and structure (Purcell et al.

2006), and regional population persistence (Harveson et al. 2004).

Determining the relationship between habitat structure or quality, movement behavior, and the spatial distribution of organisms may be of particular importance for less vagile taxa such as amphibians (Wind 1999). Historically, research on amphibian ecology has focused on aquatic life-history stages, but recent population models have shown that the growth and decline of amphibian populations are highly sensitive to changes in the survival of terrestrial life-history stages (Biek et al. 2002, Vonesh and De la Cruz 2002). In particular, amphibian declines and extinctions have been linked to fragmentation and loss of their terrestrial habitat (Stuart et al. 2004). However, mechanisms driving amphibian distributions in landscapes and the effects of these distributions on survival are not well understood.

Experimental studies have shown that the vital rates of amphibians in terrestrial habitats can differ greatly depending on density (Harper and Semlitsch 2007) and

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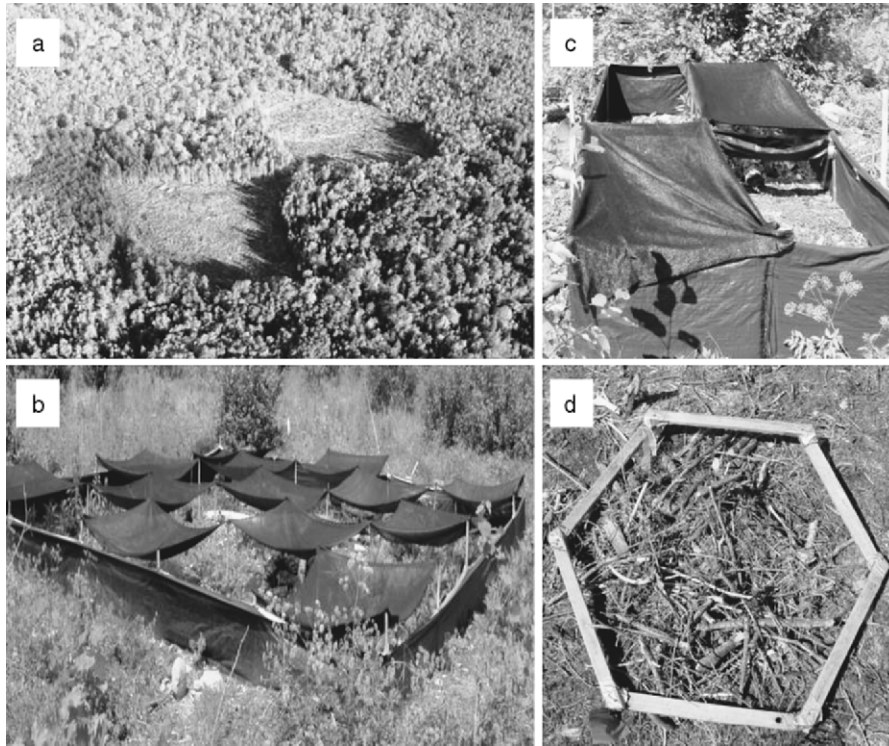


PLATE 1. The four scales at which experimental habitat manipulations were conducted (from coarsest to finest scale): (a)  $\sim 10$  ha landscapes surrounding breeding ponds; (b)  $4\text{-m}^2$  blocks of habitat within a  $100\text{-m}^2$  enclosure; (c)  $2\text{-m}^2$  blocks within  $4\text{-m}^2$  enclosures; and (d)  $1\text{-m}^2$  hexagonal patches within a  $12 \times 16$  m landscape. Photo credits: panel (a), Chick Crockett; panels (b–d), D. A. Patrick.

the type of terrestrial environment in which animals are located (Todd and Rothermel 2006, Harper and Semlitsch 2007; Rittenhouse et al., *in press*). To translate these differences in vital rates into population level effects, however, requires understanding individual habitat choice and resulting densities in a heterogeneous landscape. Field studies have shown that individual amphibians within a breeding population are not uniformly distributed in the terrestrial environment (Regosin et al. 2003, 2005), and that these patterns of spatial distribution can differ between life-history stages and behavioral “phases” (for example, emigrating compared to settled phases) (Regosin et al. 2003, Baldwin 2005, Baldwin et al. 2006b, Patrick et al. 2006). No published studies to date, however, have reported on the behavioral mechanisms that lead to these differences in the spatial distribution of populations.

In this study, we evaluate how amphibian movement and habitat choice vary in different behavioral phases, how these choices translate into variation in the abundance and density of individuals in different habitat types, and how changes in densities affect survival. Connecting these behavioral and demographic parameters forms a vital step in developing accurate predictive models of the effects of habitat change on the viability of amphibian populations (Armstrong 2005).

Our research focuses on the habitat choice of juvenile wood frogs, *Rana sylvatica*. We considered two behavioral phases, animals actively emigrating from natal ponds, and animals that have settled following this active emigration phase. Because wood frogs are a forest-dependent species (deMaynadier and Hunter 1998), we used timber harvesting (partial harvesting and clear-cutting) as a means of manipulating habitat quality. We conducted four experimental habitat manipulations representing a range of spatial scales (see Plate 1). In Experiment 1 we used replicate landscape-scale manipulations of terrestrial habitat (10-ha landscapes) around amphibian breeding ponds, a scale sufficient to contain most individuals in a local amphibian population (Semlitsch and Bodie 2003). Experiment 2 focused on the influence of fine-scale habitat heterogeneity ( $1\text{-m}^2$  patches) on individual movement behavior during the active period of emigration. In Experiment 3, we studied responses to fine-scale habitat heterogeneity in a simple enclosed landscape ( $2\text{-m}^2$  patches) during and following the active emigration phase, and examined the effect of conspecific density on survival. In Experiment 4 we studied response to a meso-scale habitat manipulation ( $100\text{-m}^2$  enclosure made up of  $4\text{-m}^2$  patches), and evaluated how the interaction between habitat heterogeneity and the density of conspecifics affected habitat choice.

## METHODS

*Study species*

The wood frog is a wide-ranging North American anuran (occurring from north of the Arctic Circle south to Missouri, and from the East Coast to Alaska) closely associated with forests (deMaynadier and Hunter 1998). In central Maine, wood frogs breed in April, with each female laying a clutch of ~1000 eggs. Tadpoles metamorphose at the end of June or early July. After emergence, juveniles emigrate away from the pond, and approximately two weeks later they begin to settle in the landscape and establish a summer foraging area (Patrick et al. 2006). In late fall, frogs move to upland areas where they overwinter in leaf litter on well-drained soils (Baldwin et al. 2006a). Adults breed one to three years following metamorphosis, with high rates of philopatry to natal ponds (Berven and Grudzien 1990, Vasconcelos and Calhoun 2004).

*Study area*

Experiments were established in the Dwight B. Demeritt (Gilman and Smith sites) and Penobscot Experimental (North and South Chemo sites) Forests, Penobscot County, Maine, USA. The area consists of mature mixed deciduous-coniferous forest (>80 years old). Dominant tree species include balsam fir (*Abies balsamea*), eastern white pine (*Pinus strobus*), northern white cedar (*Thuja occidentalis*), red maple (*Acer rubrum*), red oak (*Quercus rubra*), and paper birch (*Betula papyrifera*). We obtained weather data for the study region from a weather station at Bangor International Airport ~8 km from the study site (information available online).<sup>5</sup>

*Experiment 1: Effects of landscape-scale habitat heterogeneity on movement and habitat selection during both the active emigration and settled phases*

In Experiment 1, we assessed the effects of a large-scale habitat manipulation on the spatial distribution of juveniles in a wood frog population. This experiment was conducted as part of the Land Use Effects on Amphibian Populations project (LEAP). LEAP involves manipulation of forest habitat within large (~10 ha) experimental arrays replicated at a geographic scale, with four similar arrays each in Maine, South Carolina, and Missouri (Patrick et al. 2006).

Each of the four replicate arrays in Maine was centered on an amphibian breeding pond (10–15 m in diameter). The terrestrial habitat surrounding each of these ponds to a distance of 164 m was divided into quarters, with each quarter randomly assigned one of four forestry treatments applied between December 2003 and April 2004: an uncut control, a partial cut (PC) where 50% of the canopy was removed, and two clear-cuts, one where coarse woody debris (CWD) >10 cm in

diameter was retained (CWD-retained), and one where CWD was removed (CWD-removed) (Fig. 1). Each array was established with large areas of continuous forest extending at least 300 m beyond the outer perimeter. Arrays were at least 5 km apart except for South and North Chemo, where the outer edges were ~300 m apart.

At each array, we completely encircled the pond with a drift fence with pitfall traps every 5 m on the inside and outside. Additional drift fences were established at 16, 50, 100, and 150 m into each of the terrestrial forestry treatments; these were 10 m in length with a pitfall trap on each end, and one on each side in the center. The number of fences increased at each distance away from the ponds, such that an equal proportion of the total arc was sampled (38% of the circumference; i.e., one fence in each treatment of each array at 16 m, 3 at 50 m, 6 at 100 m, and 9 at 150 m) (Fig. 1).

We monitored pitfall traps from 24 June to 17 September in 2005, and 30 June to 22 August in 2006, checking traps every other day until the beginning of September, when we checked traps every third day. We marked all metamorph wood frogs captured emerging from the ponds according to the following protocols. In 2005, metamorphs were marked using a single toe-clip to indicate the treatment into which they emerged. In 2006, metamorphs initially were marked at the pond fences based on the treatment and the week of first capture. Animals recaptured at the terrestrial fences were marked with visible implant elastomer (VIE) (Northwest Marine Technology, Shaw Island, Washington, USA) to indicate clear-cut or forested (control and PC) treatment, and the week of first recapture. Animals recaptured following this second mark were not re-marked, but were counted as a multiple recapture. The latter data were only used for question 3 in the following paragraph.

Data from this experiment were used to evaluate three questions: (1) Did wood frogs preferentially select one or more of the terrestrial treatments? (2) Was habitat selection consistent between years? and (3) Were there differences in habitat use as animals transitioned from the active emigration phase to the subsequent settled phase?

We addressed questions 1 and 2 using ANOVA with the number of recaptures as the dependent variable, and year, site, treatment, and distance as factors. Only individuals recaptured for the first time in 2006 were included in analyses to avoid multiple counts of the same individuals. South Chemo was excluded from 2006 data due to disease-related recruitment failure. We evaluated question 3 using chi-square comparison of the proportion of first-time recaptures in 2006 in each treatment (representing emigrating animals), and animals recaptured multiple times (representing individuals that had settled in the treatments).

The remaining experiments (Experiments 2–4) were conducted in a clear-cut treatment, as it was feasible to approximate forest conditions in a clear-cut (using shade cloth and augmenting woody debris and leaf litter), but

<sup>5</sup> <http://pnwpest.org/NE/ME/index.html>

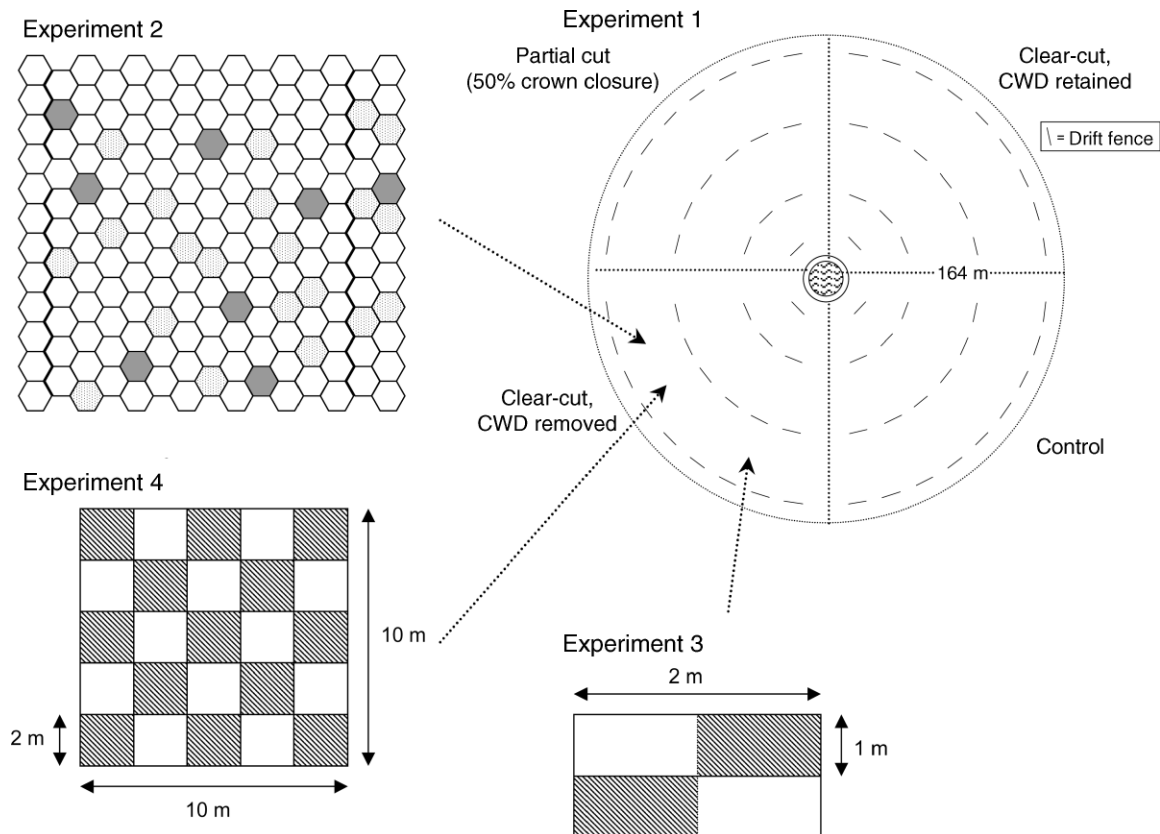


FIG. 1. Outline of experiments (not to scale). In the schematic for Experiment 2, one of the four landscape scenarios is shown for illustrative purposes. Coarse woody debris (CWD) cells are indicated by dark gray hexagons, and cells containing slash piles by black stippling. In the excerpts for Experiments 3 and 4, hatched areas indicate high-quality habitat. Arrows indicate the approximate position of experiments 2–4 within the landscape of Experiment 1. (Experiments 2–4 were all conducted within a clear-cut at the Gilman LEAP site, Maine, USA.) For Experiment 3, only one of the 12 paired pens is shown.

not clear-cut conditions in the forest due to shade from large trees. For each of these experiments we recorded the maximum daily temperature and total daily precipitation during the study periods.

*Experiment 2: Effects of fine-scale habitat heterogeneity on individual movement behavior during the active emigration phase*

In this experiment, we evaluated whether individual behavior was influenced by local habitat structure during active emigration. We established a  $12 \times 16$  m experimental landscape approximately in the center of the Gilman site (Fig. 1). We removed all vegetation and woody material  $>1$  cm in diameter and used pin flags to demarcate a honeycomb grid of  $11 \times 16$  tessellating hexagonal cells, each 1 m in width. These cells were assigned one of three possible contents: (1) bare ground (hereafter denoted as “empty”); (2) habitat containing a total of 2 m of 10–15 cm diameter, coarse woody debris (denoted “CWD”) of decay class 3 (Faccio 2003); and (3) habitat containing a 30 cm high by 1 m wide pile of fine woody material ( $<2$  cm in diameter, denoted as “slash”). There were 147 empty cells, 8 cells containing

CWD, and 21 cells containing slash (Fig. 1). These proportions were designed to mimic the relative amounts of these conditions in the LEAP clear-cut with CWD-retained treatment (D. A. Patrick, *unpublished data*). The contents of the hexagonal cells were initially assigned nonrandomly to ensure an approximately equal dispersion of the three cell contents. Following this initial landscape configuration, the contents of each of the slash and CWD cells were assigned to one of the adjoining cells on a random basis to create a new landscape configuration within the same grid. We repeated this process of randomizing the landscape three times to give four scenarios in total.

We conducted the experiment from 27 June to 3 August 2005. Wood frog metamorphs were collected on emergence from the breeding pond located 100 m to the east of the experimental landscape. We collected 30 metamorphs for each scenario, releasing the animals into the experimental landscape at dusk. Releases occurred over a period of 2–4 nights per scenario. Cells in which animals were released were randomly chosen with the condition that no other individual could be released into the same or an adjacent cell. Before release,

we liberally coated the ventral side of each frog with fluorescent powder. (The use of fluorescent powder allows the movement of individuals to be followed, while minimizing any potential effects of handling on behavior [Rittenhouse et al. 2006]). We then placed the frog under an inverted plastic cup in the center of an empty cell, removing the cup 10 minutes later, using an attached 2 m long bamboo pole. Two hours later, we followed powder trails using an ultraviolet light. This period was sufficient for the animals to move outside the experimental landscape. We marked trails with wire flags and string. Marking of a trail was terminated when the frog left the boundary of the experimental array, or when there was >50 cm between signs of fluorescent powder. Each study animal was used once. To ensure that animals were neither “homing” back to their point of initial capture nor exhibiting escape behavior, we also conducted an initial pilot study during which we monitored the movement of juvenile frogs placed outside of the experimental array. No evidence was seen to suggest that either of these behaviors was present.

Statistical analysis of the trail data compared the contents of the hexagonal cell the frog chose to move into each time a new cell was entered, with the contents of each of the six cells available for the move. This presented a number of configurations; for example, the choice frogs made when one CWD cell and five empty cells were available. We selected the four configurations that were replicated sufficiently for analysis and used chi-square tests to compare the frequency of cell contents selected against the frequency expected under a null hypothesis of random movement. To ensure that there was no overall directionality in the movement of the juvenile frogs (as might be the case if they all “homed” back to the pond from which they were collected), we used the Rayleigh test to test for nonrandomness in the overall direction of each of the frog’s trails. Analysis of circular data was conducted using Oriana 1.0 (Kovach Computing Services, Anglesey, Wales, UK).

*Experiment 3: Effects of fine-scale habitat heterogeneity and density of conspecifics on groups of juveniles, during both the active emigration and settled phases*

We designed this experiment to evaluate the effect of conspecific density and fine-scale habitat structure on habitat selection. We also assessed if habitat choice changed as animals progressed from active emigration to the settled phase, and the effects of density on short-term survival. We established 24  $1 \times 4$  m experimental pens >30 m from the edge of the clear-cut CWD-removed treatment of the Gilman site (Fig. 1). We constructed pens as 12 randomly oriented pairs, with a pair sharing a central wall along the long axis. Pens were constructed from 1 m tall silt fencing buried 30 cm into the ground. A 3-cm lip was created on the inside of each pen to prevent escapes and trespasses. We removed all vegetation and

woody material from the pens, with half of each pen ( $2 \text{ m}^2$ ) randomly assigned as either high- or low-quality habitat (Fig. 1). The second pen in each pair had the opposite configuration. To create high-quality habitat we used 30 mm deep leaf litter, a total of 3 m of 10–15 cm diameter CWD of decay class 3, and 70% shade cloth elevated 1 m from the ground. Low-quality habitat contained 25 mm deep leaf litter and was not shaded.

We conducted this experiment from 20 July to 6 August in 2005 and 31 July to 18 August in 2006. Recently metamorphosed wood frogs were released into the pens in three randomly assigned density treatments: low (2 individuals/ $\text{m}^2$ , 8 individuals per pen); medium (4 individuals/ $\text{m}^2$ , 16 individuals per pen); and high (7 individuals/ $\text{m}^2$ , 28 individuals per pen). The same treatment was assigned to each pair of pens. Densities were based on previous research showing a threshold between 4 and 7 juvenile wood frogs/ $\text{m}^2$ , at which point growth and survival decreased (Harper and Semlitsch 2007).

In 2005, eight pens were assigned to each of the three density treatments. Following release of the amphibians, we left the pens for 16 days, a sufficient period for juvenile wood frogs to transition from active emigration to a settled phase (Patrick et al. 2006). At midday, when juvenile wood frogs were not active, a barrier was then constructed between the two habitat treatments within each pen, creating two temporary  $1 \times 2$  m pens. We conducted exhaustive sampling at dusk when frogs were most active. For each captured frog we noted the treatment of capture and snout–vent length (SVL). As frogs were never seen to be active in the low-quality habitat treatments during the day, this sampling approach allowed us to assess habitat selection during the night when juvenile wood frogs move.

ANOVA was used to assess if the initial density in the pen in 2005 influenced the final proportion of recaptures in the high-quality treatment. Regression was then used to compare the total number captured in the final sample, and the proportion of recaptures in the high-quality habitat.

In 2006, six pens were assigned to each of the three density treatments. All animals were measured and individually marked before release using a combination of a single toe-clip and visible implant elastomer (VIE). Pens were sampled at 3-day intervals following the date of release, for 15 days per pen, with captured animals measured, identified individually, and the treatment of capture noted. This protocol allowed an assessment of changes in habitat selection and survival over the total sampling period. In 2006, frogs in four of the six highest-density pens showed extremely rapid mortality, likely because of disease indicated by physical signs such as hemorrhaging, with rapid mortality. These pens were excluded from further analyses following these events (no signs of disease were seen prior to mortality events).

Recaptures in 2006 were analyzed using a general linear model, with the number of recaptures in the high-

quality treatment as the dependent variable, and time, rainfall, maximum daily temperature during the period between samples, and total number captured during the sampling period as covariates.

We used a Cormack-Jolly-Seber model in program MARK (version 4.0) (White and Burnham 1999) to estimate capture probability at each sampling interval for the individually marked animals in 2006. This allowed us to assess the efficacy of our sampling efforts. Survival analysis was conducted using the individually marked animals in 2006, with the data adjusted to account for capture probability. We used a nonparametric Kaplan-Meier survival analysis to compare survival over time for wood frogs in the three density treatments.

*Experiment 4: Effects of a meso-scale habitat manipulation and varying density of conspecifics during the settled period*

In 2006, we established a single  $10 \times 10$  m pen approximately in the center of the CWD-removed clear-cut at the Gilman site. This pen was constructed of 1 m tall silt fencing buried 30 cm into the ground, with a 3-cm lip on both the inside and outside to prevent animals entering or exiting. Within this pen, all vegetation and woody material were removed. We demarcated the pen into  $25 \times 2 \times 2$  m habitat blocks alternately designated as either high- or low-quality habitat to create a regular checkerboard effect (Fig. 1). Low- and high-quality blocks consisted of the same habitat variables as in Experiment 3, but with 10 m rather than 3 m of 10–15 cm diameter CWD of decay class 3 in the high-quality blocks.

We released 200 recently metamorphosed wood frogs from 28 July to 31 July 2006, with 50 frogs placed in each of the corner habitat blocks. On 2 August 2006, temporary barriers were constructed around each of the 25 habitat blocks using 1 m tall silt fencing stapled to central posts and fixed to the ground with metal stakes. Barriers were constructed at midday when wood frogs were not active and unlikely to move in response to disturbance. Each of the 25 blocks was then sampled to determine the density of individuals (termed “sample 1”). To ensure that no animals were injured during sampling, we maintained a clear path where each barrier fell and carefully removed all CWD from each block, replacing it afterwards.

Following sampling, we raised the barriers and the pen was left for two days to allow the wood frogs to resettle. One hundred additional wood frog metamorphs were released on 4–5 August, 25 in each corner. We marked animals in this second release with a single toe-clip to distinguish them from the first batch. A week after the second release, we replaced the temporary barriers around each of the 25 habitat blocks and assessed the density of animals from both releases through exhaustive sampling (termed “sample 2”).

We used chi-square tests to ascertain if more individuals settled in high-quality habitat blocks, and whether there were any differences between edge and interior blocks. The latter analysis allowed us to evaluate if habitat selection was influenced by either escape behavior or the increased shade on the edge of the pen. The expected number of captures was adjusted by the number of blocks that fell into each of these categories (13 high quality and 12 low quality). Recaptures are reported as density per square meter, while total counts were used in statistical analyses. In sample 2, we evaluated recaptures from the first release and second release separately, due to possible correlation between the location of unmarked animals in sample 1 and sample 2.

We tested two alternative hypotheses based on the settling of marked animals from the second batch released. Hypothesis 1 was that individuals settle based on differences in habitat, not density of conspecifics (i.e., blocks with high numbers of individuals in sample 1 were presumably high quality and would have high numbers in sample 2). Hypothesis 2 was that individuals settle based on avoiding competition from those animals already released in the first batch (i.e., more animals would be captured in sample 2 in blocks that had few captures in sample 1). We grouped habitat blocks based on the number of recaptures in sample 1, regardless of habitat treatment. Three categories were used: low (1 individual,  $N = 7$  blocks); medium (2–5 individuals,  $N = 9$ ); and high (6+ individuals,  $N = 9$ ), with the cutoff point for each category based on qualitative analysis of the distribution of data. Recaptures were totaled for blocks within these groups, and the proportion of the total recaptures in each group calculated. For hypothesis 1, this proportion was used to derive the number of marked animals expected in sample 2 if the animals distributed themselves in the same way. For hypothesis 2, we postulated that marked animals would show the reverse trend, with more marked animals captured in blocks that had previously shown low captures. Based on this hypothesis, we used the proportion of captures from the low recapture blocks to estimate the number expected in high-quality blocks, and vice versa. Medium-quality blocks were presumed to have an equal proportional relationship between unmarked captures in sample 1, and marked captures in sample 2.

*Overall statistical analyses*

Statistical analyses were conducted using SYSTAT 11.0 software (Systat, San Jose, California, USA), with  $\alpha < 0.05$  for all tests. For parametric tests, normality was assessed using Shapiro-Wilk tests. If assumptions were not met, data were transformed via a logarithmic ( $X' = \log[X + 1]$ ), square-root ( $X' = \sqrt{[X + 0.5]}$ ), or arcsine function ( $p' = \arcsin \sqrt{p}$ ). The latter transformation was used for proportional data (Zar 1999).

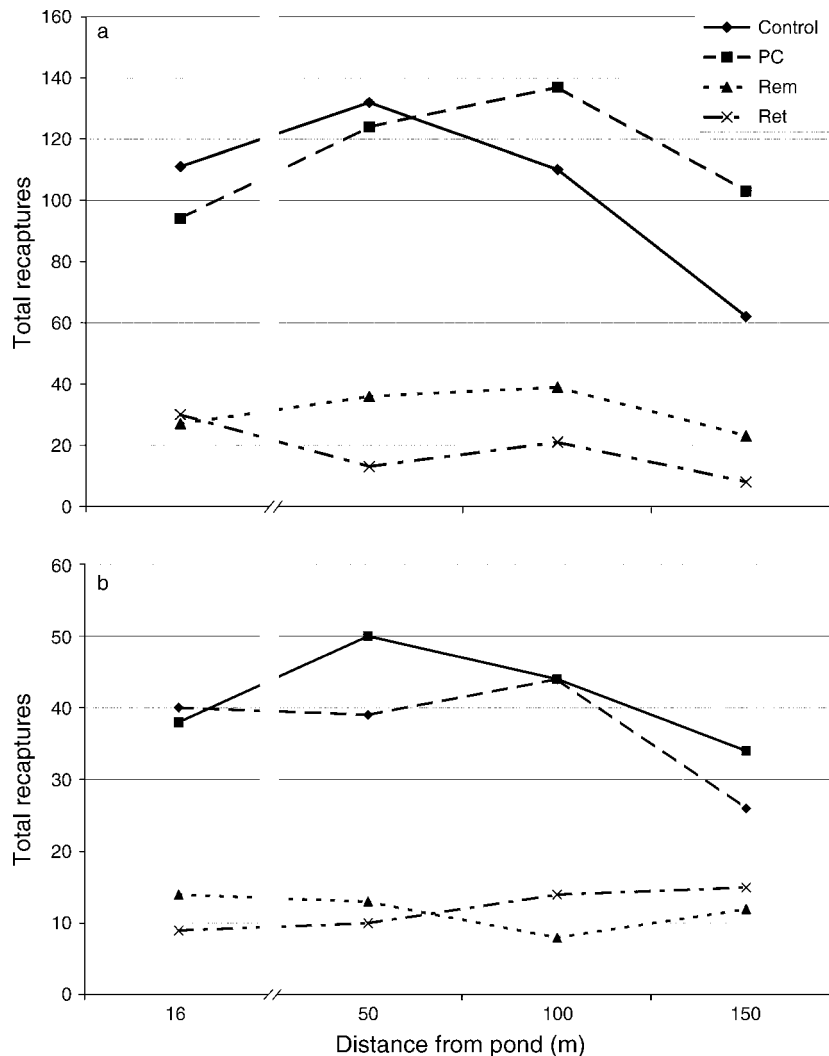


FIG. 2. Total recaptures of emigrating juvenile wood frogs (*Rana sylvatica*) at four distances from the pond in the LEAP treatments in (a) 2005 ( $n = 1084$ ) and (b) 2006 ( $n = 410$ ). The number of recaptures in 2006 represents animals recaptured for the first time only. The key refers to the four LEAP forestry treatments: Control; PC (partial cut of 50% crown closure); Rem (clear-cut with coarse woody debris [CWD] <10 cm in diameter removed); and Ret (clear-cut with CWD retained).

## RESULTS

### *Experiment 1: Effects of landscape-scale habitat heterogeneity on movement and habitat selection during both the active emigration and settled phases*

The four forestry treatments differed significantly in numbers of recaptures in both years ( $F = 8.845$ ,  $df = 3$ ,  $91$ ,  $P \leq 0.001$ ) (Fig. 2), with post hoc analyses revealing significantly more recaptures in forested treatments (control and partial cut) than in the clear-cuts ( $P \leq 0.001$ ), but no significant difference between the control and partial cut or between the two clear-cut treatments ( $P > 0.999$ ). The numbers of recaptures in the four treatments did not significantly differ over distance from the pond ( $F = 0.586$ ,  $P = 0.625$ ), suggesting that once these treatments had been entered the frogs moved through them in a similar fashion (data summarized in

Appendix A). There were significant differences among the four experimental sites ( $F = 10.155$ ,  $df = 3$ ,  $91$ ,  $P \leq 0.001$ ). The lack of a significant year, treatment, and site interaction ( $F = 0.261$ ,  $P = 0.983$ ) indicates that the differences among sites reflected variation in the overall number of juvenile wood frogs recaptured at each site, and not variation in patterns of treatment selection or captures over distance. No significant difference could be seen between the proportions of wood frogs that settled in treatments (indicated by multiple recaptures of the same individual in our 2006 experiment), and the proportions that emigrated through treatments (indicated by first-time recaptures) (for Gilman,  $\chi^2 = 0.668$ ,  $df = 3$ ,  $P \geq 0.75$ ; for North Chemo,  $\chi^2 = 1.596$ ,  $P \geq 0.5$ ; for Smith,  $\chi^2 = 10.706$ ,  $P \geq 0.1$ ; South Chemo was excluded due to disease).

TABLE 1. Habitat selection of recently metamorphosed juvenile wood frogs (*Rana sylvatica*) released in an artificial landscape of hexagonal cells (Fig. 1).

No. cells with specified contents			No. frogs entering cells			
Cells empty	Cells with slash	Cells with CWD	Empty	Slash	CWD	$P^\dagger$
5	1	0	49	16	0	>0.10
4	1	1	24	6	4	>0.25
4	2	0	13	5	0	>0.50
5	0	1	40	0	8	>0.99

Notes: Each cell (area  $\approx 1 \text{ m}^2$ ) contains one of three habitat types: empty, slash, or coarse woody debris (CWD); (see *Methods*). Four “scenarios,” each represented by a separate row, in which a frog chose between a specific combination of habitat types in the surrounding six cells, yielded sufficient data for analysis.

$^\dagger$  Chi-square  $P$  values represent comparison between the observed numbers of frogs selecting each of the habitat treatments available in each scenario and the expected number of frogs under the null hypothesis of random choice.

*Experiment 2: Effects of fine-scale habitat heterogeneity on individual movement behavior during the active emigration phase*

In the 1 m wide hexagonal cells with three contents (empty, CWD, and slash), no significant difference could be detected between the observed habitat selection of emigrating juvenile wood frogs and that expected with random movement (Table 1). This indicates that individual juvenile wood frogs were not demonstrating fine-scale habitat selection for any of these three habitats during the active emigration phase. Trails were found to be randomly oriented (Appendix B, Rayleigh's  $Z$  test:  $Z = 0.375$ ,  $df = 1$ ,  $111$ ,  $P = 0.688$ ), indicating that movement of juvenile frogs in a specific direction did not influence the results.

*Experiment 3: Effects of fine-scale habitat heterogeneity and density of conspecifics on groups of juveniles, during both the active emigration and settled phases*

More individuals in the  $1 \times 4 \text{ m}$  pens were recaptured in the high-quality treatment than in the low-quality treatment at the conclusion of the experiment (after two weeks) in 2005 (proportion of total recaptures  $= 0.881 \pm 0.116$ ; mean  $\pm$  SD). The initial density of animals released into the pens (either 2, 4, or 7  $\text{m}^2$ ) did not determine the final proportion of recaptures in the high-quality treatment ( $F = 0.895$ ,  $df = 2$ ,  $15$ ,  $P = 0.429$ ). Similarly, the final density of animals (based on the total number of recaptures in the final sample) did not significantly influence the proportion of animals found in the high-quality habitat (linear regression of the proportion of recaptures in the high-quality treatment in relation to the total number recaptured:  $F = 4.272$ ,  $df = 1$ ,  $16$ ,  $P = 0.055$ ) (Appendix C).

A higher proportion of animals was also recaptured in the high-quality treatment in 2006 ( $0.797 \pm 0.194$ ) (Appendix C). No significant relationship was found between the proportion of recaptures in the high-quality habitat and the total number recaptured in the pen ( $F = 0.991$ ,  $df = 1$ ,  $12$ ,  $P = 0.339$ ). Both mean daily maximum temperatures and precipitation were similar

during 2005 and 2006 (mean daily maximum temperature,  $28^\circ \pm 3^\circ\text{C}$  and  $25^\circ \pm 2^\circ\text{C}$ ; mean daily precipitation,  $5 \pm 8 \text{ mm}$  and  $3 \pm 5 \text{ mm}$  for 2005 and 2006, respectively).

Survivorship was significantly different among density treatments in 2006 (Wilcoxon;  $\chi^2 = 74.91$ ,  $df = 2$ ,  $P < 0.0001$ ) (Fig. 3). Wood frogs in enclosures initially stocked at the lowest density (8 frogs per pen) were more than four times as likely to survive than frogs in the highest-density enclosures. Only 7.7% of wood frogs stocked at an initial density of 28 frogs per enclosure survived to the end of the experiment at week 15, compared to 37.5% in enclosures stocked with 16 animals and 47.9% in enclosures stocked with 8 frogs.

*Experiment 4: Effects of a meso-scale habitat manipulation and varying density of conspecifics during the settled period*

Significantly more animals were recaptured in high-quality habitat in the  $10 \times 10 \text{ m}$  pen (Sample 1,  $\chi^2 = 24.762$ ; sample 2,  $\chi^2 = 52.878$ ;  $P < 0.001$ ) (Table 2). In sample 1, 119 of the 200 animals in the first release were recaptured; nine days later in sample 2, 121 animals out

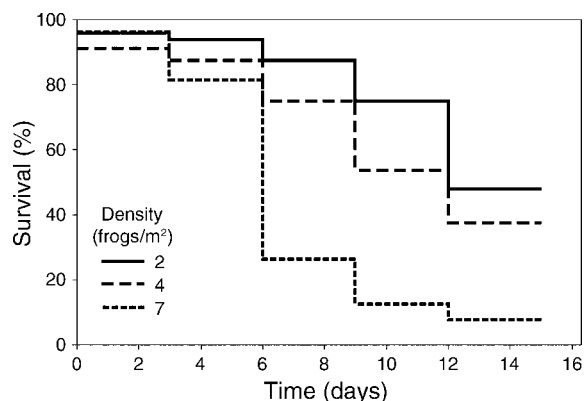


FIG. 3. Survival of juvenile wood frogs (*Rana sylvatica*) at three density treatments (2, 4, and 7 frogs/ $\text{m}^2$ ) in  $1 \times 4 \text{ m}$  pens in 2006. Survival analysis was only conducted in 2006, as frogs were not individually marked in 2005.



TABLE 2. Number and density of juvenile wood frogs recaptured in the experimental area.

Sample	Habitat quality	Mean density (no. frogs/m <sup>2</sup> )	Range (no. frogs/m <sup>2</sup> )	No. unmarked captures	No. marked captures
1	High	1.7	0.25–3.25	89	0
	Low	0.625	0.25–2.25	30	0
2	High	2.15	0.5–7.75	43	69
	Low	0.19	0–0.5	5	4

Notes: The wood frogs were recaptured in a 10 × 10 m landscape of 4-m<sup>2</sup> blocks of two habitat types (high and low quality). Sample 1 refers to the distribution of animals following an initial release of 200 frogs. Sample 2 refers to the distribution of recaptures following a second release of an additional 100 frogs.

of the total of 300 animals released (200 animals in the first release and 100 animals in the second release) were recaptured.

The mean density of animals in low-quality cells decreased substantially from sample 1 to sample 2, from 0.625 to 0.19 animals/m<sup>2</sup>, with the density in high-quality cells increasing from 3.25 to 7.25 animals/m<sup>2</sup> (Table 2). Additionally, in sample 1, at least one animal was recaptured in all of the blocks. In sample 2, however, four of the low-quality blocks had no recaptures. Temperatures during samples 1 and 2 remained consistent (mean daily maximum was 28° ± 2°C and 25° ± 1°, respectively), but there was far greater precipitation during sample 1 (mean daily precipitation was 30 ± 50 mm and 2 ± 3 mm, respectively).

High-quality blocks on the edge of the pen (where the fence itself provided extra shading) had significantly higher numbers of recaptures than those in the center of the pen in both samples (sample 1,  $\chi^2 = 11.012$ ,  $P < 0.001$ ; sample 2,  $\chi^2 = 8.940$  for unmarked, and 25.829 for marked individuals;  $P < 0.005$  for unmarked and  $P < 0.001$  for marked animals). Animals in this experiment chose blocks based on habitat quality, and not on the distribution of individuals from the first batch released (i.e., no significant difference was found in the distribution of first-release animals caught in sample 1 compared to first-release animals captured in sample 2 [ $\chi^2 = 0.900$ ,  $P > 0.50$ ]).

#### DISCUSSION

##### *The effects of habitat heterogeneity on spatial distribution*

Recent research has clearly demonstrated that changes in terrestrial habitat can lead to reductions in amphibian survival (Rothermel and Luhring 2005, Todd and Rothermel 2006, Harper 2007; Rittenhouse et al., *in press*). However, the effects of habitat alteration at the population level are determined not only by habitat-specific vital rates, but also depend on how individuals in the population are distributed in the mosaic of available habitat types. This distribution determines both local densities as well as the proportion of the population exposed to different habitat types, both of which affect vital rates. Our study demonstrates the complexity of predicting the effects of habitat heterogeneity on the spatial distribution of amphibians. Specifically, we show that the interaction between the

behavioral phase of the amphibian and the scale of habitat heterogeneity determines these patterns, rather than these factors operating independently.

The spatial distribution of juvenile wood frogs following emigration resulted from differences in the scale at which juvenile amphibians in active compared to settled phases responded to habitat heterogeneity. During active emigration, juvenile wood frogs chose habitat at a coarse spatial scale, selecting large patches (2.2 ha) of high-quality forested habitat in preference to the lower-quality clear-cuts, but not responding to differences between the uncut and partially cut forest (Experiment 1, Fig. 2). During this behavioral phase, they showed no response to finer-scale differences in habitat as represented by the ~1-m<sup>2</sup> patches of slash/CWD and bare ground of Experiment 2 (Table 1). Initially, this behavior resulted in a higher abundance of animals in high-quality forested treatments compared to clear-cuts, but similar distributions over distance within all four treatments. If habitat choice was consistent between life-history phases, juveniles would have remained distributed in this way, and animals in the clear-cuts would have been at much lower densities than those in the forested treatments. Crucially, however, after juvenile wood frogs transitioned into a post-emigration settled phase, we observed a change in the scale at which habitat heterogeneity was perceived, with choice at a much finer scale, i.e., selection for small patches of high-quality habitat in both the 1 × 4 m and 10 × 10 m pens (Experiments 3 and 4, respectively; Table 2). This behavior resulted in extremely high densities of juvenile wood frogs in localized patches of high-quality habitat (up to 7.75 individuals/m<sup>2</sup>).

##### *Density and habitat selection*

Understanding how the juvenile frogs respond to localized densities of conspecifics forms a vital connection between spatial ecology and the resulting effects on both individuals and populations. Individuals should distribute themselves within available habitat to maximize fitness, with animals preferring to be in high-quality habitat. As density increases, however, the fitness advantage of remaining in this habitat decreases, and a point should be reached at which some animals leave high-quality habitat and move into lower-quality habitat (Fretwell and Lucas 1969, Morris 1987). In our

experiments, however, we saw little evidence of density-dependent habitat choice, with juvenile frogs typically choosing to remain at extremely high densities in high-quality habitat, rather than occupying low-quality habitat. This is of particular note given that our survival analysis and similar research with the study species (Harper and Semlitsch 2007) shows how rapidly density-dependent mortality can occur. Our results suggest that the low-quality treatments in Experiment 3 (i.e., the  $1 \times 4$  m pens) and the second sample in Experiment 4 ( $2 \times 2$  m blocks) had very little use once juvenile wood frogs were in a settled phase. Given the importance of this low-quality habitat in driving the high density-dependent mortality we observed, it is important to understand when habitat falls below the threshold at which it is used. As our study did not examine a continuum of habitat quality, we cannot pinpoint this threshold. However, we did see a change in the use of low-quality habitat blocks in Experiment 4. In the first sample, all low-quality blocks (each  $4 \text{ m}^2$ ) contained at least one frog, with a mean density of  $0.625 \text{ individual/m}^2$ . In the second sample, however, four of the low-quality blocks were entirely empty (even though the overall number of frogs captured was the same in both samples), and the mean density in this treatment had dropped to  $0.19 \text{ individual/m}^2$  (Table 2). We hypothesize that this is indicative of an overall drop in habitat quality during the experiment, i.e., the low-quality habitat had decreased in quality to a point where it had become almost unusable.

#### *Temporal variability in habitat quality*

The observed variation in habitat choice between different years (Experiment 3) and different sampling periods in the same year (Experiment 4) highlights the role of temporal variability in determining habitat quality. In Experiment 4, the most likely cause of these differences was variation in precipitation, with drier conditions leading to more animals occupying shaded habitat around the edge of the pen. Alternatively, these high densities along the edge could be due to escape behavior leading to animals congregating against the pen edges. This is unlikely to be the case, given that the maximum density on the edges of the pen was lower at the end of the first sample period, when animals were most active, compared to the end of the second period (unless an overall reduction in habitat quality triggered escape behavior during the second period).

Temporal variation in abiotic factors such as weather has been shown to be an important factor determining habitat choice (Martin 2001), primarily because organisms need to remain within the limits of their physiological tolerances (Harte and Shaw 1995, Root and Schneider 1995). Long-term changes in abiotic factors drive shifts in the geographic distribution of species (McCarty 2001). Over shorter periods (for example within days or weeks), abiotic change probably causes individuals to relocate to remain within patches of

suitable habitat. The high sensitivity of amphibians to small changes in abiotic conditions (Spotila 1972; Rittenhouse et al., *in press*) means that for animals found in places with extremely limited suitable habitat (for example the clear-cut areas in our experiments), these remaining patches may act as highly isolated islands, even when large areas of suitable habitat are not far away (illustrated in Appendix D). Even if factors such as temperature and moisture are unfavorable for a short period, based on the results of our experiments, this isolation can cause rapid mortality for animals found at high densities.

#### *Isolating vital rates for population models*

Our research points to the role of habitat heterogeneity and behavioral phase in determining the spatial distribution and density-dependent survival of juvenile wood frogs. These results can be incorporated into both structured and spatially explicit population models to make predictions beyond the scope of our study. Most structured matrix population models project the change in population size over an annual cycle (Morris and Doak 2002). Models of amphibian populations have recognized differences in within-year survival rates for aquatic life-history stages (i.e., egg vs. larval survival [Vonesh and De la Cruz 2002]). However, survival estimates for early behavioral phases of the terrestrial stage of amphibians are rare. Enclosure studies have demonstrated that mortality rates are far greater within the first six weeks following metamorphosis than in subsequent weeks (Trenham et al. 2000, Rothermel and Semlitsch 2006, Harper and Semlitsch 2007). We advocate incorporating separate survival parameters for the active movement phase and the settled phase of the terrestrial juvenile stage in structured populations models. Our density-dependent survival data provide estimates for the active movement phase (Appendix E). Similar considerations of behavioral phases should be made when deriving dispersal kernels from our data on the distribution of marked juvenile wood frogs over distance from natal pools (Appendix A). These data represent the spatial distribution of juvenile wood frogs in the first two months following metamorphosis, but do not indicate how factors such as movement to overwintering sites may change these distributions.

#### *Conclusions*

Given the important role played by terrestrial stages of amphibians in driving population dynamics (Vonesh and De la Cruz 2002), the continuing degradation and loss of terrestrial habitat is of obvious concern for amphibian conservation. To date, however, evaluation of the role of terrestrial habitat heterogeneity in determining the spatial distribution of amphibians within populations has tended to focus on describing patterns of spatial distribution, rather than understanding the underlying mechanisms that generate these patterns. For example, studies have tended to operate

under the premise that all “suitable” terrestrial habitats are essentially uniform in quality (although see Conroy and Brook 2003). While such studies have greatly increased our knowledge of amphibian ecology, they are of limited value when predicting spatial distributions beyond the specific environment in which the study was conducted.

The experiments outlined in this study represent a novel approach to understanding amphibian ecology. Evaluating the influence of scale is a principal difficulty facing empirical studies of the effects of habitat heterogeneity on the spatial distribution of organisms (and resulting effects on populations) (Levin 1992, Melbourne and Chesson 2006). Small-scale studies afford much greater control of variability, but there is a concern that the results from these studies may be either artifacts of the experimental design, or influenced by processes operating at a larger scale (Thrush et al. 1997). Studies conducted at larger scales can encompass these population-level processes, but may inherently incorporate more variability and thus may require degrees of replication that are difficult to attain. The experiments we have outlined at multiple spatial scales offer one approach to addressing these issues. By conducting small-scale experiments, we were able to pinpoint specific mechanisms driving patterns of spatial distribution. The use of larger-scale experiments allowed us to evaluate how these mechanisms translated into population-level processes, and the role of forces operating at larger scales.

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#### APPENDIX A

Summary of the number of recaptures of marked juvenile wood frogs at drift fences in Experiment 1 in 2005 and 2006 (*Ecological Archives* E089-144-A1).

#### APPENDIX B

Directionality of juvenile wood frogs trails in Experiment 2 (*Ecological Archives* E089-144-A2).

#### APPENDIX C

Mean final densities of juvenile wood frogs in high-quality habitat treatments in 1 × 4 m pens two weeks after initial release (*Ecological Archives* E089-144-A3).

#### APPENDIX D

Schematic representation of the effects of changes in habitat quality due to factors such as weather (*Ecological Archives* E089-144-A4).

#### APPENDIX E

Survival of juvenile wood frogs at three density treatments (2, 4, and 7 frogs/m<sup>2</sup>) in 1 × 4 m pens in 2006 calculated using program MARK (*Ecological Archives* E089-144-A5).