

1 Terrestrial habitat selection and strong density-dependent mortality in recently  
2 metamorphosed amphibians

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15

16 ABSTRACT

17 To predict the effects of terrestrial habitat change on amphibian  
18 populations, we need to know how amphibians respond to habitat heterogeneity,  
19 and whether habitat choice remains consistent throughout the life-history cycle.  
20 We conducted four experiments to evaluate how the spatial distribution of  
21 juvenile wood frogs, *Rana sylvatica* (including both overall abundance and  
22 localized density) was influenced by habitat choice and habitat structure, and  
23 how this relationship changed with spatial scale and behavioral phase. The four

24 experiments included (1) habitat manipulation on replicated 10 ha landscapes  
25 surrounding breeding pools; (2) short-term experiments with individual frogs  
26 emigrating through a manipulated landscape of 1 m wide hexagonal patches;  
27 and habitat manipulations in (3) small (4 m<sup>2</sup>) and (4) large (100 m<sup>2</sup>) enclosures  
28 with multiple individuals to compare behavior both during and following  
29 emigration. The spatial distribution of juvenile wood frogs following emigration  
30 resulted from differences in the scale at which juvenile amphibians responded to  
31 habitat heterogeneity during active versus settled behavioral phases. During  
32 emigration, juvenile wood frogs responded to coarse-scale variation in habitat  
33 (selection between 2.2 ha forest treatments) but not to fine-scale variation. After  
34 settling however, animals showed habitat selection at much smaller scales (2-4  
35 m<sup>2</sup>). This resulted in high densities of animals in small patches of suitable habitat  
36 where they experienced rapid mortality. No evidence of density-dependent  
37 habitat selection was seen, with juveniles typically choosing to remain at  
38 extremely high densities in high-quality habitat, rather than occupying low-quality  
39 habitat. These experiments demonstrate how predicting the terrestrial distribution  
40 of juvenile amphibians requires understanding complex behavioral responses to  
41 habitat heterogeneity. Understanding these patterns is important given that  
42 human alterations to amphibian habitats may generate extremely high densities  
43 of animals, resulting in high density-dependent mortality.

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## 47 INTRODUCTION

48           Improving our understanding of habitat selection requires examining how  
49 animal behavior, environmental structure, and variation in habitat quality interact  
50 to determine the spatial distribution of organisms (Figueira and Crowder 2006).  
51 These relationships can determine density-dependent mortality through  
52 competition (Hixon and Jones 2005), predation (Johnson 2006), and disease  
53 (Bradshaw and Brook 2005). Spatial distribution can also influence the probability  
54 of dispersal between populations, in turn determining rescue effects (Hanski et  
55 al. 1994, Trenham et al. 2001) genetic variation and structure (Purcell et al.  
56 2006), and regional population persistence (Harveson et al. 2004).

57           Determining the relationship between habitat structure or quality,  
58 movement behavior, and the spatial distribution of organisms may be of  
59 particular importance for less vagile taxa such as amphibians (Wind 1999).  
60 Historically, research on amphibian ecology has focused on aquatic life-history  
61 stages, but recent population models have shown that the growth and decline of  
62 amphibian populations are highly sensitive to changes in the survival of terrestrial  
63 life-history stages (Biek et al. 2001, 2002, Vonesh and De la Cruz 2002). In  
64 particular, amphibian declines and extinctions have been linked to fragmentation  
65 and loss of their terrestrial habitat (Stuart et al. 2004). However, mechanisms  
66 driving amphibian distributions in landscapes and the effects of these  
67 distributions on survival are not well understood.

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

70 2007) and the type of terrestrial environment in which animals are located (Todd  
71 and Rothermel 2006, Harper and Semlitsch in review, Rittenhouse et al. in  
72 review). To translate these differences in vital rates into population level effects,  
73 however, requires understanding individual habitat choice and resulting densities  
74 in a heterogeneous landscape. Field studies have shown that individual  
75 amphibians within a breeding population are not uniformly distributed in the  
76 terrestrial environment (Regosin et al. 2003, Regosin et al. 2005), and that these  
77 patterns of spatial distribution can differ between life-history stages and  
78 behavioral “phases” (for example emigrating compared to settled) (Regosin et al.  
79 2003, Baldwin 2005, Baldwin et al. 2006b, Patrick et al. 2006). No published  
80 studies to date, however, have reported on the behavioral mechanisms that lead  
81 to these differences in the spatial distribution of populations.

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

89         Our research focuses on the habitat choice of juvenile wood frogs, *Rana*  
90 *sylvatica*. We considered two behavioral phases, animals actively emigrating  
91 from natal ponds and animals that have settled following this active emigration  
92 phase. Because wood frogs are a forest-dependent species (deMaynadier and

93 Hunter 1998), we used timber harvesting (partial harvesting and clearcutting) as  
94 a means of manipulating habitat quality. We conducted four experimental habitat  
95 manipulations representing a range of spatial scales. In Experiment 1 we used  
96 replicate landscape-scale manipulations of terrestrial habitat (10 ha landscapes)  
97 around amphibian breeding ponds, a scale sufficient to contain most individuals  
98 in a local amphibian population (Semlitsch and Bodie 2003). Experiment 2  
99 focused on the influence of fine-scale habitat heterogeneity (1 m<sup>2</sup> patches) on  
100 individual movement behavior during the active period of emigration. In  
101 Experiment 3, we studied responses to fine-scale habitat heterogeneity in a  
102 simple enclosed landscape (2 m<sup>2</sup> patches) during and following the active  
103 emigration phase, and examined the effect of conspecific density on survival. In  
104 Experiment 4 we studied response to a meso-scale habitat manipulation (100 m<sup>2</sup>  
105 enclosure made up of 4m<sup>2</sup> patches), and evaluated how the interaction between  
106 habitat heterogeneity and the density of conspecifics affected habitat choice.

107

## 108 METHODS

109 *Study Species:* The wood frog is a wide-ranging North American ranid (occurring  
110 from north of the Arctic circle south to Missouri, and from the East coast to  
111 Alaska) closely associated with forests (deMaynadier and Hunter 1998). In  
112 central Maine, wood frogs breed in April, with each female laying a clutch of  
113 approximately 1000 eggs. Tadpoles metamorphose at the end of June/early July.  
114 After emergence, juveniles emigrate away from the pond and approximately 2  
115 weeks later they begin to settle in the landscape and establish a summer

116 foraging area (Patrick et al. 2006). In late fall, frogs move to upland areas where  
117 they over-winter in leaf-litter on well-drained soils (Baldwin et al. 2006a). Adults  
118 breed 1 to 3 years following metamorphosis with high rates of philopatry to natal  
119 ponds (Berven and Grudzien 1990, Vasconcelos and Calhoun 2004).

120

121 *Study Area:* Experiments were established in the Dwight B. Demeritt (Gilman and  
122 Smith sites) and Penobscot Experimental (North and South Chemo sites)  
123 Forests, Penobscot Country, Maine, USA. The area consists of mature mixed  
124 deciduous/coniferous forest (>80 years old). Dominant tree species include  
125 balsam fir (*Abies balsamea*), eastern white pine (*Pinus strobes*), northern white  
126 cedar (*Thuja occidentalis*), red maple (*Acer rubrum*), red oak (*Quercus rubra*),  
127 and paper birch (*Betula papyrifera*). We obtained weather data for the study  
128 region from a weather station at Bangor International Airport approximately 8 km  
129 from the study site (<http://pnwpest.org/NE/ME/index.html>).

130

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

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

139           Each of the four replicate arrays in Maine was centered on an amphibian  
140 breeding pond (10-15 m in diameter). The terrestrial habitat surrounding each of  
141 these ponds to a distance of 164 m was divided into quarters, with each quarter  
142 randomly assigned one of four forestry treatments applied between December  
143 2003 and April 2004: an uncut control, a partial cut (PC) where 50% of the  
144 canopy was removed, and two clearcuts, one where coarse woody debris (CWD)  
145 >10 cm in diameter was retained (CWD-retained), and one where CWD was  
146 removed (CWD-removed) (Fig. 1). Each array was established with large areas  
147 of continuous forest extending at least 300 m beyond the outer perimeter. Arrays  
148 were at least 5 km apart except for South and North Chemo where the outer  
149 edges were approximately 300 m apart.

150           At each array, we completely encircled the pond with a drift fence with  
151 pitfall traps every 5 m on the inside and outside. Additional drift fences were  
152 established at 16, 50, 100, and 150 m into each of the terrestrial forestry  
153 treatments; these were 10 m in length with a pitfall trap on each end, and one on  
154 each side in the center. The number of fences increased at each distance away  
155 from the ponds, such that an equal proportion of the total arc was sampled (38 %  
156 of the circumference; i.e., one fence in each treatment of each array at 16 m, 3 at  
157 50 m, 6 at 100 m, and 9 at 150 m) (Fig. 1).

158           We monitored pitfall traps from 24 June to 17 September in 2005, and 30  
159 June to 22 August in 2006, checking traps every other day until the beginning of  
160 September when we checked traps every two days. We marked all metamorph  
161 wood frogs captured emerging from the ponds according to the following

162 protocols: In 2005, metamorphs were marked using a single toe-clip to indicate  
163 into which treatment they emerged. In 2006, metamorphs initially were marked at  
164 the pond fences based on the treatment and the week of first capture. Animals  
165 recaptured at the terrestrial fences were marked with visible implant elastomer  
166 (VIE) to indicate clearcut or forested (control and PC) treatment, and the week of  
167 first recapture. Animals recaptured following this second mark were not  
168 remarked, but were counted as a multiple recapture. The latter data were only  
169 used for question (3) below.

170 Data from this experiment were used to evaluate three questions: (1) did  
171 wood frogs preferentially select one or more of the terrestrial treatments; (2) was  
172 habitat selection consistent between years; and (3) were there differences in  
173 habitat use as animals transitioned from the active emigration phase to the  
174 subsequent settled phase.

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

184

185 Experiments 2-4: The remaining experiments were conducted in a clearcut  
186 treatment as it was feasible to approximate forest conditions in a clearcut (using  
187 shade-cloth and augmenting woody debris and leaf-litter), but not clearcut  
188 conditions in the forest due to shade from large trees. For each of these  
189 experiments we recorded the maximum daily temperature and total daily  
190 precipitation during the study periods.

191

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

194 In this experiment, we evaluated whether individual behavior was  
195 influenced by local habitat structure during active emigration. We established a  
196 12x16 m experimental landscape approximately in the center of the Gilman site  
197 (Fig. 1). We removed all vegetation and woody material >1 cm in diameter and  
198 used pin flags to demarcate a honeycomb grid of 11 by 16 tessellating hexagonal  
199 cells, each 1 m in width. These cells were assigned one of three possible  
200 contents: (1) bare ground (hereafter denoted as “empty”); (2) habitat containing a  
201 total of 2 m of 10-15 cm diameter coarse woody debris (denoted “CWD”) of  
202 decay class 3 (Faccio 2003); and (3) habitat containing a 30 cm high by 1-m wide  
203 pile of fine woody material (<2 cm in diameter, denoted as “slash”). There were  
204 147 empty cells, 8 cells containing CWD, and 21 cells containing slash (Fig. 1).  
205 These proportions were designed to mimic the relative amounts of these  
206 conditions in the LEAP clearcut with CWD-retained treatment (unpub. data). The  
207 contents of the hexagonal cells were initially assigned non-randomly to ensure an

208 approximately equal dispersion of the three cell contents. Following this initial  
209 landscape configuration, the contents of each of the slash and CWD cells were  
210 assigned to one of the adjoining cells on a random basis to create a new  
211 landscape configuration within the same grid. We repeated this process of  
212 randomizing the landscape three times to give four scenarios in total.

213         We conducted the experiment from 27 June to 3 August 2005. Wood frog  
214 metamorphs were collected on emergence from the breeding pond located 100  
215 m to the east of the experimental landscape. We collected 30 metamorphs for  
216 each scenario, releasing the animals into the experimental landscape at dusk.  
217 Releases occurred over a period of 2-4 nights per scenario. Cells in which  
218 animals were released were randomly chosen with the condition that no other  
219 individual could be released into the same or an adjacent cell. Before release, we  
220 liberally coated the ventral side of each frog with fluorescent powder. (The use of  
221 fluorescent powder allows the movement of individuals to be followed, while  
222 minimizing any potential effects of handling on behavior (Rittenhouse et al.  
223 2006). We then placed the frog under an inverted plastic cup in the center of an  
224 empty cell, removing the cup 10 minutes later using an attached 2-m long  
225 bamboo pole. Two hours later, we followed powder trails using an ultraviolet light.  
226 This period was sufficient for the animals to move outside the experimental  
227 landscape. We marked trails with wire flags and string. Marking of a trail was  
228 terminated when the frog left the boundary of the experimental array, or when  
229 there was >50 cm between signs of fluorescent powder. Each study animal was  
230 used once. To ensure that animals were neither “homing” back to their point of

231 initial capture nor exhibiting escape behavior, we also conducted an initial pilot  
232 study during which we monitored the movement of juvenile frogs placed outside  
233 of the experimental array. No evidence was seen to suggest that either of these  
234 behaviors were present.

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

248

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

252         We designed this experiment to evaluate the effect of conspecific density  
253 and fine-scale habitat structure on habitat selection. We also assessed if habitat

254 choice changed as animals progressed from active emigration to the settled  
255 phase, and the effects of density on short-term survival. We established 24 1x4  
256 m experimental pens >30 m from the edge of the clearcut CWD-removed  
257 treatment of the Gilman site (Fig. 1). We constructed pens as 12 randomly  
258 oriented pairs, with a pair sharing a central wall along the long axis. Pens were  
259 constructed from 1-m tall silt fencing buried 30 cm into the ground. A 3-cm lip  
260 was created on the inside of each pen to prevent escapes and trespasses. We  
261 removed all vegetation and woody material from the pens, with half of each pen  
262 ( $2 \text{ m}^2$ ) randomly assigned as either high- or low-quality habitat (Fig. 1). The  
263 second pen in each pair had the opposite configuration. To create high-quality  
264 habitat we used 30 mm deep leaf litter, a total of 3 m of 10-15 cm diameter CWD  
265 of decay class 3, and 70% shade cloth elevated 1 m from the ground. Low-  
266 quality habitat contained 25 mm deep leaf litter and was not shaded.

267 We conducted this experiment from 20 July to 6 August in 2005 and 31  
268 July to 18 August in 2006. Recently metamorphosed wood frogs were released  
269 into the pens in three randomly assigned density treatments: low (2 individuals  
270 per  $\text{m}^2$ , 8 per pen); medium (4 per  $\text{m}^2$ , 16 per pen); and high (7 per  $\text{m}^2$ , 28 per  
271 pen). The same treatment was assigned to each pair of pens. Densities were  
272 based on previous research showing a threshold between 4 and 7 juvenile wood  
273 frogs per  $\text{m}^2$  at which point growth and survival decreased (Harper and Semlitsch  
274 2007).

275 In 2005, eight pens were assigned to each of the three density treatments.  
276 Following release of the amphibians, we left the pens for 16 days, a sufficient

277 period for juvenile wood frogs to transition from active emigration to a settled  
278 phase (Patrick et al. 2006). At midday when juvenile wood frogs were not active,  
279 a barrier was then constructed between the two habitat treatments within each  
280 pen, creating two temporary 1x2 m pens. We conducted exhaustive sampling at  
281 dusk when frogs were most active. For each captured frog we noted the  
282 treatment of capture and snout-vent length (SVL). As frogs were never seen to  
283 be active in the low-quality habitat treatments during the day, this sampling  
284 approach allowed us to assess habitat selection during the night when juvenile  
285 wood frogs move.

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

290 In 2006, six pens were assigned to each of the three density treatments.  
291 All animals were measured and individually marked before release using a  
292 combination of a single toe-clip and visible implant elastomer (VIE). Pens were  
293 sampled at 3-day intervals following the date of release, for 15 days per pen, with  
294 captured animals measured, identified individually, and the treatment of capture  
295 noted. This protocol allowed an assessment of changes in habitat selection and  
296 survival over the total sampling period. In 2006, frogs in four of the six highest  
297 density pens showed extremely rapid mortality, likely because of disease  
298 indicated by physical signs such as hemorrhaging, with rapid mortality. These

299 pens were excluded from further analyses following these events (no signs of  
300 disease were seen prior to mortality events).

301 Recaptures in 2006 were analyzed using a general linear model, with the  
302 number of recaptures in the high-quality treatment as the dependent variable,  
303 and time, rainfall, maximum daily temperature during the period between  
304 samples, and total number captured during the sampling period as covariates.

305 We used a Cormack-Jolly-Seber model in program MARK (version 4.0) to  
306 estimate capture probability at each sampling interval for the individually marked  
307 animals in 2006. This allowed us to assess the efficacy of our sampling efforts.  
308 Survival analysis was conducted using the individually marked animals in 2006  
309 with the data adjusted to account for capture probability. We used a non-  
310 parametric Kaplan-Meier survival analysis to compare survival over time for wood  
311 frogs in the three density treatments.

312

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

315 In 2006, we established a single 10x10-m pen approximately in the center  
316 of the CWD-removed clearcut at the Gilman site. This pen was constructed of 1-  
317 m tall silt fencing buried 30-cm into the ground, with a 3-cm lip on both the inside  
318 and outside to prevent animals entering or exiting. Within this pen, all vegetation  
319 and woody material were removed. We demarcated the pen into 25 2x2-m  
320 habitat blocks alternately designated as either high or low-quality habitat to  
321 create a regular checkerboard effect (Fig. 1). Low and high-quality blocks

322 consisted of the same habitat variables as in Experiment 3, but with 10 m rather  
323 than 3 m of 10-15 cm diameter CWD of decay class 3 in the high-quality blocks.

324 We released 200 recently metamorphosed wood frogs from 28 July to 31  
325 July 2006, with 50 frogs placed in each of the corner habitat blocks. On 2 August  
326 2006, temporary barriers were constructed around each of the 25 habitat blocks  
327 using 1-m tall silt fencing stapled to central posts and fixed to the ground with  
328 metal stakes. Barriers were constructed at midday when wood frogs were not  
329 active and unlikely to move in response to disturbance. Each of the 25 blocks  
330 was then sampled to determine the density of individuals (termed "sample 1"). To  
331 ensure that no animals were injured during sampling we maintained a clear path  
332 where each barrier fell and carefully removed all CWD from each block, replacing  
333 it afterwards.

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

341 We used chi-square to test if more individuals settled in high-quality  
342 habitat blocks and whether there were any differences between edge and interior  
343 blocks. The latter analysis allowed us to evaluate if habitat selection was  
344 influenced by either escape behavior or the increased shade on the edge of the

345 pen. The expected number of captures was adjusted by the number of blocks  
346 that fell into each of these categories (13 high quality and 12 low quality).  
347 Recaptures are reported as density per  $m^2$ , while total counts were used in  
348 statistical analyses. In sample 2, we evaluated recaptures from the first release  
349 and second release separately due to possible correlation between the location  
350 of unmarked animals in sample 1 and sample 2.

351 We tested two alternative hypotheses based on the settling of marked  
352 animals from the second batch released: hypothesis (1), individuals settle based  
353 on differences in habitat, not density of conspecifics (i.e., blocks with high  
354 numbers of individuals in sample 1 were presumably high-quality and would have  
355 high numbers in sample 2); and hypothesis (2), individuals settle based on  
356 avoiding competition from those animals already released in the first batch (i.e.,  
357 more animals would be captured in sample 2 in blocks that had few captures in  
358 sample 1). We grouped habitat blocks based on the number of recaptures in  
359 sample 1, regardless of habitat treatment. Three categories were used: low (1  
360 individual,  $N = 7$  blocks), medium (2-5 individuals,  $N = 9$ ), and high (6+  
361 individuals,  $N = 9$ ), with the cut-off point for each category based on qualitative  
362 analysis of the distribution of data. Recaptures were totaled for blocks within  
363 these groups and the proportion of the total recaptures in each group calculated.  
364 For hypothesis 1, this proportion was used to derive the number of marked  
365 animals expected in sample 2 if the animals distributed themselves in the same  
366 way. For hypothesis 2, we postulated that marked animals would show the  
367 reverse trend with more marked animals captured in blocks that had previously

368 shown low captures. Based on this hypothesis, we used the proportion of  
369 captures from the low recapture blocks to estimate the number expected in high-  
370 quality blocks, and *vice versa*. Medium quality blocks were presumed to have an  
371 equal proportional relationship between unmarked captures in sample 1, and  
372 marked captures in sample 2.

373

374 *Overall statistical analyses.*

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

380

381 RESULTS

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

384 The four forestry treatments differed significantly in numbers of recaptures  
385 in both years (Fig. 2,  $F = 8.845$ ,  $df = 3,91$ ,  $P \leq 0.001$ ), with *post hoc* analyses  
386 revealing significantly more recaptures in forested treatments (control and partial  
387 cut) than in the clearcuts ( $P \leq 0.001$ ), but no significant difference between the  
388 control and partial cut or between the two clearcut treatments ( $P > 0.999$ ). The  
389 numbers of recaptures in the 4 treatments did not significantly differ over  
390 distance from the pond, ( $F = 0.586$ ,  $df 3,9,91$ ,  $P = 0.625$ ), suggesting that once

391 these treatments had been entered the frogs moved through them in a similar  
392 fashion (data summarized in Appendix 1). There were significant differences  
393 among the four experimental sites ( $F = 10.155$ ,  $df = 3,91$ ,  $P \leq 0.001$ ). The lack of  
394 a significant year, treatment, and site interaction ( $F = 0.261$ ,  $df = 1,3,3,1,3,9,91$ ,  $P$   
395  $= 0.983$ ) indicates that the differences among sites reflected variation in the  
396 overall number of juvenile wood frogs recaptured at each site, and not variation  
397 in patterns of treatment selection or captures over distance.

398         No significant difference could be seen between the proportions of wood  
399 frogs that settled in treatments (indicated by multiple recaptures of the same  
400 individual in our 2006 experiment) and the proportions that emigrated through  
401 treatments (indicated by first-time recaptures) (Gilman  $\chi^2 = 0.668$ ,  $df = 3$ ,  $P \geq$   
402  $0.75$ ; North Chemo  $\chi^2 = 1.596$ ,  $P \geq 0.5$ ; Smith  $\chi^2 = 10.706$ ,  $P \geq 0.1$ , South  
403 Chemo excluded due to disease).

404

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

407         In the 1-m wide hexagonal cells with three contents (empty, CWD, and  
408 slash), no significant difference could be detected between the observed habitat  
409 selection of emigrating juvenile wood frogs and that expected with random  
410 movement (Table 1). This indicates that individual juvenile wood frogs were not  
411 demonstrating fine-scale habitat selection for any of these three habitats during  
412 the active emigration phase. Trails were found to be randomly oriented

413 (Appendix 2, Rayleigh's Z test:  $Z = 0.375$ ,  $df = 1,111$ ,  $P = 0.688$ ) indicating that  
414 movement of juvenile frogs in a specific direction did not influence the results.

415

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

419 More individuals in the 1x4 m pens were recaptured in the high-quality  
420 treatment than in the low-quality treatment at the conclusion of the experiment  
421 (after 2 weeks) in 2005 (mean proportion of total recaptures  $\pm$  SD =  $0.881 \pm$   
422  $0.116$ ). The initial density of animals released into the pens (either 2, 4, or 7 m<sup>2</sup>)  
423 did not determine the final proportion of recaptures in the high-quality treatment  
424 ( $F = 0.895$ ,  $df = 2,15$ ,  $P = 0.429$ ). Similarly, the final density of animals (based on  
425 the total number of recaptures in the final sample) did not significantly influence  
426 the proportion of animals found in the high-quality habitat (linear regression of the  
427 proportion of recaptures in the high-quality treatment in relation to the total  
428 number recaptured  $F = 4.272$ ,  $df = 1,16$ ,  $P = 0.055$ ).

429 A higher proportion of animals were also recaptured in the high-quality  
430 treatment in 2006 ( $0.797 \pm 0.194$ ). No significant relationship was found between  
431 the proportion of recaptures in the high-quality habitat and the total number  
432 recaptured in the pen ( $F = 0.991$ ,  $df = 1,12$ ,  $P = 0.339$ ). Both mean daily  
433 maximum temperatures and precipitation were similar during 2005 and 2006  
434 (mean daily max. °C  $28 \pm 3$  and  $25 \pm 2$ ; mean daily precipitation mm:  $5 \pm 8$  and  $3$   
435  $\pm 5$  for 2005 and 2006 respectively)

436 Survivorship was significantly different among density treatments in 2006  
437 (Fig. 3. Wilcoxon;  $\chi^2 = 74.91$ ,  $df = 2$ ,  $P < 0.0001$ ). Wood frogs in enclosures  
438 initially stocked at the lowest density (8 frogs/per pen) were more than four times  
439 as likely to survive than frogs in the highest density enclosures. Only 7.7% of  
440 wood frogs stocked at an initial density of 28 frogs per enclosure survived to the  
441 end of the experiment at week 15, compared to 37.5% in enclosures stocked with  
442 16 animals and 47.9% in enclosures stocked with 8 frogs.

443

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

446 Significantly more animals were recaptured in high-quality habitat in the  
447 10x10-m pen (Table 2. Sample 1:  $X^2 = 24.762$ , sample 2:  $X^2 = 52.878$ ,  $P =$   
448  $<0.001$ ). In sample 1, 119 of the 200 animals in the first release were recaptured;  
449 9 days later in sample 2, 121 out of the total of 300 released (200 first and 100  
450 second release) were recaptured.

451 The mean density of animals in low-quality cells decreased substantially  
452 from sample 1 to sample 2 from 0.625 to 0.19  $m^2$ , with the density in high-quality  
453 cells increasing from 3.25 to 7.25  $m^2$  (Table 2.). Additionally, in sample 1, at least  
454 one animal was recaptured in all of the blocks. In sample 2, however, four of the  
455 low-quality blocks had no recaptures. Temperatures during samples 1 and 2  
456 remained consistent (mean daily max. °C:  $28 \pm 2$  and  $25 \pm 1$  respectively), but  
457 there was far greater precipitation during sample 1 (mean daily mm:  $30 \pm 50$  and  
458  $2 \pm 3$ , respectively).

459 High-quality blocks on the edge of the pen (where the fence itself provided  
460 extra shading) had significantly higher numbers of recaptures than those in the  
461 center of the pen in both samples (sample 1:  $X^2 = 11.012$ ,  $P = <0.001$ ; sample 2:  
462  $X^2 = 8.940$  for unmarked, and  $25.829$  for marked individuals,  $P = <0.005$  for  
463 unmarked and  $<0.001$  for marked animals). Animals in this experiment chose  
464 blocks based on habitat quality, and not on the distribution of individuals from the  
465 first batch released (i.e., no significant difference was found in the distribution of  
466 first release animals caught in sample 1 compared to first release animals  
467 captured in sample 2 [ $X^2 = .900$ ,  $P = >0.50$ ]).

468

469 DISCUSSION

470 *The effects of habitat heterogeneity on spatial distribution*

471 Recent research has clearly demonstrated that changes in terrestrial  
472 habitat can lead to reductions in amphibian survival (Rothermel and Luhring  
473 2005, Todd and Rothermel 2006, Harper 2007, Rittenhouse et al. in review).  
474 However, the effects of habitat alteration at the population level are determined  
475 not only by habitat-specific vital rates, but also depend on how individuals in the  
476 population are distributed in the mosaic of available habitat types. This  
477 distribution determines both local densities as well as the proportion of the  
478 population exposed to different habitat types, both of which affect vital rates. Our  
479 study demonstrates the complexity of predicting the effects of habitat  
480 heterogeneity on the spatial distribution of amphibians. Specifically, we show that  
481 the interaction between the behavioral phase of the amphibian and the scale of

482 habitat heterogeneity determines these patterns, rather than these factors  
483 operating independently.

484         The spatial distribution of juvenile wood frogs following emigration resulted  
485 from differences in the scale at which juvenile amphibians in active compared to  
486 settled phases responded to habitat heterogeneity. During active emigration,  
487 juvenile wood frogs chose habitat at a coarse spatial scale, selecting large  
488 patches (2.2 ha) of high-quality forested habitat in preference to the lower-quality  
489 clearcuts, but not responding to differences between the uncut and partially cut  
490 forest (Experiment 1, Fig. 2). During this behavioral phase, they showed no  
491 response to finer scale differences in habitat as represented in Experiment 2's ~1  
492 m<sup>2</sup> patches of slash/CWD and bare ground (Table 1). Initially, this behavior  
493 resulted in a higher abundance of animals in high-quality forested treatments  
494 compared to clearcuts, but similar distributions over distance within all four  
495 treatments. If habitat choice was consistent between life-history phases, juveniles  
496 would have remained distributed in this way, and animals in the clearcuts would  
497 have been at much lower densities than those in the forested treatments.  
498 Crucially, however, after juvenile wood frogs transitioned into a post-emigration  
499 settled phase we observed a change in the scale at which habitat heterogeneity  
500 was perceived, with choice at a much finer scale, i.e., selection for small patches  
501 of high-quality habitat in both the 1x4 m and 10x10 m pens (Experiments 3 and 4  
502 respectively, Table 2). This behavior resulted in extremely high densities of  
503 juvenile wood frogs in localized patches of high-quality habitat (up to 7.75  
504 individuals per m<sup>2</sup>).

505 *Density and habitat selection*

506           Understanding how the juvenile frogs respond to localized densities of  
507 conspecifics forms a vital connection between spatial ecology and the resulting  
508 effects on both individuals and populations. Individuals should distribute  
509 themselves within available habitat to maximize fitness, with animals preferring to  
510 be in high-quality habitat. As density increases, however, the fitness advantage  
511 of remaining in this habitat decreases, and a point should be reached at which  
512 some animals leave high-quality habitat and move into lower-quality habitat  
513 (Fretwell and Lucas 1969, Morris 1987). In our experiments, however, we saw  
514 little evidence of density-dependent habitat choice, with juvenile frogs typically  
515 choosing to remain at extremely high densities in high-quality habitat, rather than  
516 occupying low-quality habitat. This is of particular note given that our survival  
517 analysis and similar research with the study species (Harper and Semlitsch  
518 2007) shows how rapidly density-dependent mortality can occur. Our results  
519 suggest that the low-quality treatments in Experiment 3 (i.e., the 1x4 m pens) and  
520 the second sample in Experiment 4 (2x2 m blocks) had very little use once  
521 juvenile wood frogs were in a settled phase. Given the importance of this low-  
522 quality habitat in driving the high density-dependent mortality we observed,  
523 understanding when habitat falls below the threshold at which it is used is  
524 important. As our study did not examine a continuum of habitat quality, we  
525 cannot pinpoint this threshold. However, we did see a change in the use of low-  
526 quality habitat blocks in Experiment 4: In the first sample, all low-quality blocks  
527 (each 4 m<sup>2</sup>) contained at least one frog, with a mean density of 0.625/m<sup>2</sup>. In the

528 second sample, however, four of the low-quality blocks were entirely empty (even  
529 though the overall number of frogs captured was the same in both samples), and  
530 the mean density in this treatment had dropped to  $0.19/\text{m}^2$  (Table 2). We  
531 hypothesize that this is indicative of an overall drop in habitat quality during the  
532 experiment, i.e., the low-quality habitat had decreased in quality to a point where  
533 it had become almost unusable.

534 *Temporal variability in habitat quality*

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

547         Temporal variation in abiotic factors such as weather has been shown to  
548 be an important factor determining habitat choice (Martin 2001), primarily  
549 because organisms need to remain within the limits of their physiological  
550 tolerances (Harte and Shaw 1995, Root and Schneider 1995). Long-term

551 changes in abiotic factors drive shifts in the geographic distribution of species  
552 (McCarty 2001). Over shorter periods (for example within days or weeks), abiotic  
553 change probably causes individuals to relocate to remain within patches of  
554 suitable habitat. The high sensitivity of amphibians to small changes in abiotic  
555 conditions (Spotila 1972, Rittenhouse et al. in review) means that for animals  
556 found in places with extremely limited suitable habitat (for example the clearcut  
557 areas in our experiments), these remaining patches may act as highly isolated  
558 islands, even when large areas of suitable habitat are not far away (illustrated in  
559 Appendix 3). Even if factors such as temperature and moisture are unfavorable  
560 for a short period, based on the results of our experiments, this isolation can  
561 cause rapid mortality for animals found at high densities.

562 *Isolating vital rates for population models*

563 Our research points to the role of habitat heterogeneity and behavioral phase in  
564 determining the spatial distribution and density-dependent survival of juvenile  
565 wood frogs. These results can be incorporated into both structured and spatially  
566 explicit population models to make predictions beyond the scope of our study.  
567 Most structured matrix population models project the change in population size  
568 over an annual cycle (Morris and Doak 2002). Models of amphibian populations  
569 have recognized differences in within-year survival rates for aquatic life history  
570 stages (i.e. egg vs. larval survival; (Vonesh and De la Cruz 2002)); however,  
571 survival estimates for early behavioral phases of the terrestrial stage of  
572 amphibians are rare. Enclosure studies have demonstrated that mortality rates  
573 are far greater within the first 6 weeks following metamorphosis than in

574 subsequent weeks (Trenham et al. 2000, Rothermel and Semlitsch 2006, Harper  
575 and Semlitsch 2007). We advocate incorporating separate survival parameters  
576 for the active movement phase and the settled phase of the terrestrial juvenile  
577 stage in structured populations models. Our density-dependent survival data  
578 provide estimates for the active movement phase (Appendix 5). Similar  
579 considerations of behavioral phases should be made when deriving dispersal  
580 kernels from our data on the distribution of marked juvenile wood frogs over  
581 distance from natal pools (Appendix 1). These data represent the spatial  
582 distribution of juvenile wood frogs in the first 2 months following metamorphosis,  
583 but do not indicate how factors such as movement to overwintering sites may  
584 change these distributions.

#### 585 *Conclusions*

586         Given the important role that terrestrial stages of amphibians play in  
587 driving population dynamics (Vonesh and De la Cruz 2002), the continuing  
588 degradation and loss of terrestrial habitat is of obvious concern for amphibian  
589 conservation. To date, however, evaluation of the role of terrestrial habitat  
590 heterogeneity in determining the spatial distribution of amphibians within  
591 populations has tended to focus on describing patterns of spatial distribution,  
592 rather than understanding the underlying mechanisms that generate these  
593 patterns. For example, studies have tended to operate under the premise that all  
594 “suitable” terrestrial habitats are essentially uniform in quality (although see  
595 Conroy and Brook 2003). While such studies have greatly increased our  
596 knowledge of amphibian ecology, they are of limited value when predicting

597 spatial distributions beyond the specific environment in which the study was  
598 conducted.

599         The experiments outlined in this study represent a novel approach to  
600 understanding amphibian ecology. Evaluating the influence of scale is a principle  
601 difficulty facing empirical studies of the effects of habitat heterogeneity on the  
602 spatial distribution of organisms (and resulting effects on populations) (Levin  
603 1992, Melbourne and Chesson 2006). Small-scale studies afford much greater  
604 control of variability, but there is a concern that the results from these studies  
605 may either be artifacts of the experimental design, or influenced by processes  
606 operating at a larger scale (Thrush et al. 1997). Studies conducted at larger  
607 scales can encompass these population-level processes, but inherently  
608 incorporate more variability and thus may require degrees of replication that are  
609 difficult to attain. The experiments we have outlined at multiple spatial scales  
610 offer one approach to addressing these issues. By conducting small-scale  
611 experiments, we were able to pinpoint specific mechanisms driving patterns of  
612 spatial distribution. The use of larger-scale experiments allowed us to evaluate  
613 how these mechanisms translated into population-level processes, and the role  
614 of forces operating at larger scales.

615

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625 Paper XXX

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## 643 LITERATURE CITED

644

645 Armstrong, D. P. 2005. Integrating the metapopulation and habitat paradigms for  
646 understanding broad-scale declines of species. *Conservation Biology*  
647 **19**:1402-1410.

648 Baldwin, R. F. 2005. Pool-breeding amphibian habitat use and conservation in  
649 southern Maine's urbanizing landscapes. PhD. University of Maine, Orono,  
650 Orono.

651 Baldwin, R. F., A. J. K. Calhoun, and P. G. deMaynadier. 2006a. Conservation  
652 planning for amphibian species with complex habitat requirements: a case  
653 study using movements and habitat selection of the wood frog *Rana*  
654 *sylvatica*. *Journal of Herpetology* **40**:443-454.

655 Baldwin, R. F., A. J. K. Calhoun, and P. G. deMaynadier. 2006b. The significance  
656 of hydroperiod and stand maturity for pool-breeding amphibians in  
657 forested landscapes. *Canadian Journal of Zoology* **84**:1604-1615.

658 Berven, K. A., and T. A. Grudzien. 1990. Dispersal in the wood frog (*Rana*  
659 *sylvatica*): implications for genetic population structure. *Evolution* **44**:2047  
660 - 2056.

661 Biek, R., W. C. Funk, and B. A. Maxell. 2001. What is missing in amphibian  
662 decline research: insights from ecological sensitivity analysis.

663 Biek, R., W. C. Funk, and B. A. Maxell. 2002. What is missing in amphibian  
664 decline research: insights from ecological sensitivity analysis.  
665 *Conservation Biology* **16**:728-734.

- 666 Bradshaw, C. J. A., and B. W. Brook. 2005. Disease and the devil: density-  
667 dependent epidemiological processes explain historical population  
668 fluctuations in the Tasmanian devil. *Ecography* **28**:181-190.
- 669 Conroy, S. D. S., and B. W. Brook. 2003. Demographic sensitivity and  
670 persistence of the threatened white- and orange-bellied frogs of Western  
671 Australia. *Population Ecology* **45**:105-114.
- 672 deMaynadier, P. G., and M. L. J. Hunter. 1998. Effects of silvicultural edges on  
673 the distribution and abundance of amphibians in Maine. *Conservation*  
674 *Biology* **12**:340-352.
- 675 Faccio, S. D. 2003. Postbreeding emigration and habitat use by Jefferson and  
676 Spotted salamanders in Vermont. *Journal of Herpetology* **37**:479-489.
- 677 Figueira, W. F., and L. B. Crowder. 2006. Defining patch contribution in source-  
678 sink metapopulations: the importance of including dispersal and its  
679 relevance to marine systems. *Population Ecology* **48**.
- 680 Fretwell, S. D., and J. Lucas, H. L. 1969. On territorial behavior and other factors  
681 influencing habitat distribution in birds. *Acta Biotheoretica* **19**:16-36.
- 682 Hanski, I., M. Kuussaari, and M. Nieminen. 1994. Metapopulation structure and  
683 migration in the butterfly *Melitaea cinxia*. *Ecology* **75**:747-762.
- 684 Harper, E. B. 2007. The role of terrestrial habitat in the population dynamics and  
685 conservation of pond-breeding amphibians. University of Missouri,  
686 Columbia.
- 687 Harper, E. B., and R. D. Semlitsch. 2007. Density dependence in the terrestrial  
688 life history stage of two anurans. *Oecologia* **153**:879-889.

- 689 Harper, E. B. H., and R. D. Semlitsch. in review. Density dependence in the  
690 terrestrial life history stage of two anurans.
- 691 Harte, J., and R. Shaw. 1995. Shifting dominance within a montane vegetation  
692 community: results of a climate warming experiment. *Science* **267**:8767-  
693 8880.
- 694 Harveson, P. M., W. E. Grant, R. R. Lopez, N. J. Silvy, and P. A. Frank. 2004.  
695 The role of dispersal in Florida Key deer metapopulation dynamics.  
696 *Ecological Modelling* **195**:393-401.
- 697 Hixon, M. A., and G. P. Jones. 2005. Competition, predation, and density  
698 dependent mortality in demersal marine fishes. *Ecology* **86**:2847-2859.
- 699 Johnson, D. W. 2006. Predation, habitat complexity, and variation in density-  
700 dependent mortality of temperate reef fishes. *Ecology* **87**:1179-1188.
- 701 Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* **73**:1943-  
702 1967.
- 703 Martin, T. E. 2001. Abiotic vs. biotic influences on habitat selection of co-existing  
704 species: climate change impacts. *Ecology* **82**:175-188.
- 705 McCarty, J. P. 2001. Ecological consequences of recent climate change.  
706 *Conservation Biology* **15**:320-331.
- 707 Melbourne, B. A., and P. Chesson. 2006. The scale transition: scaling up  
708 population dynamics with field data. *Ecology* **87**:1478-1488.
- 709 Morris, D. W. 1987. Tests of density-dependent habitat selection in a patchy  
710 environment. *Ecological Monographs* **57**:269-281.

- 711 Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: theory  
712 and practice of population viability analysis. Sinauer Associates, Inc.,  
713 Sunderland, Massachusetts U.S.A.
- 714 Patrick, D. A., M. L. Hunter Jr., and A. J. K. Calhoun. 2006. Effects of  
715 experimental forestry treatments on a Maine amphibian community. *Forest*  
716 *Ecology and Management* **234**:323-332.
- 717 Purcell, J. F. H., R. K. Cowen, C. R. Hughes, and D. A. Williams. 2006. Weak  
718 genetic structure indicates strong dispersal limits: a tale of two coral reef  
719 fish. *Proceedings of the Royal Society of London Series B-Biological*  
720 *Sciences* **273**:1483-1490.
- 721 Regosin, J. V., B. S. Windmiller, R. N. Homan, and J. M. Reed. 2005. Variation in  
722 terrestrial habitat use by four pool-breeding amphibian species. *Journal of*  
723 *Wildlife Management* **69**:1481-1493.
- 724 Regosin, J. V., B. S. Windmiller, and J. M. Reed. 2003. Terrestrial Habitat Use  
725 and Winter Densities of the Wood Frog (*Rana sylvatica*). *Journal of*  
726 *Herpetology* **37**:390-394.
- 727 Rittenhouse, T. A. G., T. T. Altnether, and R. D. Semlitsch. 2006. Fluorescent  
728 powder pigments as a harmless tracking method for Ambystomatids and  
729 Ranids. *Herpetological Review* **37**:188-191.
- 730 Rittenhouse, T. A. G., E. B. H. Harper, L. R. Rehard, and R. D. Semlitsch. in  
731 review. The role of microhabitats in the desiccation and survival of  
732 amphibians in recently harvested oak-hickory forest.

- 733 Root, T. L., and S. H. Schneider. 1995. Ecology and climate: research strategies  
734 and implications. *Science* **269**:334-341.
- 735 Rothermel, B., B., and T. M. Luhring. 2005. Burrow availability and desiccation  
736 risk of mole salamander (*Ambystoma talpoideum*) in harvested versus  
737 unharvested forest stands. *Journal of Herpetology* **39**:619-626.
- 738 Rothermel, B., B., and R. D. Semlitsch. 2006. Consequences of forest  
739 fragmentation for juvenile survival in spotted (*Ambystoma maculatum*) and  
740 marbled (*A. opacum*) salamanders. *Canadian Journal of Zoology* **84**:797-  
741 807.
- 742 Semlitsch, R. D., and J. R. Bodie. 2003. Biological Criteria for Buffer Zones  
743 around Wetlands and Riparian Habitats for Amphibians and Reptiles.  
744 *Conservation Biology* **17**:1219-1228.
- 745 Spotila, J. R. 1972. Role of temperature and water in the ecology of lungless  
746 salamanders. *Ecological Monographs* **42**:95-125.
- 747 Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. Rogrigues, D. L.  
748 Fischman, and R. M. Waller. 2004. Status and trends of amphibian  
749 declines and extinctions worldwide. *Science* **306**:1783-1786.
- 750 Thrush, S. F., V. J. Cummings, P. K. Dayton, R. Ford, J. Grant, J. E. Hewitt, A. H.  
751 Hines, S. M. Lawrie, R. D. Pridmore, and P. Legendre. 1997. Matching the  
752 outcome of small-scale density manipulation experiments with larger scale  
753 patterns an example of bivalve adult/juvenile interactions. *Journal of*  
754 *Experimental Marine Biology and Ecology* **216**:153-169.

- 755 Todd, B., and B. Rothermel, B. 2006. Assessing quality of clearcut habitats for  
756 amphibians: Effects on abundances versus vital rates in the southern  
757 toad (*Bufo terrestris*). *Biological Conservation* **133**:178-185.
- 758 Trenham, P. C., W. D. Koenig, and H. B. Shaffer. 2001. Spatially autocorrelated  
759 demography and interpond dispersal in the salamander *Ambystoma*  
760 *californiense*. *Ecology* **82**:3519 - 3530.
- 761 Trenham, P. C., H. B. Shaffer, W. D. Koenig, and M. R. Stromberg. 2000. Life  
762 history and demographic variation in the California tiger salamander  
763 (*Ambystoma californiense*). *Copeia* **2000**:365 - 377.
- 764 Vasconcelos, D., and A. J. K. Calhoun. 2004. Movement patterns of adult and  
765 juvenile *Rana sylvatica* (LeConte) and *Ambystoma maculatum* (Shaw) in  
766 three restored seasonal pools in Maine. *Journal of Herpetology* **38**:551-  
767 561.
- 768 Vonesh, J. R., and O. De la Cruz. 2002. Complex life cycles and density  
769 dependence: assessing the contribution of egg mortality to amphibian  
770 declines. *Oecologia* **133**:325 - 333.
- 771 Wind, E. 1999. Effects of habitat fragmentation on amphibians: what do we know  
772 and where do we go from here. *in* *Biology and management of species and*  
773 *habitats at risk*. B.C. Ministry of Environment, Lands, and Parks, Victoria,  
774 B.C., Kamloops, British Columbia.
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## TABLES

779

780

781 Table 1. Habitat selection of recently metamorphosed juvenile wood frogs  
 782 released in an artificial landscape of hexagonal cells (each approximately 1 m<sup>2</sup>  
 783 [Figure 1]). Each cell contains one of three habitat types: empty, CWD, or slash.  
 784 Four “scenarios”, where a frog chose between a specific combination of habitat  
 785 types in the surrounding six cells, yielded sufficient data for analysis. These  
 786 scenarios are each represented by a separate line in the table.

787

Contents of adjacent cells			Frogs (N) entering cells			X <sup>2</sup> P value
N cells Empty	N cells Slash	N cells CWD	Empty	Slash	CWD	
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

788

789 Table 2. Summary of the number and density of juvenile wood frogs recaptured  
 790 in a 10x10 m landscape of 4 m<sup>2</sup> blocks of two habitat types, high and low-quality.  
 791 Sample 1 refers to the distribution of animals following an initial release of 200  
 792 frogs. Sample 2 refers to the distribution of recaptures following a second release  
 793 of an additional 100 frogs.  
 794

Sample	Treatment	Mean density (m <sup>2</sup> )	Range in density (m <sup>2</sup> )	Unmarked captures (N)	Marked captures (N)
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

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## LIST OF FIGURES

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802

803 Figure 1. Outline of experiments (not to scale). In the schematic for Experiment  
804 2, one of the four landscape scenarios is shown for illustrative purposes. Coarse  
805 woody debris cells are indicated by gray hexagons, cells containing slash piles  
806 by black stippling. In excerpts for Experiments 3 and 4, hatch marks indicate  
807 high-quality habitat. Arrows indicate the approximate position of experiments 2-4  
808 within the landscape of experiment 1 (Experiments 2-4 were all conducted within  
809 a clearcut at the Gilman LEAP site). For Experiment 3, only one of the 12 paired  
810 pens is shown.

811

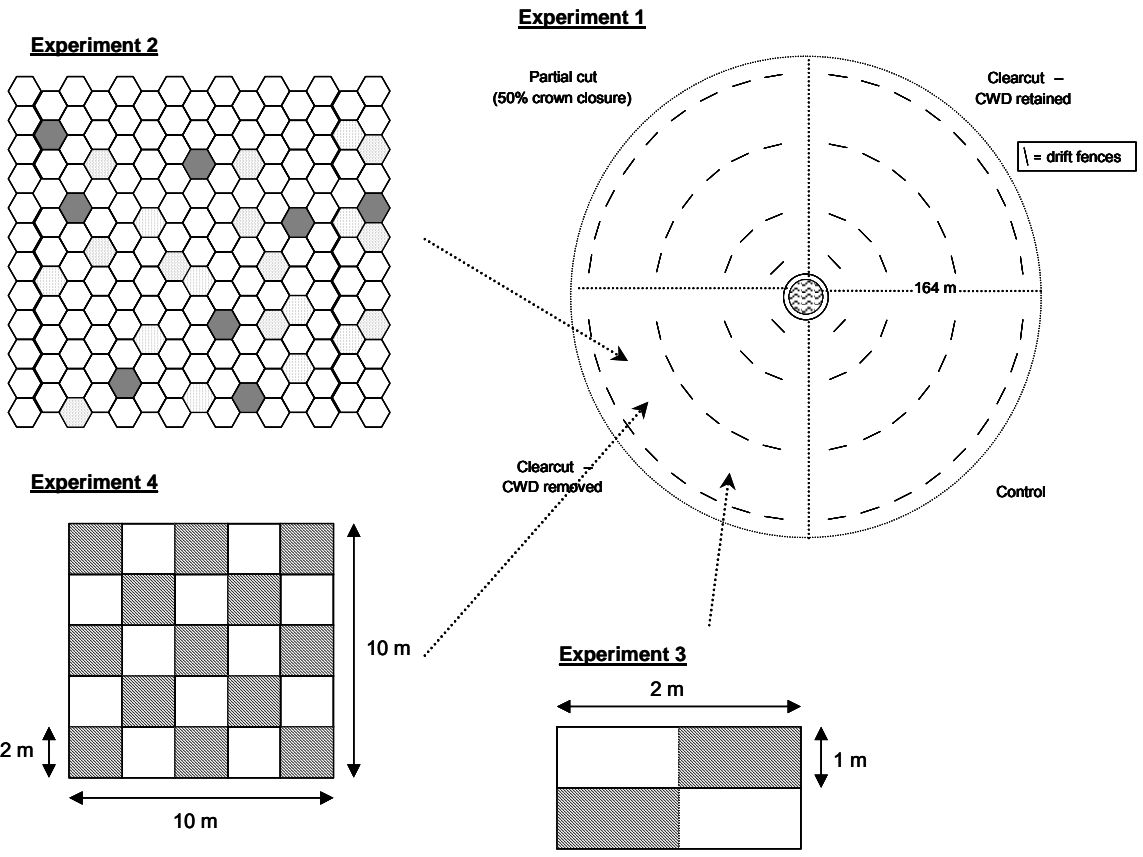
812 Figure 2. Total recaptures of emigrating juvenile wood frogs over distance from  
813 the pond in the LEAP treatments in (a) 2005 (n = 1084) and (b) 2006 (n = 410).  
814 The number of recaptures in 2006 represents animals recaptured for the first  
815 time only. The figure legend refers to the four LEAP forestry treatments (Control,  
816 PC = partial cut of 50 % crown closure, Rem = clearcut with CWD < 10cm in  
817 diameter removed, and Ret = clearcut with CWD-retained).

818

819 Figure 3. Survival of juvenile wood frogs at three density treatments (2, 4, and 7  
820 per m<sup>2</sup>) in 1x4 m pens in 2006. Survival analysis was only conducted in 2006 as  
821 in 2005 frogs were not individually marked.

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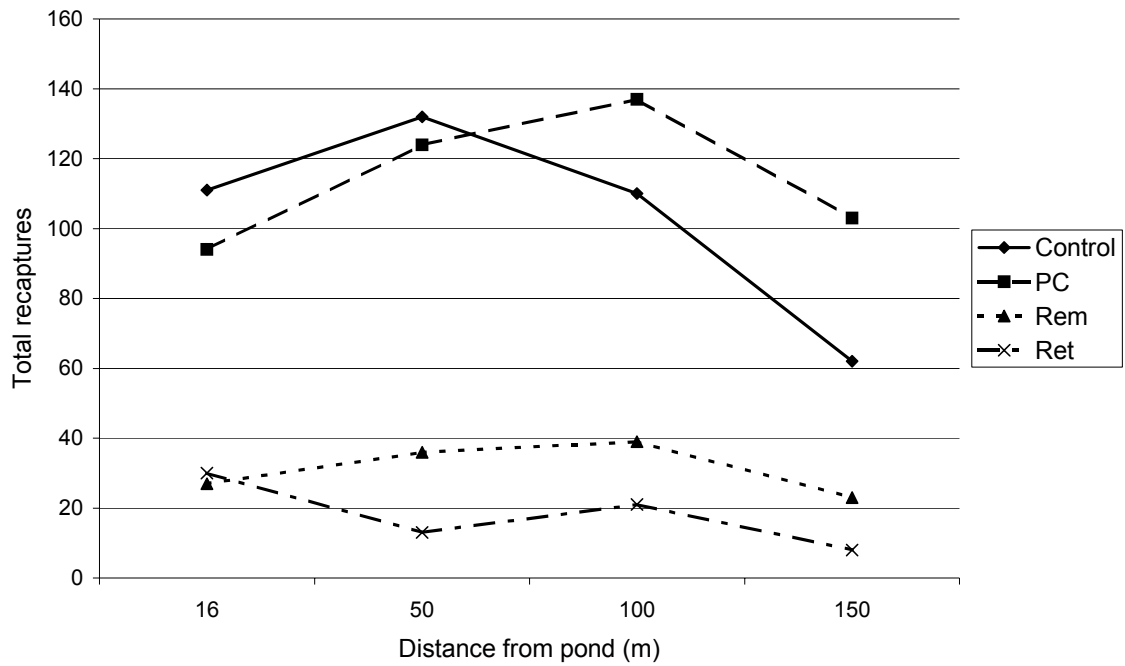
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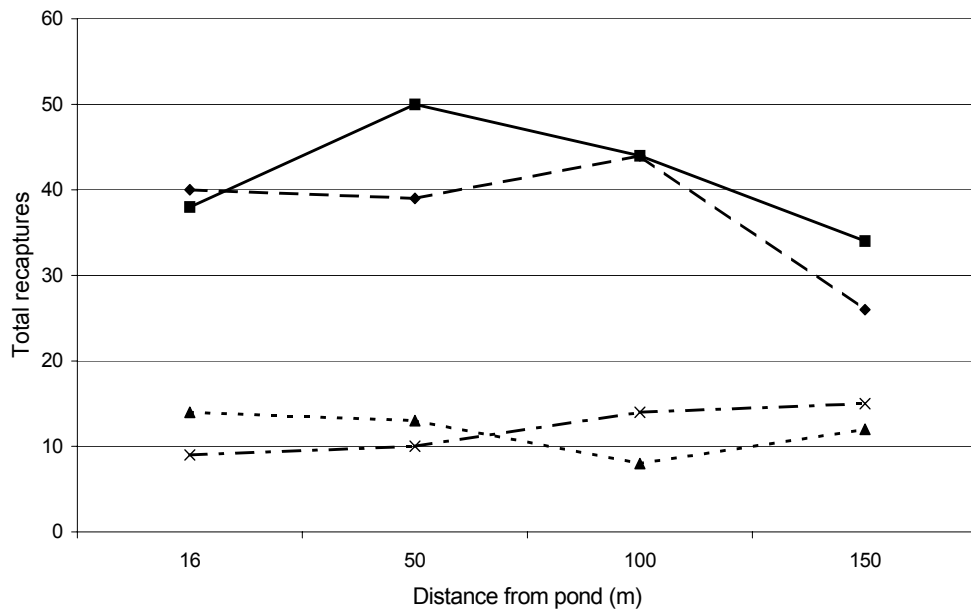
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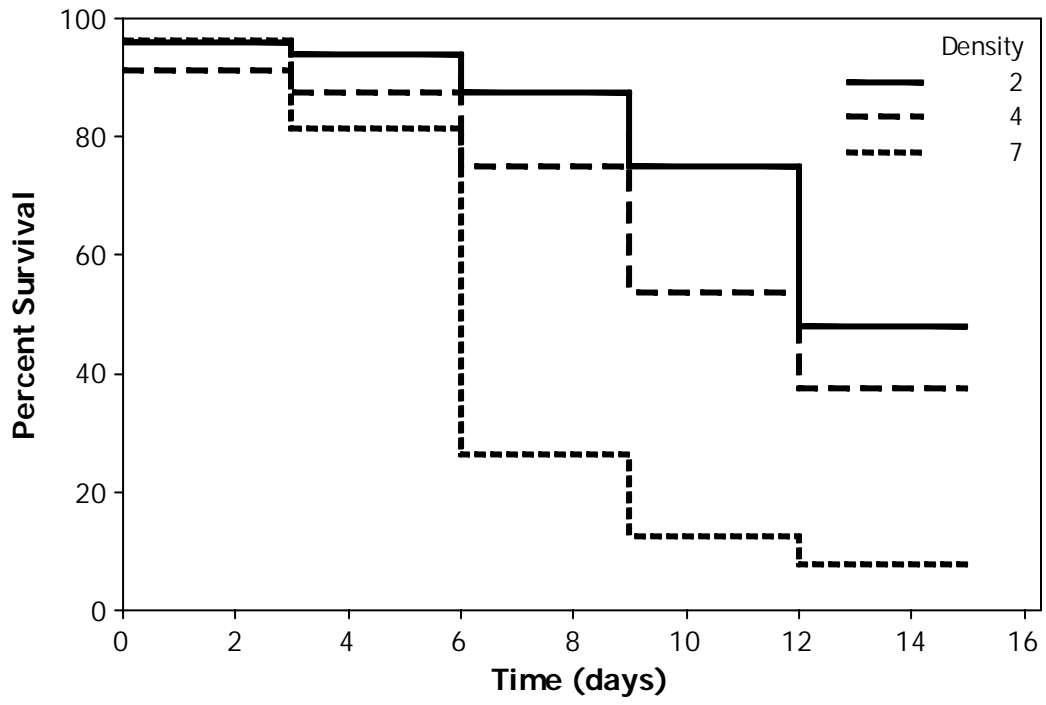


830 (a).  
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832 (b).  
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