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The Effects of Forest Practices on a Maine Amphibian Community

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THE EFFECTS OF FOREST PRACTICES ON A MAINE AMPHIBIAN

COMMUNITY

By

David A. Patrick

BS University of North Wales, Bangor, 1999

MS Durrell Institute of Conservation and Ecology, 2000

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of Doctor of Philosophy

(in Wildlife Ecology)

The Graduate School,

The University of Maine,

May, 2007

Advisory Committee:

Malcolm L. Hunter Jr., Libra Professor of Conservation Biology and Professor

of Wildlife Ecology, Co-Advisor

Aram J. K. Calhoun, Associate Professor of Wetland Ecology, Co-Advisor

James P. Gibbs, Associate Professor, Conservation Biology and Wildlife

Management

David Hiebeler, Assistant Professor of Mathematics

William B. Krohn, Professor of Wildlife Ecology and Leader, Maine

Cooperative Fish and Wildlife Research Unit

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THE EFFECTS OF FOREST PRACTICES ON A MAINE AMPHIBIAN

COMMUNITY

By

David A. Patrick

Thesis Advisors: Dr. Malcolm Hunter and Dr. Aram Calhoun

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy
(in Wildlife Ecology)
May, 2007

Changes in forest habitat have been linked to global declines in amphibian populations, but little research has been conducted into the mechanisms causing these declines. This study evaluated the effects of changes in forest habitat on the spatial distribution of a Maine amphibian community, focusing on juvenile wood frogs, *Rana sylvatica*. Juvenile wood frogs emerging from artificial ponds did not orient towards preferred habitat and a significant number of animals maintained the same directionality documented at the site from which larval individuals were collected. Abundance and habitat use differed among adults of 9 species of amphibians in a replicated landscape (n = 4, each 10 ha in size) of 4 forestry treatments (clearcut with coarse woody debris [CWD] removed, clearcut with CWD retained, partial-cut of 50% of canopy cover, and an uncut control) centered on a breeding pool. Lower captures of juveniles of all species (statistically significant for 7 of 9 species) were seen in clearcuts compared to forested treatments. Juvenile wood frogs marked as they emerged from the breeding pools

preferred forested treatments to the clearcuts, but patterns of captures within each treatment at different distances from the pond's edge did not differ. The response of juvenile wood frogs to habitat heterogeneity (in the 10 ha landscapes, a 12x16 m area of hexagonal patches, 1x4 m pens, and a 10x10 m pen) changed from coarse scale habitat selection during emigration, to fine scale selection when settling.

Spatial simulations designed to predict the effects of habitat change on the spatial distribution of juvenile wood frogs best predicted field data when specific movement behavior, and a heterogeneous landscape were included. Model results demonstrated the importance of comparing densities of frogs in different habitat types following emigration, as well as the distribution of frogs over distance when considering effects of habitat change on local populations.

The study demonstrated the complex responses of amphibians to habitat change and the importance of conducting research at multiple spatial and temporal scales. Simulations highlighted the need for species-specific information when predicting the effects of habitat change on the spatial distribution of amphibians, and managing habitat accordingly.

ACKNOWLEDGEMENTS

This thesis is dedicated to David Michael Veverka and Raymond O'Connor, two individuals who exemplified everything that is decent in the world, and whom are sorely missed.

Lastly I would like to thank my wife, Elizabeth Harper, for putting up with me and regularly truthing my reality map.

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PREFACE

Globally many species of amphibians are suffering dramatic population declines with habitat loss and degradation cited as a causative factor in many of these cases (Stuart *et al.* 2004). However, little understanding of the mechanisms by which change in terrestrial habitat causes the resulting effects on the population has been developed. The goal of my dissertation research was to understand the mechanisms by which habitat change influenced the spatial distribution of amphibians, especially juvenile wood frogs *Rana sylvatica*, and to develop spatial models to predict these patterns. Ecological processes are typically hierarchically structured, with multiple factors operating across a range of scales (Franklin *et al.* 2000, Cushman and McGarigal 2002). Because of this, I conducted a series of experimental habitat manipulations at multiple spatial and temporal scales. I simultaneously developed candidate simulation models to predict the effects of habitat change on the spatial distribution of juvenile wood frogs. Habitat manipulations were conducted as part of the Land-use Effects on Amphibian Populations project (LEAP) underway at the University of Maine, the University of Missouri-Columbia, the University of Georgia, and the State University of New York, Syracuse, USA.

In chapter 1, I examined how juvenile wood frogs responded to preferable habitat when leaving natal ponds. Studies have shown that amphibians can orient non-randomly when moving (Dodd and Cade, 1998; Bulger et al., 2003; Mazerolle and Desrochers, 2005). Two hypotheses predict how this orientation may occur: (1) animals directly detect the habitat features towards which they are moving; or (2) animals rely on indirect cues to orient towards the habitat feature. I focused on a population of *Rana sylvatica* indigenous to Sears Island, Maine, where juveniles emerging from a natal pond from 1999 to 2002

consistently oriented towards a closed canopy forested wetland to the northeast

(Vasconcelos and Calhoun, 2004). The experiment assessed whether *Rana sylvatica*

translocated from Sears Island oriented in the same direction as at the original site, or if

they detected and actively oriented towards suitable habitat (forested wetland) located in

the opposite direction of their natal pond. I also assessed whether orientation occurred

immediately upon emergence from the natal pond or after experience in the terrestrial

environment, and if the distance between the natal pond and a potential cue had any

influence on orientation ability.

Chapter 2 broadly compared the effects of the four LEAP forestry treatments

(clearcut with coarse woody debris [CWD] removed, clear-cut with CWD retained,

partial-cut of 50% of canopy cover, and an uncut control) on movement, habitat selection,

and abundance of amphibians in Maine. Four landscape-scale replicates of these four

forestry treatments were created with each replicate centered on a breeding pool. This

research had two foci. First, mark-recapture of emerging juvenile wood frogs was used to

examine how differences in terrestrial habitat quality affect movement and habitat

selection during dispersal, and the abundance of individuals in the different treatments

during and following this period. Second, I looked at how the different forestry treatments

influenced the use of habitat by most members of the amphibian community in the study

area.

Chapter 3 specifically examined how factors determining the spatial distribution

of juvenile wood frogs varied across ecological scales. This study consisted of four

experimental habitat manipulations at different spatial and temporal scales including (1)

the LEAP habitat manipulations (10 ha landscapes); (2) short-term experiments with

individual organisms emigrating through a manipulated landscape of 1 m wide hexagonal

patches; and (3) and (4) habitat manipulations in small (4 m^2) and large (100 m^2)

enclosures with multiple individuals where I compared behavior both during and

following emigration.

In Chapter 4, I integrated the results of these habitat manipulations with cellular

automata models designed to simulate the spatial distribution of emigrating wood frogs.

Models varied in complexity from random diffusion in a uniform landscape to models

specifically designed to mimic habitat and behavioral characteristics seen in my empirical

studies. Models were tested using data gathered on the spatial distribution of juvenile

wood frogs following emigration within the LEAP treatments (10 ha replicates).

The results of my experiments demonstrate how habitat change influences

movement behavior and habitat selection of amphibians, and how this in turn determines

the spatial distribution of animals across the landscape. The importance of understanding

the role of ecological scale when evaluating this relationship and predicting the likely

effects of further habitat change were also evident. Chapter 4 highlighted the need for

careful consideration of response metrics when reaching conclusions as to how habitat

change is likely to affect amphibian populations. My research offers useful information

for those looking to manage habitat for amphibians as well as furthering my

understanding of the terrestrial ecology of amphibians in general.

CHAPTER 1

THE ORIENTATION OF JUVENILE WOOD FROGS, *RANA SYLVATICA*, LEAVING EXPERIMENTAL PONDS.

1.1 Abstract

Some amphibians are able to orient towards habitat features, but it is not always clear whether: (a) these animals can directly detect the habitat towards which they are moving (e.g., scenting water from a wetland); or (b) they are detecting an indirect cue that is consistently correlated with the location of suitable habitat (e.g., the location of sunrise). In 2004 I translocated 400 *Rana sylvatica* tadpoles from an isolated population on Sears Island in Maine, where emerging metamorphs travel northeast towards a forested wetland. I placed study animals in arrays consisting of a central artificial pool, with a circular drift-fence at 0.2 m from the pool's edge to assess orientation of metamorphs at emergence, and a similar fence at 5 m to assess orientation post-emergence. Arrays were placed at 10 m and 50 m from a forested wetland, with the wetland cue to the southwest (i.e., the opposite direction of the wetland at Sears Island). *Rana sylvatica* exhibited significant orientation towards the northeast at the 0.2 m fence, indicating that emerging metamorphs retained the same directionality as at the site where they were hatched. A significant result at the 5 m fence indicated that animals continued to head towards the northeast. These results suggest that the population of *Rana sylvatica* on Sears Island may rely on indirect cues for orientation. Relying on indirect cues offers less adaptability to changes in habitat such as breeding site loss or road construction, and thus could lead frogs into ecological traps.

1.2. Introduction

Juvenile and adult amphibians move up to several kilometers for a variety of reasons, including traveling between summer foraging areas and overwintering sites (Regosin et al., 2003), migrating to and from breeding sites (Stenhouse, 1985), and dispersing to new habitats (Berven and Grudzien, 1990). Numerous studies have shown that amphibians can orient non-randomly when making such long-distance movements (Dodd and Cade, 1998; Bulger et al., 2003; Mazerolle and Desrochers, 2005). Two hypotheses predict how this orientation may occur: (1) animals directly detect the habitat features towards which they are moving (e.g., via a scent or visual cue); or (2) animals rely on indirect cues to orient towards the habitat feature (e.g., the location of the sun). Under the second hypothesis, animals may not be able to directly detect the habitat feature.

A few studies have documented the use of direct cues. Olfactory detection of home ponds has been demonstrated for *Ambystoma maculatum* (McGregor and Teska, 1989), *Taricha rivularis* (Grant et al., 1968), and *Notophthalmus v. viridescens* (Hershey and Forester, 1980). The use of indirect cues has been more widely explored, with mechanisms including sun-compass orientation in *Acris crepitans* and *Rana catesbeiana* (Ferguson et al., 1966, 1967), detection of magnetic fields in *Notophthalmus v. viridescens* (Phillips, 1986; Fischer et al. 2001; Phillips et al., 2001) and *Rana catesbeiana* tadpoles (Freake and Phillips, 2005), and the potential to use plane-polarized light in *Ambystoma tigrinum* (Taylor and Adler, 1973).

The use of indirect cues has principally been shown in the laboratory, and its prevalence under natural conditions is unclear. Relying on indirect cues limits the ability

of amphibians to respond to changes in habitat location whether due to natural (e.g., beaver dam construction) or anthropogenic causes (e.g., wetland destruction). Such changes in habitat features could occur between amphibian breeding seasons and direct detection of the actual habitat feature would allow more rapid adaptation.

This study focused on a population of *Rana sylvatica* indigenous to Sears Island, Maine, where juveniles emerging from a natal pond from 1999 to 2002 consistently orient towards a closed canopy forested wetland to the northeast (Vasconcelos and Calhoun, 2004). My objective was to assess whether *Rana sylvatica* translocated from Sears Island orient in the same cardinal direction as at the original site, or if they detected and actively orient towards suitable habitat (forested wetland) located in the opposite direction of their natal pond. I also assessed whether orientation occurred immediately upon emergence from the natal pond or after experience in the terrestrial environment, and if the distance between the natal pond and a potential cue had any influence on orientation ability.

1.3 Methods

Study sites: Sears Island (380 ha) is situated in Penobscot Bay, Searsport, Maine (44°27'N, 68°53'W), and is connected to the mainland by a 200 m long causeway. I removed *Rana sylvatica* from 1 of 3 breeding ponds (namely VP3) that were constructed on the island in 1997 to replace a natural wetland (Vasconcelos and Calhoun, 2004). The constructed ponds are in a seasonally saturated wet meadow with the bay located 100 m to the southwest. A closed-canopy forested wetland is located 15 m to the northeast of VP3, with wet meadow habitat extending 60 to 100 m to the south and east before reaching further closed canopy forest. The remainder of the island is an area of undeveloped forest, dominated by red spruce (*Picea rubens*), balsam fir (*Abies*

balsamea), northern white cedar (*Thuja occidentalis*), red maple (*Acer rubrum*), and yellow birch (*Betula alleghaniensis*).

My experimental site is located in the University of Maine Dwight B. Demeritt Forest, Orono, Maine (approximately 55 km inland from Sears Island). I constructed experimental arrays in continuous forest of eastern white pine (*Pinus strobes*), balsam fir (*Abies balsamea*), and northern white cedar (*Thuja occidentalis*), with a forested wetland located to the southwest. This wetland has similar floral composition to the forested wetland on Sears Island, indicative of similar hydrology. No other wetlands are located within 100 m of any of the arrays. I established my study site at this location so that metamorphosing wood frogs orienting toward the nearby wetlands would have to shift 180° from the preferred direction at their natal pond on Sears Island (Vasconcelos and Calhoun, 2004).

Experimental design: Two experimental sites were chosen approximately 1 km apart. Site choice was based on maintaining a standard species, age-composition, and disturbance pattern of forest stands, and so that a clear distinction existed between the forested wetland and the surrounding upland forest. At each site, 2 arrays were placed at 10 m and at 50 m from the wetland edge (Figure 1). At 1 site, an additional 2 arrays were constructed at the 10 m distance, for a total of 10 arrays (the latter 2 arrays were not coupled with arrays at 50 m due to the presence of a small area of damp ground ($<4 \text{ m}^2$) approximately 80 m north of the wetland). All arrays were spaced >60 m apart in each distance class. Also, the nearest forest edge or change in stand type was >60 m away. All woody debris (>1 cm in diameter) was removed from the arrays.

Forested Wetland
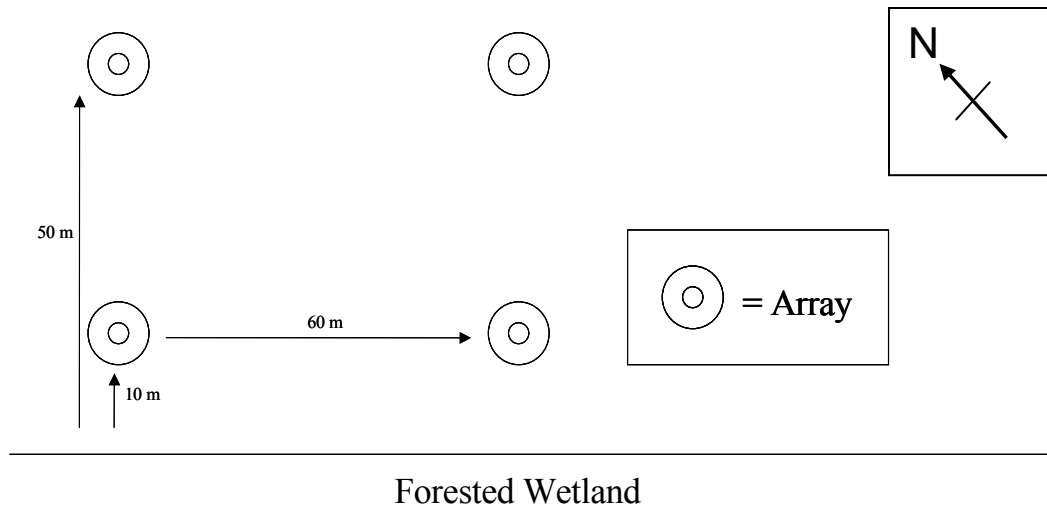
Figure 1. Layout of artificial arrays at each site (figure approximately to scale).

An array consisted of a 60 L plastic wading pool, 1.5 m in diameter, and 25 cm deep. Pools were placed on a leveled surface, and filled to the top with water from a nearby stream that emerged from the forested wetland (approximately 100 m west-southwest of the nearest array in site 1, and > 1 km from site 2). The pools were stocked with a 5 L bucket of packed wet leaf litter collected adjacent to the same stream a week prior to introduction of the tadpoles. The water level was maintained throughout the study, although consistent rainfall meant that little additional water was needed. Silt fencing was attached to the rim of the pool to form a continuous ramp down to the ground at an angle of approximately 45°. Two circular silt-fencing drift-fences were constructed around each pool at 0.2 m and 5 m from the pools edge. The fences were 30 cm in height, with the bottom buried 10 cm into the ground. Eight pitfall traps were equally spaced at the 0.2 m fence, and 12 traps at the 5 m fence. Pitfall traps consisted of a single #10 aluminum food can 22.5 cm deep, with a 10 cm deep funnel extending down into the trap,

and were aligned at both fences such that one trap faced each of the cardinal directions, with the remaining traps equally spaced between these (i.e., 1 trap in between at the 0.2 m fence, and 2 traps at the 5 m fence). Traps remained moist throughout the study period, so no means of preventing dehydration (such as sponges) were needed.

On 29 June 2004 I translocated 40 randomly selected *Rana* sylvatica tadpoles of Gosner stage 31 – 41 (Duellman and Trueb, 1986) from Sears Island into each artificial pool. The number of tadpoles was based on viable ranid tadpole densities in artificial pools (Alford and Wilbur, 1985).

From 2 July through 19 July 2004, I checked pitfall traps daily except for the final week of the experiment when checks occurred every other day. Juveniles captured in pitfall traps at the enclosing 0.2 m drift-fence were released on the outside of the fence directly opposite the point of capture. Juveniles recaptured at the 5 m drift-fence were removed and returned to Sears Island.

Analysis: I examined the data using both qualitative and quantitative methods (circular statistics). Graphical analysis was used as a qualitative means of looking for general patterns in orientation that may not have been evident from circular statistics. For these analyses I pooled the circular data from all of the arrays, comparing mean directionality and the circular dispersion of individuals at the 0.2 m and 5 m fences.

I used Oriana 1.0 (Kovach Computing Services, Anglesey, Wales, U.K.) to quantitatively analyze circular data. I used the Rayleigh test to test for non-random directionality in animals leaving the ponds at the 0.2 m and 5.0 m fences, and to compare between arrays at 10 m and 50 m. Although a V test is more powerful than a Rayleigh test when there is an expected direction of movement, the design of the experiment presented

two alternative hypotheses: (1) that the emerging juveniles would orient towards the northeast; or (2) that they orient towards the southwest. The V test would only have indicated whether the frogs had oriented in the same direction, and the multiple comparisons needed to evaluate several alternative hypotheses would have reduced the power of the test (Batschelet, 1981). Because of the small circumference of the 0.2 m drift fence, I felt that to be able to evaluate these hypotheses, one would need evidence of specific directionality towards the northeast or the southwest, rather than simply non-random movement. A significance level of 0.05 was used for all tests, corrected for the grouping of data due to the low number of traps at both fences (Batschelet, 1981). Watson-Williams tests were used to test for differences in the mean angles of those arrays that demonstrated significant results with the Rayleigh test. If no significant differences were shown in these mean angles, the data were pooled, and a further Rayleigh's test was conducted.

1.4 Results

Of the 400 tadpoles released, 346 were captured as metamorphs at the 0.2 m drift fences, and 195 were recaptured at the 5 m fence. Those individuals that were not captured at the 0.2 m fence presumably died before leaving the artificial ponds; individuals not captured at the 5 m fence presumably either settled or died between the two drift fences.

Graphical analysis of all the data (pooled for all arrays regardless of individual significance levels) showed mean directions of 57.35° at the 0.2 m fence, and 41.84° at the 5 m fence (Figure 2). This analysis also revealed that at the 5 m fence, 14 % of

captures were in traps to the south of the artificial ponds, i.e., the direction of the wetland at the experimental site.

The results of statistical analyses showed similar patterns to the graphical analyses. Juvenile frogs were significantly oriented in a specific direction at 5 of the 10 arrays at the 0.2 m drift fences (Table 1). Watson-Williams tests of these five significant arrays showed a significant difference between sample means, indicating that one or more of the arrays differed in directionality (Watson-Williams $F_{4,176} = 8.271$; $P < 0.001$). Analysis showed that the 95% confidence intervals for the mean directions overlapped for four of the arrays, with one array differing in directionality. When this one array was removed from the analysis, the remaining arrays did not significantly differ in mean directionality (Watson-Williams $F_{3,141} = 2.024$; $P = 0.093$). The removal of this array from the pooled data is justified as it had little effect on the mean directionality (a change from 57.076° to 71.647° after removal) and no effect on the significance level of the Rayleigh's test ($P < 0.001$). Mean directionality was 71.647° for these pooled data (95% CI from 52.044° to 91.250°; Figure 3).

Significant orientation was also seen in 3 of the 10 arrays at the 5 m fence (Table 2), with Watson-Williams tests revealing no significant differences between these mean directions. The pooled data had a mean direction of 44.541° (95% CI: 23.247° to 65.836°; Figure 3). Both of these mean angles at the 0.2 m and 5m fences approximate a northeasterly direction (45°). The lack of significant differences in the Watson-Williams tests also indicates that there were no significant differences in the directionality of juvenile frogs when comparing between arrays at 10 m and 50 m from the wetland.
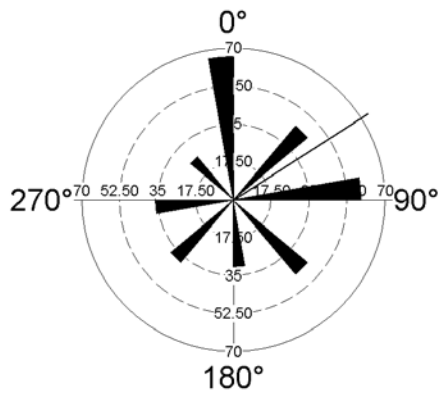
a)
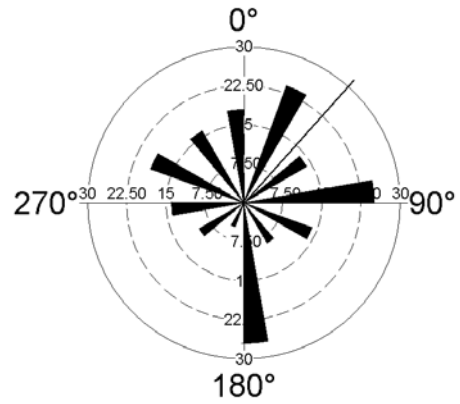
b)

Figure 2. Orientation of all juvenile *Rana sylvatica* captured at the inner (a) and outer (b) drift fences (pooled for all arrays). The length of the bars represents the total number of captures in each trap, with the abundance scale indicated on the concentric circles. The solid line represents the mean vector.

Table 1. Results of Rayleigh's test for the directionality of juvenile *Rana sylvatica* captured at the 0.2 m drift fence.

Array	Distance from wetland (m)	Sample Size (*N)*	Mean vector (°)	Length of Mean vector (r_c)	Circular Variance	Sig. level
1a	10	28	300.83	0.195	0.81	0.373
1b	50	33	87.02	0.144	0.86	0.521
1c	10	32	180.85	0.267	0.74	0.123
1d	50	36	184.43	0.113	0.89	0.674
1e	10	31	58.97	0.472	0.54	0.001 *
1f	10	37	50.86	0.349	0.66	0.012 *
2a	10	40	82.72	0.287	0.72	0.043 *
2b	50	37	333.07	0.328	0.68	0.020 *
2c	10	36	12.64	0.287	0.72	0.053
2d	50	36	98.79	0.339	0.67	0.018 *
All**		144	71.647	0.328	0.67	<0.001 *

* Indicates a significant directionality as indicated by a Rayleigh $P < 0.05$. The   arrays number refers to the site where it was located.

** Shows the analysis of the pooled data for those arrays that showed significant directionality in individual Rayleigh's tests
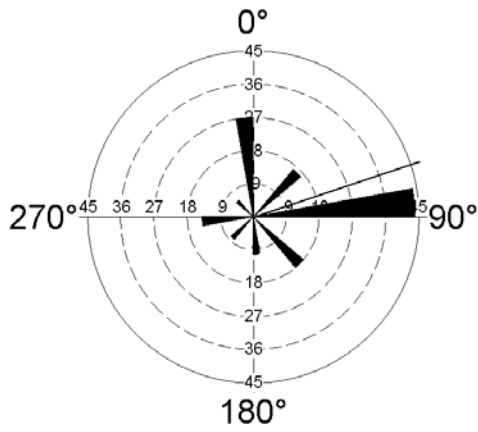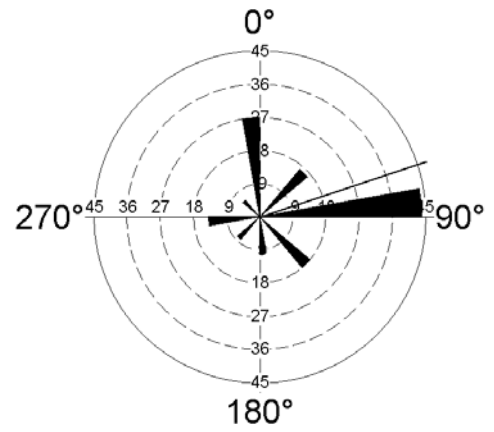
Figure. 3. Orientation of juvenile *Rana sylvatica* captured at the 0.2 m (a) and 5 m (b) drift fences. The figures represent pooled data from those individual arrays that showed significant directionality as evaluated by Rayleigh's test. The length of the bars represents the total number of captures in each trap, with the abundance scale indicated on the concentric circles. The solid line represents the mean vector.

Table 2. Results of Rayleigh's test for the directionality of juvenile *Rana sylvatica* captured at the 5 m drift fence.

Array	Distance from wetland (m)	Sample Size (*N)*	Mean vector (α)	Length of Mean vector (r$_c$)	Circular Variance	Sig. level
1a	10	20	245.10	0.020	0.98	0.992
1b	50	23	178.71	0.263	0.74	0.215
1c	10	19	355.14	0.607	0.40	0.001 *
1d	50	24	320.49	0.293	0.71	0.141
1e	10	18	80.68	0.779	0.23	<0.001 *
1f	10	21	254.14	0.223	0.78	0.363
2a	10	18	48.43	0.425	0.58	0.042 *
2b	50	25	75.60	0.263	0.74	0.179
2c	10	16	90.57	0.222	0.78	0.452
2d	50	11	270.00	0.273	0.73	0.451
All**		55	44.54	0.473	0.527	<0.001*

* Indicates a significant directionality as indicated by a Rayleigh *P* < 0.05. The arrays number refers to the site where it was located.

** Shows the analysis of the pooled data for those arrays that showed significant directionality in individual Rayleigh's tests

1.5 Discussion

Finding that emerging juvenile *Rana* sylvatica showed evidence of orientation

towards the northeast, i.e., the same directionality found at Sears Island from 1999-2002

(Vasconcelos and Calhoun, 2004), and the opposite direction to the forested wetland at

the experimental arrays, was unexpected given that previous research indicates that

emerging wood frog juveniles move towards wetlands (Heatwole, 1961; Bellis, 1965;

Mazerolle, 2001). It is important to notice that this directionality was only seen at 5 out

of the 10 inner fences, and 3 out of the 10 outer fences. However, there were no arrays

where frogs were significantly oriented in a direction corresponding to my alternative

hypothesis of southwest. At the one statistically significant array where frogs at the 0.2 m

fence did not orient northeast, the frogs exhibited a mean orientation of 333˚ (i.e., north-

northwest). This represents <1 m change in direction as represented by position on the

circumference of the 0.2 m fence). At Sears Island the frogs emerging from the pools

showed highly significant directionality (Rayleigh *P* <0.001 for all tests) moving towards

a forested wetland and away from open habitat (Vasconcelos and Calhoun, 2004).

Although sites were uniformly forested, I also documented a similar significant

directionality. The mean direction at Sears Island was 57° (Vasconcelos and Calhoun,

2004), compared with 71.6° at my 0.2 m fence, and 44.5° at my 5 m fence.

The results were unlikely to be a function of suitable habitat being too distant for

direct-cue detection, as there were no significant differences when comparing orientation

at 10 and 50 m from the wetland edge at the experimental sites. The wetlands at the

experimental sites were suitable habitat for juvenile *Rana sylvatica* (Heatwole, 1961;

Bellis, 1965), and presumably would have generated direct cues similar to those of the

Sears Island wetland. Although 50 m could be too distant for animals to detect direct cues, it is unlikely 10 m is too distant, especially if the cue is of value in orientation. The use of a drift fence to capture animals may have presented a barrier to olfactory cues, although this is unlikely as a porous fencing material was used and previous studies have indicated that drift fences do not block such cues (Hershey and Forester, 1980). Visual cues could have been limited, but Maine forests are usually too dense to allow visual detection of forest wetlands at 50 m even without a fence.

I documented that some of the frogs moved northeast even though the habitat located in this direction was less suitable than in other directions. This suggests that the movement of some of the translocated *Rana sylvatica* is based on the use of indirect cues that remain consistent between Sears Island and my experimental site (e.g., the direction of the sun, or the earth's magnetic field). Those animals that showed significant directionality at the 0.2 m fence provide evidence that orientation in response to indirect cues may manifest itself prior to, or during emergence from, the natal pond. Orientation prior to emergence has been demonstrated for other amphibian species such as *Triturus vulgaris* (Malmgren, 2002) and *Rana catesbeiana* (Justis and Taylor, 1976), but I believe that this is the first time the use of indirect cues has been shown as a potential mechanism for orientation of larval *Rana sylvatica*.

Although I found evidence that dispersing wood frog metamorphs use indirect environmental cues, I were not able to determine specifically which cue(s) the metamorphs were using to orient. Nevertheless, my results raise the question as to how widespread the use of indirect cues is in amphibian orientation. At Sears Island, I expected strong selection for directionality of emerging metamorphs due to the ocean's

proximity to the southwest of the breeding pond. The size of the wood frog population is not known, but as an island population, immigration is most likely reduced, and thus selection pressure increased (Ridley, 1993). The fact that amphibians in large populations (e.g., those found at the Savannah River Site, Aiken, South Carolina), continue to show philopatry following destruction of their breeding sites (Pechmann et al., 2001), suggests that indirect cues may be prevalent in many populations.

Using indirect cues could lead metamorphs into an ecological trap where the proximate cues used to orient in the terrestrial environment no longer maximize survival and fitness (Schlaepfer et al., 2002). Evidence for this has been shown for several species of amphibian including *Ambystoma talpoideum* and *Notophthalmus viridescens*, with adults continuing to return to breeding pools that have been destroyed (Pechmann et al., 2001). If the use of indirect cues is widespread in amphibian populations, the potential for disrupted breeding success due to habitat loss will be increased. Wetland mitigation often involves wetlands being created to replace those that are lost (Roberts, 1993). If wetland removal not only leads to the loss of a breeding site, but also to high rates of breeding failure due to adults returning to the destroyed location, effects on amphibian populations may be more significant than first thought.

In addition to potentially creating an ecological trap, the use of indirect cues may have a strong link to the degree of philopatry in a population. If all the juvenile amphibians emerging from a natal pond head in the same direction, then the chance of their locating a different breeding site will be reduced. High levels of philopatry for *Rana sylvatica* have been demonstrated; for example approximately 80% of adults breeding at study ponds in Appalachia emerged as juveniles from the same pond (Berven and

Grudzien, 1990). Interestingly, the 14% of juveniles I documented changing direction towards the wetland at the 5 m drift fence is similar to the 18% of juveniles dispersing to different breeding sites found by Berven and Grudzien (1990).

My results highlight the need for more research into how amphibian populations respond to changes in the location of potential breeding sites, and links between directionality and levels of philopatry. The extension of experimental studies to different locations and species would help in determining how widespread the use of indirect cues is.

CHAPTER 2

EFFECTS OF EXPERIMENTAL FORESTRY TREATMENTS ON A MAINE AMPHIBIAN COMMUNITY

2.1 Abstract

Predicting how timber harvesting will influence sensitive taxa such as amphibians is of critical importance for sustainable management of forests. In 2004 and 2005, I studied the effects of four forestry treatments (clearcut with coarse woody debris [CWD] removed, clear-cut with CWD retained, partial-cut of 50% of canopy cover, and an uncut control) on movement, habitat selection, and abundance of amphibians in Maine. Four landscape-scale replicates of these four forestry treatments were created with each replicate centered on a breeding pool. A total of 8632 emerging juvenile wood frogs were captured and marked at drift fences encircling breeding pools, with 1166 marked wood frogs (*Rana sylvatica*), and 13,727 unmarked amphibians captured in drift fence/pitfall arrays at 16, 50, 100, and 150 m from the pools. My capture results in the different treatments were consistent with previous studies in showing that adult abundance and habitat use differed among species, with wood frogs, spotted salamanders (*Ambystoma maculatum*), and eastern red-backed salamanders (*Plethodon cinereus*) preferring uncut and partial-cut habitat, and adult green frogs (*Rana clamitans*) and American bullfrogs (*Rana catesbeiana*) being more tolerant of clearcutting. Spotted salamanders also showed reduced captures with partial canopy removal and increased captures with the retention of CWD. My results for juvenile amphibians differed from previous research, with lower captures of all study species (statistically significant for 7 of 9 species) in clearcuts

compared to uncut and partial-cut treatments. Clearcuts did not reduce habitat

permeability for the low number of marked wood frogs that entered these treatments.

Data from marked wood frogs also suggest that both density of conspecifics and habitat

quality can influence habitat selection, and potentially dispersal of juvenile amphibians.

The avoidance of clearcuts by juveniles of all study species suggests that this silvicultural

technique may reduce both abundance and dispersal of many species, rather than just

species where adults are known to be forest-dependent. Species may also be affected by

partial as well as full canopy removal, and the retention of CWD may play a role in

mitigating some of the effects of clearcutting.

2.2 Introduction

When considering biodiversity in forest management planning it is crucial to

understand how habitat changes will affect the distribution and abundance of species.

Amphibians form a large part of the vertebrate biomass in forested ecosystems in north-

eastern North America and play an important role in ecosystem processes (Burton and

Likens, 1975a,b; Wyman, 1998). Furthermore there is a great deal of debate as to how

forest management influences amphibians because of uncertainty in how severely

practices such as clearcutting affect populations, and how long such effects may last

following harvesting (Petranka et al., 1993, 1994; Petranka, 1994; Ash, 1997; Chazal and

Niewiarowski, 1998; Harper and Guynn, 1999; Ford et al., 2002; Ash et al., 2003). There

is also uncertainty as to the relative effects of different management practices on

amphibians, for example the frequency and intensity of harvesting efforts (Bennett et al.,

1980; Aubry, 2000; Bartman et al., 2001; Ryan et al., 2002) and the retention of

biological legacies such as leaf litter and coarse woody debris (CWD) (Aubry, 2000; Moseley et al., 2004; Strojny, 2004).

Predicting the effects of habitat change on amphibian populations is complicated by the bi-phasic life history of most species. This makes them especially prone to changes in population dynamics caused by habitat alteration (Wilbur, 1980; Semlitsch, 1998). Previous amphibian population research has tended to focus on aquatic breeding habitat rather than the terrestrial environment used during the non-breeding season (Trenham and Shaffer, 2005; although see deMaynadier and Hunter,1995; Regosin et al., 2003). Even within the terrestrial environment, habitat change may differentially affect each life-history stage. For example, juvenile amphibians have been shown to be the primary dispersing stage for many species, with adults often showing high philopatry (Vasconcelos and Calhoun, 2004; Berven and Grudzien, 1990). Because of this, changes in juvenile life history traits due to habitat alteration can have repercussions in terms of metapopulation dynamics (Green, 2003).

To understand and predict how alteration in forested habitat quality will affect amphibian community dynamics, I used a replicated experimental design with forestry treatments large enough to incorporate population processes (e.g., dispersal) that occur over a wide spatial scale, i.e., a landscape scale in terms of amphibian ecology. By blocking different treatments within the same location, I was able to account for temporal and spatial variation. My experimental design allowed direct comparison of changes in abundance and habitat use by amphibians among treatments, and also allowed us to link movement and habitat selection paradigms, a critical step in understanding population dynamics in changing environments (Armstrong, 2005).

Our research had two foci. First, mark-recapture of emerging juvenile wood frogs was used to examine how differences in terrestrial habitat quality affect movement and habitat selection during dispersal, and the abundance of individuals in the different treatments during and following this period. Second, I looked at how the different forestry treatments influenced the use of habitat by most members of the amphibian community in the study area. This included examining potential differences in temporal patterns of use throughout the study period.

2.3 Methods

2.3.1. *Study area and experimental design*

This study was conducted in the Dwight B. Demeritt and Penobscot experimental forests, Orono, Maine, as part of the Land-use Effects on Amphibian Populations project (LEAP) underway at the University of Maine, the University of Missouri-Columbia, and the University of Georgia, USA. I created four replicates of four forestry treatments with each replicate centered around a breeding pool approximately 10 m in diameter (Figure 4). Treatments extended 164 m in radius from the pond, giving a total area of 2.11 hectares for each treatment per site.

Partial cut
(50% crown closure)

Clearcut –
CWD retained

\ = drift fences

Drift fence and pitfall
traps (not to scale)

164 m

Clearcut –
CWD removed

Control
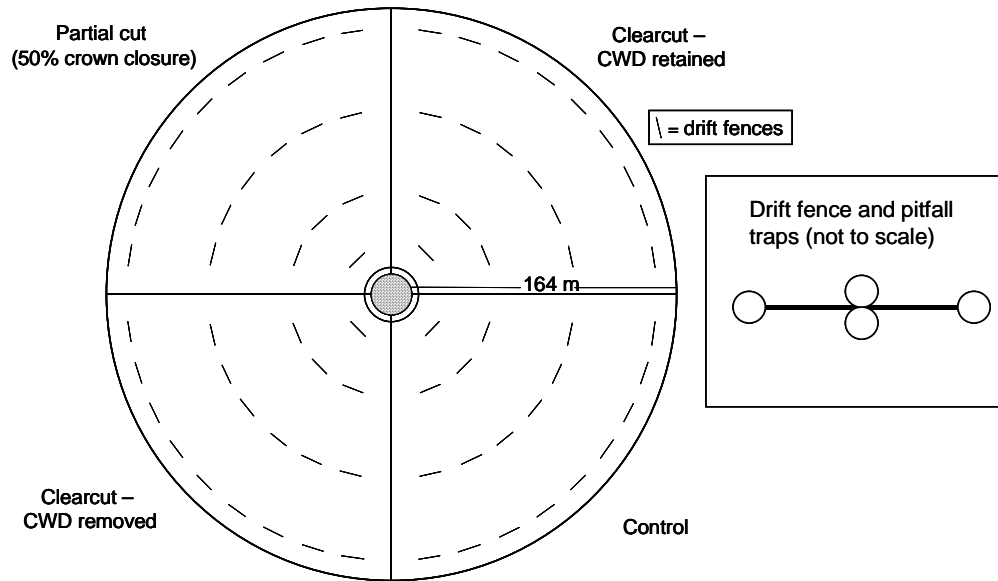
Figure 4. Outline of the LEAP experimental array, showing locations of drift fences. The inset shows the design of each drift fence.

The four treatments were a clearcut with coarse woody debris (CWD) > 10 cm in diameter removed, a clearcut with CWD retained, a partial cut where the canopy was reduced by 50 %, and an uncut control. All merchantable timber was removed from harvested treatments using a cable skidder. Harvesting was conducted between November 2003 and April 2004. Treatments were randomly assigned, with the caveat that the clearcut treatments were opposite one another. Breeding pools were constructed from naturally occurring forested wetlands in 2003 with the goal being to create the vernal breeding sites used by my focal study species, wood frogs and spotted salamander. Initially, three of my four sites were areas where less than 6" of surface water remained for 1-2 months following spring snow-melt, but no amphibians bred. The other site was a natural vernal pool where small numbers of wood frog and spotted salamander bred (<10 egg masses). Following deepening with a backhoe, the pools averaged 25-40cm in depth

and 10m in diameter. A pond liner was also used at one site to extend the hydroperiod long enough for successful amphibian reproduction. Soils in the study area are a mosaic of glaciomarine hydric soils, with well-drained till soils in upland areas (Natural Resources Conservation Service, 1962).

Before the establishment of experimental treatments, forests in the study areas were mixed coniferous and deciduous stands, with the dominant tree species being balsam fir (*Abies balsamea*), eastern white pine (*Pinus strobes*), northern white cedar (*Thuja occidentalis*), red maple (*Acer rubrum*), eastern hemlock (*Tsuga canadensis*), red oak (*Quercus rubra*), and paper birch (*Betula papyrifera*). Understory tree species included American beech (*fagus* grandifolia), bigtooth aspen (*Populus grandidenta*), quaking aspen (*P. tremuloides*), and balsam poplar (*P. balsamifera*). Stands were predominantly even-aged, with some stratified mixed stands (no more than three age classes). Sites had a simple stand history, with 2 sites on regenerating agricultural lands (cleared at least 80-100 years prior to the study), and 2 sites in areas harvested at least 60 years prior to my study. Of the 4 sites, 3 were located in forested lowland areas, with the last being in an upland area. Sites were selected such that the vegetation was as homogeneous as feasible before the establishment of experimental treatments. None of the sites contained any additional natural breeding locations for the focal amphibian species during the duration of my study, although construction of experimental arrays did result in several depressions where egg masses were laid by wood frogs and spotted salamanders. These egg masses were removed. The nearest breeding ponds outside of the arrays were at least 50 m from the outer treatment edge.

At each pool, I used 1m tall silt fencing to make a complete encircling drift fence approximately 1m from the water's edge. Pitfall traps were placed at 5 m intervals on both the inside and outside of each fence. Drift fences/pitfalls were also constructed at 50, 100, and 150 m from the pool's edge (Figure 4). In each treatment, there were three fences at 50 m, six at 100 m, and nine at 150 m, with a total of 18 fences per treatment, and 72 per site. This allowed the same proportion (38%) of the circumference at each distance to be sampled. I constructed an additional drift fence in each treatment at 16.6 m from the pool in 2005 to allow an examination of short-distance dispersal.

Each drift fence consisted of 4 pitfalls and 10 m of silt fencing buried approximately 30 cm in the ground. Two number-ten aluminum cans were taped together to form each pitfall trap, with a plastic container used to make a 10 cm deep entrance funnel around the trap. A single pitfall trap was placed at the end of each fence, plus one on each side at the center of the fence. Trapping was conducted for 2 years following forest harvesting, from 1 July to 27 October in 2004, and 24 June to 17 September in 2005. The 4 sites were split into pairs of sites, with one pair being checked approximately every other day. During sampling, I removed water from traps using a hand bilge pump to reduce amphibian mortality.

2.3.2. *Study species*

Our study focused on 9 species of amphibians commonly found in Maine forests: wood frogs, green frogs, American bullfrogs, northern leopard frogs (*Rana pipens*), pickerel frogs (*Rana palustris*), spotted salamanders, blue-spotted salamanders (*Ambystoma laterale*), red-spotted newt (*Notophthalmus viridescens viridescens*), and eastern red-backed salamanders. These species cover a diversity of life-history strategies

allowing evaluation of how such differences may influence the effects of forest

management on amphibians (summarized in Table 3).

2.3.3. *Data collection*

      In 2004, wood frog metamorphs emerging from the focal pools were individually

marked at the encircling fence using a combination of a single toe clip and visible implant

elastomer (VIE) (Heyer et al., 1994). In 2005 a single mark was given depending on the

treatment the individual entered post-emergence. Age (juvenile or adult based on the

presence of secondary sexual characteristics and/or size), sex of adults, and snout-vent

length (SVL) were recorded for all captures of marked and unmarked amphibians at the

terrestrial fences. I released captured animals on the opposite side of the fence to the point

of capture.

Table 3. Life-history traits of amphibian species captured in the LEAP project, Maine, 2004-2005.

Trait	Wood frog[1]	Green frog[2]	American bullfrog[3]	Northern leopard frog[4]	Pickerel frog[5]	Spotted salamander[6]	Blue spotted salamander[7]	E. Red-backed salamander[8]	Red-spotted newt[9]
Life-cycle	Bi-phasic	Bi-phasic	Bi-phasic	Bi-phasic	Bi-phasic	Bi-phasic	Bi-phasic	Uni-phasic	Bi-phasic
Juvenile habitat	Forested wetlands	Wetlands	na	na	na	Forest	Forest	Forest	Forest
Juvenile dispersal habitat	Forest	Drainages/ vernal pools	Streams/ drainages	Streams/ drainages	na	na	Na	na	forest
Adult summer habitat	Forested wetlands	Pool edge, dense vegetation	Primarily near water	Forest, fields, and meadows	Forest, fields, and meadows	Underground in forest	Underground in forest	Forest in moist conditions	Aquatic
Adult Winter habitat	Upland forest	Underwater/ underground	Underwater/ underground	Underwater	Underwater	Underground in forest	Underground in forest	In forest soil	Terrestrial
Max. Juv. dispersal distance (km)	2.530	4.800	0.914	5.200	na	na	0.92	na	na
Adult dispersal distance (km)	0.43	1.260	1.600	3.218	na	0.756	0.405	0.090	1.000

[1] Based on data from (Heatwole, 1961; Bellis, 1965; Howard and Kluge, 1985; Berven and Grudzien, 1990; deMaynadier and Hunter, 1998; Gibbs, 1998; Guerry and Hunter, 2002; Petranka et al., 2003; Regosin et al., 2003, Vasconcelos and Calhoun, 2004; Baldwin, 2005)

[2] Based on data from (Martof 1953, 1956; Schroeder, 1976; Hunter et al., 1999; Carr and Fahrig, 2001; Guerry and Hunter, 2002; Lamoureux et al., 2002; Livingston Birchfield, 2002)

[3] Based on data from (Raney, 1940; Ingram and Raney, 1943; Willis et al., 1956)

[4] Based on data from (Force, 1933; Merrell, 1970; Dole, 1971; Seburn et al., 1997; Hunter et al., 1999; Pope et al., 2000; Carr and Fahrig, 2001)

[5] Based on data from (Hunter et al., 1999)

[6] Based on data from (Douglas and Monroe, 1981; Kleeberger and Werner, 1983; Madison, 1997; Semlitsch, 1998; Guerry and Hunter, 2002; Rothermel and Semlitsch, 2002; Faccio, 2003; Vasconcelos and Calhoun, 2004)

[7] Based on data from (Douglas and Monroe, 1981; Semlitsch, 1998; Faccio, 2003)

[8] Based on data from (Vernberg, 1953; Heatwole, 1962; Burton and Likens, 1975b; Gill, 1978; Pough et al., 1987; deMaynadier, 2000)

[9] Based on data from (Gill, 1978; Jaeger, 1980; Jaeger et al., 1995; Kleeberger and Werner, 1982; Pough et al., 1987; Gibbs, 1998; Hunter et al., 1999).

We sampled habitat variables from 16 to 23 August 2004, and 5 to 26 August 2005 to assess how the forestry treatments influenced environmental factors. Sampling in each treatment was based on arrays of 7 hexagonal plots, each hexagon being 1 m in length at the longest axis, with 6 plots encircling a 7th plot. Eighteen of these arrays were located in each treatment, with one array associated with each fence. The arrays were placed 25 m towards the focal pool from the central trap of each drift fence.

Variables sampled included percent canopy cover per array using a densiometer, leaf litter depth per plot, percent cover of standing water > 1 cm in depth per plot, and vegetation as percent cover in two height classes per plot (0 – 50 cm, 50 – 100 cm). Variables sampled in 2005 were those that would have changed as a result of succession between years, with canopy cover and CWD only measured in 2004.

We sampled CWD using three 50-m line transects in each treatment. Each transect had a fixed starting point and random angle, with one transect originating between the 50 m and 100 m fences, and two originating between the 100 and 150 m fences. Coarse woody debris > 10 cm in diameter and within 2.5 cm of the ground intercepting this line was measured, including diameter at the point of intersection, length, and decay class (scale of 1 – 5) (Faccio, 2003). This allowed a calculation of the volume of CWD (m^3 per ha) in each treatment (Bate et al., 2004).

Statistical analysis was conducted using SYSTAT 11.0. (Systat Software Inc.). For parametric tests, all data were assessed for normality and homogeneity of variance using Shapiro-Wilk and Bartletts tests respectively, with data transformed via the square-root function where assumptions of normality were not met.

Differences in the number of wood frogs recaptured at successive distances from the pond were analyzed using three-factor analysis of variance (ANOVA) with site as a blocking factor, and site, treatment, and distance as the main factors. Recaptures of marked wood frogs were grouped by one-week intervals starting from the date of the first capture and analyzed graphically to determine temporal patterns. In 2004 a low sample size meant I could only compare changes in the total number of captures at all sites and treatments over the one-week intervals. Sufficient recaptures in 2005 allowed assessment of both individual treatment recaptures and the overall totals.

Analysis of differences in unmarked captures of adults and juveniles of each species in the LEAP treatments were conducted using chi square tests of the observed number captured in the 2 years combined. Captures of the 2 most numerous species of unmarked amphibians (wood frogs and spotted salamanders were assessed via two-factor ANOVA with site and treatment as the main effects, excluding sites with fewer than 5 individuals captured in any treatment (Zar, 1996). Captures were compared for the 2 years combined, as patterns of captures remained consistent between years. Only adults of 6 species, wood frogs, green frogs, American bullfrogs, northern leopard frogs, spotted salamanders, and eastern red-backed salamanders, yielded sufficient data for analysis. I did not have sufficient data for analyses on blue-spotted salamander and pickerel frog juveniles.

Seasonal changes in abundance of unmarked animals in each treatment were evaluated graphically using the mean proportion (± S.E.) of the total captures per site per year, caught in each two-week interval. To compare the mean size of juvenile amphibians

captured, I used two-way analysis of variance (ANOVA), with site and treatment as the main factors.

2.4 Results

2.4.1 *Marked wood frogs*

In 2004, 2547 emerging juvenile wood frogs were individually marked from the 2 July to 14 August. Eighty-two wood frog juveniles were recaptured, with only 16 % of these recaptures in the clearcuts (28 in the control, 41 in the partial-cut, 8 in the clearcut with CWD removed, and 5 in the clearcut with CWD retained). The first individual was recaptured on the 17 July, and the peak recaptures occurred 2 to 6 August (Figure 5a).

In 2005, 6085 emerging juveniles wood frogs were marked between 30 June and 7 August. Recaptures totaled 1084 individuals, again with relatively few (18%) of captures in the clearcuts (425 in the control, 460 in the partial-cut, 125 in the clearcut with CWD removed, and 74 in the clearcut with CWD retained). The first recapture was on the 2 July, and the peak recaptures occurred 16 to 22 July (Figure 5b). There was a significant difference in the number of recaptures at different distances from the pool (d.f. 3,3,3, $F =$ 3.177, $P = 0.031$) and no significant interaction between treatment and distance indicating that differences in captures at different distances remained consistent between treatments (d.f. 3,3,3,9, $F = 0.633$, $P = 0.645$) (Figure 6). The highest number of recaptures was at 100 m, with a peak in the captures in the partial-cut and clearcut with CWD removed treatments at this distance.

a) 2004
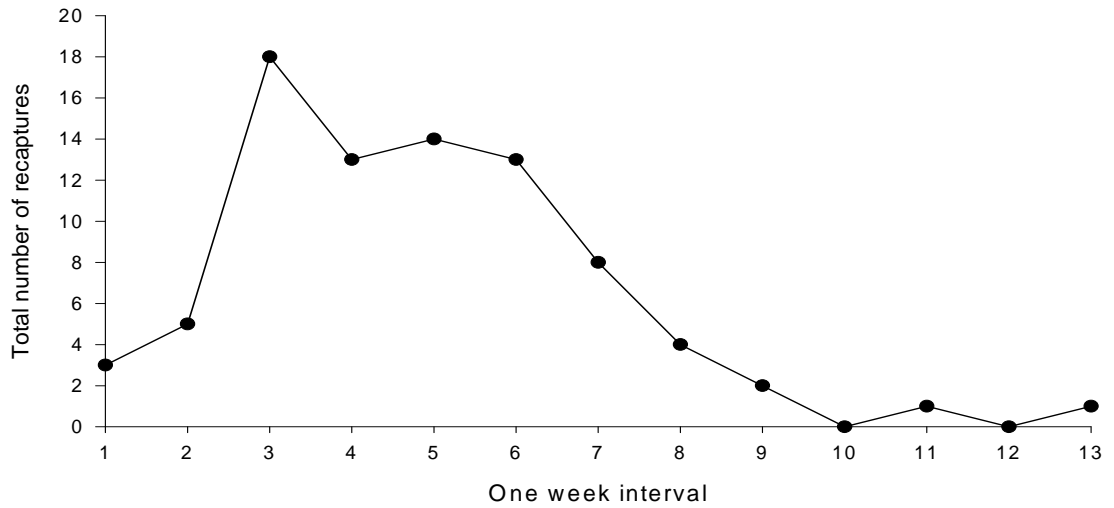
b) 2005
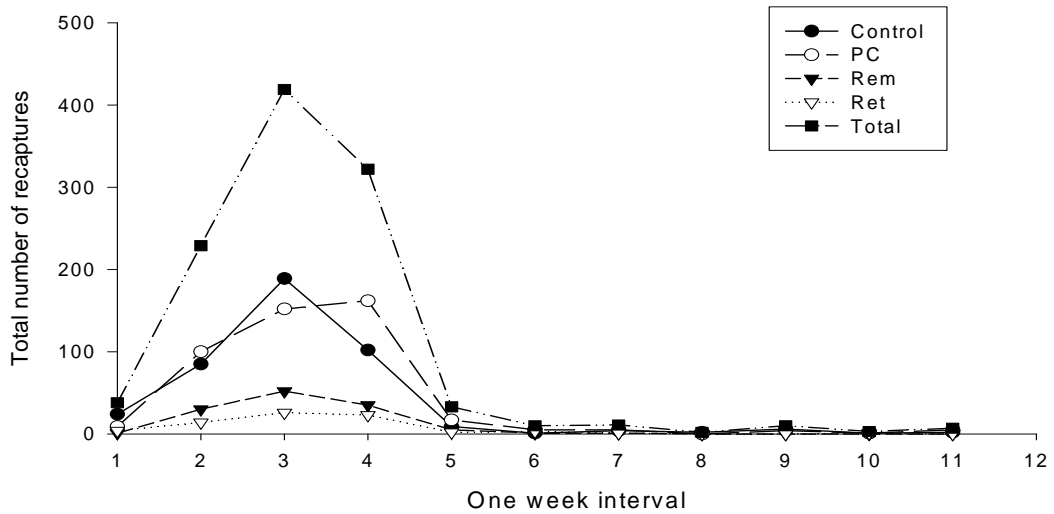
Figure 5. Total number of recaptures of marked juvenile wood frog over one week time intervals in 2004 (n = 82), with individual LEAP treatments total shown for 2005 (n = 1084).
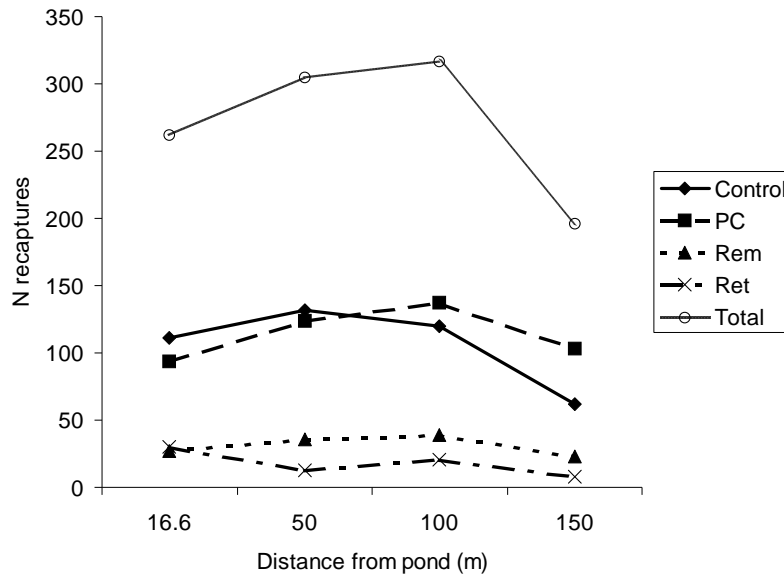
Figure 6. Total number of recaptures of marked juvenile wood frogs in the LEAP treatments at successive distances from the pools in 2005 (n=1084).

2.4.2 *Unmarked study species*:

We captured 7379 unmarked amphibians in 2004, and 6350 in 2005, representing 11 species (Table 4). Wood frogs, green frogs, and spotted salamanders were found in high abundance at all four of the sites, and these species collectively constituted 90.4 % of the total captures during the study. Traps did not adequately sample gray tree frog (*Hyla versicolor*) and spring peeper (*Pseudacris crucifer*), which were excluded from future analyses. Four-toed salamanders (*Hemidactylium scutatum*) and American toads (*Bufo americanus*) were rarely captured, and therefore were also excluded from analyses. Data for pickerel frog and blue-spotted salamander are presented but only discussed qualitatively.

Adults made up a smaller proportion of the total captures for all species except for blue-spotted and eastern red-backed salamanders (Table 4). Four species (wood frogs, northern leopard frogs, spotted salamander, and eastern red-backed salamanders) showed consistently higher adult captures in uncut and partial-cut treatments than in clearcuts, with patterns being less clear for the remaining species (Table 4). Significantly more wood frog adults were captured in the control forest compared to the partial-cut, and in the partial-cut compared with the clearcut treatments (ANOVA: 3,9, d.f. $F = 16.520$, $P = < 0.001$, Tukey pairwise comparisons $P = 0.045$, < 0.001, and < 0.001, respectively). Spotted salamanders showed higher number of adult captures in the control, partial-cut, and clearcut with CWD retained compared to the clearcut with CWD removed (ANOVA: 3, 7 d.f., $F = 5.279$, $P = 0.032$, Tukey pairwise comparison 0.034).

All of the study species showed higher juvenile captures in the uncut and partial-cut treatments compared to the clearcuts, although the results were not statistically significant for pickerel frogs and blue-spotted salamanders (Table 4). Wood frog juveniles showed significantly higher captures when comparing the uncut and partial-cut treatments to the clearcuts, but no significant differences within these groups (Table 4) (ANOVA 3, 8 d.f., $F = 17.711$, $P = < 0.001$, Tukey pairwise comparisons $P = 0.001$ for control compared to both clearcuts, $P = 0.022$ for partial-cut compared to clearcut with CWD removed, and $P = 0.019$ for partial-cut compared to clearcut with CWD retained). Significantly more juvenile spotted salamanders were captured in the clearcut with CWD retained compared to the clearcut with CWD removed (ANOVA 3, 7 d.f., $F = 27.544$, $P = < 0.001$, Tukey pairwise comparison $P = 0.028$). Captures of juveniles of this species were also significantly lower in the partial-cut compared to the control treatments

(ANOVA 3, 7 d.f., $F = 27.544$, $P = < 0.001$, Tukey pairwise comparison $P = < 0.001$) (Table 4).

Temporal patterns in juvenile captures were generally similar among treatments for all species: representative figures for wood frogs and spotted salamanders are shown in Figures 7 and 8 respectively. The temporal peaks in these captures also remained quite consistent between both field seasons for all species except green frogs. A distinct peak in eastern red-backed salamander captures (adults and juveniles combined) was seen at the end of the 2004 field season, but traps were closed before this period in 2005 (Figure 9). This difference in field season duration may also have lead to the lack of selection seen for any treatment in 2004, with strong selection for the control treatment seen in 2005.

Unmarked juvenile wood frog showed a significant size difference, with larger animals found in the uncut and partial-cut treatments compared to the clearcuts (3, 1574 d.f., $F = 8.858$, $P < 0.001$). Individual mean sizes (mm ± S.E.) were 24.5 (0.2) for the control, 24.9 (0.2) for the partial-cut, 23.4 (0.3) for the clearcut with CWD removed, and 23.5 (0.3) for the clearcut with CWD retained.
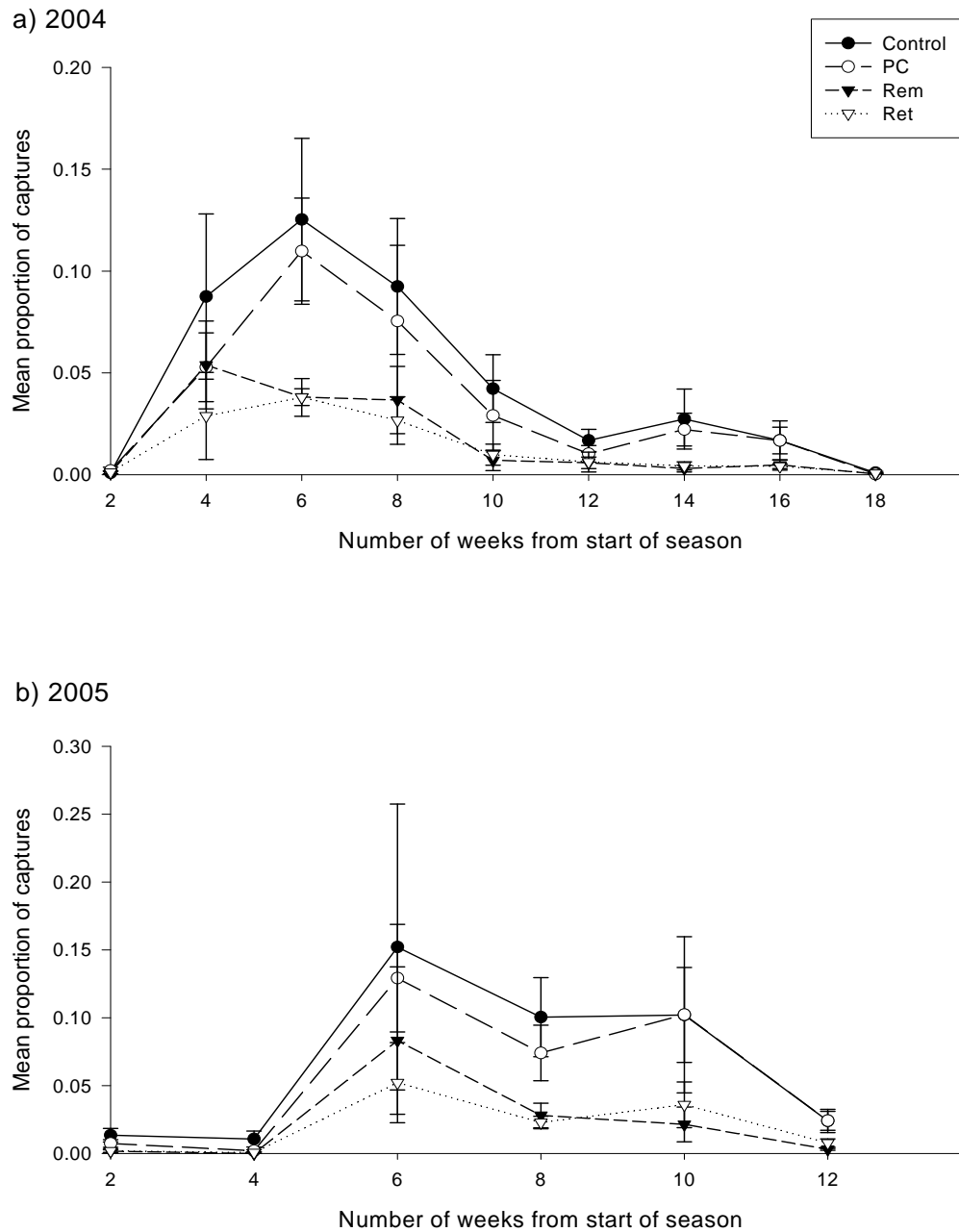
Figure 7. Temporal changes in the mean proportion of the total number of juvenile wood frog captures grouped by two week intervals from the start of the field season (n sites = 4).

a) 2004

b) 2005
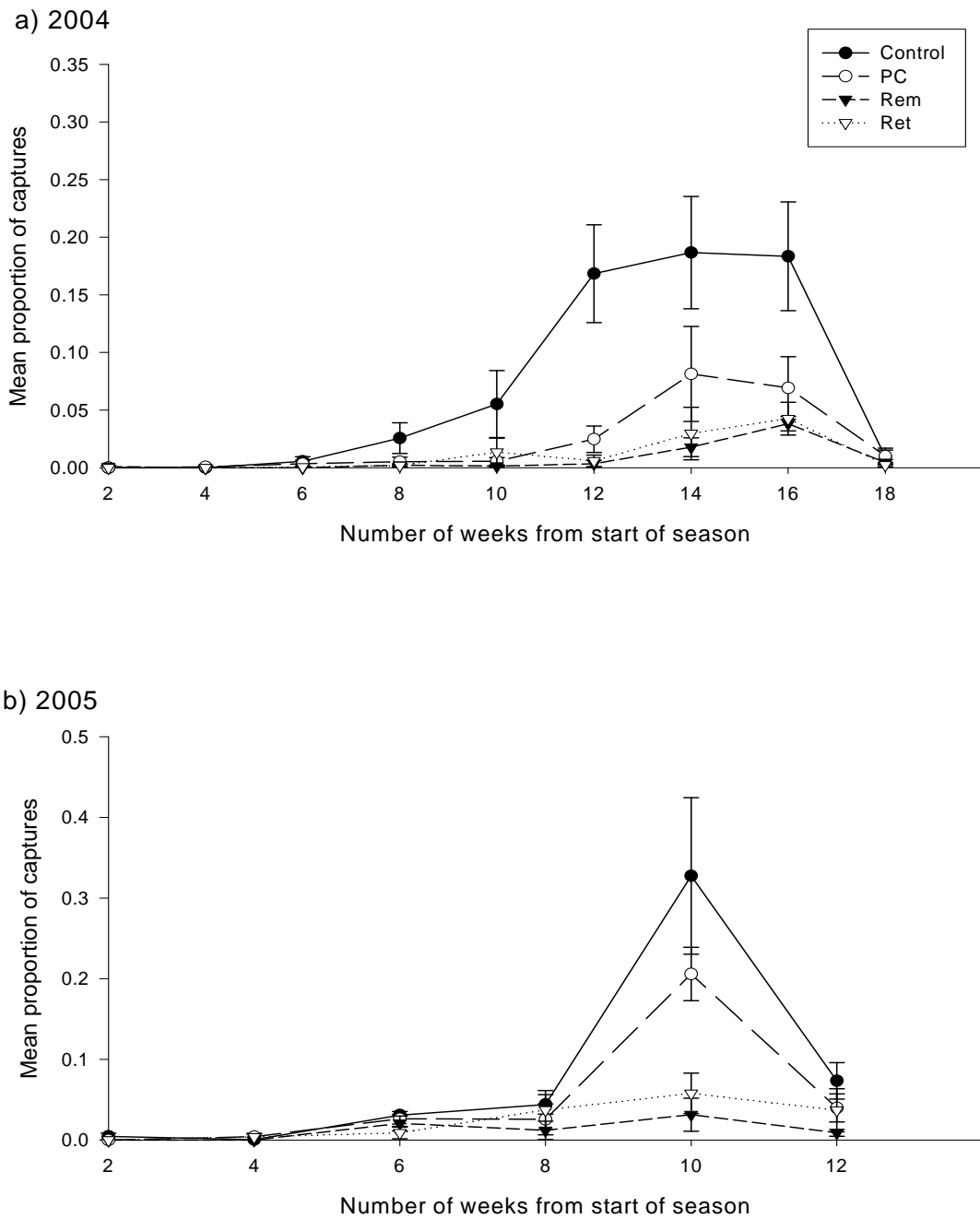
Figure 8. Temporal changes in the mean proportion of the total number of juvenile spotted salamander captures grouped by two week intervals from the start of the field season (n sites = 4).
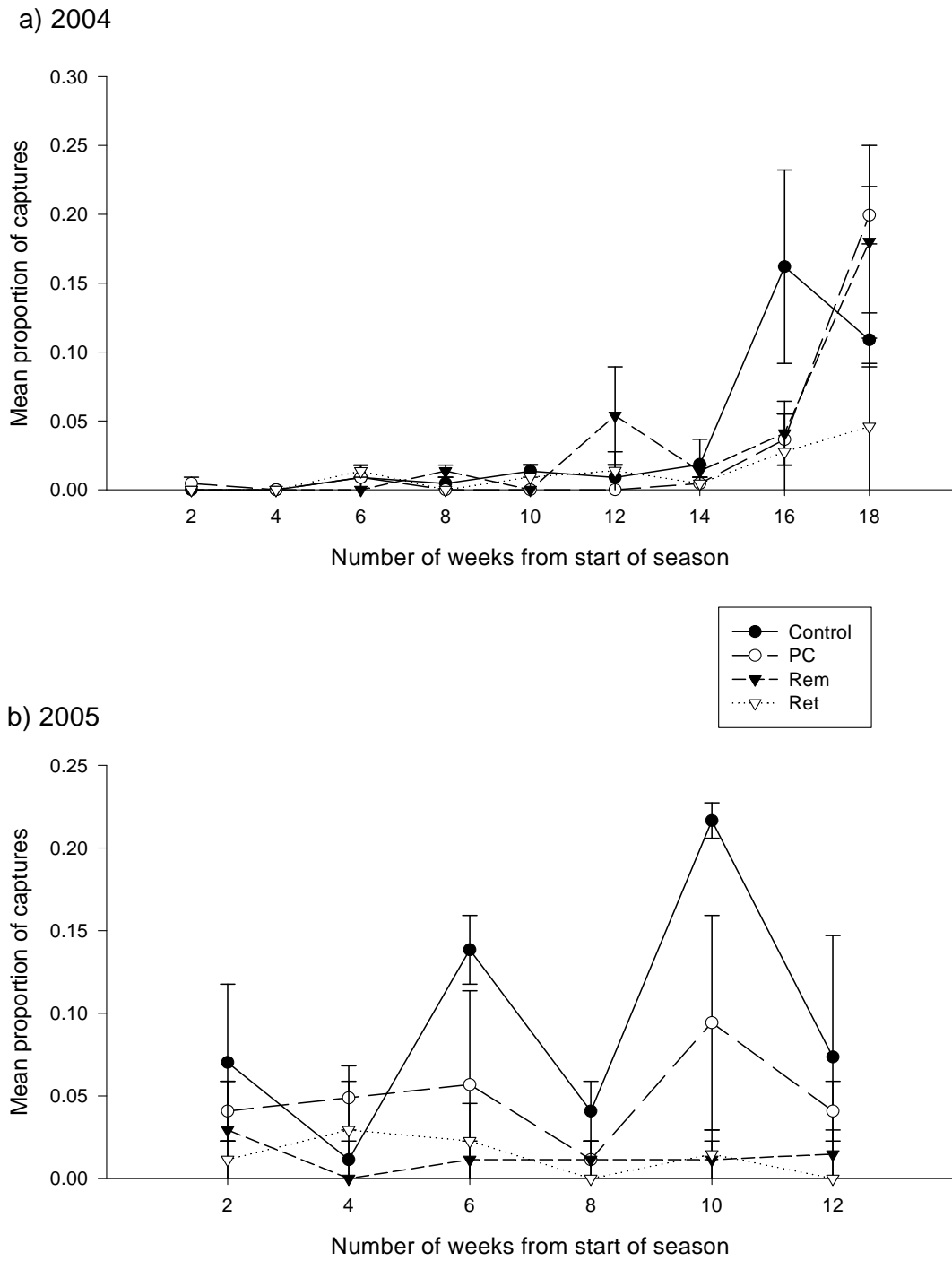
Figure 9. Temporal changes in the mean proportion of the total number of eastern red-backed salamander captures grouped by two week intervals from the start of the field season (n sites = 2).

Table 4. Captures of unmarked amphibians in the LEAP treatments in 2004 and 2005.

Species	Chi-square value[1]		Total juvenile captures		Total adult captures		% adults in both seasons combined[2,3,4]				% juveniles in both seasons combined[2,3,4]			
	Adult	Juv.	2004	2005	2004	2005	Con	PC	Rem	Ret	Con	PC	Rem	Ret
Wood frog	313.22*	1375.34*	4097	3033	262	466	51.2 [A]	26.5 [B]	11.3 [C]	11.0 [C]	40.2[A]	30.8 [A]	14.3 [B]	14.7 [B]
American bullfrog	15.30*	15.30*	137	238	35	34	37.7	13.0	27.5	21.7	32.8	25.3	18.9	22.9
Green frog	11.53**	79.95*	582	1160	181	153	25.1	16.8	32.3	19.8	32.8	27.0	21.1	19.1
Pickerel frog	Na	na	33	24	8	7	40.0	6.7	33.3	20.0	36.8	36.8	15.8	10.5
Northern leopard frog	20.40*	19.11*	132	142	24	6	30.0	46.7	16.7	6.7	32.8	29.6	21.5	16.
Blue-spotted salamander	Na	na	10	21	13	2	40.0	20.0	6.7	33.3	58.1	9.7	9.7	22.6
Spotted salamander	39.18*	1653.29*	1303	871	279	25	37.2 [AB]	28.9 [A]	13.2 [B]	20.7 [AB]	61.9 [A]	20.1 [B]	7.0 [C]	11.0 [B]
Red-spotted newt	Na	57.157*	75	52	5	11	25.0	43.8	12.5	18.8	52.8	23.6	13.4	10.0
E. red-backed salamander	19.49*	11.79*	67	27	122	69	33.5	30.9	22.5	13.1	38.3	27.7	18.1	16.0
Total			6444	5570	929	773								

[1] Calculated from captures in both seasons combined. The critical value of the chi-square distribution with 3 d.f. and α of 0.05 is 7.815. Significant results are indicated by *

[2] For wood frogs and spotted salamanders, pairwise comparison of significant ANOVA results ($p < 0.05$) are indicated by letters grouping similar data (A,B,C).

[3] Con = control, PC = partial cut, Rem = clearcut coarse woody debris removed, and Ret = clearcut coarse woody debris retained, na = insufficient data

[4] Peak captures were measured in weeks from the start of the field season

2.4.3 *Habitat*

Mean canopy cover in the uncut forest was 73.8 %, with harvesting reducing this to 53.0 % in the partial-cut and 0 % in the clearcuts (Table 5). Volume of CWD differed dramatically between treatments, with the greatest amount in the clearcut with CWD retained (Table 5). The uncut and partial-cut treatments had a greater mean leaf litter depth than the clearcuts in both years, with a reduction in this depth in both clearcuts in 2005. Regeneration of ground vegetation in the clearcuts was rapid, with approximately a 36 % increase in cover in the 50 – 100 cm height category in both clearcuts from 2004 to 2005. Much of this regeneration was in the form of dense stands of red maple (*Acer rubrum*), growing from cut stumps, and balsam poplar (*Populus balsamifera*), with the latter having reached heights of up to 3 m in two years of growth.

Table 5. Habitat variables sampled in LEAP treatments in 2004 and 2005. Values shown represent treatment means ± one standard error.

Treatment	Leaf litter depth (mm)		% cover of vegetation < 0.5m		% cover of vegetation 0.5m – 1m		% standing water		CWD (m^3 per ha)	Canopy cover (%)
	2004	2005	2004	2005	2004	2005	2004	2005		
Control	30 ± 5.8	18.9 ± 4.6	8.4 ± 1.0	0 ± 0	4.8 ± 2.2	10.5 ± 3.2	2.2 ± 1.3	2.6 ± 1.0	22.9 ± 11.8	73.8 ± 22.7
Partial cut	28 ± 5.9	13.5 ± 1.1	11.9 ± 4.4	0.05 ± 0.0	3.6 ± 1.9	14.0 ± 1.2	4.3 ± 2.51	5.2 ± 1.2	33.9 ± 7.3	53.0 ± 33.5
Clearcut (CWD removed)	24 ± 5.7	8.8 ± 2.5	10.6 ± 0.5	2.82 ± 2.3	2.1 ± 0.5	38.6 ± 7.2	5.3 ± 2.1	15.0 ± 3.2	12.7 ± 7.5	0
Clearcut (CWD retained)	19 ± 4.5	5.9 ± 1.0	10.1 ± 2.2	2.59 ± 1.5	1.1 ± 0.6	36.0 ± 5.0	3.0 ± 2.63	12.9 ± 1.9	45.6 ± 21.6	0

2.5 Discussion

Our results corroborate findings of previous studies on the effects of forest management practices on amphibians, with lower overall abundance of amphibians in clearcuts (Pough et al., 1987; Raymond and Hardy, 1991; Petranka et al., 1993, 1994; Ash, 1997; Harpole and Haas, 1999; Grialou, et al., 2000; Ash et al., 2003; Knapp et al., 2003; Renken et al., 2004). As previously found, adult habitat use differed among species (deMaynadier and Hunter, 1998; Strojny 2004), with wood frogs, spotted salamanders, and eastern red-backed salamanders preferring uncut or partially cut forest, and adult green frogs and American bullfrogs being more tolerant of canopy removal. The reported sensitivity of ambystomatid salamander species to reduced canopy cover (deMaynadier and Hunter, 1998; Cromer et al., 2002; Guerry and Hunter, 2002; Rothermel and Semlitsch, 2002), and to the retention of CWD in clearcuts (Moseley et al., 2004) was also seen in my results. Eastern red-backed salamanders showed a low number of captures during summer when individuals are territorial and limited in movement (Jaeger et al., 1995). During the late fall movement of this species documented in 2004 it appears that eastern red-backed salamanders were moving through all four treatments (Figure 6).

Much of the research on terrestrial habitat use of amphibians to date has focused on adults (although see deMaynadier and Hunter, 1999; Rothermel and Semlitsch, 2002; Vasconcelos and Calhoun, 2004), with the ranid species in my study (except wood frogs) typically being described as generalists rather than forest-dependent species (Table 3). This highlights the importance of my results showing that juvenile habitat use differed from that of adults, with 7 of 9 species showing statistically more juvenile captures in the uncut and partial-cut treatments and lower in clearcuts. In other words, my results clearly

show that the habitat selection of adult amphibians does not necessarily make a good surrogate for that of juveniles of the same species, and that the majority of juvenile amphibians will choose to move through forest rather than open-canopy areas. The results also suggest that partial canopy removal may reduce the relative abundance of many species (all species except pickerel frogs had fewer juvenile captures in the PC compared to the control, although a statistical difference could only be shown for spotted salamander), and that the retention of CWD may serve to mitigate some of the effects of clearcutting for ambystomatid salamanders.

Our experimental design assessed two components of habitat selection during movement of marked juvenile wood frogs. The first of these was the initial choice made as to which treatment is entered. The second component related to how treatments such as clearcuts affect habitat resistance, i.e., movement through the habitat following this initial selection (Ricketts et al., 2001; Rothermel and Semlitsch, 2002; Mazerolle and Desrochers, 2005). Recaptures did not decline until 150 m from the pond in any of the treatments suggesting that for the few juvenile wood frogs that chose to move through clearcuts, the habitat did not offer greater resistance. Although this suggests that clearcuts do not present a significant barrier to movement and potentially to dispersal and connectivity between populations, I am hesitant to draw this conclusion. Clearcuts have been shown to increase dehydration and reduce survival of juvenile amphibians (Rothermel and Semlitsch, 2002). My study did not address such effects, and further research is clearly needed to understand how clearcuts may affect long-term survival.

The marked wood frog data also show that the highest total number of recaptures was at 100 m from the pond. This suggests that there were more recaptures of the same

individuals at 100 m (assuming that efficacy of the fences did not change with distance), which could indicate that the animals had settled in an area suitable for summer foraging and were not actively dispersing. In other words, juvenile wood frogs may have a predisposition to move some minimum distance from the source pools. Such a predisposition has been suggested for adult female wood frogs (Regosin et al., 2003), but to the best of my knowledge this is the first time that a similar pattern has been shown for juvenile wood frogs. This finding has important implications when protecting terrestrial habitat near pools, as it suggests that the population may not be most concentrated directly adjacent to the pool.

The marked wood frog data also suggest that habitat selection during movement is not purely a function of habitat quality, given that some juvenile wood frogs chose to remain in clearcuts. Competitive exclusion by a high density of conspecifics in the high-quality (uncut and partial-cut) treatments might explain this result (Fretwell and Lucas, 1969). The significantly larger mean sizes of unmarked juvenile wood frog captured in the uncut and partial-cut treatments in 2005 supports this idea.

The sensitivity to clearcutting of juvenile amphibian species in my study may have important implications when considering the linkage between forest management and amphibian populations. Juveniles have been shown to be the dispersing life-history stage for many amphibian species (Gill, 1978; Breden, 1987; Berven and Grudzien, 1990). Reductions in abundance and changes in dispersal patterns can have critical effects on population viability and processes such as the probability of recolonization of extinct populations, and gene flow between populations (Frankham et al., 2002). Although my results do not explicitly measure the effects of forest management on juvenile dispersal,

my data on habitat selection, abundance, and long-distance movement of marked wood frogs provides a surrogate measure of these effects. If fewer juvenile amphibians choose to enter clearcuts, then the probability of successful dispersal through these habitats is obviously reduced when compared to dispersal through uncut or partially cut habitat. Similarly, if juvenile amphibians avoid settling in clearcuts following dispersal, the available habitat is reduced, along with the population abundance. To critically assess the importance of these patterns I would need to have information on many other factors, notably the extent of clearcutting in the region and the duration of any responses to clearcutting (i.e., how soon would regeneration restore habitat for juvenile amphibians).

Although my study species are common and probably not jeopardized by the limited clearcutting that currently occurs in Maine, these results suggest that biologists should investigate the effects of major habitat change on juveniles of other amphibian species, especially those at risk of local or global extinction. Furthermore, diminished abundance of common species could compromise their ecological role (Wyman, 1998).

Future research efforts should focus on understanding the long-term patterns of juvenile abundance and how they affect the viability of amphibian populations. Such an understanding will need to include factors such as the survival of juveniles to adulthood in different treatments, as well as the effects on subsequent life-history stages for example adult survival and reproduction. By understanding such effects, forest management can be designed to incorporate both connectivity between areas of suitable habitat, and sufficient areas of habitat to maintain population viability.

CHAPTER 3

HABITAT STRUCTURE, TERRESTRIAL HABITAT USE, AND EMIGRATION OF JUVENILE AMPHIBIANS: A MULTI-SCALE EXPERIMENTAL EVALUATION.

3.1 Abstract

The interactions between behavior and habitat structure that determine the spatial distribution of organisms may vary across different ecological scales. Understanding these patterns is important when predicting the effects of habitat change on populations. I conducted four experiments at different ecological scales to evaluate how the spatial distribution of juvenile wood frogs was influenced by behavior and habitat structure, and how this relationship changed with spatial scale, and life-history mode. The four experiments included (1) a replicated population level habitat manipulation (10 ha landscapes) with multiple habitat treatments; (2) short-term experiments with individual organisms emigrating through a manipulated landscape of 1 m wide hexagonal patches; and (3) and (4) habitat manipulations in small (4 m^2) and large (100 m^2) enclosures with multiple individuals where I compared behavior both during and following emigration. Results indicated that the scale at which juveniles responded to habitat changed depended on whether animals were emigrating or settling post-emigration. During emigration, juvenile wood frogs responded to large-scale habitat differences (selection between 2.2 ha patches of different forestry treatments), and not to fine-scale variation in habitat. Post-emigration however, animals showed habitat selection for much smaller patches (2-4 m^2). This resulted in high densities of animals in patches of suitable habitat, where they

experienced rapid mortality. Habitat selection was found to be dynamic, with temporal variation both within a season and annually. My field experiments show that habitat heterogeneity can have effects at multiple spatial and temporal scales, and that to understand these effects I need to conduct experiments at multiple scales. Focusing on a single scale could lead to dramatically different conclusions about animal/habitat relationships.

3.2 Introduction

Understanding the spatial distribution of species is a critical component of ecology and conservation. Paradigms developed in population biology theory are often aimed at specific levels of ecological organization for example models of local populations (e.g., Leslie 1945) or regional populations such as island biogeography and metapopulation theory (MacArthur and Wilson 1963, Levins 1969). Constraining my view of ecological systems to these scale-dependent paradigms can be at odds with ecological scale theory, however (summarized in Peterson and Parker 1998). Ecological processes are typically hierarchically structured, with multiple factors operating across a range of scales (Franklin *et al.* 2000, Cushman and McGarigal 2002). Changing spatial or temporal scale can therefore influence both the suite of factors determining patterns of spatial distribution, and the relative strengths of the role played by each of these factors (Wiens 1989, Sale 1998). Consequently, experiments conducted at different scales may lead to different and apparently contradictory results (Benhamou 2006).

The relationship between ecological scale and factors determining patterns of spatial distribution has been explored in a number of studies (Peterson and Parker 1998). This body of research has shown that focusing on individual behavior may not detect

population level processes such as density dependent movement (e.g., Kauffman *et al.* 2004). Conversely, population level studies may not recognize the role of individual behavior (Benhamou 2006). Similar issues arise when considering changing temporal scale: animals may alter individual movement behavior within a matter of minutes in response to weather changes, whereas metapopulation events, such as localized extinctions, may take decades to occur (Mackey and Lindenmayer 2001). Additional factors that have been shown to change with ecological scale include habitat structure and quality (e.g., Garcia-Charton *et al*. 2004, Akcakaya *et al*. 2004, Thompson and McGarigal 2002); seasonal resource use (e.g., Regosin *et al*., 2003); and the response of different life-history stages (Turchin 1996, Harveson *et al.* 2004, Vasconcelos and Calhoun 2004).

The scale-dependent nature of ecological processes means that to draw comprehensive conclusions about factors determining spatial distribution, research should be conducted at multiple scales (Wiens 1989, Mackey and Lindenmayer 2001, Cushman and McGarigal 2002). This approach allows both the factors determining patterns of spatial distribution, and how these factors change with spatial and temporal scale, to be evaluated. By providing a mechanistic rather than phenomenistic understanding, models predicting the effects of habitat change on patterns of spatial distribution can be readily applied at multiple scales (Levin 1992).

Accurate predictive models of the effects of habitat change on species distributions are essential in the development of effective conservation strategies for species at high risk of extinction due to habitat loss and degradation. Amphibians, with 1,896 species threatened globally, are a taxa for which such models could prove especially useful (Stuart et al. 2004). Recent studies have indicated the importance of

terrestrial life-history stages in driving amphibian population trends (Biek *et al.* 2001, Vonesh and De la Cruz 2002), with fragmentation and loss of terrestrial habitat contributing directly to the vulnerability of species to extinction (e.g., Sjogren Gulve 1994). However, the mechanisms driving patterns of amphibian distribution and abundance are still not well understood (Marsh and Trenham 2001, Cushman 2006). The majority of studies of natural amphibian populations have focused on aquatic breeding sites, but less is known about amphibian distributions outside of the breeding season when adults and juveniles are foraging and overwintering in terrestrial habitat (Regosin *et al*. 2003, Semlitsch and Bodie 2003, Baldwin *et al.* 2006). This is partly because of methodological limitations, such as the difficulty of tracking individual juvenile amphibians, and the limited battery life of radio-transmitters for adults.

The goal of my research is to understand the interplay between behavior, habitat structure, and ecological scale within the context of habitat selection during and immediately following emigration of juvenile wood frogs (*Rana sylvatica*) from natal ponds. I used timber harvesting (partial harvesting and clearcutting) as a means of manipulating habitat structure/quality because wood frogs are a forest-dependent species (deMaynadier and Hunter 1998). I conducted four experimental habitat manipulations representing a range of spatial and temporal scales. Experiment 1 involved replicated 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 1998). Experiment 2 focused on the influence of fine-scale habitat heterogeneity (1 m^2 patches) on individual movement behavior during emigration. In Experiment 3, I studied the response of multiple individuals to fine-scale habitat

heterogeneity in a simple enclosed landscape (2 m² patches) during and following emigration, and examined the role of the density of con-specifics. Experiment 4 studied the response of multiple individuals to a meso-scale habitat manipulation (100 m² enclosure made up of 4m² patches), and evaluated the interaction between habitat heterogeneity and the density of con-specifics on patterns of settling.

3.3 Methods

3.3.1 *Study Area*

The study was conducted in the Dwight B. Demeritt and Penobscot Experimental Forests, Penobscot Country, Maine, USA, as part of the Land Use Effects on Amphibians Population (LEAP) project (details provided in Patrick *et al.* 2006). At each of the 4 Maine LEAP 4 forestry treatments extending 164 m into the terrestrial environment are centered on an amphibian breeding pond. Treatments were harvested in December 2003, and include an uncut control, a partial cut (PC) where 50% of the canopy was removed, and 2 clearcuts, one where CWD >10 cm in diameter was retained (CWD retained), and 1 where CWD was removed (CWD removed). Experiments 2-4 were established in the clearcut with CWD removed treatment at the Gilman site.

3.3.2 *Study Species*

The wood frog is a wide-ranging North American ranid with a close association with forests (deMaynadier and Hunter 1998). Wood frogs at my sites breed in vernal pools in April, with each female laying a clutch of approximately 1000 eggs. Tadpoles metamorphose simultaneously at the end of June/early July. After emergence, juveniles emigrate away from the pond. After approximately 2 weeks, juveniles 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 over-winter in hummocks of sphagnum moss and leaves (Baldwin *et al.* 2006). Adults breed in their third year, with high rates of philopatry to native ponds (Berven and Grudzien 1990, Vasconcelos and Calhoun 2004).

Experiment 1: *Effects of landscape-scale habitat heterogeneity on movement and habitat selection during and following emigration.*

In Experiment 1, I assessed the effects of habitat manipulation on the spatial distribution of juveniles in a wood frog population within the LEAP landscape of forestry treatments (each of the 4 replicate landscapes approximately 10 ha). I also evaluated potential effects of the density of con-specifics on spatial distribution, and changes within seasons and between 2 years of data collection. Drift fences established at the pond's edge, and at 16, 50, 100, and 150 m into each of the 4 terrestrial forestry treatments were used to catch juvenile wood frogs as they moved away from the breeding ponds. Pitfall traps were monitored from 24 June to 17 September in 2005, and 30 June to 22 August in 2006. Further details of experimental design and data collection in 2005 are provided in Patrick *et al.* 2006.

In 2005, metamorphs were marked using a single toe-clip to indicate which treatment they emerged into. In 2006, metamorphs were marked based on the treatment and the week of first capture. Recaptured animals were marked with visible implant elastomer (VIE) to indicate clearcut or forested (control and PC) treatment, and the week of first recapture. Animals recaptured following this second mark were not remarked, but were counted as a multiple recapture.

I evaluated 3 questions with recapture data: (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 emigration to a settled, summer foraging phase.

I evaluated questions (1) and (2) using ANOVA with year, site, treatment, and distance as factors. Only individuals recaptured for the first time in 2006 were included in analyses. One site was excluded from 2006 data due to disease-related recruitment failure. Question (3) was evaluated 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).

Experiment 2: Effects of fine-scale habitat heterogeneity on individual movement behavior during emigration.

I evaluated whether individual behavior was influenced by local habitat structure during emigration. I established a 12x16 m experimental landscape approximately in the center of the clearcut CWD removed treatment at the one of the LEAP sites, removing all vegetation and woody material >1 cm in diameter. Pin flags were used to demarcate a grid of 11 by 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 as "CWD") of decay class 3 (Faccio 2003); and (3) habitat containing a 30 cm high by 1 m wide heap of fine woody material (<2 cm in diameter, denoted as "slash"). There were a total of 147 empty cells, 8 cells containing CWD, and 21 cells containing slash. These proportions were designed to mimic the relative amounts of these conditions in the LEAP clearcut with CWD retained treatment (see experiment 4 methods). Cell contents were initially assigned non-randomly to ensure an approximately equal dispersion of the 3 cell

contents. Following this initial landscape configuration, the contents of each of the slash and CWD cells were assigned to 1 of the adjoining cells on a random basis to create a new landscape. This process of randomizing the landscape was repeated 3 times to give a total of 4 scenarios.

I 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. For each scenario, 30 metamorphs were collected and released into the experimental landscape on the same day at dusk. 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. Immediately prior to release, the ventral side of each frog was liberally coated with fluorescent powder (Rittenhouse *et al.,* 2006), then it was placed under an inverted plastic cup in the center of an empty cell. After waiting 10 minutes I removed the cup using an attached bamboo pole, allowing the observer to remain 2 m away. Two hours after release of the frog I followed their trail using an ultraviolet light. This period was sufficient for the animals to move > 30 m (i.e., outside the experimental landscape, Patrick *unpub. data*). I 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. None of the individual frogs was confronted with the same scenario twice due to the limited number of cells containing CWD or slash.

We conducted statistical analysis of the trails by comparing the contents of the hexagonal cell the frog chose to move into each time a new cell was entered, with the 6 cell contents available. This presented a number of configurations; for example the choice

frogs made when 1 CWD cell and 5 empty cells were available. I selected the
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.

Experiment 3: *Effects of fine-scale habitat heterogeneity and density of con-specifics on*
groups of frogs, both during and following emigration.

I designed this experiment to evaluate the effect of con-specific density and local
habitat structure on habitat selection. I also assessed if any behavioral responses changed
over time as animals progressed from emigration to a more settled phase, and the effects
of density on short-term survival. I established 24 1x4 m experimental pens >30 m from
the edge of the clearcut CWD removed treatment at one of the LEAP sites. These pens
were constructed 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. All
vegetation and woody material were removed from the pens, with half of each pen then
being designated as either high- or low-quality habitat. In the context of this study, the
label "high" quality is used to refer to the presence of shade, increased leaf litter, and
CWD, factors that have been shown to increase survival of amphibians (Rittenhouse *et al.*
in review). This assignation was conducted randomly for 1 pen in each pair, with the 2nd
pen having the opposite configuration. High-quality habitat contained 30 mm deep leaf
litter, a total of 3 m of 10-15 cm diameter CWD of decay class 3, and was covered by
70% shade cloth raised 1m from the ground. Low-quality habitat contained 25 mm deep
leaf litter and was not covered.

I conducted this experiment from 20 July to 6 August 2005, and 31 July to 18 August 2006. Three density treatments of recently metamorphosed wood frogs were released into the pens: low (2 individuals per m^2/ 8 per pen); medium (4 per m^2/ 16 per pen); and high (7 per m^2/ 28 per pen). The same treatment was assigned to each pair of pens. Densities were based on previous research indicating that there is a threshold between 4 and 7 juvenile wood frogs per m^2 at which growth and survival decreases significantly (E. Harper *unpub. data*).

In 2005, 8 pens were assigned to each of the density treatments. Following release, pens were left for 16 days, a sufficient period for juvenile wood frogs to transition from emigration to a settled summer foraging phase (Patrick *et al.* 2006). A barrier was then constructed at midday between the 2 habitat treatments within each pen. At dusk when frogs were most active I conducted exhaustive sampling until no more individuals were found. For each captured frogs were I noted the treatment in which they were captured and SVL.

In 2006, 6 pens were assigned to each density treatment (3 pairs of pens). I staggered releases over a period of a week. All animals were measured and individually marked upon 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 a total of 15 days, with captured animals measured and the treatment of capture noted. This allowed an assessment of changes in habitat selection and density due to mortality over the total sampling period. In 2006, frogs in 4 of the 6 highest density pens showed signs 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 die-offs).

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.

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 sample as covariates. I obtained climatic data for the study region from a weather station approximately 5 miles from the study site (weather underground [wunderground.com]).

I used a Cormack-Jolly-Seber model to estimate capture probability at each sampling interval for the individually marked animals in 2006. This allowed me to assess the efficacy of my sampling efforts. Survival analysis was conducted using the individually marked animals in 2006 with the data adjusted to account for capture probability. I used a non-parametric 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 con-specifics.

I evaluated the effects of variation in habitat and density of con-specifics on the spatial distribution of juveniles settling following emigration. In 2006 I established a single 10x10 m pen approximately in the center of a CWD removed clearcut at one of the

LEAP sites. This pen was constructed of 1 m tall silt fencing buried 30 cm into the ground. A 3 cm lip was placed on both the inside and outside to prevent animals entering or exiting. Within this pen all vegetation and woody material were removed. I divided the pen into 25 2x2 m habitat blocks alternately designated as either high or low-quality habitat to create a regular checkerboard effect. High-quality blocks contained 30 mm deep leaf litter, a total of 10 m of 10-15 cm diameter CWD of decay class 3, and were covered by 4 m^2 of 70% shade cloth raised approximately 1m from the ground. Low-quality blocks were unshaded and contained 25 mm deep leaf litter and no CWD.

I released 200 recently metamorphosed wood frogs from 28 July to 31 July 2006, with a total of 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 using metal stakes. Barriers were constructed at midday when wood frogs were less active and likely to move in response to disturbance. Each of the 25 blocks was then sampled to estimate the density of individuals (termed "sample 1"). Following sampling, barriers were raised, and the pen left for 2 days to allow the wood frogs to resettle in the landscape. One hundred additional wood frog metamorphs were released on the 4 to 5 August, 25 in each corner. Animals in this second release were marked with a single toe-clip to allow them to be distinguished from the first batch released. A week after the release of the additional frogs, I replaced the temporary barriers around each of the 25 habitat blocks and the density of animals from both releases was assessed through exhaustive sampling (termed "sample 2").

I used chi-square to test if more individuals settled in high-quality habitat blocks, and whether there were any differences between edge blocks and interior blocks. The expected number of captures was adjusted by the number of blocks that fell into each of these categories. Recaptures are reported as density per m^2, while total counts were used in statistical analysis. In sample 2, unmarked and marked recaptures were evaluated separately due to possible correlation between the location of unmarked animals in sample 1 and sample 2.

I tested two alternative hypotheses based on the settling of marked animals from the second batch released: hypothesis (1), individuals settle based on differences in habitat, not density of con-specifics (i.e., blocks with high numbers of individuals in sample 1 were presumably high-quality and would have high numbers in sample 2); and hypothesis (2), 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). To evaluate these hypotheses, I 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 cut-off point for each category based on qualitative analysis of the distribution of data. Recaptures were totalled 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 I 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, I

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.

3.3.3 *Overall statistical analyses.*

Statistical analyses were conducted using SYSTAT 11.0 (Systat software inc.),

with α = <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).

3.4 Results

Experiment 1: Effects of landscape scale habitat heterogeneity on movement and habitat

selection during and following emigration.

The four LEAP treatments differed significantly in numbers of recaptures in both

years (Figure 10, ANOVA d.f. 3,91, F = 8.845, P ≤ 0.001), with *post hoc* analyses

revealing significant differences between forested treatments and clearcuts ($P ≤ 0.001$),

but not within each of these groups ($P > 0.999$). There were also significant differences

when comparing among sites (d.f. 3,91, F = 10.155, $P ≤ 0.001$). The lack of a significant

year, treatment, and site interaction (d.f. 1,3,3,1,3,9,91, F = 0.261, P = 0.983) showed

that these differences 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. The numbers of recaptures in the 4 LEAP treatments did not significantly

differ over distance from the pond, (d.f. 3,9,91, $F = 0.586$, $P = 0.625$), although having

four replicates of each treatment led to low statistical power to detect differences.

In 2006, wood frogs settled in treatments (indicated by multiple recaptures of the

same individual) in the same proportions as they emigrated through treatments (indicated

by first time recaptures) (Gilman $X^2 = 0.668$, critical value with 3 d.f. 12.838, $P \geq 0.75$;

North Chemo $X^2 = 1.596$, $P \geq 0.5$; Smith $X^2 = 10.706$, $P \geq 0.01$).
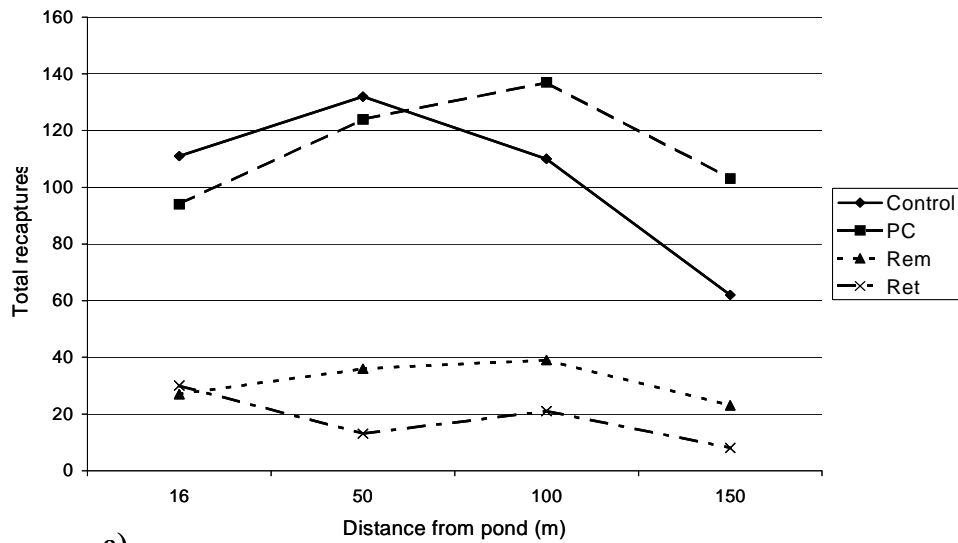
a)
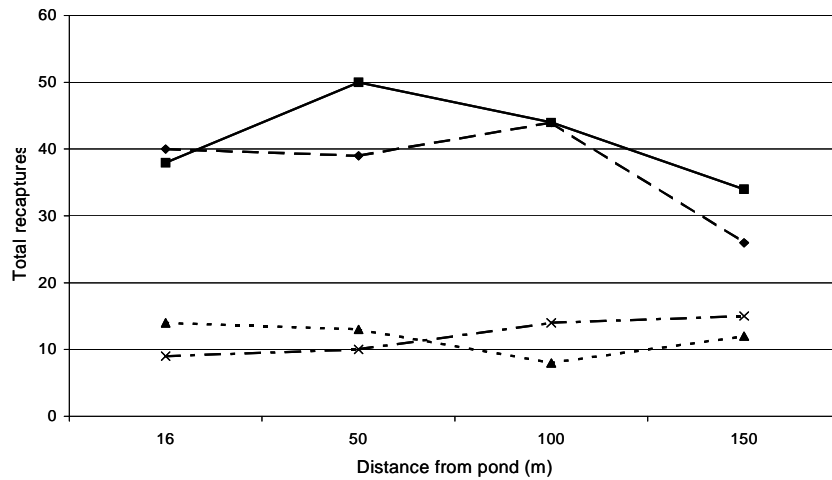
b)

Figure 10. Total recaptures of emigrating juvenile wood frogs over distance 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 figure
legend refers to the four LEAP forestry treatments (Control, PC = partial cut of 50 %
crown closure, Rem = clearcut with CWD > 10cm in diameter removed, and Ret =
clearcut with CWD retained).

Experiment 2: Effects of fine-scale habitat heterogeneity on individual movement

behavior during emigration.

In the manipulated area of 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 6). Of the complete suite of different cell configurations, 4 were

common enough to yield sufficient data for analyses.

Table 6. Habitat selection of recently metamorphosed juvenile wood frogs released in an
artificial landscape of hexagonal cells (each approximately 1 m^2), with cells containing
one of three habitat types, empty, CWD, or slash. Each line in the table represents a
different choice scenario with which frogs were confronted.

Contents of adjacent cells		Frogs (N) entering cells			
N cells slash	N cells CWD	Empty	Slash	CWD	X^2 P value
1	0	49	16	0	>0.10
1	1	24	6	4	>0.25
2	0	13	5	0	>0.50
0	1	40	0	8	>0.99

Experiment 3: *Effects of fine-scale habitat heterogeneity and density of con-specifics on*

groups of frogs, both during and following emigration.

More individuals in the 1x4 m pens in 2005 were recaptured in the high-quality

treatment at the conclusion of the experiment (mean proportion of total recaptures ± std.

dev = 0.881 ± 0.116). The initial density of animals released into the pens (either 2, 4, or

7 m^2) did not determine the final proportion of recaptures in the high-quality treatment

(ANOVA d.f. = 2,15, F = 0.895, P = 0.429). Regressing the proportion of recaptures in

the high-quality treatment against the total number recaptured in the pen revealed a marginally significant relationship, with more animals in the low-quality habitat as density in the entire pen increased (linear regression d.f. 1,16, $F = 4.272$, $P = 0.055$).

A higher proportion of animals was recaptured in the high-quality treatment in 2006 (mean ± std. dev. = 0.797 ± 0.194). No significant relationship was found between the proportion of the total recaptures in the control treatment and the maximum daily temperature, rainfall, time, and the total number recaptured in the pen (d.f. = 5,71, $F = 1.071$, $P = 0.384$), indicating that animals were selecting for the high-quality treatment regardless of the total density in the pen and weather conditions.

Percent survival over time in 2006 was significantly different among density treatments (Figure 11. Wilcoxon; df = 2; $\chi^2 = 74.91$; p < 0.0001). Wood frogs in enclosures initially stocked at the lowest density (8 frogs/per pen) were more than 4 times more 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.
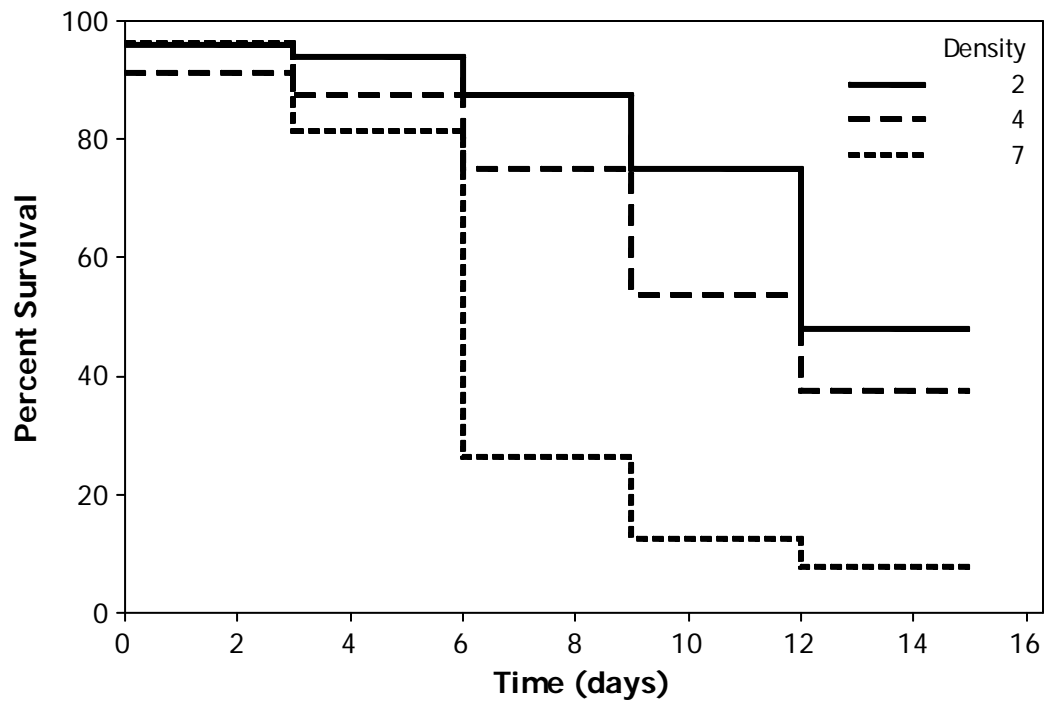
Figure 11. Survival of juvenile wood frogs at 3 density treatments (2, 4, and 7 per m^2) in 1x4 m pens in 2006.

Experiment 4: *Effects of a meso-scale habitat manipulation and varying density of con-specifics.*

Significantly more animals were recaptured in high-quality habitat in the 10x10 m pen when grouping animals from both releases (Table 7. Sample 1: $X^2 = 24.762$, sample 2: X^2 for marked animals only $= 52.878$, critical value with 1 d.f. $= 3.841$, $P = <0.001$). In sample 1, 119 of the initial 200 animals released into the pen were recaptured; in sample 2, 121 out of the total of 300 released were recaptured (48 marked and 73 unmarked).

Table 7. Summary of the number and density of juvenile wood frogs recaptured in a 10x10 m landscape of 4 m^2 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 a further 100 frogs. Edge captures refers to habitat blocks immediately adjacent to the outer wall of the pen (n = 8 high-quality blocks, and 8 low-quality), and interior captures refers to the remaining blocks (n = 5 high-quality blocks, and 4 low-quality blocks).

Sample	Treatment	Mean density (m^2)	Range in density (m^2)	Unmarked captures (N)	Marked captures (N)	Mean edge density (m^2)	Mean interior density (m^2)
1	High	1.7	0.25-3.25	89	0	2.19	0.95
	Low	0.625	0.25-2.25	30	0	0.72	0.44
2	High	2.15	0.5-7.75	43	69	3.09	0.65
	Low	0.19	0-0.5	5	4	0.19	0.19

Variation was seen in the number of recaptures within habitat treatments. High-quality blocks on the edge of the pen had significantly higher numbers of recaptures than those in the center of the pen in both samples (sample 1: $X^2 = 11.012$, critical value with 1 d.f. = 3.841, $P = <0.001$; sample 2: $X^2 = 8.940$ for unmarked, and 25.829 for marked individuals, critical value with 1 d.f. = 3.841, $P = <0.005$ for unmarked and <0.001 for marked animals). No difference was seen in recaptures in low-quality edge and interior blocks (sample 1: $X^2 = 1.35$, critical value with 1 d.f. = 3.841, $P = >0.25$; sample 2: insufficient data for statistical analysis).

Animals apparently 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 marked animals found in sample 1 compared to unmarked animals captured in sample 2 (X^2 = .900, critical value with 2 d.f. = 5.991, P = >0.50).

3.5 Discussion

My results illustrate the complex response of emigrating juvenile wood frogs to different spatial and temporal scales. During emigration, wood frogs viewed habitat heterogeneity at a coarse spatial scale, selecting the forested LEAP treatments (each 2.2 ha) over clearcuts (Figure 10). After frogs had entered these treatments, however, they showed no response to fine-scale habitat heterogeneity (at a scale of approx. 1 m^2) in a clearcut treatment (Table 6). No differences among treatments were seen in the proportional distance distribution of animals away from the pond, which suggests that differences in habitat determined the overall number of animals entering treatments, but did not affect the way in which juveniles then emigrated within these large patches.

Once animals began to settle following emigration, however, wood frogs exhibited strong selection for small patches of high-quality habitat in both the 1x2 m and 10x10m pens. I also observed variation in selection when comparing between small patches of the same habitat type in the 10x10 m landscape of multiple patches (Table 7). My results suggest that juvenile wood frogs exhibit a bi-phasic behavioral response to habitat heterogeneity, with clear differences between emigration and settling following this period. This bi-phasic response is likely to play an important role in determining the density of juvenile wood frogs in different habitat types following emigration. My results suggest that in forested areas similar to the forested LEAP treatments, the entire habitat is likely to be suitable post-emigration (albeit of variable quality). Thus although more animals choose forested habitats on initial emigration from the pond, they will occur at

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relatively low densities because they are distributed throughout the forest. In areas of largely unsuitable habitat such as clearcuts, fewer individuals enter the treatment, but following emigration most of these individuals are likely to be found within the few small patches of suitable habitat, potentially resulting in locally high densities.

Previous research has shown the importance of density in defining vital rates through factors such as mortality through competition (e.g., Hixon and Jones 2005), predation (e.g., Johnson 2006), and disease (e.g., Bradshaw and Brook 2005). Few estimates of terrestrial amphibian density are available (although see Regosin 2003), however, and studies have not been able to link terrestrial habitat heterogeneity and the resulting effects on density. My results clearly demonstrate the importance of understanding this relationship, rather than solely focusing on the abundance of amphibians in the terrestrial environment as a metric of the effects of habitat change. I found that even in areas of relatively low overall density when considered from a large patch perspective (i.e., 2.2 ha clearcuts), extremely high densities of wood frogs may be found in localized patches (up to 7.75 individuals/m^2). Survival analysis also showed how density dependent mortality could dramatically reduce overall abundance even if animals are only exposed to these conditions for a few weeks (Figure 11).

Temporal variation in habitat heterogeneity should be considered when relating habitat structure to eventual population processes. I documented annual changes in habitat use in the 1x4 m pens; in 2005, con-specific density played a role in habitat selection whereas in 2006 no relationship was seen. I also observed changes over much shorter periods of time in the 10x10m pen experiment in 2006, with far fewer frog selecting low-quality blocks in the second sample even though the overall density was similar in both

samples. My results suggest that these differences were due to behavioral responses to changes in the same habitat over time: reduced use of low-quality areas resulted in higher densities in high-quality habitat in both the 1x4 m and 10x10 m pens and thus to high density dependent mortality. Based on fitness theory, the high cost of the densities I observed should be a result of other options (i.e., selecting low-quality habitat) having an even greater cost in terms of fitness. Amphibians are known to be physiologically vulnerable to apparently small changes in habitat such as temperature and moisture (Rittenhouse *et al*. *in prep*). The extremely low densities I observed in low-quality habitat at certain points during my experiments are indicative of habitat quality being close to the threshold at which it can be physiologically tolerated (Table 7). I was not, however, able to determine the factors that caused these changes in habitat quality.

Our results reinforce the need to conduct research at multiple scales if I are to fully understand animal/habitat relationships. Were I to have only conducted experiments at the scale of the entire LEAP project (i.e. 2.2 ha patches/10 ha landscapes), I would not have understood the critical role that fine-scale habitat heterogeneity within these patches plays. Fine-scale experiments such as experiments 2-4 would also not have shown the importance of coarse-scale habitat selection. Similarly, by only focusing on juvenile amphibians during emigration, I would not have noted the behavioral shift following this movement. This study is far from comprehensive, however, and further research into the relationship between habitat structure and other life-history stages of amphibians is needed. Of particular importance is a greater focus on the factors linking micro-climatic variation in habitat with the quality of that habitat for amphibians. Reduction in habitat quality due to factors such as global climate change may lead to both an increase in areas

of non-habitat, and a long-term reduction in overall abundance of populations, in turn

increasing vulnerability to extinction. The effects of reduced areas of high-quality habitat

on density and the resulting mortality of juvenile amphibians documented in my study,

suggests that an overall reduction in terrestrial habitat quality could have far reaching

effects on the viability of amphibian populations.

CHAPTER 4

FACTORS DETERMINING THE SPATIAL DISTRIBUTION OF JUVENILE WOOD FROGS: COMBINING SIMULATIONS WITH MULTI-SCALE FIELD EXPERIMENTS

4.1 Abstract

Some amphibian population declines have been linked to loss and degradation of forest habitat, but a mechanistic understanding of this relationship has yet to be fully developed. Without this understanding it is difficult to predict the consequences of further habitat change on populations. I evaluated the effects of changes in forest habitat on the spatial distribution of emigrating juvenile wood frogs, *Rana sylvatica*, using a combination of multi-scale experimental habitat manipulations and predictive spatial modeling. Habitat manipulations were used to estimate variables shown to determine spatial distribution including habitat heterogeneity and movement behavior such as autocorrelation in random walks and habitat selection. The estimates of these variables were included in candidate models designed to simulate emigration of juvenile wood frogs. Models varied in complexity from random diffusion in a uniform landscape to models specifically designed to mimic habitat and behavioral characteristics seen in my empirical studies. I tested models using data gathered on the spatial distribution of juvenile wood frogs following emigration over a large area (10 ha replicates) of experimentally manipulated forest.

Our results demonstrated the complex relationship between habitat heterogeneity, wood frog behavior, and spatial distribution following emigration. In empirical studies

the response of wood frogs to habitat heterogeneity changed from coarse-scale habitat selection during active emigration, to fine-scale selection when settling. This behavior resulted in some localized densities above carrying capacity in clearcut habitat causing rapid mortality. Inclusion of specific movement behavior (autocorrelation and habitat selection), as well as habitat heterogeneity resulted in the best fit between my models and field data. My combination of empirical and theoretical approaches also demonstrates the importance of looking at both the resulting density of frogs in different habitat types following emigration, as well as the overall distribution of organisms over distance when considering effects of habitat change on juvenile wood frogs.

4.2 Introduction

Developing models to accurately predict the effects of environmental change on biodiversity is a principal goal of conservation science. Predictive models allow *a priori* identification of threats, giving time for the development of management plans and contingency strategies (e.g., Rustigan *et al.* 2003). In addition to this preemptive role, predictive models also allow the identification of life history stages or demographic factors that are likely to be driving the changes seen, allowing research to be directed to where it will be most effective (Crouse *et al.* 1987, Caswell 2001).

My research uses predictive modeling and directed empirical research to understand the relationship between animal behavior, landscape structure, and the spatial distribution of amphibians in the terrestrial environment. Amphibians are known to be highly sensitive to habitat change (e.g., Ray *et al.* 2002), with population declines reported globally (Wake 1991, Lips 1998, Pounds *et al*. 2006). Some of these declines have been linked to loss and degradation of forest habitats (Stuart *et al.* 2004), but a

mechanistic link between habitat change and the resulting population level effects has yet to be made (Cushman 2006).

The sensitivity of amphibians to terrestrial habitat change is likely to be at least partially reflected in their spatial distribution because fragmentation, loss, and/or degradation of habitat can change both the spatial arrangement and quality of different habitat types. Amphibians respond to these changes by selecting preferred habitat (e.g., Rothermel and Semlistch 2002, Rittenhouse *et al.* 2004), with selection manifested as changes in movement characteristics such as the rate of movement, directionality, and where animals settle at the conclusion of movement (Turchin 1998, Johnson *et al.* 1992). These behavioral changes affect the distribution of animals in the landscape; for example species may respond to habitat fragmentation by occupying a smaller area at higher densities. Changes in spatial distribution can have demographic consequences including effects on local populations through density dependent mortality (e.g., Bradshaw and Brook 2005, Hixon and Jones 2005, Johnson 2006), and regional population dynamics through reduced dispersal between populations (e.g., Greenberg and Tanner 2005).

In this paper I specifically focus on the effects of change in forest habitat on emigration of juvenile wood frogs, *Rana sylvatica*. For many amphibian species, juveniles are the dispersing life-history stage, with adults showing high rates of philopatry (e.g., Berven and Grudzien 1990, Vasconcelos and Calhoun 2004). Focusing on juveniles therefore offers information relevant to both local and regional population persistence. I first developed a series of experimental habitat manipulations to evaluate the effects of habitat heterogeneity on movement behavior and habitat selection by juvenile frogs (Patrick *et al.* 2006, Patrick *et al. in prep*). I next simulated amphibian emigration using

cellular automata models that varied in complexity from random diffusion to spatially explicit models that included specific estimates of behavioral and habitat characteristics from my field experiments. The models were tested using data from a landscape-scale habitat manipulation involving mark-recapture of juvenile amphibians using drift fence/pitfall trap arrays (details of experimental design are provided below and in Patrick *et al.* 2006).

4.3 Methods

4.3.1 *Study species*

The wood frog is a wide-ranging North American ranid with a close association with forests (deMaynadier and Hunter 1998). Wood frogs at my study sites breed in vernal pools in April, with each female laying a clutch of approximately 1000 eggs. Tadpoles metamorphose simultaneously at the end of June/early July. After emergence, juveniles emigrate away from the pond. After approximately two weeks, juveniles 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 over-winter in shallow leaf litter depressions (Baldwin *et al.* 2006). Adults breed in their third year, with high rates of philopatry to native ponds (Berven and Grudzien 1990, Vasconcelos and Calhoun 2004).

4.3.2 *Field experiments*

Landscape-scale mark-recapture

Empirical studies were conducted within the Land Use Effects on Amphibian Populations project (LEAP), at the University of Maine. This landscape-scale forest manipulation has been replicated in Maine, Missouri, and South Carolina. At each of these sites, four experimental arrays have been created, with each replicate centered on an

amphibian breeding pond, and consisting of four forestry treatments extending 164 m in radius from the central pond. Treatments include an uncut control, a partial harvest with 50% canopy removal, and two clearcuts; one with coarse woody debris (CWD) >10 cm in diameter removed, and one with CWD retained. Experiments were conducted from 2004-2006, with juvenile wood frogs marked on emerging from the pond and recaptured at terrestrial drift fences at 16, 50, 100, and 150 m from the pond. Further details of the design of this experiment are provided in Chapters 2 and 3.

Habitat selection and autocorrelation

Habitat selection and autocorrelation in random walks were evaluated via an experimental habitat manipulation within one of the LEAP clearcuts. A 12x16 m area was cleared of all vegetation and woody material. Within this area, I demarcated a lattice of 1 m wide hexagons with pin flags. Each of these hexagonal cells was assigned to one of three habitat types: containing CWD, slash, or empty. Recently emerged juvenile wood frogs were released into this landscape and their trails followed using fluorescent powder. Further details of experimental design are provided in Patrick *et al. in prep*.

Autocorrelation was evaluated by calculating the probability of a frog continuing to move in the same direction when each new hexagonal cell was entered. An overall mean was calculated from individual means for each trail that yielded sufficient data (at least three hexagonal cells moved through). Because the hexagonal landscape had six available neighbors and the spatial simulation models eight neighbors, the probability of autocorrelation was converted accordingly. Autocorrelation was calculated as a binary probability for model input: either a frog moved in the same or a different direction.

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Estimation of the density of frogs in low and high-quality habitat

Frog densities in simulated low and high-quality habitat were evaluated using two experiments described in Patrick *et al. in prep*. The first involved 1x4 m pens constructed out of 1 m tall silt fencing in one of the LEAP clearcuts. These pens consisted of half low and high-quality habitat (i.e. 1x2 m of each). Low-quality habitat consisted of 25 mm of leaf litter, while high-quality habitat had 30 mm of leaf litter, a total of 3 m of CWD of decay class 3 (Faccio 2003), and a covering of 70% shade cloth. Three densities of juvenile wood frogs were released into the pens (2, 4, and 7 per m2). These animals were left for two weeks, before a temporary barrier was erected between the two habitat types, and removal sampling used to estimate density.

In the second experiment, a larger manipulated landscape of the two habitat types was produced: a 10x10 m area of clearcut was fenced with 1 m high silt fencing and further demarcated into 2x2 m blocks in a regular checkerboard pattern. Each of these blocks was alternately designated as either low or high-quality habitat. Leaf litter depth and shade cover were the same in these habitats as in the previous experiments. High-quality blocks contained a total of 10 m of CWD. I released 200 juvenile wood frogs into this landscape, then returned one week later to erect temporary barriers around each habitat block and sample the number of frogs in each block. I next removed the temporary barriers, and released a further 100 marked frogs. After a further week, the temporary barriers were replaced, and the number of marked and unmarked animals in each of the blocks was calculated via removal sampling.

Estimation of habitat heterogeneity

To estimate habitat quality (for the purpose of model development) within each of the LEAP treatments, I established 18 permanent vegetation arrays. Each array consisted of seven 1 m wide tessellating hexagons. Within these arrays I measured leaf litter depth, standing water, and vegetation in 2 height classes (< 0.5 m, and > 1 m). Not all arrays were measured in both years due to logistical constraints. CWD was estimated using three 50 m line transects in each treatment. Further details of experimental design are provided in Patrick *et al*. 2006.

For modeling purposes, habitat measurements were converted to binary categorical data: low and high-quality habitat. For each habitat variable, this conversion compared the mean measurement per array with the overall mean (based on both years and all sites and treatments). If the array mean was less than the overall mean, it was considered low-quality habitat, and if it was equal to or greater than the overall mean it was considered to be high-quality. Variables for which I calculated the proportion of low and high-quality arrays per treatment included leaf litter depth, % vegetation cover 0-1 m in height (composite of 0-0.5, and 0.5-1 m categories), and % standing water separately. To derive a relative measure of CWD in each treatment, I calculated the proportion of the total volume in all the LEAP sites that was found in each of the treatments. The individual proportions for each of the four habitat variables were used to calculate a combined mean proportion of low and high-quality habitat for each LEAP treatments. As my field data indicated no difference between the forested cuts (partial cut and control) in terms of the response of amphibians, I considered the presence of canopy cover (both partial and full) as overriding the effects of the other variables listed above. Based on this

assumption, candidate models 1-7 had uniform landscapes of high-quality habitat in the control and partial cut treatments.

4.3.3 *Model development- simulating emigration of juvenile wood frogs.*

We developed cellular automata models using Matlab 7.0.1. The seven candidate models varied from generalized diffusion to models specifically recreating frog behavior and landscape attributes documented in the LEAP study (Table 8).

Models were run in a 200 by 200 lattice with continuous time and wrap-around boundaries. For each simulation I created a bi-layered matrix, with one layer documenting the frog state (the number of frogs in each cell), and the other documenting the landscape state (habitat quality, represented by the number of frogs allowed in a cell). Each cell within the lattice represented a 4 m2 area (i.e., the model landscape represented a 400x400 m lattice), allowing simulation of animals leaving the boundaries of the LEAP landscape (which measures 328 m in diameter). For each of the models except 7, the four LEAP treatments were simulated separately. For the forested treatments, landscapes were uniformly high-quality. For the two clearcuts, landscapes consisted of low and high-quality habitat. Landscapes were randomly generated with the proportion of each of these habitat types estimated from my field experiments.

Frogs were seeded into the central four cells of the frog state matrix to simulate natal ponds. The numbers of frogs seeded into simulations were based on the mean number per treatment captured at the LEAP pond fences in 2005 (Table 9). This allowed us to more directly compare my field data with model outputs. For each event in the model, an individual frog was randomly chosen (with replacement) and moved to one of

the eight adjacent cells based on the rules of the particular simulation. If the cell to which it was destined to move was already at full capacity based on the number of frogs allowed in the cell in the landscape matrix, the individual was returned to the source cell. Because these were continuous time stimulations, only one event occurred at a time. Every set of F successful moves was defined as a time step, where F was the number of frogs seeded into the model. Note that because of the stochastic nature of the model, and the fact that sampling was done with replacement, some frogs had more than one successful move during a time step while other frogs had none, but on average each frog had one successful move per time step. A counter recorded the number of times a frog successfully changed position, allowing direct comparison of models where differences in model rules meant variation in the proportion of attempted moves that were successful.

Table 8. Candidate models for predicting the spatial distribution of juvenile wood frogs following dispersal in the 4 LEAP treatments. Variables listed as 'yes' indicate the inclusion of an estimate of the mean of this variable from field studies in the model. A heterogeneous landscape includes 2 habitat types, low and high-quality, with the proportion of each based on data from the LEAP project. High-quality habitat has an unlimited number of animals allowed to settle. Low-quality habitat had a maximum density of 1 animal per cell. Bi-phasic behavior refers to models with a switch from autocorrelation to local habitat selection after two-thirds of the total number of successful time-steps. The number of frogs seeded into the model was based on the mean number of frogs that entered each of the 4 LEAP treatments, multiplied by 4 to simulate a single landscape of each of the treatments.

Model	Landscape	Initial directionality	Autocorrelation	Habitat selection	Bi-phasic behavior
1) Random diffusion.	Uniform	No	No	No	No
2) Autocorrelation in a uniform landscape.	Uniform	No	Yes	No	No
3) Autocorrelation in a heterogeneous landscape.	Heterogeneous	No	Yes	No	No
4) Habitat selection.	Heterogeneous	No	No	Yes	No
5) Autocorrelation or habitat selection.	Heterogeneous	No	Yes	Yes	No
6) Bi-phasic autocorrelation or habitat selection in a heterogeneous landscape.	Heterogeneous	No	Yes	Yes	Yes
7) Bi-phasic autocorrelation or habitat selection in a simulated LEAP landscape.	Heterogeneous including 4 LEAP treatments	Yes	Yes	Yes	Yes

I ran models for two durations (600 and 10,500 time-steps). Models run for 10,500 time-steps allowed frog's sufficient time to distribute themselves across the entire matrix, i.e., to simulate both emigration and settling. The short-term models (600 time-steps) were used to evaluate the behavior of models during active emigration (i.e., not necessarily to predict the final distribution of frogs in the landscape).

For bi-phasic models (6 and 7), frogs shifted from emigrating to settling behavior after two-thirds of the total number of successful time-steps (i.e., simulated emigration occurred for twice as long as simulated settling). For model 5 where both autocorrelation and habitat selection were included without a bi-phasic behavioral switch, it was first determined if a frog demonstrated autocorrelation at each move. If it did not, then localized habitat selection occurred.

Autocorrelation between movement was modeled based on my field estimates of the probability an individual would continue in the same direction as its previous move. Habitat selection was modeled by assigning the eight cells adjacent to a frog's position with probabilities proportional to their habitat quality, e.g., a cell with habitat quality 6 would be twice as likely to be chosen as a cell with habitat quality 3. More precisely, if the eight neighbors had habitat qualities h_i for $1 <= i <= 8$, then cell i would be chosen with probability $h_i / \Sigma h_i$.

I considered three outputs from my models: (1) The mean number of frogs reaching 10 different distances from the central pond (16, 40, 50, 60, 80, 100, 120, 150, 164, and 200 m) for each model; (2) a qualitative measure of the degree of clustering of frogs in the landscape; and (3) the mean density of frogs in occupied high-quality habitat cells. The predictive accuracy of each of the models was calculated by comparing the

simulated distribution of frogs following dispersal with that seen in the LEAP fences. The LEAP field data covered 2 years (2005, and 2006) during which there were sufficient recaptures of wood frogs to allow comparison with models. As terrestrial drift fences did not completely encircle the pond (only 38 % of the circumference was sampled) data were converted to estimate the total number of frogs that would have been captured if the entire circumference had been sampled.

4.4 Results

4.4.1 *Empirical studies*

Landscape-scale mark-recapture

Results of the landscape-scale mark-recapture experiment have previously been published in *Patrick et al.* 2006, and are reproduced in Table 9. More juvenile wood frogs were recaptured in the forested treatments than in the clearcuts (ANOVA d.f. 3,91, $F = 8.845$, $P = <0.001$). The number of recaptures at different distances from the ponds did not differ between treatments (d.f. 3,3,91, $F = 0.586$, $P = 0.625$).

Table 9. Total number of recaptured juvenile wood frogs from the LEAP fences in 2005 (both initial and multiple recaptures) and 2006 (initial captures only). Distance of 0 m represents the total initially marked and released into each of the 4 LEAP treatments.

Year	Distance (m)	Treatment				Total recaptures
		Control	PC	CWD retained	CWD removed	
2005	0	1438	1985	1360	1305	na
	16	111	94	30	27	262
	50	132	124	13	36	305
	100	110	137	21	39	307
	150	62	103	8	23	196
2006	0	408	545	600	505	na
	16	40	38	9	14	101
	50	39	50	10	13	112
	100	45	44	14	8	111
	150	28	35	15	12	90

Habitat selection and autocorrelation

Juvenile wood frogs did not show significant selection for any of the 3 habitat types (empty, containing slash, or containing CWD) in the artificial landscape of hexagonal blocks (*X* square *P* >0.1 for all tests). The probability of a frog showing autocorrelation in directionality between successive movement steps during dispersal was calculated as 21.9% (n = 71 trails), indicating that frogs tended towards more linear paths than would have been expected under random movement (where there would be a 16.67% chance of moving in the same direction as a previous step).

Estimation of the density of frogs in low and high-quality habitat

Mean densities (± SD) calculated from the final samples in the 1x4 m pens in 2005 were 0.69 (±1.0) individuals per m^2 in low-quality habitat and 3.73 (±2.87) in high-quality habitat. In 2006 low-quality cells had a mean density of 0.29 (±0.47) and high-quality cells a mean of 3.0 (±1.27). Mean densities in the 10x10 m pen varied between the first and second sample (even though the overall number of recaptures was very similar). In the first sample, low-quality habitat had a mean of 0.63 individuals per m2 and high-quality habitat a mean of 1.7. In the second sample, low-quality mean was 0.19, and the mean for high-quality blocks was 2.15. The highest density observed in a high-quality block was 7.75 individuals/m2. Based on these figures, the maximum number of frogs allowed in low-quality habitat in my models was 0.25 per m2 (or 1 per 4 m2), with an unlimited number of frogs allowed in high-quality habitat.

Estimation of habitat heterogeneity

We calculated that the clearcut with CWD retained averaged 36 % high-quality habitat, and the clearcut with CWD removed 31 % (Table 10). I have included calculations of the proportion of high-quality arrays in the control and partial cut, although I incorporated these treatments into models as uniformly high-quality habitat (due to the presence of forest canopy overriding the effects of variables shown in Table 10).

Table 10. Mean proportion of habitat variables designated as high-quality, measured in the LEAP treatments (data from 2005-2006 combined). Sample sizes for 2005 were control n = 31, partial cut n = 54, clearcut CWD retained n = 59, clearcut CWD removed n = 71. Sample sizes in 2006 were n = 24 for all treatments.

Treatment	Proportion of high-quality leaf litter depth arrays	Proportion of high-quality 0-1m vegetation arrays	Proportion of high-quality standing water arrays (measured in 2005 only)	Proportion of high-quality CWD arrays	Mean proportion high-quality cells
Control	0.84	0.09	0.00	0.20	0.28
Partial cut	0.62	0.13	0.02	0.30	0.27
Clearcut (CWD retained)	0.20	0.61	0.11	0.40	0.36
Clearcut (CWD removed)	0.35	0.60	0.18	0.11	0.31

4.4.2 Candidate models

Little difference was seen between randomly generated heterogeneous landscapes representing the two clearcuts (Figure 12). After 10,500 time-steps, models had diverged in their predictions of the distribution of frogs over distance (Figure 13). In the control and partial cut treatments, Model 7 (with the explicit LEAP landscape), provided the closest fit to the actual LEAP data (Figure 13a.), with all other models demonstrating similar predictions, and greatly overestimating the number of frogs. When considering model predictions in the clearcuts, however, Model 7 provided the worst fit (Figure 13b). This was due to animals moving into the clearcuts from the forested treatments, a process that could not occur in Models 1-6. Model 4 provided the closest fit to the LEAP data for clearcuts, but the relationship was still extremely poor. Models 1-3 and 5-6 showed similar results.
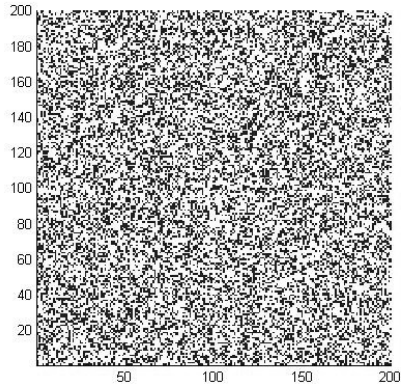
a) Clearcut with CWD retained
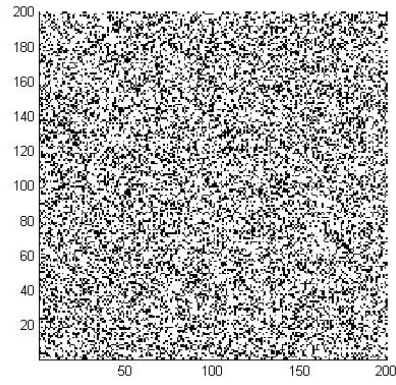
b) Clearcut with CWD removed
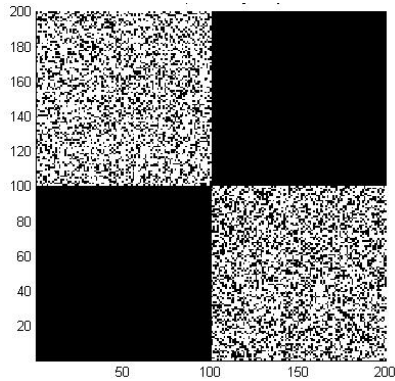
c) Explicit LEAP landscape

Figure 12. Sample modeling landscapes representing the clearcut with CWD retained, clearcut with CWD removed, and all the LEAP treatments. Each landscape is made up of two habitat types, low-quality, representing a maximum density of 0.25 frog per m2 indicated by white cells, and high-quality with an unlimited maximum density indicated by black cells. The CWD retained treatment consists of 64 % low-quality habitat (randomly located within the grid), and the CWD removed treatment 69 %. The control and partial cut treatments consist entirely of high-quality habitat.
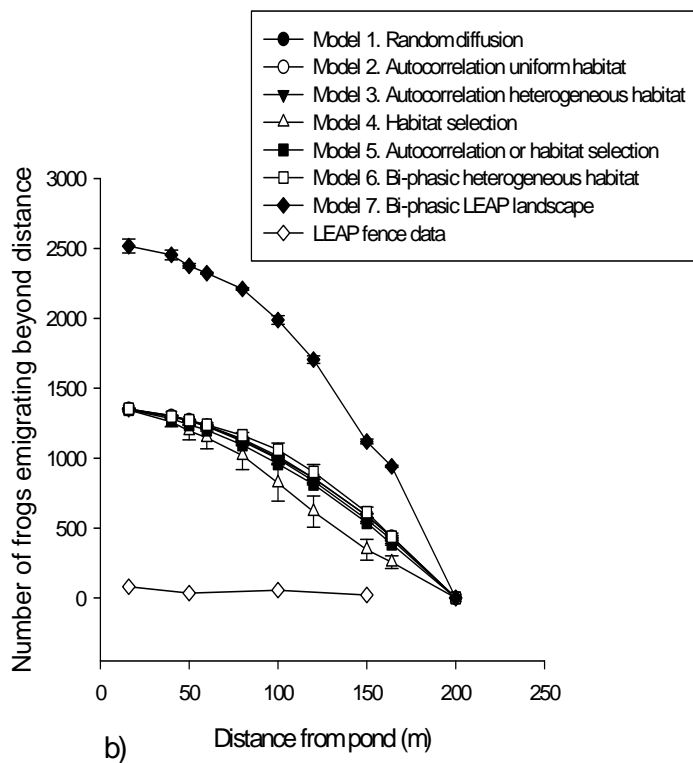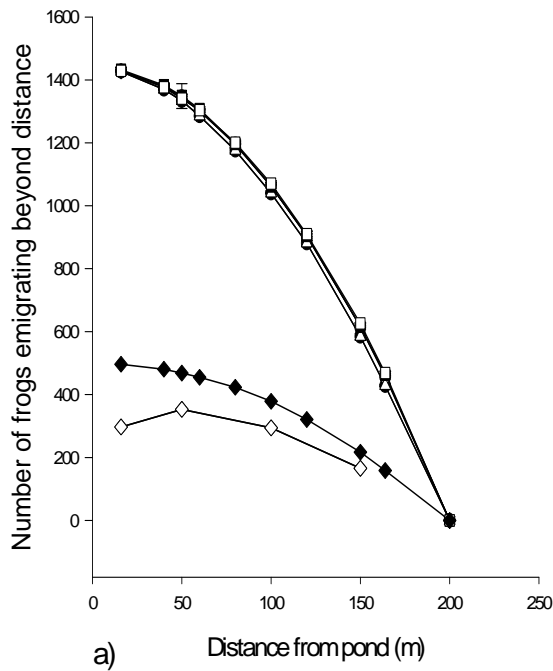
Figure 13. Numbers of frogs moving beyond successive distances from the source pond in candidate models run for 10,500 time-steps (mean ± std. dev.). Results are shown for the control (a) and clearcut with CWD retained (b) treatments. The partial cut and control showed very similar results to one another, as did the two clearcut treatments.

Differences between models were also apparent when comparing the distribution of frogs across the landscape (see Figures 15 and 16). After 600 time-steps, inclusion of habitat selection and a heterogeneous landscape in models resulted in a high degree of clustering of occupied cells (Figure 14a and the clearcut treatments in 15c). Models without habitat selection (i.e., Models 1-3), and simulated treatments with a uniform landscape (i.e., the control and partial cut) showed a more uniform distribution of frogs away from the source (Figure 14b and the control and partial cut in 15c). After 10,500 time-steps all models showed a greater dispersion of frogs across the available landscape (Figure 15), but the clustering seen in Figure 14 was still apparent when comparing different models. In Model 7 where the coarse scale habitat heterogeneity of the LEAP landscape was recreated (i.e., the 4 LEAP treatments), the clearcut treatments had far more frogs than the forested treatments (Figure 15c).
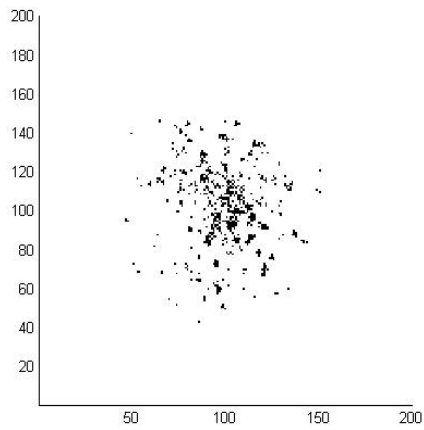
a) Habitat selection model
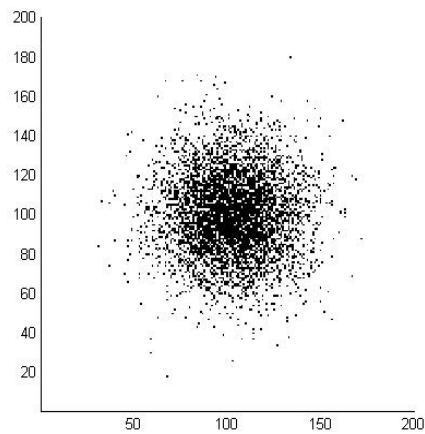
b) Autocorrelation in heterogeneous landscape model
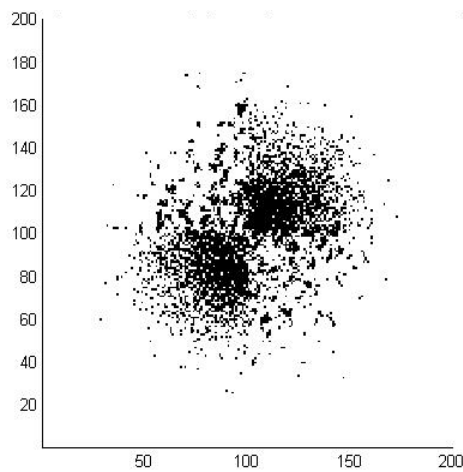
c) Bi-phasic model with explicit LEAP landscape

Figure 14. Spatial distribution of juvenile wood frogs following running candidate models for 600 successful time-steps. Figures shown are the combined results of three replicated simulations. Frogs started from the center of the landscape. Figures (a) and (b) represent models run in the clearcut with CWD retained treatment, Figure (c) the explicit LEAP landscape (in this figure the control is in the bottom left quarter, and the partial cut top right).
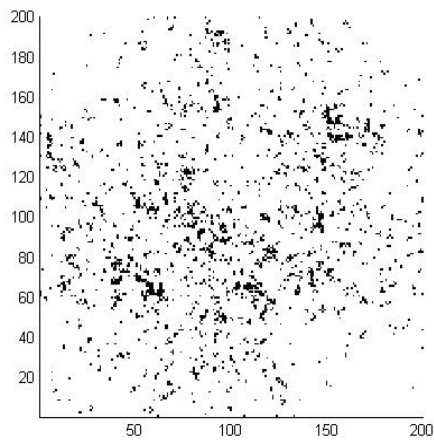
a) Habitat selection model
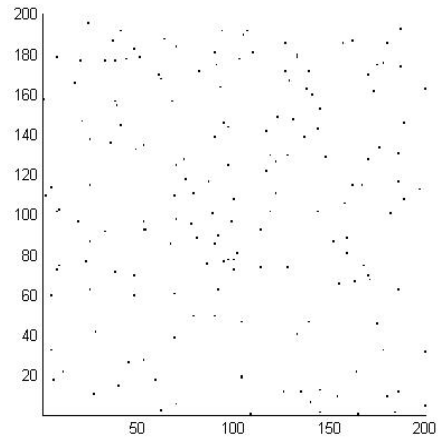
b) Autocorrelation in heterogeneous landscape model
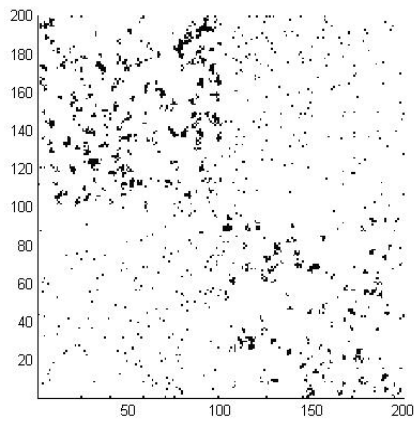
c) Bi-phasic model with explicit LEAP landscape

Figure 15. Spatial distribution of juvenile wood frogs following running candidate models for 10,500 successful time-steps. Figures shown are the combined results of three replicated simulations. Frogs started from the center of the landscape. Figures (a) and (b) are for the clearcut with CWD retained treatment, Figure (c) for the explicit LEAP landscape (in this figure the control is in the bottom left quarter, and the partial cut top right).

Comparing the mean densities of frogs in occupied high-quality cells highlighted model differences that were not apparent from either the 2–dimensional distribution of frogs from the source (i.e., Figure 13), or the spatial clustering of individuals (Figures 15 and 16). For models without habitat selection (i.e., Models 1-3) and simulated uniform quality treatments (control and partial cut), the mean density of frogs was consistently slightly higher than 1 per cell (i.e., 0.25/m2) (Table 11). In clearcut treatments for models including habitat selection, however, densities in occupied high-quality cells increased. The highest densities were observed in Model 7 where mean densities exceeded 5.5 frogs per cell (1.375 m2). The two models with the highest densities (models 5 and 7) also showed a difference between the clearcuts, with the clearcut with CWD removed, i.e., the clearcut with the most poor quality habitat (69% compared to 64% in the clearcut CWD retained treatment), having higher mean densities among occupied high-quality sites.

Table 11. Predicted mean densities per cell (i.e., 4 m2) of frogs in occupied high-quality habitat patches in the four LEAP treatments (control, partial cut, clearcut with CWD retained, and clearcut with CWD removed) for candidate models run for 10,500 time-steps. Low-quality occupied cells had a mean density of 1 frog per cell due to constraints placed by models.

Model	Mean density per occupied high-quality cell in simulated LEAP treatments			
	Control	Partial Cut	Clearcut (CWD retained)	Clearcut (CWD removed)
1) Random diffusion.	1.018	1.025	1.018	1.015
2) Autocorrelation in a uniform landscape.	1.015	1.026	1.017	1.016
3) Autocorrelation in a heterogeneous landscape.	1.016	1.027	1.019	1.018
4) Habitat selection.	na	na	1.859	1.679
5) Autocorrelation or habitat selection.	1.023	1.029	1.043	1.056
6) Bi-phasic autocorrelation or habitat selection in a heterogeneous landscape.	1.018	1.028	1.530	1.450
7) Bi-phasic autocorrelation or habitat selection in a simulated LEAP landscape.	1.006	1.008	5.574	6.032

4.5 Discussion

4.5.1 Empirical studies

My field experiments revealed significant differences in the behavior of juvenile wood frogs in different terrestrial habitats. At the scale of the LEAP treatments, juvenile wood frogs preferred to emigrate through forested treatments compared to clearcuts, but showed no difference in selection for the control compared to the partial cut, or between the two types of clearcuts (Table 8). Although clearcuts had lower overall abundance of juvenile wood frogs than forested treatments, I observed frogs moving up to 150 m in all treatments, and the patterns of recaptures over distance did not differ when comparing between treatments. This indicates that during emigration, frogs showed coarse but not fine-scale habitat preference. This conclusion is supported by the experiments in the manipulated landscape of 1 m wide hexagons where no fine-scale habitat selection was seen. This experiment also indicated that during emigration, frogs tended to move in more linear paths than would have been expected with random movement.

My experiments focusing on habitat selection following emigration indicated that frogs exhibited fine-scale habitat selection after settling. I observed strong selection for high-quality habitat in both 2 and 4 m^2 patches. I also observed extremely high densities of frogs in some of these high-quality patches (up to 7.75 individuals/m^2) and extremely low densities in low-quality patches. These localized densities, and the strength of selection for low and high-quality habitat areas, changed both within the same season in subsequent experiments, and when comparing between seasons (Patrick *et al. in prep*), indicating the dynamic nature of habitat heterogeneity.

Wood frogs have been shown to be closely associated with forests (e.g., Guerry and Hunter 2002, deMaynadier and Hunter 1998), and to exhibit local variation in density (Regosin *et al.* 2003, 2005). My results concur with these studies, and demonstrate how coarse-scale habitat selection during emigration followed by fine-scale habitat selection during settling could cause these patterns of spatial distribution.

4.5.2 Autocorrelation and habitat selection

The inclusion of simple autocorrelation (where frogs either headed in the same direction or a random direction) in models with a uniform landscape resulted in an increase in the mean step length of movement paths, but no difference when compared to the behavior of a random diffusion model (Figure 13). The addition of habitat heterogeneity to autocorrelation models (i.e., Model 3) also had no effect on the number of frogs over distance from the source.

Localized habitat selection reduced the average distance moved by frogs in clearcut treatments for Models 4 and 5, resulting in more animals close to the pond (Figure 13b). In Model 6 where behavior changed from autocorrelation to habitat selection after 2/3 of the total time-steps, the effects of habitat selection in reducing movement were not seen, and the results closely matched those seen from models 1-3. In Model 7, the overwhelming effects of frogs transitioning from one treatment to another masked any effects of the initial directionality of movement included in the model.

When using the simulated density of animals across the landscape as a response variable, models solely based on random diffusion (Model 1), autocorrelation (Model 2), or with uniform habitat quality treatments (i.e., forested treatments) failed to show a

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response to local habitat heterogeneity (Table 11). In contrast, Models 4-7 where localized habitat selection and habitat heterogeneity were included resulted in consistently higher densities in occupied high-quality cells (Table 11). This difference could most clearly be seen in Model 7, where the effects of coarse-scale selection between treatments, and fine-scale selection within treatments resulted in the highest densities of all the models. This was presumably a function of habitat selection operating to "trap" individuals where a high-quality cell was surrounded by low-quality cells.

4.5.3 Combining information from empirical studies and modeling simulations

By incorporating the juvenile wood frog species-environment relationships seen in my field experiments into my models, I greatly simplified the inherent complexity observed. I acknowledge that my estimate for autocorrelation in the directionality of movement represents a single suite of conditions, and that I have no knowledge how paths would have changed were these to have differed. Similarly my conversion of complex habitat heterogeneity into binary low and high habitat cells is based on the limited scope of my field experiments, within which I deliberately tried to manipulate habitat such that it represented profound differences in habitat quality.

Bearing these caveats in mind, my candidate models offer valuable information concerning the relationship between emigrating juvenile wood frogs and habitat heterogeneity. In predicting the two dimensional distribution of juvenile amphibians away from a source site following emigration, I found that Model 7 provided the best fit to the data from the LEAP fences for the forested treatments (Figure 13a). None of the models

provided good fits to the clearcut data, although Model 4 provided the best fit (Figure 13b).

When comparing among candidate models, differences in the simulated density of animals across the landscape are of particular importance. my field experiments clearly show that post-emigration, juvenile amphibians respond to local patchiness, resulting in isolated high-density patches of frogs in a sea of low-density matrix. Model 7 also highlights the importance of habitat heterogeneity at multiple scales in changing overall spatial patterns, including predicted differences in density at a fine (within the LEAP treatments), and coarse (comparing between treatments) scales. Clearly this model presents a far more accurate representation of the distribution of juveniles in the LEAP landscape than do models where the entire landscape is viewed as being of uniform habitat quality. The failure of my models to provide accurate predictions of the field data from the clearcut fences is almost certainly a function of excluding mortality. Were density dependent mortality to have been included in my models, I predict that Model 7 would have provided a good fit for both forested and clearcut treatments. This prediction is based on the fact that model 7 most accurately portrayed the localized high-density patches of frogs seen in clearcuts in my field experiments.

4.5.4 Management implications

Much of the existing spatial dynamic theory assumes that dispersal is a random process and does not depend on the response of organisms to habitat heterogeneity (e.g., Okubo and Levin 2001). While such theory provides an important heuristic tool in intact landscapes, it offers little predictive power when assessing the effects of continued habitat

fragmentation on animal species. My study demonstrates the dramatic effects behavioral responses to habitat heterogeneity can have on the spatial distribution of organisms, both from an empirical and theoretical standpoint.

Our results also show the importance of the metric used to determine the response of organisms to habitat change. Traditionally, including spatially explicit information when modeling the spatial distribution of amphibian populations has been limited due to data deficiencies (although see Rustigan *et al.* 2003). For example, management recommendations based on the use of terrestrial buffer zones have considered the population to be uniformly spread away from the source pond (e.g., Semlitsch 1998). My own results and those of other studies (e.g., Armsworth and Roughgarden 2005) show that any differences in movement behavior due to habitat heterogeneity can lead to unequal clumping of individuals in space. Importantly, these results also show that the resulting density of frogs in these patches can be well above the likely carrying capacity for juvenile wood frogs resulting in rapid mortality (Patrick *et al. in prep*, and Harper and Semlitsch *in review*). Accurately predicting the effects of habitat heterogeneity and change on amphibian populations will require data on multiple life-history stages and the inclusion of mortality in models. Ultimately I hope such multi-stage models can be incorporated with population viability analyses to predict the long-term effects of habitat change on amphibian populations.

BIBLIOGRAPHY

Akcakaya, H. R., Radeloff, V. C., Mladenoff, D. J., and He, H. S. 2003. Integrating
Landscape and metapopulation modeling approaches: viability of the Sharp-
Tailed Grouse in a dynamic landscape. Conservation Biology 18:526-537.

Alford, R., A., and Wilbur, H. M. 1985. Priority effects in experimental pond
communities: competition between *Bufo* and *Rana*. Ecology 66:1097-1105.

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

Armsworth, P. R., and Roughgarden, J. 2005. The impact of directed versus random
movement on population dynamics and biodiversity patterns. The American
Naturalist **165**:449-465.

Ash, A. N., 1997. Disappearance and return of plethodontid salamanders to clearcut plots
in the southern Blue Ridge Mountains. Conservation Biology 11:983 - 989.

Ash, A. N., R. C. Bruce, J. Castanet, and H. Francillon-Viellot., 2003. Population
parameters of *Plethodon metcalfi* on a 10-year-old clearcut and in nearby forest
in the southern Blue Ridge Mountains. Journal of Herpetology 37:445-452.

Aubry, K. B. 2000. Amphibians in managed, second-growth douglas-fir forests. Journal
of Wildlife Management 64:1041 - 1052.

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

Bartman, C. E., K. C. Parker, J. Laerm, and T. S. McCay. 2001. Short-term response of
    Jordan's salamander to a shelterwood timber harvest in western North Carolina.
    Physical Geography. 22:154 - 166.

Batschelet, E. 1981. Circular statistics in biology. Academic Press, London.

Bate, L. J., Torgersen, T. R., Wisdom, M. J., and Garton, E. O., 2004. Performance of
    sampling methods to estimate log characteristics for wildlife. Forest Ecology and
    Management in press.

Bellis, E. D., 1965. Home range movements of the wood frog in a northern bog. Ecology
    46:90-98.

Benhamou, S. 2006. Detecting an orientation component in animal paths when the
    preferred direction is individual-dependent. Ecology 87:518-528.

Bennett, S. H., Gibbons, J. W., and Glanville, J., 1980. Terrestrial activity, abundance and
    diversity of amphibians in differently managed forest types. American Midland
    Naturalist 103:412-416.

Berven, K. A. 1990. Factors affecting population fluctuation in larval and adult stages of
    the wood frog (Rana sylvatica). Ecology 71:1599 - 1608.

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

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

Bradshaw, C. J. A., and Brook, B. W. 2005. Disease and the devil: density-dependent epidemiological processes explain historical population fluctuations in the Tasmanian devil. Ecography **28**:181-190.

Breden, F. 1987., The effect of post-metamorphic dispersal on the population genetic structure of Fowler's Toad. Copeia 1987:386 - 395.

Buechner, M. 1987. A geometric model of vertebrate dispersal: tests and implications. Ecology 68:310-318.

Bulger, J. B., N. J. Scott, and Seymour, R.B. 2003. Terrestrial activity and conservation of adult california red-legged frogs *Rana aurora draytonii* in coastal forests and grasslands. Biological Conservation 110:85-95.

Burton, T. M., and Likens, G. F., 1975a. Energy flow and nutrient cycling in salamander populations in the Hubbard Brook Experiment Forest, New Hampshire. Ecology 56:1068-1080.

Burton, T. M., and Likens, G. F., 1975b. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. Copeia 175:541-546.

Carr, L. W., and Fahrig, L., 2001. Effects of road traffic on two amphibian species of different vagility. Conservation Biology 15:1071-1078.

Caswell, H. 2001. Matrix Population Models. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts.

Chazal, A. C., and P. H. Niewiarowski., 1998. Responses of mole salamanders to

clearcutting: using field experiments in forest management. Ecological

Applications 8:1133 - 1143.

Chelgren, N. D., Rosenberg, D. K., Heppell, S. S., and Gitelman, A. I. 2006. Carryover

aquatic effects on survival of metamorphic frogs during pond emigration.

Ecological Applications **16**:250-261.

Cromer, R. B., J.D. Lanham, and Hanlin H. G.. 2002. Herpetofaunal response to gap and

skidder-rut wetland creation in a southern bottomland hardwood forests. Forest

Science 48:407-413.

Crouse, D. T., Crowder, L. B., and Caswell, H. 1987. A stage-based population model for

loggerhead sea turtles and implications for conservation. Ecology **68**:1412-1423.

Cushman, S. A. 2006. Effects of habitat loss and fragmentation on amphibians: a review

and prospectus. Biological Conservation 128:231-240.

Cushman, S. A., and McGarigal, K. 2002. Hierarchical, multi-scale decomposition of

species-environment relationships. Landscape Ecology 17:637-646.

deMaynadier, P.G. and M.L. Hunter, Jr., 1995. The relationship between forest

management and amphibian ecology: a review of the North American literature.

Environmental Reviews 3:230-261.

deMaynadier, P. G., and Hunter, M. L. Jr., 1998. Effects of silvicultural edges on the

distribution and abundance of amphibians in Maine. Conservation Biology

12:340-352.

deMaynadier, P. G., and M. L. Hunter., 1999. Forest canopy closure and juvenile emigration by pool-breeding amphibians in Maine. Journal of Wildlife Management 63:441-450.

deMaynadier, P. G., and M.L. Hunter, Jr. 2000. Road effects on amphibian movements in a forested landscape. Natural Areas Journal 20:56 - 65.

Dodd Jr, C. K. J. and Cade, B.S. 1998. Movement patterns and the conservation of amphibians breeding in small, temporary wetlands. Conservation Biology 12:331 - 339.

Dole, J. W., 1971. Dispersal of recently metamorphosed leopard frogs, *Rana pipiens*. Copeia 1971:221-228.

Douglas, M. E., and Monroe, B. L., 1981. A comparative study of topographical orientation in *Ambystoma* (Amphibia: Caudata). Copeia 1981:460-463.

Duellman, W. E., and Trueb, L. 1986. Biology of Amphibians. The Johns Hopkins University Press.

Faccio, S. D., 2003. Postbreeding emigration and habitat use by jefferson and spotted salamanders in Vermont. Journal of Herpetology 37:479-489.

Ferguson, D. E., H. F. Landreth, and McKeon, J. P. 1967. Sun-compass orientation of the northern cricket Frog, *Acris crepitans*. Animal Behaviour 15:45-53.

Ferguson, D. E., McKeown, J. P., Bosarge, D. S., and Landreth, H. F. 1966. Sun-compass orientation of bullfrogs. Copeia 1966: 230-235.

Fischer, J. H., Freake, M. J., Borland, S. C., and Phillips, J. B. 2001. Evidence for the use of magnetic map information by an amphibian. Animal Behaviour 62:1-10.

Force, E. R., 1933. The age of attainment of sexual maturity of the leopard frog *Rana pipiens* (Schreber) in Northern Michigan. Copeia 1933:128-131.

Ford, W. M., B.R. Chapman, M.A. Menzel, and Odom, R. H.. 2002. Stand age and habitat influences on salamanders in Appalachian cove hardwood forests. Forest Ecology and Management 155:131-141.

Frankham, R., Ballou, J. D., and Briscoe, D. A., 2002. Introduction to conservation genetics. Cambridge University Press, New York, New York.

Franklin, A. B., Anderson, D. R., Gutierrez, R. J., and Burnham, K. P. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs 70:539-590.

Freake, M. J., and Phillips, J. B. 2005. Light-dependent shift in bullfrog tadpole magnetic compass orientation: Evidence for a common magnetoreception mechanism in anuran and urodele amphibians. Ethology 111:241-254.

Fretwell, S. D., and H.L. Lucas, Jr., 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16-36.

GAA. 2004. www.globalamphibians.org.

Garcia-Charton, J. A., Perez-Ruzafa, A., Sanchez-Jerez, P, Bayle-Sempere, J. T., Renones, O., and Moreno, D. 2004. Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. Marine Biology 144:161-182.

Gibbs, J. P., 1998. Distribution of woodland amphibians along a forest fragmentation gradient. Landscape Ecology 13:262-268.

Gill, D. E., 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). Ecological Monographs 48:145-166.

Grant, D., O. Anderson, and Twitty, V. 1968. Homing orientation by olfaction in newts (*Taricha rivularis*). Science 160:1354-1356.

Green, D. M., 2003. The ecology of extinction: Population fluctuation and decline in amphibians. Biological Conservation. 111:331-343.

Greenberg, C. H., and Tanner, G. W. 2005. Spatial and temporal ecology of oak toads (*Bufo quercicus*) on a florida landscape. Herpetologica **61**:422-434

Grialou, J. A., S. D. West, and R. N. Wilkins., 2000. The effects of forest clearcut harvesting and thinning on terrestrial salamanders. Journal of Wildlife Management 64:105-113.

Guerry, A. D., and Hunter, M. L.Jr., 2002. Amphibian declines in a landscape of forests and agriculture: an examination of landscape composition and configuration. Conservation Biology 16:745-755.

Harpole, D. N., and Haas, C. A. 1999. Effects of seven silvicultural treatments on terrestrial salamanders. Forest Ecology and Management 114:349-356.

Harper, C. A., and Guynn, D. C. 1999. Factors affecting salamander density and distribution within four forest types in the Southern Appalachian Mountains. Forest Ecology and Management 114:245-252.

Heatwole, H. 1961. Habitat selection and activity of the wood frog, *Rana sylvatica* Le Conte. American Midland Naturalist 66:301-313.

Heatwole, H., 1962. Environmental factors influencing local distribution and activity of the salamander, *Plethodon cinereus*. Ecology 34:460-472.

Hershey, J. L., and Forester, D.C. 1980. Sensory orientation in *Notophthalmus v. viridescens* (Amphibia: Salamandridae). Canadian Journal of Zoology 58:266-276.

Heyer, W. R., Donnelly, M. A., McDiarmid, R. W., Hayek, L. C., and Foster, M. S., 1994. Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians. Smithsonian Institution Press.

Hixon, M. A., and Jones, G. P. 2005. Competition, predation, and density-dependent mortality in demersal marine fishes. Ecology 86:2847-2859.

Howard, R. D., and Kluge, A. G., 1985. Proximate mechanisms of sexual selection in wood frogs. Evolution 39:260-277.

Hunter, M. L. Jr., Calhoun, A, J. K., and McCollough, M., 1999. Maine Reptiles and Amphibians. The University of Maine Press.

Ingram, W. M., and Raney, E. C., 1943. Additional studies on the movement of tagged bullfrogs. American Midland Naturalist 29:239-241.

Jaeger, R. G., 1980. Microhabitats of a terrestrial forest salamander. Copeia 1980:265-268.

Jaeger, R. G., Wicknick, J. A., Griffis, M. R., and Anthony, C. D., 1995. Socioecology of a terrestrial salamander: juveniles enter adult territories during stressful foraging periods. Ecology 76:533-543.

Johnson, D. W. 2006. Predation, habitat complexity, and variation in density-dependent mortality of temperate reef fishes. Ecology 87:1179-1188.

Johnson, M. L., and Gaines, M. S. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annual Review of Ecology and Systematics 21:449-480.

Johnson, A. R., Wiens, J. A., Milne, B. T., and Crist, T. O. 1992. Animal movements and population dynamics in heterogeneous landscapes. Landscape Ecology **7**:63-75.

Justis, C. S., and Taylor, D. H. 1976. Extraocular photoreception and compass orientation in larval bullfrogs, *Rana catesbeiana*. Copeia 1976:98-105.

Kauffman, M. J., Pollock, J. F., and Walton, B. 2004. Spatial structure, dispersal, and management of a recovering raptor population. The American Naturalist 164:582-597.

Kleeberger, S. R., and Werner, J. K., 1982. Home range and homing behavior of *Plethodon cinereus* in northern Michigan. Copeia 1982:409-415.

Kleeberger, S. R., and Werner, J. K., 1983. Post-breeding migration and summer movement of *Ambystoma maculatum*. Journal of Herpetology 17:176-177.

Knapp, S. M., C.A. Haas, D.N. Harpole and Kirkpatrick, R. L. 2003. Initial effects of clearcutting and alternative silivicultural practices on terrestrial salamander abundance. Conservation Biology 17:752-762.

Lamoureux, V. S., J. C. Maerz, and D. M. Madison., 2002. Premigratory autumn foraging forays in the green frog, *Rana clamitans*. Journal of Herpetology 36:245-254.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183-212.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943-1967.

Levins, R. 1969. Some demographic and genetic consequences of environmental

    heterogeneity for biological control. Bulletin of the Entomological Society of

    America 12:237-240.

Lips, K. R. 1998. Decline of a Tropical Montane Amphibian Fauna. Conservation

    Biology 12:106-117.

Livingston Birchfield, G., 2002. Adult green frog (*Rana clamitans*) movement behavior

    and terrestrial habitat use in fragmented landscapes in central Missouri. Doctor

    of Philosophy. University of Missouri-Columbia, Columbia.

MacArthur, R. H., and Wilson, E. O. 1963. An equilibrium theory of insular

    zoogeography. Evolution 17:373-387.

Mackey, B. G., and Lindenmayer, D. B. 2001. Towards a hierarchical framework for

    modelling the spatial distribution of animals. Journal of Biogeography 28:1147-

    1166.

Madison, D. M., 1997. The emigration of radio-implanted spotted salamanders,

    Ambystoma maculatum. Journal of Herpetology 31:542-551.

Malmgren, J. C. 2002. How does a newt find its way from a pond? Migration patterns

    after breeding and metamorphosis in great crested newts (*Triturus cristatus*) and

    smooth newts (*T. vulgaris*). Herpetological Journal 12:29-35.

Marsh, D. M., and P.C. Trenham. 2001. Metapopulation dynamics and amphibian

    conservation. Conservation Biology 15:40 - 49.

Martof, B., 1953. Home range and movements of the green frog, *Rana clamitans*.

    Ecology 34:529-543.

Martof, B., 1956. Growth and development of the green frog, *Rana clamitans*, under natural conditions. American Midland Naturalist 55:101-117.

Mazerolle, M. J. 2001. Amphibian activity, movement patterns, and body size in fragmented peat bogs. Journal of Herpetology 35:13-20.

Mazerolle, M. J., and Desrochers, A., 2005. Landscape resistance to frog movements. Canadian Journal of Zoology 83:455-464.

McGregor, J. H., and Teska, W.R. 1989. Olfaction as an orientation mechanism in migrating *Ambystoma maculatum*. Copeia 1989:779-781.

Merrell, D. J., 1970. Migration and gene dispersal in *Rana pipiens*. American Zoologist 10:47-52.

Moseley, K. R. C., Castelberry, S. B., and Ford, W. M., 2004. Coarse woody debris and pine manipulation effects on movement and microhabitat use of *Ambystoma talpoideum* in a *Pinus taeda* stand. Forest Ecology and Management 2004.

Natural Resources Conservation Service, 1962. Penobscot County Soil Survey.

Okubo, A., and Levin, S. A. 2001. Diffusion and ecological problems: modern perspectives. Springer Publishers, New York.

Patrick, D. A., Hunter Jr., M. L., and Calhoun, A. J. K. 2006. Effects of experimental forestry treatments on a Maine amphibian community. Forest Ecology and Management 234: 323-332.

Pechmann, J. H. K., Estes, R. A., Scott, D., E., and Gibbons, J. W. 2001. Amphibian colonization and use of ponds created for trial mitigation and wetland loss. Wetlands 21:93-111.

Peterson, D. L., and Parker, V. T. 1998. Ecological scale. Columbia University Press, New York.

Petranka, J. W., 1994. Response to impact of timber harvesting on salamanders. Conservation Biology 8:302-304.

Petranka, J. W., Brannon, M. P., Hopey, M. E., and Smith, C. K., 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. Forest Ecology and Management 67:135-147.

Petranka, J. W., Eldridge, M. E., and Haley, K. E., 1993. Effects of timber harvesting on southern appalachian salamanders. Conservation Biology 7:363-370.

Petranka, J. W., S. S. Murray, and Kennedy, C. A., 2003. Responses of amphibians to restoration of a southern Appalachian wetland: perturbations confound post-restoration assessment. Wetlands 23:278 - 290.

Phillips, J. B. 1986. Two magnetoreception pathways in a migratory salamander. Science 233:765-767.

Phillips, J. B., M. E. Deutschlander, M. J. Freake, and Borland, S. C. 2001. The role of extraocular photoreceptors in newt magnetic compass orientation: parallels between light-dependent magnetoreception and polarized light detection in vertebrates. Journal of Experimental Biology 204:2543-2552.

Pope, S. E., Fahrig, L., & Gray Merriam, H., 2000. Landscape complementation and metapopulation effects on leopard frog populations. Ecology 81:2498-2508.

Pough, F. H., Smith, E. M., Rhodes, D. H., and Collazo, A., 1987. The abundance of salamanders in forest stands with different histories of disturbance. Forest Ecology and Management 20:1-9.

Pounds, J. A., Bustamante, M. R., Coloma, L. A., Consuegra, J. A., Fogden, M. P. L.,
Foster, P. N., La Marca, E., Masters, K. L., Merino-Viteri, A., Puschendorf, R.,
Ron, S. R., Sanchez-Azofeifa, G. A., Still, C. J., and Young, B. E. 2006.
Widespread amphibian extinctions from epidemic disease driven by global
warming. Nature 439:161-167.

Raney, E. C., 1940. Summer movements of the bullfrog, *Rana catesbeiana* Shaw, as
determined by the jaw-tag method. American Midland Naturalist 23:733-745.

Ray, N., Lehmann, A., and Joly, P. 2002. Modeling spatial distribution of amphibian
populations: a GIS approach based on habitat matrix permeability. Biodiversity
and Conservation **11**:2143-2165.

Raymond, L. R., and Hardy, L. M. 1991. Effects of a clearcut on a population of the mole
salamander, Ambystoma talpoideum, in an adjacent unaltered forest. Journal of
Herpetology 25:509-512.

Regosin, J. V. W., B.S. Windmiller, and Reed, M.J. 2003. Terrestrial habitat use and
winter densities of the wood frog (*Rana sylvatica*). Journal of Herpetology
37:390-394.

Regosin, J. V., Windmiller, B. S., Homan, R. N., and Reed, J. M. 2005. Variation in
terrestrial habitat use by four pool-breeding amphibian species. Journal of
Wildlife Management **69**:1481-1493.

Renken, R. B., Gram, W. K., Fantz, D. K., Richter, S. C., Miller, T. J., Ricke, K. B.,
Russell, B., and Wang, X., 2004. Effects of forest management on amphibians
and reptiles in Missouri Ozark forests. Conservation Biology 18:174-188.

Revilla, E., Wiegand, T., Palomares, F., Ferreras, P., and Delibes., M. 2004. Effects of matrix heterogeneity on animal dispersal: from individual behavior to metapopulation-level parameters. The American Naturalist 164:130-153.

Ricketts, T. H., E. Dinerstein, T. Boucher, T. M. Brooks, S. H. M. Butchart, M. Hoffmann, J. F. Lamoreux, J. Morrison, M. Parr, J. D. Pilgrim, A. S. L. Rodrigues, W. Sechrest, G. E. Wallace, K. Berlin, J. Bielby, N. D. Burgess, D. R. Church, N. Cox, D. Knox, C. Loucks, G. W. Luck, L. L. Master, R. Moore, R. Naidoo, R. Ridgely, G. E. Schatz, G. Shire, H. Strand, W. Wettengel, and E. Wikramanayake., 2005. Pinpointing and preventing imminent extinctions. PNAS 102:18497-18501.

Ridley, M. 1993. Evolution. Blackwell Scientific Publications, Boston.

Rittenhouse, T. A. G., Altnether, T. T., and Semlitsch, R. D. 2006. Fluorescent powder pigments as a harmless tracking method for Ambystomatids and Ranids. Herpetological Review 37:188-191.

Rittenhouse, T. A. G., Doyle, M. C., Mank, C. R., Rothermel, B. B., and Semlitsch, R.D. 2004. Substrate cues influence habitat selection by spotted salamanders. Journal of Wildlife Management **68**:1151-1158.

Rittenhouse, T.A.G., E.B. Harper, L.R. Rehard and R.D. Semlitsch. (in review) The role of microhabitats in the desiccation and survival of amphibians in recently harvested oak-hickory forest.

Roberts, L. 1993. Wetlands trading is a loser's game, say ecologists. Science 260:1890-1892.

Rothermel, B., and Semiltsch, R. D., 2002. An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. Conservation Biology 16:1324-1332.

Rothermel, B., B. 2004. Migratory success of juveniles: a potential constraint on connectivity for pond-breeding amphibians. Ecological Applications **14**:1535-1546.

Rustigian, H. L., M. V. Santelmann, and N. H. Schumaker. 2003. Assessing the potential impacts of alternative landscape designs on amphibian population dynamics. Landscape Ecology **18**:65 - 81.

Ryan, T. J., T. Philippi, Y. A. Leiden, M. E. Dorcas, T. B. Wigley, and J. W. Gibbons., 2002. Monitoring herpetofauna in a managed forest landscape: effects of habitat types and census techniques. Forest Ecology and Management 167:83 - 90.

Sale, P. F. 1998. Appropriate spatial scales for studies of reef-fish ecology. Australian Journal of Ecology 23:202-208.

Schlaepfer, M. A., M. C. Runge, and Sherman, P. W. 2002. Ecological and evolutionary traps. Trends in Ecology and Evolution 17:474-480.

Schroeder, E. E., 1976. Dispersal and movement of newly transformed green frogs, *Rana clamitans*. American Midland Naturalist 95:471-474.

Seburn, C. N. L., Seburn, D. C., and Paszkowski, C. A., 1997. Northern leopard frog (*Rana pipiens*) dispersal in relation to habitat. Pages 64-72 in D. M. Green, editor. Amphibians in decline. Canadian studies of a global problem. Society for the study of amphibians and reptiles.

Semlitsch, R. D., 1998. Biological delineation of terrestrial buffer zones for salamanders. Conservation Biology 12:1113-1119.

Semlitsch, R. D., and J. R. Bodie. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology:1219 - 1228.

Sjogren Gulve, P. 1994. Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*. Ecology 75:1357-1367.

Smith, A. M., and D. M. Green. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography 28:110-128.

Stenhouse, S. L. 1985. Migratory orientation and homing in *Ambystoma maculatum* and *Ambystoma opacum*. Copeia 1985:633-637.

Strojny, C. A., 2004. Effects of harvest created gaps on forest amphibians. MSc. University of Maine, Orono.

Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. Rogrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783 - 1786.

Sutherland, W. J. 2006. Predicting the ecological consequences of environmental change: a review of the methods. Journal of Applied Ecology 43:599-616.

Taylor, D. H., and Adler, K. 1973. Spatial orientation by salamanders using plane-polarized light. Science 181:285-287.

Thompson, C. M., and McGarigal, K. 2002. The influence of research scale on bald eagle habitat along the lower Hudson River, New York (USA). Landscape Ecology 17:569-586.

Trenham, P. C., and Shaffer, H. B., 2005. Amphibian upland habitat use and its consequences for population viability. Ecological Applications. 15:1158-1168.

Turchin, P. 1996. Fractal analysis of animal movement: a critique. Ecology 77:2086-2090.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants.

VanBuskirk, J., and D. C. Smith. 1991. Density-dependent population regulation in a salamander. Ecology 72:1747 - 1756.

Vasconcelos, D., and Calhoun, A. J. K. 2004. Movement patterns of adult and juvenile *Rana sylvatica* (LeConte) and *Ambystoma maculatum* (Shaw) in three restored seasonal pools in Maine. Journal of Herpetology 38:551-561.

Vernberg, F. J., 1953. Hibernation studies of two species of salamanders, *Plethodon cinereus cinereus* and *Eurycea bislineata bislineata*. Ecology 34:55-62.

Vonesh, J. R., and O. De la Cruz. 2002. Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. Oecologia 133:325 - 333.

Wake, D. B. 1991. Declining amphibian populations. Science **253**:860.

Waser, P. M. 1985. Does competition drive dispersal? Ecology 66:1710-1175.

Wilbur, H. M., 1980. Complex life cycles. Annual Review of Ecology and Systematics 11:67 - 93.

Wiens, J. A. 1989. Spatial scaling in ecology. Fuctional ecology 3:385-397.

Willis, Y. L., Moyle, D. L., and Baskett, T. S., 1956. Emergence, breeding, hibernation, movements and transformations of the bullfrog, *Rana catesbeiana*, in Missouri. Copeia 1956:30-41.

Wyman, R. L., 1998. Experimental assessment of salamanders as predators of detrital food webs: effects on invertebrates, decomposition and the carbon cycle. Biodiversity. Conservation 7:641-650.

Yoo, H. J. S. 2006. Local population size in a flightless insect: importance of patch structure-dependent mortality. Ecology 87:634-647.

Zar, J. H., 1996. Biostatistical Analysis, 3rd edition. Prentice Hall.

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David Patrick was born in Devon in the southwest of England in July 1977. He attended secondary school at Torquay Boys' Grammar School, graduating in 1995. This was followed by teaching English in Eastern Nepal as a GAP Fellow, then an undergraduate degree in Zoology and Animal Ecology from the University of Wales, Bangor. During this time he spent a year at Oregon State University and worked as a Wilderness Ranger in Eagle Cap Wilderness in Eastern Oregon.

In the second year of his undergraduate he was awarded a Guinness Earth Science Fellowship in the Tanzanian Rainforest. He continued working in Tanzania for his Masters degree in Conservation Biology at the Durrell Institute of Conservation and Ecology. Following his MS, he carried on working in Tanzania, as well as beginning two summers where he worked as the senior Roseate Tern warden on Rockabill Island, Ireland. David has published four papers in peer-reviewed journals and two in publications for the Irish government.

David began his PhD research in November of 2003. While at the University of Maine he designed and taught WLE 455 "advanced problem solving in conservation biology", and was a teaching assistant for WLE 440 "wildlife habitat relationships". Following completion of his degree he will start a postdoctoral position with Professor James Gibbs at SUNY ESF. He is a member of the Society for Conservation Biology, and currently serves as Chair of the North American Student Affairs Committee of the Society, on the North American Section Board, and on the Student Chapters Board of

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