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Relative Fitness and Behavioral Compensation of Amphibians in a Managed Forest

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RELATIVE FITNESS AND BEHAVIORAL COMPENSATION OF AMPHIBIANS IN A MANAGED FOREST

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By Sean Michael Blomquist

Thesis Advisor: Dr. Malcolm L. Hunter, Jr.

An Abstract of the Thesis Presented in
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Habitat loss and degradation are two of the most important factors leading to the imperilment of species worldwide including amphibians, but mechanisms underlying these changes are poorly understood. To understand the fitness potential of harvested forests, I conducted studies of a forest specialist, *Rana sylvatica* (Wood Frogs) and compared these results with those from identical studies with an open canopy specialist, *R. pipiens* (Northern Leopard Frogs) in response to an unharvested control and three forest harvesting treatments: clearcutting (with removal of all merchantable timber > 10 cm diameter), clearcutting with coarse woody debris retention, and partial harvesting with removal of < 25% canopy cover. First, I used radio-telemetry data collected on 72 adult *R. sylvatica* and 40 *R. pipiens* and logistic regression modeling to assess habitat selection Second, I predicted and quantified the plasticity of the two frogs with respect to survival, time to metamorphosis, and growth rate. My results suggest that *R. pipiens* may use clearcut areas during the spring and summer that are within migration distance of

breeding and overwintering habitats if dense ground vegetation has regenerated. However, the fitness potential of the clearcut treatments for *R. sylvatica* is lower than that of the forested treatments, and coarse woody debris retention may ameliorate some of the effects of clearcut harvesting. Further, partial harvesting with removal of < 25% canopy cover is a forest management technique that may not adversely influence the fitness of *R. sylvatica*. Larval *R. sylvatica* from open-canopy treatments reached a minimum size and metamorphosed earlier than other treatments, but ultimately, juveniles attained the same mass in all four treatments; open-canopy treatments, however, had 35 ± 2% fewer survivors than forested treatments. In contrast, survival of *R. pipiens* larvae increased with decreasing canopy cover, increasing water temperature, and increasing food availability, and juveniles remained larger and had higher survival in open-canopy treatments. In summary, the treatments induced opposing changes in the fitness correlates at the aquatic and terrestrial life stages of *R. sylvatica* but not *R. pipiens*. Further, each species selected different harvest treatments, and havesting affected the habitat selection of both species at multiple scales.

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CHAPTER 1

EXTERNALLY ATTACHED RADIO-TRANSMITTERS HAVE LIMITED EFFECTS ON THE ANTIPREDATOR BEHAVIOR AND VAGILITY OF *RANA PIPIENS* AND *RANA SYLVATICA*

Abstract

Anurans display a variety of antipredator behaviors from flight and crypsis to defensive postures. External attachment of a radio-transmitter is a commonly used technique that could potentially interfere with the antipredator behavior of anurans. I investigated the effect of an externally attached radio-transmitter on the antipredator behavior and vagility of adult Northern Leopard Frogs (*Rana pipiens*) and adult Wood Frogs (*R. sylvatica*). I simulated attacks by birds and snakes and used fluorescent powder to follow the path of individuals through natural habitats. Both species displayed a different frequency of behaviors in response to each predator, but the presence of a transmitter did not affect the frequency of antipredator behaviors. When carrying a transmitter, *R. pipiens* exhibited a different escape angle during attacks by simulated aerial predators, and exhibited a change in the mean turn angle over 4 h movement paths. *Rana sylvatica*'s escape behavior and vagility were unaffected by a transmitter during simulated attacks, although frogs with a transmitter did take more jumps per 4 h movement paths and followed straighter paths than did frogs without a transmitter. The body mass of the individual did not affect any of my behavior or movement metrics. While most of my metrics did not change markedly in response to the presence of a

transmitter, the subtle changes in vagility and escape behavior are analogous to the negative effects of externally attached transmitters seen in birds and mammals. These results suggest that transmitters may have consequences for the energetics, survival, and reproduction of anurans.

Introduction

Anurans display a variety of antipredator behaviors from flight and crypsis to defensive postures (Marshisin and Anderson, 1978; Williams et al., 2000). Along with morphological and physiological adaptations such as coloration, cryptic appendages, and skin secretions, these behaviors function to deter or elude predators by making the animal look too large to ingest or difficult to find, catch, or handle (Schall and Pianka, 1980; Duellman and Trueb, 1986).

Because anurans rely on morphology, behavior, and vagility to avoid predation, it is possible that constraints on any of these mechanisms could lead to increased predation. This phenomenon has been seen in other animals such as Snow Geese (*Chen caerulescens*), which became more susceptible to hunting by humans after attachment of a backpack radio-transmitter (Withey et al., 2001). The attachment of radio-transmitters could make an animal slower, more visible, or unable to assume certain postures (Kenward, 2001). For example, diving ducks (*Aythya* spp.) increased preening, stretching, and fluffing of feathers in response to the attachment of a backpack radio-transmitter (Withey et al., 2001).

External attachment of a radio-transmitter is a commonly used technique for studying behavior in a variety of anurans that has been used for over four decades (Tester

1963; van Nuland and Claus, 1981; Hodgkison and Hero, 2001; Watson et al., 2003). External attachment of transmitters has two advantages over implanted transmitters: no surgery is required and detection range can be greatly increased (Richards et al., 1994). Increased detection range is advantageous with the small transmitter size necessary to study relatively small bodied, yet highly mobile, anurans that use refugia below the water or ground surface (e.g., Eggert, 2001). Possible disadvantages of using an externally attached radio-transmitter include increased stress to the animal, altered behavior, decreased vagility, harm to the animal's skin, and increased susceptibility to predation (Richards et al., 1994; Goldberg et al., 2002; Weick et al., 2005), although these effects have not been experimentally addressed for anurans. These effects are thought to be minimized if the transmitter's mass is < 10% of the animal's body mass (White and Garrott, 1990; Richards et al., 1994). However, effects have been found in birds and mammals with a transmitter as light as 3% of the body mass (Kenward, 2001), and external attachment of a transmitter with a harness had effects in most studies on birds (Withey et al., 2001).

I investigated the effect of an externally attached radio-transmitter on antipredator behavior and vagility of adult Northern Leopard Frogs (*Rana pipiens*) and adult Wood Frogs (*R. sylvatica*) in two experiments. First, I simulated attacks on frogs with and without a transmitter by models of ground (garter snakes, *Thamnophis* spp.) and aerial (raptors) predators. Second, I marked frogs with fluorescent powder and followed the movement paths of frogs with and without a transmitter through the terrestrial environment.

Materials and Methods

Study animals

I collected wild frogs from the University of Maine Demeritt and Penobscot Experimental Forests 1–13 days prior to the predation and vagility experiments described below. I captured frogs by hand, dip net, and in pitfall traps. I used telemetry to follow frogs with transmitters in the vagility experiment for 1–40 days prior to tracking with fluorescent powder. When in captivity, I housed all frogs individually in 2.3 L plastic storage bins or in small groups (< 5 frogs) in 38 L glass aquaria. Each container had ca. 5 mm of standing water, holes in the top, and a wet paper towel for cover. I fed all frogs crickets *ad libitum* prior to the start of the trials and at the end of the trials. After each experiment was completed, I collected all frogs and released them at dusk at the original capture location.

Predation experiment

I conducted all trials in a 48 m^2 fenced experimental arena in the northeast corner of a 0.5 ha forest clearing near the University of Maine campus. Surrounding forest canopy trees were gray birch (*Betula populifolia*), white pine (*Pinus strobus*), balsam fir (*Abies balsamea*), and American beech (*Fagus grandifolia*). Ground cover in the arena included grasses, bracken fern (*Pteridium aquilinum*), shrubs (*Spiraea* spp.), saplings of *A. balsamea* and *P. strobus*, haircap moss (*Polytrichum commune*), woody debris, and coniferous and deciduous leaf litter. The experimental arena was similar in vegetation to areas where I collected both species. I chose this area to standardize the cover available to

each species because cover availability is an important variable in the risk perception of frogs (Hayes, 1990; Martin et al., 2005).

I randomly assigned each frog to a transmitter or no transmitter category prior to each trial. I attached a transmitter (Holohil BD-2, 0.9 g, 14 cm external whip antennae, 40 day battery life) with elastic thread beaded with glass beads snug enough to prevent slippage over the rear legs when extended, but not so snug as to constrict the skin (Muths, 2003; Weick et al., 2005). The 24 (11 males, 13 females) *R. sylvatica* used in the experiment were 47±1 mm (mean±SE) (range 40–56) snout-vent length (SVL) and weighed 10.1±0.6 g (range 6.1–17.0). The 18 (8 males, 10 females) *R. pipiens* used in the experiment were 65±2 mm (range 50–84) SVL and weighed 27.3±3.1 g (range 9.5–54.2). Transmitters plus harness weighed 0.96–0.98 g and were on average 9.6% (range 5.7–15.8%) of the body mass for *R. sylvatica* and 3.5% (range 1.8–10.0%) for *R. pipiens*.

I used model predators to simulate attacks (Hayes, 1989; Brodie et al., 1998; Gomes et al., 2002; Meehan and Nisbet, 2002). These models work well because anurans rely primarily on visual cues to elicit antipredator behavior (Gregory, 1979; Heinen, 1994; Martin et al., 2005; Wirsing et al., 2005). *Rana pipiens* and *R. sylvatica* responded similarly to the movement of all models I tried in preliminary trials (e.g., a dipnet, brown plastic bucket, and model bird moved towards the frog through the air; and aluminum pole, bamboo pole, and model snake moved along the ground towards the frog). For my model of an aerial predator, I attached a three-dimensional, black model of a flying bird to a monofilament fishing line (5.4 kg [12 lb] test) that was anchored to the ground 0.4 m from the trial location and to a metal fencepost 2.6 m above the ground and 10 m from

the trial location. I used a 1.2 m long by 1.5 cm diameter bamboo pole as my model of a ground predator.

I first simulated an attack by an aerial predator and then, if the frog did not move from its original location, I simulated an attack with a ground predator. I placed an individual frog at the trial location under a 2 L plastic bucket, and then I allowed it to acclimate for 1 min. I removed the bucket and waited 2–5 sec before I released the bird model from the high end of the fencepost so that it slid down the line toward the frog. I coded the frog's behavior during the attack following Marshisin and Anderson's (1978) classification of 14 antipredator behaviors, and used video recordings of each attack (taken with a Canon NTCA ZR 60 digital video camera mounted on a tripod outside the experimental arena) to proof my coding and distinguish between behaviors. I also recorded the distance and direction the frog moved immediately after the attack.

If the frog did not exhibit flight behavior during the initial aerial attack, I simulated an attack by a ground predator 5–10 sec later. I crouched on the edge of the experimental arena (hidden by black silt fencing), held the bamboo pole 1–5 cm above the ground, and slowly moved the pole toward the frog until the frog fled or the pole touched the frog. As for the aerial attack, I coded the frog's behavior during the attack and recorded the distance and direction the frog moved after the ground attack.

I repeated trials over the span of four days (24 July–27 July 2006) during 0800–1800 h until I evaluated ten trials for each frog and at least 150 trials for each species and predator type. I conducted four or fewer trials per day with each frog and allowed a resting time of $\geq$ 2 h between trials, so as not to physically stress the frogs and allow for trials to function as independent replicates. I chose timing and weather conditions to

mimic when predation was likely to occur. The weather during trials was partly sunny to overcast with temperatures in the experimental arena of 23.7–33.8°C, relative humidity of 54–81%, and wind < 16 km/h. I terminated trials on 26 July when wind speed increased to > 24 km/h and a thunderstorm began. Both *R. pipiens* and *R. sylvatica* are primarily nocturnal, but are frequently active during daylight hours during summer in Maine (Hinshaw, 1999; Knox, 1999; Redmer and Trauth, 2005; Rorabaugh, 2005). The aerial predators (raptors) and ground predators (snakes) I were mimicking are primarily diurnal and forage visually (Goodwin, 1976; Drummond, 1985; Sullivan and Dinsmore, 1992; Marzluff and Angell, 2005).

The data were primarily nonnormal based on histograms, skewness, and kurtosis of each variable; thus, I transformed each variable to achieve normality and homogeneity of variance for all comparisons between transmittered and non-transmittered frogs. I used repeated measures analysis of variance (rmANOVA; PROC MIXED; Wallace and Green, 2002) to compare the total distance a frog traveled, number of jumps a frog took to travel that distance, and the angle a frog moved in response to attacks with and without a transmitter. I used multiple linear regression (PROC GLM) to investigate the relationship between frog mass and mean coded behavioral response (following Marshisin and Anderson's [1978] classification), mean distance traveled, mean angle of the jumps, and the mean number of jumps per escape. I also investigated the frequency distribution of the coded behavioral response (following Marshisin and Anderson's [1978] classification) between species, predator types, and frogs with or without a transmitter using a chi-square or Fisher's exact test. I analyzed only the behaviors the frog exhibited in response to the approach and first contact with the ground predator. I performed all

tests using SAS (SAS Institute, Cary, North Carolina). I accepted significance at $P < 0.05$ for the multiple linear regression and used Bonferonni adjusted *P*-values for each set of univariate comparisons ($P < 0.017$ for rmANOVA and $P < 0.013$ for chi-square and Fisher's exact tests). I also performed comparisons between transmittered and non-transmittered frogs using nonparametric tests. I report only parametric results because the results were qualitatively identical.

Vagility experiment

To compare vagility and movement patterns of frogs with and without radio-transmitters, I tracked the movement paths of 26 (17 males, 9 females) *R. sylvatica* and 33 (16 males, 17 females) *R. pipiens* with fluorescent powder (DayGlo Color Corporation, Cleveland, Ohio). Fluorescent powders are an effective, non-invasive way to track the movements of small, ground-dwelling animals, and these powders do not affect the movement patterns or physiology of amphibians (Graeter, 2005; Rittenhouse et al., 2006). I tracked 18 and 15 *R. pipiens* and 16 and 10 *R. sylvatica* without and with transmitters respectively. *Rana pipiens* were tracked in June 2006, and *R. sylvatica* were tracked in June 2005. The 26 *R. sylvatica* were 48±1 mm (range 43–58) SVL (mean±SE) and 11.1±0.3 g (range 9.1–16.7). The 33 *R. pipiens* were 77±1 mm (range 66–87) SVL and 40.7±1.8 g (range 24.6–66.0). Transmitters plus harness were on average 8.7% (range 6.4–10.5%) of the body weight for *R. sylvatica* and 2.4% (range 1.5–3.6%) for *R. pipiens*.

Frogs were captured in clearcut, partially harvested, or unharvested forest, and individuals were released at dusk at a central location in each area at least 75 m from the

nearest edge. I applied powder to each individual prior to release by dipping the ventral ¾ of the body into powder avoiding the frog's head. Approximately 4 h after I released the frogs, I tracked the paths with a handheld ultraviolet light (Versalume, Raytech, Middletown, Connecticut) and marked the path with nylon thread or pin flags. I followed the paths until no more powder could be seen or I found the frog. The following day, I used a meter stick and compass to record the distance and turn angle of each jump, which I defined as the distance between each turn of ≥ 10°, for the entire path. I used ArcGIS 9 (Environmental Systems Research Institute, Redlands, California) to plot paths and calculate total path lengths for each species and VFractal (Nams, 1996) to calculate fractal dimension (a measure of how many turns the path contains) with the dividers method (see Mandelbrot, 1967) for each path.

The data were primarily nonnormal based on histograms, skewness, and kurtosis of each variable; thus, I transformed each variable to achieve normality and homogeneity of variance for all comparisons between transmittered and non-transmittered frogs. To investigate the effect of the radio-transmitter on long-distance vagility and behavior, I used multivariate analysis of variance (MANOVA statement in PROC GLM) to compare total path length, number of jumps, mean turn angle, and fractal dimension of frogs with and without a transmitter. I used multiple linear regression (PROC GLM) to investigate the relationship between frog mass and total distance traveled, angle of the jumps, the number of jumps per path, and fractal dimension. I accepted significance at $P < 0.05$ for all tests.

Results

Predation experiment

I observed 420 simulated attacks by aerial predators and 322 simulated attacks by ground predators. During these attacks, I observed eight of the 14 behaviors described by Marshisin and Anderson (1978): remain motionless, crouch, chin tuck, body inflation, flight, hide, walk, and vocalize. The two species differed from one another in their frequency of antipredator behaviors in response to both predator types (Figure 1.1; aerial, $\chi^2_6 = 89.1$, Fisher's exact $P < 0.001$; ground, $\chi^2_7 = 100.1$, Fisher's exact $P < 0.001$), and each species differed in their frequency of behaviors in response to aerial and ground attacks (*R. pipiens*, $\chi^2_7 = 197.9$, $P < 0.001$; *R. sylvatica*, $\chi^2_5 = 96.4$, Fisher's exact $P < 0.001$). These differences were primarily due to *R. pipiens* remaining motionless in response to both attack types and the broader range of behaviors used by *R. pipiens* in reaction to ground attacks. *Rana sylvatica* never vocalized or inflated its body in response to either predator.

The antipredator behavior and vagility of *R. pipiens* and *R. sylvatica* were not greatly affected by the presence of a transmitter in response to simulated attacks. *Rana pipiens* with a transmitter exhibited a change in the escape angle of 1.5 rad (a sharper angle and in the opposite direction) in response to aerial predator attacks (Table 1.1A) and a marginally significant decrease in total escape distance (47 vs. 39 cm) in response to ground predator attacks (Table 1.1B). *Rana sylvatica* with a transmitter did not exhibit a change in the total distance moved, the number of jumps, or the angle of escape in response to attacks by aerial or ground predators. The presence of a transmitter did not

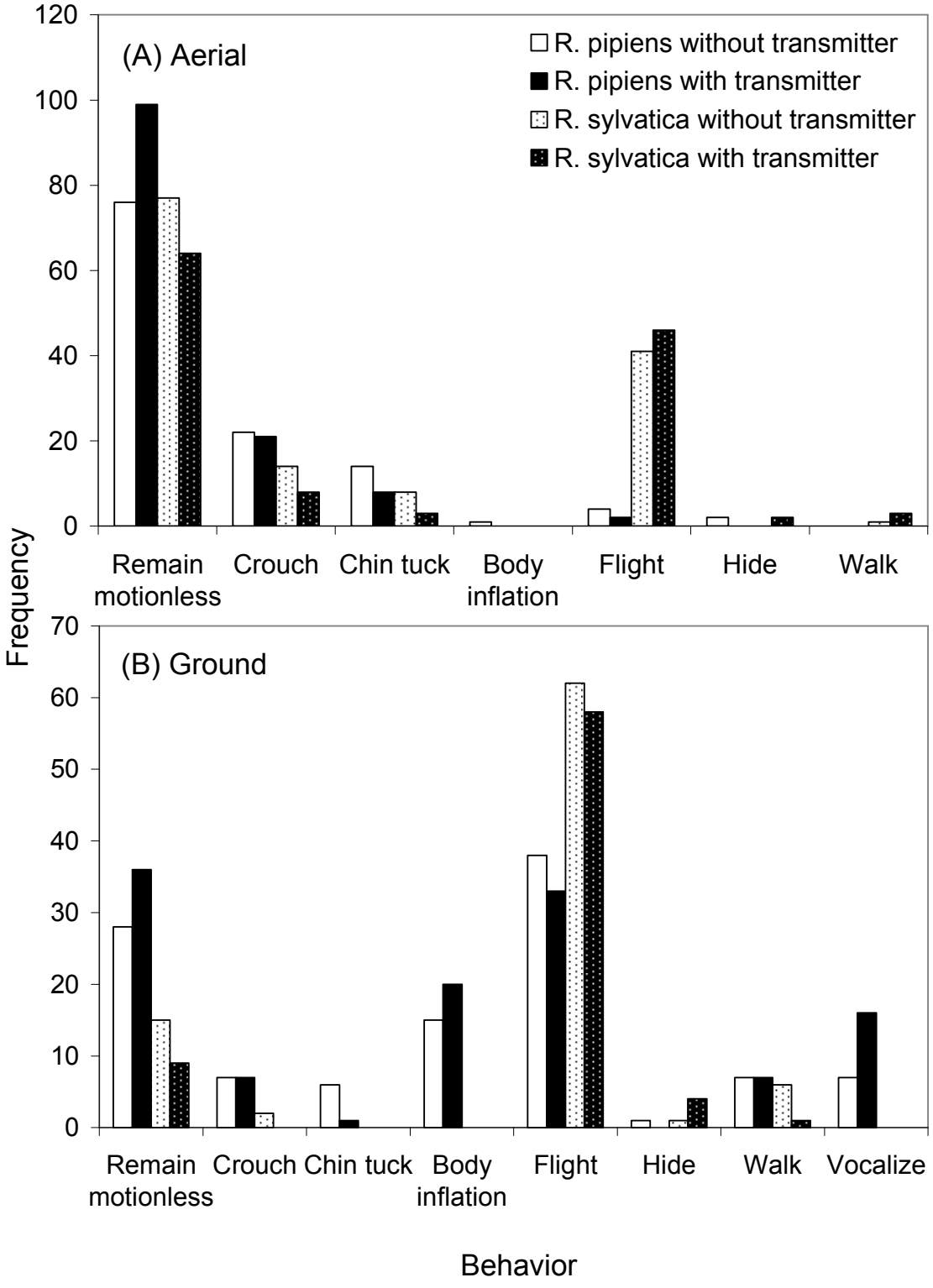

Figure 1.1. Behaviors exhibited by *Rana pipiens* (solid bars) and *R. sylvatica* (stippled bars) with (dark bars) and without (light bars) a radio-transmitter in response to simulated aerial (A) and ground (B) attacks.

Table 1.1. Characteristics of escapes (mean ± 1 SE) by *Rana pipiens* and *R. sylvatica* with and without a radio-transmitter in response to a simulated attack by an aerial (A) or ground (B) predator.

(A)	*R. pipiens*				*R. sylvatica*			
	With transmitter	Without transmitter	$F_{1,4}$	P	With transmitter	Without transmitter	$F_{1,67}$	P
N Attacks (Escapes)	95 (2)	85 (4)			114 (46)	126 (46)		
Total distance (cm)	68 ± 16	128 ± 44	1.09	0.356	56 ± 4	61 ± 5	1.03	0.314
Number of jumps	1.0 ± 0.0	1.3 ± 0.3	0.44	0.542	1.0 ± 0.0	1.0 ± 0.0	0.50	0.479
Escape angle (rad)	0.69 ± 0.28	-0.99 ± 0.22	21.24	0.010	-0.21 ± 0.16	-0.18 ± 0.21	0.06	0.815

(B)	*R. pipiens*				*R. sylvatica*			
	With transmitter	Without transmitter	$F_{1,155}$	P	With transmitter	Without transmitter	$F_{1,123}$	P
Total distance (cm)	39 ± 3	47 ± 3	4.34	0.039	48 ± 3	52 ± 3	0.63	0.428
Number of jumps	1.0 ± 0.0	1.0 ± 0.0	0.16	0.688	1.1 ± 0.0	1.0 ± 0.0	1.13	0.289
Escape angle (rad)	-0.53 ± 0.17	-0.82 ± 0.18	0.91	0.343	-0.56 ± 0.19	-0.74 ± 0.18	0.32	0.575

Table 1.2. Characteristics of movement paths (mean ± 1 SE) by *Rana pipiens* and *R. sylvatica* with and without radio-transmitters over a 4 h period.

	R. pipiens				*R. sylvatica*			
	With transmitter	Without transmitter	$F_{1,31}$	P	With transmitter	Without transmitter	$F_{1,24}$	P
Number of Paths	15	18			10	16		
Path length (m)	13.14 ± 1.80	15.20 ± 3.40	0.06	0.813	9.67 ± 2.82	9.91 ± 3.08	0.05	0.824
Number of jumps	10 ± 1	10 ± 2	0.22	0.640	25 ± 6	11 ± 3	7.06	0.014
Turn angle (rad)	0.39 ± 0.06	0.59 ± 0.06	5.21	0.023	0.60 ± 0.07	0.45 ± 0.11	0.64	0.430
Fractal dimension	1.18 ± 0.06	1.11 ± 0.02	1.85	0.184	1.08 ± 0.01	1.21 ± 0.05	5.11	0.033

change the frequency of antipredator behaviors for either *R. pipiens* (aerial, $\chi^2_5 = 7.9$, Fisher's exact $P = 0.140$; ground, $\chi^2_7 = 9.7$, Fisher's exact $P = 0.200$) or *R. sylvatica* (aerial, $\chi^2_5 = 7.6$, Fisher's exact $P = 0.192$; ground, $\chi^2_4 = 7.8$, Fisher's exact $P = 0.097$). For both species, the escape angle, escape distance, number of jumps, or coded behavioral response were not affected by the mass of the frog with a transmitter in response to either predator (*R. pipiens,* aerial: inadequate sample size ($N = 2$), ground: $F_{6,11} = 0.56$, $P = 0.810$; *R. sylvatica,* aerial: $F_{9,11} = 0.42$, $P = 0.898$, ground: $F_{7,15} = 2.72$, $P = 0.049$).

Vagility experiment

Rana pipiens with and without a radio-transmitter did not differ overall in movement path characteristics (Wilk's $\lambda_{4,28} = 1.34$; $P = 0.278$), but frogs with a transmitter did exhibit a change in mean turn angle of 0.2 rad (Table 1.2). In contrast, *Rana sylvatica* with and without a transmitter differed overall in movement path characteristics (Wilk's $\lambda_{4,21} = 8.99$; $P < 0.001$): individuals with a transmitter exhibited an increase of 14 steps per path and followed a straighter path than did frogs without a transmitter. For both species, the mean turn angle, distance traveled, number of jumps, or fractal dimension were not affected by the mass of the frog with a transmitter (*R. pipiens,* $F_{4,10} = 0.71$; $P = 0.605$; *R. sylvatica,* $F_{4,5} = 0.14$; $P = 0.959$).

Discussion

Transmitter effects

These experiments revealed some subtle, short-term, effects of an externally attached radio-transmitter on the escape behavior and vagility of two amphibian species. During both experiments, each species responded differently to the presence of a transmitter. *Rana pipiens* exhibited a different angle of escape (Table 1.1A) and a marginally significant decrease in total escape distance (Table 1.1B) in the predation experiment, and a change in turn angle in the vagility experiment (Table 1.2). *Rana sylvatica* exhibited an increase in the number of jumps per path and followed a straighter path in the vagility experiment (Table 1.2), and the frog's body mass was a marginally significant predictor of the antipredator behaviors and escape metrics in the predation experiment. While most of my metrics did not change in response to the presence of a transmitter, these subtle changes are not surprising given that externally attached transmitters have negative effects on other taxa (Kenward, 2001). Multiple factors of a species' biology; including morphology, energetic constraints, and habitat use; will affect the sensitivity of a species to the external attachment of a transmitter. For example, waterfowl and upland game birds were very sensitive to a transmitter attached as a backpack, but raptors were affected only during times of limited resources (Withey et al., 2001).

A possible explanation for the differences in behavioral response between the two ranids could be the different ratio of body size to transmitter size. The mass and bulk of the transmitter, including battery placement and length of the transmitter antenna, could affect the frog's behavior. Bulk can increase drag in swimming animals, including *R.*

sylvatica in the breeding pond (Kenward, 2001; Muths 2003), and whip antennae have caused decreased mobility and mortality in birds (e.g., Dunstan, 1977). Transmitter size has important implications for flying animals, which have high energetic demands (Gessamen and Nagy, 1988; Withey et al., 2001). The energetic demands of jumping through a complex environment and the added mass or bulk from a transmitter could have similar consequences for using and storing energy in anurans. Energetic constraints can have negative implications for survival and reproduction and lead to reduced fitness. These questions have been addressed in some larger animals (White and Garrott, 1990; Withey et al., 2001), but not in small animals. However, I did not find a significant relationship with body mass for my movement metrics. While I did not find a strong effect of body size on my movement metrics within each species, the larger and heavier *R. pipiens* was similarly affected by the presence of a radio-transmitter when compared to *R. sylvatica*. The size range of frogs I used overlapped between the two species, but on average *R. sylvatica* were approximately 2/3 the length and 1/3 the mass of *R. pipiens*. Body size is an important variable in the risk perception of frogs (Martin et al., 2005) and warrants future consideration.

Differences in sensitivity to the presence of a radio-transmitter between the species could result from differences in other antipredator mechanisms (Hayes, 1990). While both *Rana pipiens* and *R. sylvatica* routinely use the terrestrial environment (Hinshaw, 1999; Knox, 1999; Redmer and Trauth, 2005; Rorabaugh, 2005), they differ in their palatability to predators, skin secretions, jumping ability, habitat preferences, cryptic coloration, body size (Formanowicz and Brodie, 1979; Heinen and Hammond, 1997; Choi et al., 1999), and antipredator behaviors (this study). *Rana pipiens* exhibited a

broader range of behaviors than *R. sylvatica* in response to simulated aerial and ground attacks and used behaviors that may be constrained by the presence of a transmitter such as inflation of the body. I speculate that the diverse range of antipredator behaviors exhibited by *R. pipiens* may make it more sensitive to the presence of a transmitter than expected based on its body size.

While I found some limited effects of a radio-transmitter on the vagility and escape behavior of *R. pipiens* and *R. sylvatica*, the frequency of antipredator behaviors was not profoundly affected by the presence of a radio-transmitter. *Rana pipiens* exhibited changes in both experiments, and *R. sylvatica* changed its behavior only in the longer vagility experiment, despite the short duration (< 1 min for predator attacks and 4 h for movement paths) of both experiments. These differences between the species may indicate there is a different sensitivity of each species to a transmitter. The behavioral response of each may be susceptible to change at different temporal scales and have different energetic consequences for each species. Escape is only one strategy for avoiding predation, and a diverse suite of antipredator behaviors is essential to avoiding predators that form search images (Schall and Pianka, 1980).

Behavioral differences in response to different predators

I observed some differences in behavior between the two species of frog, and each species used different strategies in their response to simulated aerial and ground attacks (Figure 1.1). These differences in behavioral response between predators could be considered a product of my experimental design. By attacking first with the aerial predator and then with the ground predator, the timing of the simulated attacks could

have biased the frogs' antipredator response to ground predators. However, the order of repeated stimuli did not cause a bias toward active antipredator behaviors (e.g., fleeing) in *Scinax hiemalis* (Gomes et al., 2002), and I could not find an example where an amphibian was more likely to respond to repeated stimuli with flight, unless the animal was touched with excessive force (e.g., Williams et al., 2000). In addition, a passive antipredator response (e.g., remaining motionless, crouching, and chin tucking) was more likely if the amphibian was not touched (Ducey and Brodie, 1983; Dowdey and Brodie, 1989; Gomes et al., 2002). Both *R. sylvatica* and *R. pipiens* relied primarily on remaining motionless in response to aerial attacks in my predation experiment. Remaining motionless is a common antipredator behavior (Marshisin and Anderson, 1978; Heinen and Hammond, 1997; Williams et al., 2000), which complements cryptic coloration and decreases the risk of predation by predators that hunt visually (Heinen, 1994; Martin et al., 2005).

Both species relied more on flight behavior in response to ground attacks than in response to aerial attacks (Figure 1.1). Such rapid movements followed by immobility can take the prey out of the predator's search window, and this behavior has been seen in newly metamorphosed *R. pipiens* (Heinen and Hammond, 1997). *Rana pipiens* exhibited a broader range of behaviors in response to ground attacks than aerial attacks including inflation of the body and vocalization. These behaviors can startle the predator, accentuate skin glands, and make the frog look too big to ingest (Duellman and Trueb, 1986; Williams et al., 2000). While *R. sylvatica* relied on flight from both predators more than *R. pipiens*, it used flight most frequently in response to ground attacks. *Rana sylvatica* has less elaborate dorsal patterning, which may make this species rely more on

flight behavior than *R. pipiens*. *R. sylvatica* may also be able to find cover from predators more readily than *R. pipiens* because it is smaller.

I conclude that the presence of an externally attached radio-transmitter had some limited effects on the vagility and escape behavior of *R. pipiens* and *R. sylvatica*. I also conclude that these two species differ in their response to an attack from the air versus an attack from the ground. Behavior and vagility are two important antipredator mechanisms, and the subtle effects that I observed could lead to increased predation and affect energetic balance.

CHAPTER 2

EFFICACY OF PIT TAGS FOR TRACKING THE TERRESTRIAL ANURANS *RANA PIPIENS* AND *RANA SYLVATICA*

Introduction

The terrestrial ecology of many amphibians is poorly known compared with the aquatic stages (e.g., Regosin et al. 2003). Although advances have employed radiotelemetry on terrestrial adults (e.g., Hodgkison and Hero 2001; Watson et al. 2003), the size and battery life of transmitters are limitations on the use of radiotelemetry for smaller amphibian species and life stages. Other approaches for following small amphibians have included powder tracking, radioactive tags, and harmonic radar diodes, but each of these techniques has significant limitations (Heyer et al. 1994; Langkilde and Alford 2002).

Passive integrated transponders (PIT tags) overcome many limitations of these other techniques. PIT tags are small, glass-encased electromagnetic coils with a microchip containing a 10-space unique alphanumeric code that is emitted at a radio frequency (typically 134.2 kHz) when the coil is activated. PIT tags are easily applied and relatively benign to the tagged animal, provide a unique and essentially permanent mark, and can be cost-effective (Arntzen et al. 2004; Gibbons and Andrews 2004; Ott and Scott 1999). As a result, PIT tags have been increasingly used for marking fish, amphibians, reptiles, and other animals for demographic and behavioral studies (e.g., Camper and Dixon 1988; Kurth et al. 2007; Reaser 2000; Rowe and Kelly 2005; Sinsch 1992). Usually, PIT tag detection relies on the physical recapture of the tagged organism

because the tag needs to be within range (usually ~ 0.3 m) of an antenna to transmit the alphanumeric identification code to the transceiver (see review by Gibbons and Andrews 2004). Portable antenna and transceiver systems (PIT-packs) are a new approach to locating and identifying a tagged organism without physical recapture, thereby minimizing associated disturbances (Hill et al. 2006; Kurth et al. 2007; Zydlewski et al. 2001).

I evaluated a PIT-pack as a tool to locate and identify confined individuals of two pond-breeding amphibian species, recently metamorphosed *Rana pipiens* (Northern Leopard Frogs) and adult *R. sylvatica* (Wood Frogs). I evaluated the detection range of the PIT-pack using PIT tags alone and the detection probability of frogs implanted with PIT tags and held in terrestrial enclosures. I used the PIT-pack to identify breeding pairs in a small vernal pool and collect information on the breeding ecology of *R. sylvatica*. In addition, I evaluated three surgical implant locations and PIT-tag retention in recently metamorphosed *R. pipiens*.

Materials and Methods

The PIT-pack consisted of a battery-powered Destron-Fearing transceiver (Model FS 2001A-ISO; Digital Angel Co., St. Paul, Minnesota, USA) and custom-built antenna. The antenna head was constructed in an airtight oval (0.20 × 0.25 m) with 1.27-cm schedule 40 PVC. The antenna consisted of 20-gauge multi-strand wire wrapped 26 times through the PVC frame until an inductance of approximately 425 μH was reached. Capacitors were attached to the antenna lead cable and enclosed in the PVC, fixing the capacitance at ~ 3300 pF. Fine-scale tuning was achieved with a 400-1600 pF variable

capacitor. The head of the antenna was mounted on an adjustable 1.5-m long handle at an angle of ~ 120° (Figure 2.1). The instrument was tuned in water or air immediately prior to use at each site to maximize current at 3.0 to 3.3 Amps. In theory, changes in soil or water density and chemistry can affect the electromagmetic field generated by the antenna, and consequently it is necessary to tune the antenna prior to use in the medium (i.e., air or water) in which it will be used to achieve the maximum detection range. The PIT-pack is light (3.1 kg) and portable in the terrestrial environment (Figure 2.1), but the transceiver is small and low-powered. Heavier equipment with a larger antenna head size (e.g., 0.55 × 0.40 m and 19.3 kg in Hill et al. 2006) would probably have greater detection ranges but would sacrifice the convenience of the smaller unit (Kurth et al. 2007; Zydlewski et al. 2001). I used 12-mm PIT tags (134.2 kHz ISO tag; Model TX1411SST, Digital Angel Co., St. Paul, Minnesota, USA) in all experiments because the small size of my study frogs. Tag size may contribute to performance, and larger tags may increase the detection range for other applications (Hill et al. 2006; Roussel et al. 2000).

Prior research with larger 23-mm tags and more powerful readers reported detection ranges of 30-38 cm in air and 60-91 cm in water (Cucherousset et al. 2005; Hill et al. 2006). With a blind observer, I evaluated the PIT-pack detection range for 30 PIT tags in 30 mL polyethylene vials in each of two soil types commonly found in Maine, USA, forests (N = 60 total tags). I visually evaluated each area and assessed one to be predominantly glaciomarine hydric soils found in wetlands and the second to be predominantly well-drained till soils found in uplands (Natural Resources Conservation Service, 1963). One observer dispersed PIT tags in a 16 m^2 area (4 x 4 m) at depths

Figure 2.1. Using a PIT-pack to search for PIT-tagged, recently metamorphosed *Rana pipiens* in a terrestrial enclosure in a three-year old clearcut in Maine, USA. I held the transceiver in a shoulder bag, and constructed the antenna using a modified forearm crutch for ergonomics. I varied the angle of the antenna to increase the detection probability as I searched for concealed frogs, and an audible beep from the transceiver alerted us to detection of a tag. Photograph by Valerie Moreau.

ranging from the soil surface to 76 cm by driving a measured metal rod to the desired depths in the soil. A second observer, naive to the location and number of tags, searched the area with the PIT-pack by walking in a systematic zig-zag pattern through the area and making three passes through the area to find the tags. The first observer, who placed the tags, recorded the number and identity of the tags found on each pass. The first, informed observer then made one pass though the area and attempted to detect tags that were missed using the PIT-pack.

I collected recently metamorphosed *R. pipiens* and adult *R. sylvatica* from the University of Maine's Dwight B. Demeritt and Penobscot Experimental Forests (Penobscot County, Maine, USA, 44° 50' N, 68° 35' W) with hand capture and pitfall traps in August 2006. I housed all frogs in 125 L plastic tanks or 38 L glass aquaria in small groups (≤ 20 recently metamorphosed frogs and ≤ 5 adult frogs) for 1–16 days prior to experiments (described below). Each container had leaf litter for cover, holes in the top, and a wet paper towel on the bottom to maintain moisture. I fed captive frogs crickets *ad libitum*. I measured (snout-vent length [SVL], mass) and marked each animal individually with a PIT tag.

I surgically implanted PIT tags sub-dermally as recommended for small amphibians (Ott and Scott 1999). I anesthetized all frogs using 0.5g/L MS-222 (tricaine methanesulfonate; Sigma Aldrich, St. Louis, Missouri, USA) in well water prior to surgery. I lightly anesthetized the frogs to minimize mortality associated with small frogs (e.g., Cecala et al. 2007), and held frogs in anesthesia only until they lost their righting response but remained responsive to touch (< 15 min in most cases). I made a 2-mm long incision with a sterile, single-use blood lancet (Propper Mfg. Co., Long Island City, New

York, USA). To cut only the skin, I placed the blood lancet at an acute angle to the body of the frog and lightly pressed it into the skin until the skin began to fold upwards. I continued to apply pressure until I pierced the skin. After making the incision, I slipped a sterile PIT tag through the incision, and placed one drop of Bactine (Bayer Co., Pittsburgh, Pennsylvania, USA) on the wound to sterilize the incision and promote healing. Frogs recovered from surgery for ≥ 6 hours before release, and I assessed tag retention and the condition of the wound after the frog recovered.

I conducted a 2-week laboratory trial to determine the best position for PIT tag placement in small ranids. Three positions (scapula insertion, pubis insertion, ilium insertion) were tested in recently metamorphosed *R. pipiens* (n = 20 for each position). For scapula insertion, a longitudinal incision on the dorsum was made above the scapula ~ 3 mm posterior to the eye and ~ 2 mm medial to the tympanum. For pubis insertion, a lateral incision was made ~ 2 mm anterior to the posterior end of the urostyle. For ilium insertion, a longitudinal incision was made ~ 1 mm anterior to the anterior end of the ilium and centered on the dorsum. The frogs used in the experiment were 34 ± 1 mm (mean ± SE; range 31–38) SVL and weighed 4.0 ± 0.3 g (range 2.8–6.1). Frogs were checked twice daily for tag retention and healing of the surgical wound.

Based on the results of the retention study, I PIT tagged (scapula insertion) 50 adult *R. sylvatica* (26 males, 24 females; 46 ± 1 mm SVL, range 41–55 mm; 14.5 ± 0.5 g, range 10.1–24.9 g) and 52 recently metamorphosed *R. pipiens* (37 ± 1 mm SVL, range 31–48; 4.5 ± 0.2 g, range 1.0–8.7 g) in August 2006. Tagged frogs were placed into uninhabited 3.8 x 3.8 m (14.4 m^2) terrestrial enclosures constructed 15 months prior to data collection in an unharvested forest (unharvested), a forest partially harvested to 50%

crown closure (partial), and a 3-year old clearcut with coarse woody debris removed (removed) on the Dwight B. Demeritt and Penobscot Experimental Forests (see Patrick et al. 2006 for a description of the sites). Enclosure walls were 1.2 m tall galvanized steel hardware cloth (3.2 mm square mesh; TWP Inc., Berkeley, California, USA) supported with wooden garden stakes. Enclosure walls were buried 20–30 cm in the ground and bent 10 cm at the top toward the inside of the pen to prevent escape of animals.

I stocked terrestrial enclosures with recently metamorphosed *R. pipiens* and adult *R. sylvatica*. Recently metamorphosed *Rana pipiens* were stocked to three enclosures: one enclosure in the removed treatment at a density of 12 per enclosure (0.83 m^{-2}), one in the removed treatment at a density of 20 per enclosure (1.39 m^{-2}), and one in the unharvested treatment at a density of 20 per enclosure (1.39 m^{-2}). I was unable to capture enough recently metamorphosed *R. pipiens* at my study sites to replicate each density and treatment combination. For *R. sylvatica* adults, I stocked each of 10 enclosures at a density of five per enclosure (0.35 m^{-2}): five enclosures in the partial treatment and five in the unharvested treatment. I located recently metamorphosed *R. pipiens* every three days during 23 August – 7 September 2006 and once weekly thereafter through 11 October (the end of the growing season in central Maine). I located *R. sylvatica* adults once weekly from 26 August to 27 September 2006. I removed dead frogs and did not include them in subsequent detection probability calculations.

Lastly, I captured (drift fences and by hand) 139 adult *R. sylvatica* (61 females, 78 males) returning to breed at a single, ~ 80-m^2 vernal pool on the University of Maine's Dwight B. Demeritt Experimental Forest in April 2007. Each frog was PIT tagged (scapula insertion), and held in captivity for < 9 h prior to release at ~ 1 h before sunset.

Nightly during 22 April – 2 May I located pairs in amplexus with a spotlight and by scanning the surface of the water with the PIT-pack. I attempted to identify both members of each located pair with the PIT-pack without disturbing the frogs. I relocated the pair visually and with the PIT-pack until the female oviposited. Each morning I counted the number of fresh egg masses in the pond. I conducted all statistical analyses in SAS (SAS Institute, Cary, North Carolina, USA) with $\alpha = 0.05$.

Results and Discussion

My mean detection probability was 0.65 ± 0.14 (± 95% confidence interval), and I detected 100 ± 0% of the tags at 13 cm and 33 ± 7% of PIT tags at 43 cm in the soil (Figure 2.2). The informed observer (i.e., who knew the location of the tags) detected a higher proportion of tags in a single pass (0.76) than the blind observer (0.61 ± 0.03; range 0.57–0.67) did in three passes. This higher success in detecting tags is probably due to increased effort in an area known to have a tag versus the systematic pattern employed by the blind observer. Subtle changes in antenna orientation associated with concentrated effort in one area can change detection success without a change in detection range. The antenna is most effective at detecting a tag if the tag is perpendicular to the face of the antennae (Cucherousset et al. 2005).

No frogs died during the 2-week tag retention experiment. Tag retention after two weeks was highest with the scapula insertion technique; all *R. pipiens* retained their tags. Retention also was high with ilium insertion (90%), but retention with pubis insertion was poor (55%). All tag loss occurred before the incision healed, generally in < 6 days during these laboratory trials. The scapula and ilium insertion techniques will probably

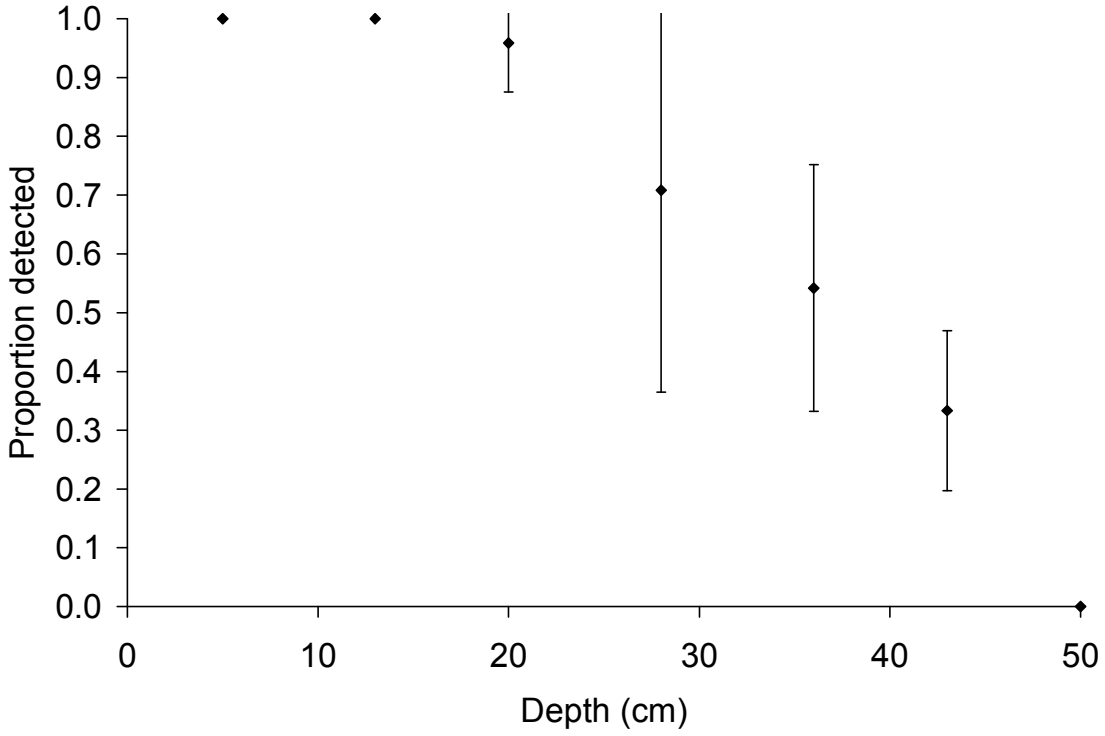

Figure 2.2. Mean (± 95% confidence interval) proportion of PIT tags detected per depth in the soil using a PIT-pack in two 16 m^2 areas. Each depth had six tags available for detection and means were calculated from all four passes with the PIT-pack. All depths ≥ 50 cm were lumped.

result in high tag retention rates in other similar sized frogs, although retention rates are important to quantify for any field study.

The proportion of recently metamorphosed *R. pipiens* detected with a PIT-pack was not affected by harvesting treatment or density, and the proportion detected in the three terrestrial enclosures remained at 1.00 throughout the study (Figure 2.3). The proportion of adult *R. sylvatica* detected remained high (> 0.90) until the first time the minimum daily temperature (MDT) was < 0°C, but declined over subsequent surveys. Because the proportion detected remained high until 11 October 2006 for the aquatic hibernator *R. pipiens* (Rorabaugh 2005), I speculate that adult *R. sylvatica* began to enter

subterranean hibernacula (Redmer and Trauth 2005) in refugia below my detection range with the PIT-pack, and thereby reduced the proportion of frogs detected. I am confident that the enclosures were escape proof (only one of 1600 *R. sylvatica* and *Ambystoma maculatum* stocked into 64 enclosures in 2005 escaped; SMB and MLH, unpublished data). Although the steel walls reduced detection range when the antenna was nearby, I detected adult *R. sylvatica* within ~ 5 cm of the fences at depths of ≤ 16 cm deep on 27 September.

A PIT-pack is a non-invasive method for locating tagged individuals, and this technique can make multiple recapture studies in confined areas more feasible. Most studies using terrestrial enclosures use destructive sampling (e.g., Rodda et al. 2001) or pitfall trapping to sample or census animals in enclosures (e.g., Bailey et al. 2004). With a PIT-pack, a user can repeatedly search an enclosure with minimal disturbance. Advantages of this technique for sampling enclosures are that it is relatively noninvasive, the user can search until all animals are detected, and detection probability should remain at 1.00 unless the study animal is likely to move below a depth of 13 cm (detection range of the PIT-pack; Figure 2.2). The effectiveness of the PIT-pack would be limited for species that burrow deeper than 13 cm. For example, *Ambystoma maculatum* burrows up to 1.3 m in winter (Semlitsch 1983). In addition, some species may not be detected during some seasons. For example, *Spea multiplicata* burrows 1.3-10 cm deep in summer and up to 90 cm in winter (Rubial et al. 1969).

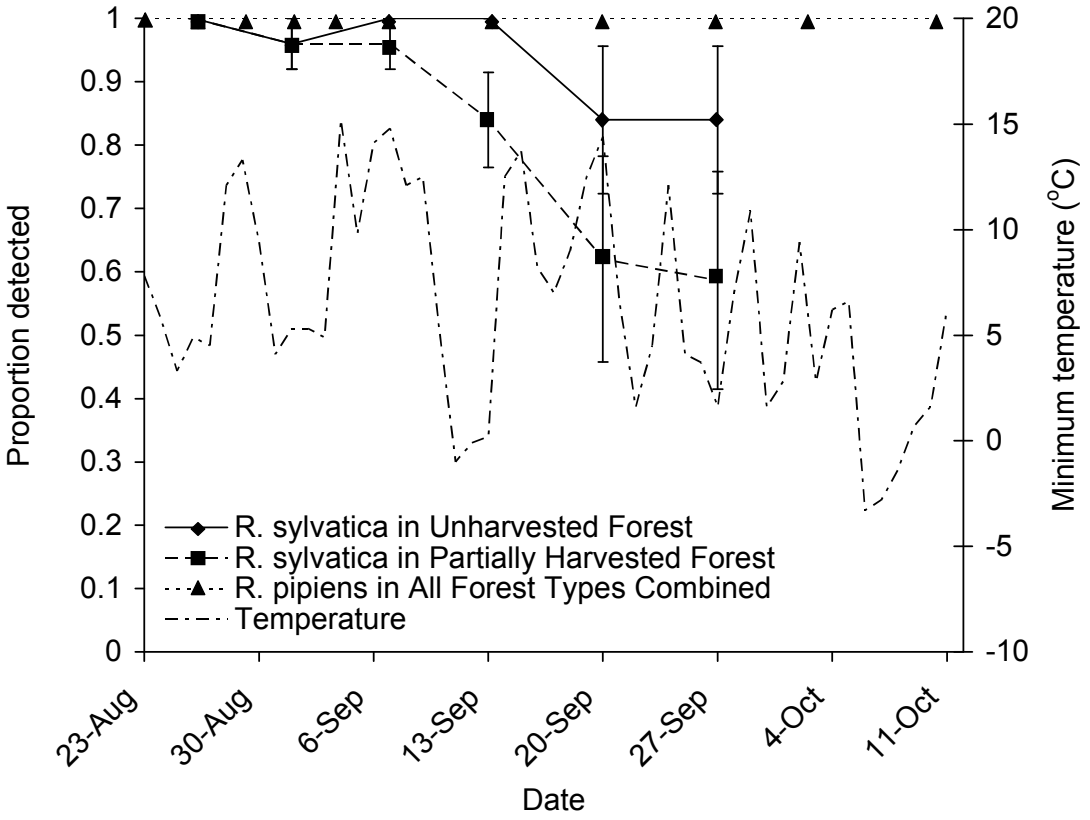

Figure 2.3. Mean (± SE) proportion of PIT-tagged frogs detected with a PIT-pack in 14.4-m^2 terrestrial enclosures in unharvested forest (recently metamorphosed *Rana pipiens*: one enclosure with 20 frogs; adult *R. sylvatica*: five enclosures with five frogs each), a forest partially harvested to 50% crown closure (adult *R. sylvatica*: five enclosures with five frogs each), and a 3-year old clearcut (recently metamorphosed *Rana pipiens*: one enclosure with 20 frogs and one enclosure with 12 frogs) in Maine, USA, in 2006. Data for the three enclosures containing *R. pipiens* are presented together because the proportion of frogs detected was always 100%. Proportion of frogs detected dropped for *R. sylvatica* after the minimum daily temperature fell below 0°C for the first time.

Two potential future applications for this technology are tracking in subterranean environments and tracking juvenile anurans. Anurans, especially bufonids (e.g., Eggert 2002), are known to use the subterranean environment as a refuge from thermal extremes and to conserve water (Duellman and Trueb 1986). Ranid frogs can dig their own burrows (Parris 1998), and many species use burrows excavated by other animals (e.g.,

Blomquist and Tull 2002; Lips 1991). However, the duration of time spent in the subterranean environment is not well studied, and PIT-tag telemetry could be used to non-invasively monitor amphibians in shallow subterranean habitats (see the study design of Quintella et al. 2005 for a possible method). A PIT-pack would be an effective technique for tracking burrowing species that use shallow burrows < 13 cm deep (e.g., *Spea hammondii*; Morey 2005).

Juvenile survival and movement can be important factors in population persistence (e.g., Red-legged Frogs in Biek et al. 2002; Conroy and Brook 2003). For example, dispersal in most amphibian species probably occurs as juveniles (e.g., Berven and Grudzen 1990; Dole 1971). Survival and movement probably are quite different in many anuran species, and PIT-based telemetry could be used to improve knowledge about the ecology of juvenile and small adult amphibians. However, the applicability of PIT-tag telemetry to free-ranging individuals could be limited. The technique will probably work best with animals that have small home range sizes and are not likely to use the subterranean habitat deeper than 13 cm during the period of study. Searching the terrestrial habitat for moving individuals (e.g., dispersing juveniles) could be labor-intensive and thus costly and only generate low recaptures of marked animals (see Arntzen et al. 2004 for a detailed analysis of the use of PIT tags and associated costs of a capture-mark-recapture studies). For example, searching the 14.4-m^2 enclosures took 6 ± 4 (± SD) minutes with the 0.20 x 0.25 m head antenna across all forest types. In addition, dispersing or migrating animals can move relatively long distances in a short period when environmental conditions are conducive to movement (e.g. a warm, rainy night for pond-

breeding amphibians in Maine, USA), which would necessitate more frequent relocation in these conditions.

I used a PIT-pack to non-invasively identify 40 pairs of PIT-tagged *R. sylvatica* in amplexus (Table 2.1), and relocate and monitor 25 of these pairs until the female oviposited. The number of pairs I identified and monitored until the female oviposited each night was highly correlated with the number of new egg masses in the pond the following morning (Pearson's correlation $r = 0.983$, $p < 0.0001$). This result indicates that I identified most of the frogs that successfully bred in the pond and the other 59 frogs I captured entering the pond did not successfully breed. In most instances where both male and female were identified, I was able to position the antenna underwater below the pair to read the female's tag. In seven instances, I was able to identify only the male because his PIT tag interfered with detection of the female's tag (Table 2.1, additional pairs observed column). I lost track of one pair prior to observing oviposition. The male stopped amplexus by releasing the female (Table 2.1, pairs disturbed column) when I placed the antennae near seven pairs. This disturbance typically occurred after I identified the male and moved the water and vegetation while moving toward the pair with the antenna to identify the female. I speculate that using a PIT-pack to identify breeding pairs of *R. sylvatica* was much less invasive than would be required using other techniques. Identifying animals marked with visual implant elastomer or toe clipping usually requires handling, and externally attached radio-transmitters can interfere with swimming and amplexus in some frogs (e.g., Muths 2003).

Table 2.1. Number of pairs of adult *Rana sylvatica* identified and observed ovipositing at a breeding pond in Maine, USA, in 2007; number of pairs disturbed with a PIT-pack prior to laying or identification of both individuals; additional pairs observed and not disturbed but both individuals were not identified or the pair was not observed ovipositing; and new egg masses observed the next morning. Males began calling on 16 April 2007, but females were not present until 22 April at which time I began nightly observations at this vernal pool.

Date	Pairs identified and observed ovipositing	Pairs disturbed	Additional pairs observed	New egg masses observed
22 April	0	0	0	0
23 April	0	0	0	0
24 April	16	4	3	17
25 April	2	0	0	2
26 April	4	2	2	4
27 April	0	0	0	0
28 April	3	1	2	3
29 April	0	0	1	0
30 April	0	0	0	0
1 May	0	0	0	0
2 May	0	0	0	0
Total	25	7	8	26

In summary, I successfully used PIT-tag telemetry to track recently metamorphosed and adult ranids in the terrestrial and aquatic environments, and this technique has potential for many more applications in anurans and other small animals, such as monitoring of animals in the shallow subterranean environment. Limitations for PIT tag and PIT-pack use are tag size and limited detection range. I successfully implanted 12-mm tags into ranids > 30 mm SVL. Currently available, 8-mm tags should be suitable for frogs > ~ 20 mm SVL and ~ 0.7 g, but use with smaller animals is not possible due to tag size. Also, additional work is needed to assess the long-term effects of tagging on animals of this size. A PIT-pack can detect 100% of tags in the terrestrial environment to a depth of 13 cm and > 90% of tags to a depth of 20 cm.

CHAPTER 3

ENVIRONMENTAL STOCHASTICITY INDUCES SPECIES AND LIFE-STAGE-SPECIFIC CHANGES IN FITNESS CORRELATES OF TWO ANURAN SPECIES

Abstract

Plasticity at different life-history stages evolves when populations experience diverse environments, multiple phenotypes can exist at each stage, and alternative phenotypes have superior fitness in different environments. I predicted and quantified the plasticity of *Rana pipiens* and *R. sylvatica* with respect to survival, time to metamorphosis, and growth rate in four different environments created by forest harvesting. *Rana sylvatica* larvae attained the highest survival to metamorphosis in partially harvested treatments, but they metamorphosed 13 ± 1 (mean ± SE) days later than larvae in open-canopy treatments and were 173 ± 35 mg lighter than larvae in unharvested treatments. Ultimately, juvenile *R. sylvatica* attained the same mass in all four treatments, but open-canopy treatments had 35 ± 2% fewer survivors than forested treatments. Survival of *R. pipiens* larvae increased with decreasing canopy cover, increasing water temperature, and increasing food availability, and juveniles remained larger and had higher survival in open-canopy treatments. In summary, the treatments induced opposing changes in the fitness correlates at the aquatic and terrestrial life stages of *R. sylvatica* but not *R. pipiens*, and each species' performance fit a pattern that followed the predictions of a different theoretical model.

Introduction

Many organisms have evolved complex life cycles that exploit diverse environmental conditions, and typically each stage in their life history is specialized for growth, dispersal, or reproduction in different environments (e.g., Wilbur 1980; Werner 1988). The ability to adapt to changes in the environment (i.e., phenotypic plasticity) can confer advantages and enhance fitness relative to conspecifics in the same environment. Both theory and empirical studies indicate that plasticity at different stages in an organism's life history evolves when: 1) populations experience diverse environments, 2) multiple phenotypes can exist at each stage, and 3) alternative phenotypes have superior fitness in different environments (Via and Lande 1985; Van Buskirk and Relyea 1998; Relyea 2002a; Benard 2004).

Increasing empirical evidence indicates that the plastic response of an organism to the environmental conditions experienced during one life stage can have positive or negative impacts on the organism in subsequent stages (i.e., latent effects, *sensu* Pechenik 2006) and ultimately affect its fitness (see reviews by Gimenez 2006; Pechenik 2006). For example, earlier hatching at a smaller size due to high predation risk resulted in reduced success at avoiding predators after metamorphosis in frogs (Vonesh 2005), but lower mass at hatching due to food stress was compensated for later with increased larval growth and larger mass at metamorphosis in crabs (Gimenez et al. 2004).

Animals using aquatic and terrestrial environments at different stages of their life cycle are ideal for studying latent effects. In particular, components of fitness are well studied for the aquatic stages of some taxa with complex, multiphasic life cycles, such as pond-breeding amphibians (Kaplan 1980; Semlitsch et al. 1988; Wilbur 1997; Relyea

2005). Additionally, size at metamorphosis and time to metamorphosis are thought to be directly related to lifetime fitness (reviewed by Wilbur 1980, 1997; but see De Block and Stoks 2005), and these traits are heritable in some instances (Van Buskirk et al. 1997; Dziminski and Roberts 2005; Laugen et al. 2005; Relyea 2005). For amphibians, larger animals that metamorphose earlier have higher survival through life, attain larger body sizes as adults, reproduce earlier, and have higher lifetime reproductive outputs (e.g., Gibbons and McCarthy 1984, 1986; Smith 1987; Reading 1991). Such empirical results have been formalized into theory on the optimal timing and size at metamorphosis for animals with complex life-cycles (e.g., Wilbur and Collins 1973; Werner 1986; Rowe and Ludwig 1991; Day and Rowe 2002).

Size at metamorphosis and time to metamorphosis are highly plastic traits in most amphibian species, and they can change with density, presence of predators, food availability, temperature, precipitation, and hydroperiod (Berven and Gill 1983; Scott 1994; Relyea 2002a,b). This plasticity allows individuals to gain advantages over conspecifics in different, unpredictable environments (Mauer and Sih 1996; Merilä et al. 2000; Camp et al. 2007; Rudolf and Rödel 2007). The effects of some of these environmental variables have been formalized into theory, but no one current model adequately predicts the response of animals with complex life cycles to all of these environmental variables (Benard 2004; Rudolf and Rödel 2007). Most models predict that larvae should metamorphose at a smaller size and earlier in response to increased risk or poor resources at the larval stage, but these predictions were supported in only two of 40 experiments on larval predation risk reviewed by Benard (2004). Additionally, risk of predation in two instances (Laurila et al. 1998, Chivers et al. 1999) actually had a positive

impact on fitness correlates by causing larvae to metamorphose earlier and at the same size.

One cause of the poor predictive power of current models is that studies measuring fitness components for both the terrestrial and aquatic stages of amphibians under natural or semi-natural conditions are rare (for other reasons see De Block and Stoks 2005). Additionally, little is known about the terrestrial ecology of most pond-breeding amphibians (Paris 2001; Regosin et al. 2003, 2005). Where empirical evidence exists, strong latent effects of size at metamorphosis and timing of metamorphosis on juvenile performance are typical (e.g., Altwegg and Reyer 2003; Chelgren et al. 2006; Capellán and Nicieza 2007), but the response of different species to different forms of environmental variability remains poorly known (Pechenik 2006). For example, *Bufo woodhousii* larvae exposed to pesticide metamorphosed earlier, but compensated for poor larval growth with increased growth in the terrestrial environment; however, a similar response was not observed in *Rana clamitans* (Boone 2005).

To evaluate how different environments affect fitness components of pond-breeding amphibian species at the aquatic and terrestrial stages, I devised an experiment to test the effect of three forest harvesting treatments and an unharvested control on the performance of two pond-breeding amphibian species, *Rana pipiens* and *R. sylvatica*. More specifically, I first quantified the effects of an open-canopy, partial-canopy, and full-canopy environment on larval growth and survival and time spent in the aquatic stage. Then, I transferred metamorphosing individuals to forests that had been clearcut (with and without coarse woody debris retained), partially harvested, or unharvested to quantify the effects of the terrestrial environment on growth, survival, and juvenile

duration. I further correlated the performance of each species with uncontrolled environmental parameters including canopy cover, temperature, and food availability.

Materials and Methods

Study environments and study species

I used four experimental, forest-harvesting arrays which incorporate a control (unharvested forest; hereafter "unharvested") and three forest management strategies (clearcut with coarse woody debris [CWD] removed ["removed"], clearcut with CWD retained ["retained"], partial cut with 50% canopy closure ["partial"]). These forest harvesting practices have been correlated with reductions in abundance of some amphibian populations (e.g., clearcutting and removal of CWD; Gibbs 1998a,b; Herbeck and Larsen 1999) and hypothesized to prevent the loss of amphibian populations (e.g., retention of CWD in clearcuts, partial harvesting with removal of < 25% of basal area; deMaynadier and Hunter 1995). The four harvesting arrays were located on the University of Maine Demeritt and Penobscot Experimental Forests (Penobscot County, Maine, USA, 44° 50' N, 68° 35' W), and harvesting was conducted during November 2003 – April 2004 (see Patrick et al. 2006 for a description of the sites and harvesting).

These four forest harvesting treatments created environmental stochasticity for organisms with complex life cycles. Amphibian distribution on the landscape and amphibian population dynamics are linked to environmental gradients (e.g., hydroperiod, wetland size; Snodgrass et al. 2000), including those created by forest dynamics (e.g., disturbance and succession; deMaynadier and Hunter 1995; Skelly et al. 1999; Werner et al. 2007a,b). These gradients change the thermal and hydric conditions available to

amphibians, and are important factors governing the behavior and performance of anurans (Tracy 1976). At the aquatic stage, theoretical models predict that organisms should respond to the stimuli in the aquatic environment because they cannot assess the terrestrial environment, and the optimal time to metamorphose is when size-specific mortality and growth rate in the aquatic environment is less than that in the post-metamorphic environment (Wilbur and Collins 1973; Werner and Gilliam 1984; Werner 1986; Rowe and Ludwig 1991). For example, an organism may experience an environment that has poor resources, a metabolically stressful thermal regime, or high predation risk at the aquatic stage. However, the conditions of the post-metamorphic environment are unknown and variation in the post-metamorphic environment is not explicitly taken into account in current models. Metamorphosing into such an unpredictable environment should be a poor decision if an individual is unlikely to survive or grow.

Rana pipiens and *R. sylvatica* should vary in growth, survival, and timing to metamorphosis due to the environmental stochasticity produced by the forest harvesting treatments, especially in the terrestrial environment. Both *R. pipiens* and *R. sylvatica* are pond-breeding amphibians with a biphasic life cycle, but differ in their habitat preferences (Hinshaw 1999; Knox 1999; Redmer and Trauth 2005; Rorabaugh 2005). More specifically, adult and juvenile *R. sylvatica* are captured in higher numbers in intact forest away from forest edges and reduced canopy cover created by forest harvesting (deMaynadier and Hunter 1998; Gibbs 1998a,b; Patrick et al. 2006), and metamorphosing animals emerge from ponds and selectively orient towards forested areas (deMaynadier and Hunter 1999; Vasconcelos and Calhoun 2006). In contrast, populations of *R. pipiens*

are more likely to be present in ponds surrounded by a landscape with little forest cover (Pope et al. 2000; Guerry and Hunter 2002). Furthermore, canopy cover at breeding ponds depressed growth rates slightly and had no effect on survival of *R. sylvatica* larvae (Werner and Glennemeier 1999; Skelly et al. 2002; but see Skelly et al. 2005), but *R. pipiens* performed poorly in closed canopy ponds (Werner and Glennemeier 1999).

Thus, I predicted *R. sylvatica* larvae to perform equally well in open-, partial-, and full-canopy environments with regards to survival and have depressed growth rates in the partial-and full-canopy environments. I expected *R. pipiens* larvae to have increased growth and survival and emerge earlier in the open-canopy environments through metamorphosis because increased sunlight should increase primary production and food availability. I predicted juvenile *R. sylvatica* to have decreased growth and survival in the clearcuts at the terrestrial stage because of this species' lower thermal tolerances and preference for forested environments (e.g., Heatwole 1961; Bellis 1962, 1965; Brattstrom 1968). I expected juvenile *R. pipiens* to have increased growth and survival to the clearcut environments because of this species' preference for open-canopy environments and ability to recover from dehydration (Whitaker 1961; Dole, 1971, 1972a,b; Merrell 1977; but see Patrick et al. 2006).

Experimental systems

Experimental units were 28 aquatic mesocosms (tanks) and 28 terrestrial enclosures (pens). I placed seven tanks each (polyethylene cattle tanks, 1,514 L, Toter Inc., Statesville, North Carolina) in the full- and partial-canopy treatments and 14 tanks in the open-canopy treatment above ground at the University of Maine's Demeritt

Experimental Forest in canopy conditions similar to the mean of each harvesting treatment (see sampling description below) and ≥ 30 m from the nearest forest edge (edge effects for amphibians persist to ca. 30 m; deMaynadier and Hunter 1998). This site allowed us to control canopy cover and forest conditions surrounding each tank and manage the logistics of maintaining water levels and checking tanks for emerging metamorphs. At least seven days prior to addition of anuran larvae, I filled each tank with 1,500 L of well water, and added 1 kg dried leaf litter, 1 L of zooplankton and phytoplankton, and 100 g commercial rabbit chow to form a self-sustaining aquatic community (e.g., Wilbur 1997). I collected zooplankton and phytoplankton samples from three (89%, 62%, and 40% canopy cover) local vernal pools with an 80 μm plankton tow (Wildlife Supply Co., Saginaw, Michigan) to ensure a representative food source for the larval anurans. I maintained water levels at approximately 1,500 L using an L-shaped PVC drain set to the appropriate height and by adding well water as necessary. Screen lids (50% white shade cloth; Greenhouse Supply Inc., Brewer, Maine) were used to keep out litter, prevent colonization by unwanted amphibians and predators (e.g., *Anax* spp.), and retain metamorphs.

Across the four experimental arrays (see Figure 1 in Patrick et al. 2006 for the layout of arrays), I constructed seven pens in randomly selected locations between 110 m and 140 m from the breeding ponds in each of the four forest harvesting treatments and ≥ 30 m from the edge of the treatment (deMaynadier and Hunter 1998). An additional pen was constructed in each treatment and used to estimate mortality and changes in density of study animals in the pens in 2006 (see description below). I constructed pens from 1.2 m tall galvanized steel hardware cloth (3.2 mm square mesh; TWP Inc., Berkeley,

California) supported with wooden garden stakes. I buried the fencing 20 – 30 cm in the ground, sewed any seams in the mesh fencing with 24 gauge bailing wire, and bent the top 10 cm of the fence over toward the inside of the pen to prevent escape of animals. In each corner of the pen, I placed a pitfall trap consisting of two #10 tin cans taped end to end so as to be approximately 38 cm deep. After construction, each pen was stocked with a leaf litter depth and coarse woody debris volume equal to the mean of that treatment based on habitat sampling (see Patrick et al. 2006 for a description of sampling). After initial stocking, pens were allowed to accumulate leaf litter and other debris naturally.

I measured effective canopy cover with hemispherical photography (Nikon Coolpix 995 digital camera with FC-E8 fisheye converter lens on a 35-cm tripod) when animals were present in the tanks (mid-June) and pens (mid-August). I used the Gap Light Analyzer (Version 2.0, Simon Fraser University, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York) to analyze hemispherical photographs (Frazer et al. 1999). Tanks and pens were monitored for temperature at the water and ground surface using HOBO dataloggers (Onset Computer Corp., Bourne, Massachusetts) recording temperature at 6-h intervals. I also monitored temperature at depths of 5, 15, 25, and 35 cm in the tanks to quantify the thermal regime available to the larvae by placing four HOBO dataloggers at each depth in representative tanks in the three treatments.

Larval and juvenile performance

The experiment started at the beginning of the natural breeding season (April for *R. sylvatica* and May for *R. pipiens*). Multiple clutches of eggs were collected from three

(*R. sylvatica*) and two (*R. pipiens*) natural ponds from the University of Maine Demeritt and Penobscot Experimental Forests and hatched in plastic wading pools (60 L). Eggs from each clutch at each breeding pond were divided and randomly assigned to wading pools in each treatment so each treatment contained eggs from each breeding site to ensure genetic diversity. Eggs were monitored daily and potential predators removed. At hatching (~ Gosner stage 25; Gosner 1960), larvae were randomly assigned to tanks. I added 60 *R. sylvatica* in 2005 and 40 *R. pipiens* in 2006 to each tank so the biomass added to each tank was approximately equal between years. I checked tanks at least weekly and captured 30 larvae per treatment (no more than four per tank) to measure growth (total length [TL]). I allowed larvae to mature through metamorphosis (emergence of front limbs at Gosner stage 42) then removed them for measurement of mass.

At the end of the larval period, I sampled zooplankton as a measure of food availability. *Rana* spp. tadpoles are omnivores and consume both phytoplankton and zooplankton, but I measured zooplankton because zooplankton are thought to be an important source of protein (Altig et al. 2007). I stirred the tank with a dipnet by sweeping clockwise once around the tank and took three 1-L samples at a depth of 30 cm. I isolated and preserved the zooplankton by pouring each sample through an 80μm filter, narcotizing for 5 min using Alka Seltzer (Bayer Co., Pittsburgh, Pennsylvania), rinsing in tap water, and storing in 70% ethanol. At a later date, I counted the number of zooplankton from each tank.

I held metamorphosing frogs for 6 – 72 h for tail resorption before stocking. When in captivity, I housed all recently metamorphosed frogs in 125 L plastic storage

bins in small groups (≤ 25 frogs). Each container had 1 kg of leaf litter for cover, holes in the top, and a wet paper towel on the bottom to maintain moisture. I fed all frogs pinhead crickets (*Acheta domesticus*) *ad libitum* while in captivity. Before stocking juveniles into pens, I measured the mass and marked each animal individually by marking one leg with visible implant elastomer (Nauwelaerts et al. 2000; NMT Inc., Shaw Island, Washington). were randomly transferred to 14.4 m^2 pens within the same treatment from which they emerged (e.g., unharvested to unharvested). I did not test for interactions among treatments because of the additional replication required. In 2005, I stocked each pen with *R. sylvatica* juveniles at a density of 25 per pen or 1.73/m^2. In 2006, I stocked each pen with *R. pipiens* juveniles at a density of 20 per pen or 1.39/m^2. Metamorphosing frogs of both species can be found in very high densities in the terrestrial environment near the breeding pond but density drops as individuals move farther into the terrestrial environment (e.g., Heatwole 1961; Dole 1971; Regosin et al. 2003).

Mortality of juveniles in terrestrial pens can be high (e.g., Pechmann 1995; Parris 2001), and density can have dramatic effects on survival, growth, and development in recently metamorphosed ranids (Altwegg 2003; Harper and Semlitsch 2007); therefore, I quantified how density changed in the pens in 2006 using *R. pipiens* tagged with passive integrated transponders (PIT tags). I collected recently metamorphosed, wild *R. pipiens* (3.1 ± 0.4 g; range 1.6–4.8 g) from the experimental arrays by hand and pitfall traps in August 2006. I implanted 12-mm long PIT tags (Digital Angel, St. Paul, Minnesota) under the dermis by making a 2-mm longitudinal incision with a sterile, single-use blood lancet (Propper Mfg. Co., Long Island City, New York) on the dorsal side of the frog ~ 3 mm posterior to the eye and 2 mm medial to the tympanum. I slipped a sterilized PIT tag

through the incision and placed one drop of Bactine (Bayer Co., Pittsburgh, Pennsylvania) on the wound to sterilize the area and promote healing. This surgical procedure resulted in 100% survival and tag retention over 2 weeks in lab trials (Gibbons and Andrews 2004; Blomquist et al. 2008). I released the PIT-tagged *R. pipiens* juveniles to two uninhabited pens at a density of 20 per pen (1.39 m^{-2}) in the unharvested and removed treatments. These treatments were chosen to represent the extremes of my treatments. I located *R. pipiens* juveniles using a "PIT-pack" (Hill et al. 2006) and measured the mass of the frogs every 3 days from 18 August to 7 September and once weekly thereafter through 10 October (the end of the growing season in central Maine). Each visit served as a census of the pen as I was able to locate every frog or its tag on every visit (Blomquist et al. 2008).

In 2005 and 2006, the non-PIT-tagged *R. sylvatica* and *R. pipiens* stocked into the 28 terrestrial pens in all four treatments were left to grow and develop in the pens until the end of the growing season (September – October in Maine). At this time, I conducted a 19-day and 17-day census of the pens in 2005 and 2006, respectively. In both years, this period included both clear and rainy nights and warm and cool temperatures, and the timing of the census was intended to maximize activity levels of the frogs (i.e., capture the fall migration to overwintering habitat; Hinshaw 1999; Knox 1999; Redmer and Trauth 2005; Rorabaugh 2005; Baldwin et al. 2006). I conducted removal sampling consisting of at least three 20-minute, time-constrained searches once every 5 to 7 days, and I checked the pitfall traps daily for the duration of the census. During both 2005 and 2006, I continued the census until no new animals were captured for consecutive samples

using both time-constrained searches and pitfall traps. Upon capture, I identified and measured the mass of each animal.

At the end of the growing season (11 October), I collected, sacrificed in MS-222, and preserved by freezing as many frogs as possible for analysis of lipid content as a measure of the health and body condition (and consequently food available) to juveniles in the pens. At a later date, I thawed each animal, dried it to a constant mass in a 70°C oven, ground it with a mortar and pestle, and placed it in a preweighed cellulose thimble for lipid extraction in a Soxtec System HT2 extraction unit (Tecator, Höganäs, Sweden). I determined total nonpolar lipid levels by a 70-min extraction using methylene chloride. I weighed each sample before and after extraction, calculated lipid amounts as the change in mass during extraction, and expressed total lipid content in the animal as lipid mass per dry mass (Scott 1994; Scott and Fore 1995).

Statistical analyses

I used univariate repeated-measures analysis of variance (rmANOVA; PROC GLM in SAS [SAS Institute, Cary, North Carolina]; Scheiner and Gurevitch 2001) on three performance metrics (proportion surviving, time in tank or pen, and mass) for larvae through metamorphosis and for juveniles through the end of the growing season to quantify the response of each species to the harvest treatments (Roff 1992). I used species and treatment as the main effects and tested for interactions between species, treatment, and life stage (e.g., larvae vs. juvenile). I also used rmANOVA to investigate weekly larval growth for Gosner stages 25-42 based on total length for larvae sampled from each treatment. I used logistic regression (PROC LOGISTIC) to determine if treatment,

growth, or density affected survival of PIT-tagged, juvenile *R. pipiens* over the 48-day period based on frogs sampled from the unharvested and removed treatments.

To further examine possible causes for treatment differences, I used linear regression (PROC REG) to investigate the effects of four potential environmental differences (proportion canopy cover, maximum and minimum temperature, and food availability) on the time to metamorphosis, proportion surviving, and mass. For food availability, I converted the abundance of zooplankton to a relative measure by dividing the absolute values of each tank or pen by the maximum value I observed. I initially ran a model with all environmental variables, but I selected variables for the final model using a stepwise selection procedure. I performed this analysis for each species and life stage individually only where I found significant or marginally significant differences ($P < 0.100$) with rmANOVA.

I used histograms, skewness, and kurtosis of each variable to assess normality and homogeneity of variance. I arcsine-square root transformed proportional variables (survival, canopy cover, and food availability); other variables fit the assumption of normality. I used Bonferonni adjusted α-levels to evaluate each set of univariate comparisons using rmANOVA ($\alpha = 0.017$), post-hoc pairwise comparisons, and linear regression on environmental variables ($\alpha = 0.013$). I report unadjusted *P*-values in all cases, and used $\alpha = 0.05$ to evaluate all other tests.

Results

Time to metamorphosis

Rana sylvatica larvae from the open-canopy treatment metamorphosed earlier ($F_{2,25} = 298.8$, $P < 0.001$) and spent longer in the terrestrial environment ($F_{3,24} = 86.6$, $P < 0.001$) than larvae from other treatments (Figure 3.1A). Higher maximum water temperature predicted a shorter larval duration for *R. sylvatica* ($r^2 = 0.92$; $F_{1,26} = 303.0$, $P < 0.001$), but other environmental variables (food availability, minimum temperature, and canopy cover) were not significant and were removed from the final model (Table 3.1). *R. pipiens* larvae showed the same pattern, although the differences among the treatments were less pronounced than for *R. sylvatica* (Figure 3.1B). *Rana pipiens* larvae from the full-canopy treatment metamorphosed later ($F_{2,25} = 10.0$, $P < 0.001$) and spent less time in the terrestrial environment ($F_{3,24} = 20.3$, $P < 0.001$). None of the environmental variables predicted duration of the larval period for *R. pipiens* ($F_{4,23} = 2.0$, $P = 0.055$). These species-specific patterns were corroborated by the overall rmANOVA analysis (Table 3.2 – Stage × Species effect, Stage × Treatment effect, and Stage × Species × Treatment effect).

Survival

Survival at the larval stage through metamorphosis was higher overall for *R. sylvatica* (0.80 ± 0.05 vs. 0.24 ± 0.06 for *R. pipiens*), but the two species survived equally well during the terrestrial stage to the end of the first active season (0.36 ± 0.09 for *R.*

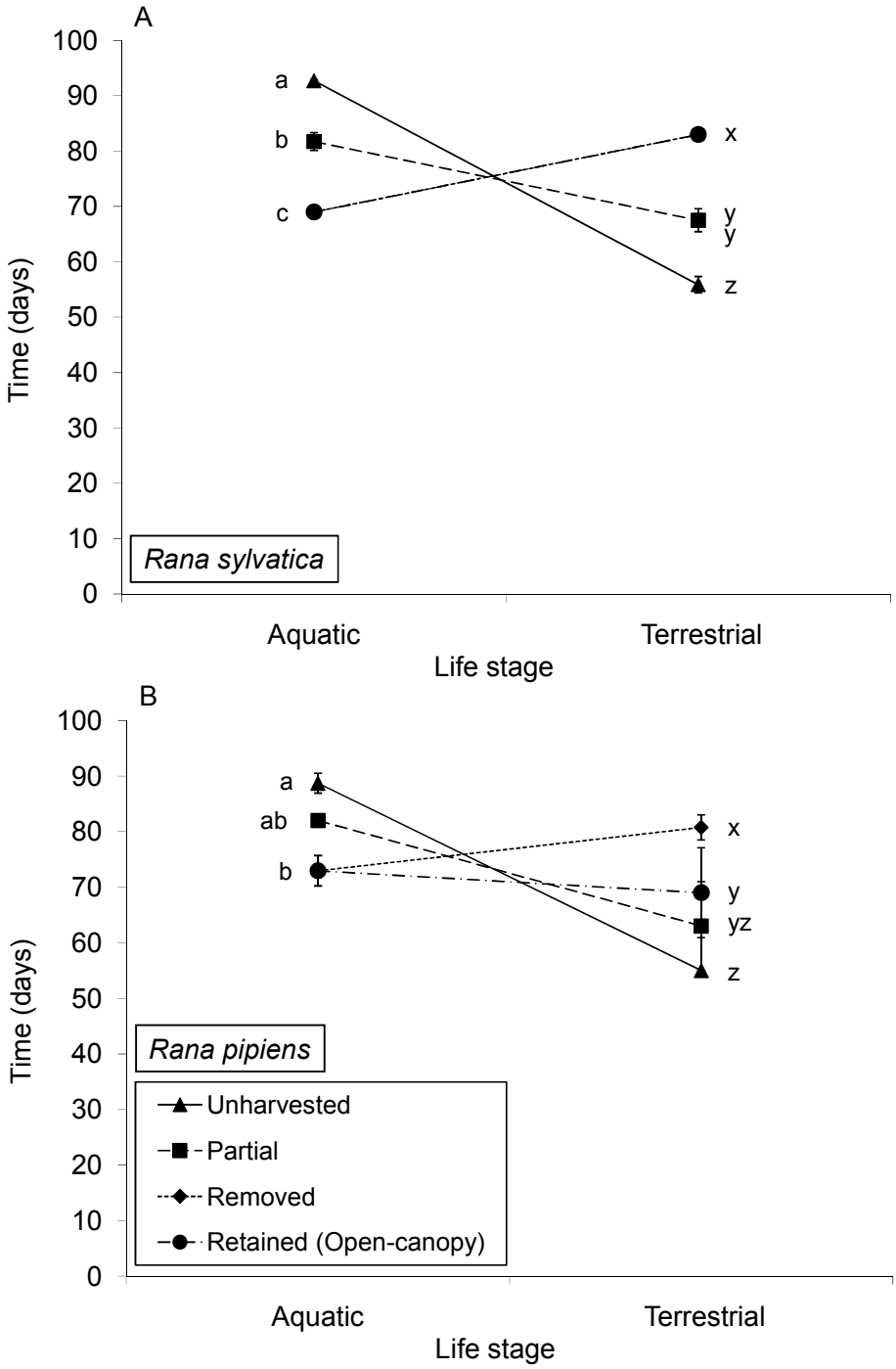

Figure 3.1. The number of days spent (± 1 SE) in the aquatic and terrestrial environment by *Rana sylvatica* (A: top panel) and *R. pipiens* (B: bottom panel) in the unharvested forest (Unharvested), 50% partial harvest (Partial), clearcut with coarse woody debris (CWD) retained (Retained), and clearcut with CWD removed treatments (Removed). Letters indicate significant differences based on Bonferonni post-hoc pairwise comparisons. Forest harvesting affected the time spent by each species at each life stage, but this effect was more pronounced for *R. sylvatica*.

Table 3.1. Means of environmental variables measured for each forest harvesting treatment. I calculated canopy cover based on hemispherical photographs. Food availability metrics are counts of zooplankton from 3 L samples for the aquatic tanks and percent fat content from juvenile frogs for terrestrial pens. *N* = number of animals sampled for fat content; SE = standard error.

Species	Environment	Treatment	Canopy cover	SE	Maximum temperature	SE	Minimum temperature	SE	Food availability	SE	*N*
Rana pipiens	Aquatic	Unharvested	0.88	0.00	19.5	0.2	17.0	0.6	46	14	
		Partial	0.83	0.02	23.2	1.9	17.3	0.2	152	18	
		Open-canopy	0.43	0.00	31.6	0.2	19.6	0.1	418	40	
	Terrestrial	Unharvested	0.88	0.01	20.1	0.4	15.1	0.9	4.482		1
		Partial	0.84	0.01	22.5	1.9	13.9	0.8	5.104	0.098	4
		Retained	0.36	0.01	26.6	1.4	13.3	0.7	7.214	0.295	5
		Removed	0.36	0.01	26.6	1.4	13.3	0.7	6.841	0.043	9
Rana sylvatica	Aquatic	Unharvested	0.88	0.00	17.9	0.3	14.6	0.4	125	9	
		Partial	0.84	0.01	20.1	0.6	15.0	0.3	289	14	
		Open-canopy	0.43	0.00	27.4	0.1	16.0	0.1	447	38	
	Terrestrial	Unharvested	0.88	0.01	20.3	0.3	14.0	0.1	4.997	0.728	6
		Partial	0.84	0.01	22.4	0.2	14.1	0.2	5.466	1.074	3
		Retained	0.35	0.01	28.2	0.6	12.7	0.2	5.917		1
		Removed	0.37	0.01	27.4	0.8	27.4	0.8	4.632		1

Table 3.2. Summary of repeated-measures analyses of variance on the effects of forest harvesting treatment and life stage on the number of days spent in the aquatic and terrestrial environment, survival, and mass of *Rana pipiens* and *R. sylvatica*. I report raw *P*-values but used Bonferonni-adjusted α-levels to assess significance and to control Type I error (α = 0.017) (df = degrees of freedom; λ = Wilk's λ).

	Days				Survival				Mass			
Between-subject	df	MS	*F*	*P*	df	MS	*F*	*P*	df	MS	*F*	*P*
Treatment	3	60	1.2	0.253	3	0.119	3.4	0.025	3	1310408	29.3	**< 0.001**
Species	1	159	3.7	0.059	1	2.770	79.4	**< 0.001**	1	24532295	548.2	**< 0.001**
Species × Treatment	3	34	0.8	0.501	3	0.299	8.6	**< 0.001**	3	2229275	48.8	**< 0.001**
Error	48	42			48	0.035			48	44747		
Within-subject	df	MS	λ	*P*	df	MS	λ	*P*	df	MS	λ	*P*
Stage	1,48	2161	114.2	**< 0.001**	1,48	0.452	13.4	**< 0.001**	1,48	8106468	67.9	**< 0.001**
Stage × Treatment	3,48	3095	163.5	**< 0.001**	3,48	0.114	3.4	0.252	3,48	419817	3.5	0.022
Stage × Species	1,48	329	17.4	**< 0.001**	1,48	1.995	59.2	**< 0.001**	1,48	425063	3.6	0.065
Stage × Species × Treatment	3,48	134	7.1	**< 0.001**	3,48	0.227	6.6	**< 0.001**	3,48	113136	1.0	0.425

sylvatica vs. 0.39 ± 0.09 for *R. pipiens*; Table 3.2 – Species × Treatment effect, Stage × Species effect, and Stage × Species × Treatment effect). For both species, larvae in the open- and partial-canopy treatments survived better than in the unharvested forest (Figure 3.2A, *R. sylvatica*: $F_{2,25} = 7.3$, $P = 0.003$), although this was trend was not statistically significant for *R. pipiens* (Figure 3.2B, $F_{2,25} = 3.5$, $P = 0.044$). Higher minimum temperature and higher food availability predicted higher survival of *R. pipiens* larvae in each tank ($r^2 = 0.36$; $F_{2,25} = 7.0$, $P = 0.004$), but none of the environmental variables predicted survival of *R. sylvatica* larvae (Table 3.1, $F_{4,23} = 1.0$, $P = 0.445$).

There was a trend that juvenile *R. sylvatica* survived better in the unharvested and partial treatments ($F_{3,24} = 3.8$, $P = 0.024$), but in contrast, juvenile *R. pipiens* survived better in the clearcut and partial treatments ($F_{3,24} = 11.0$, $P < 0.001$; Figure 3.2). For both species, canopy cover over the pen predicted survival in the pen (Table 3.1; *R. sylvatica*: $r^2 = 0.50$, $F_{1,26} = 12.5$, $P < 0.001$; *R. pipiens*: $r^2 = 0.22$, $F_{1,26} = 7.5$, $P = 0.011$), but in opposite directions: survival of *R. sylvatica* increased with increasing canopy cover whereas it decreased for *R. pipiens*.

Lower density within the pen positively affected the survival of *R. pipiens* juveniles (Figure 3.3; Hosmer and Lemeshow goodness-of-fit $\chi^2_6 = 7.7$, $P = 0.262$; density: Wald $\chi^2 = 6.1$, $P = 0.014$). As frogs in the pen died and consequently decreased the density of conspecifics remaining in the pen, the surviving frogs were 67% more likely to survive (odds ratio range: 11–153%). Additionally, treatment (Wald $\chi^2 = 0.7$, $P = 0.392$) and growth prior to death (Wald $\chi^2 = 0.0$, $P = 0.937$) were not significant

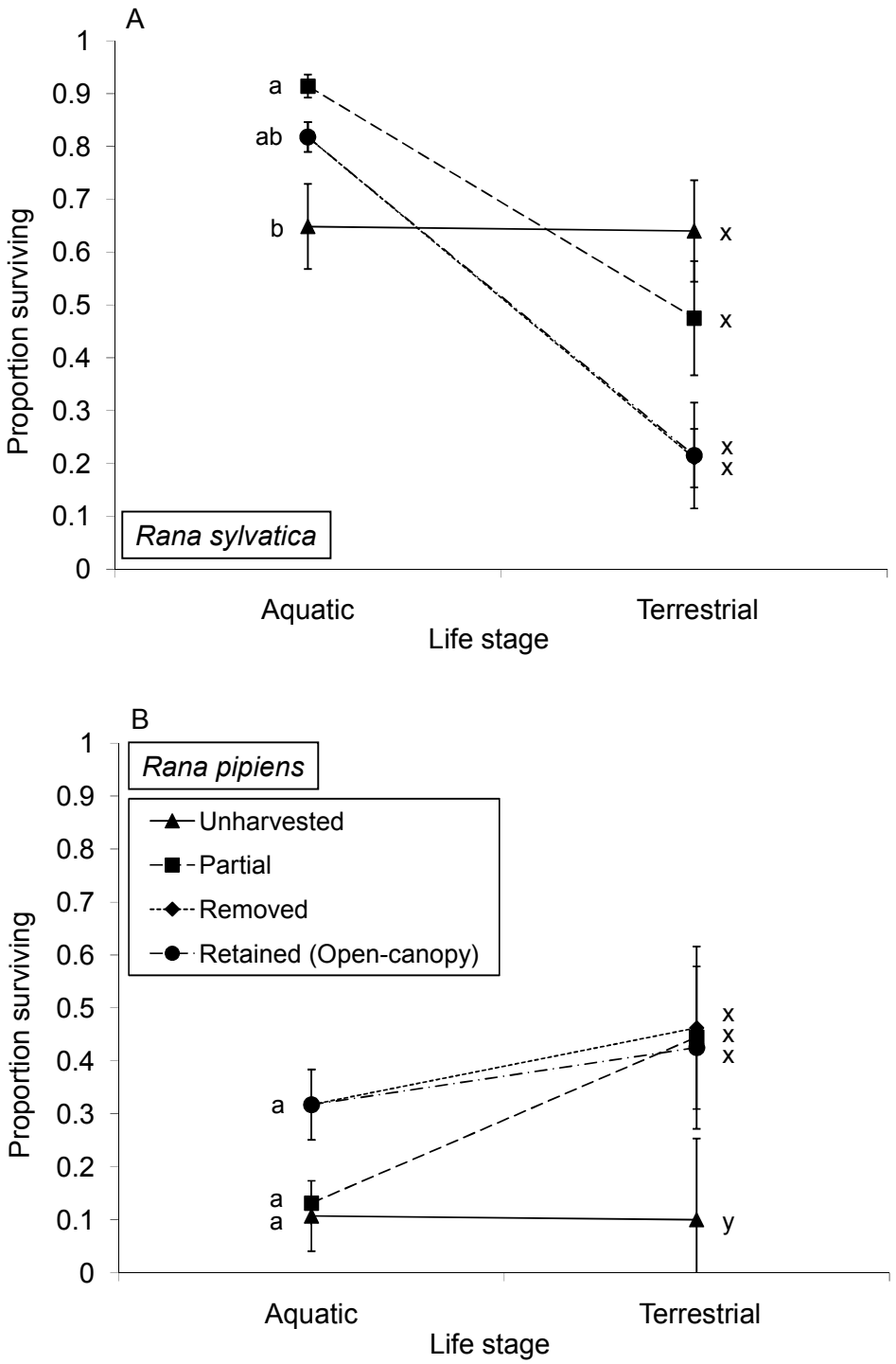

Figure 3.2. The survival (± 1 SE) of *Rana sylvatica* (A: top panel) and *R. pipiens* (B: bottom panel) aquatic larvae through metamorphosis and terrestrial juveniles through the end of the first active season in the unharvested forest (Unharvested), 50% partial harvest (Partial), clearcut with coarse woody debris (CWD) retained (Retained), and clearcut with CWD removed (Removed) treatments. Letters indicate significant differences based on Bonferonni post-hoc pairwise comparisons. The three harvesting treatments reduced survival at the terrestrial stage for *R. sylvatica*, but not for *R. pipiens*.

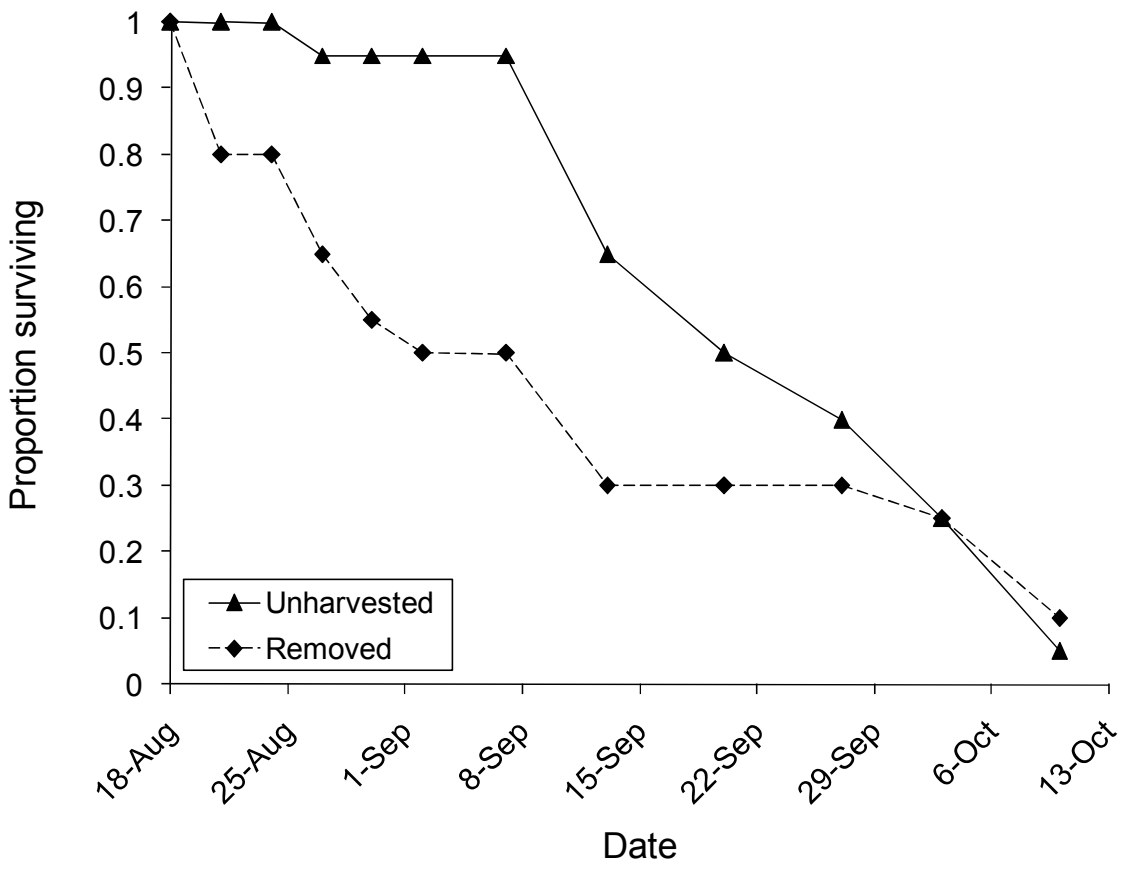

Figure 3.3. The survival of juvenile *Rana pipiens* marked with passive integrated transponders (PIT tags) in the unharvested forest (Unharvested) and clearcut with coarse woody debris removed treatments (Removed). As density decreased in each pen, the surviving frogs were 67% more likely to survive, and this effect did not vary with treatment.

explanatory variables in the regression explaining survival of *R. pipiens* over 48 days, and these variables were removed from the final model.

Growth

Larvae in the open-canopy treatment grew longer faster for both species (Figure 3.4; Treatment effect: $F_{2,174} = 241.3$, $P < 0.001$; Species effect: $F_{2,174} = 77.3$, $P < 0.001$; Table 3.2 – Species effect). However, *R. sylvatica* were heavier at metamorphosis after rearing in the partially harvested and unharvested forest than in the open-canopy (Figure

3.5A; $F_{2,25} = 19.9$, $P < 0.001$; Table 3.2 – Treatment effect and Species × Treatment effect). Additionally, higher maximum temperature predicted lower mass of recently metamorphosed *R. sylvatica* emerging from each tank (Table 3.1; $r^2 = 0.61$; $F_{1,26} = 39.9$, $P < 0.001$). In contrast, recently metamorphosed *R. pipiens* were heavier in the open-canopy forest upon emergence from the aquatic environment (Figure 3.5B; $F_{2,25} = 10.4$, $P < 0.001$), and this was associated with lower canopy cover (Table 3.1; $r^2 = 0.44$; $F_{1,26} = 20.8$, $P < 0.001$).

The mass of juvenile *R. sylvatica* was similar in all treatments at the end of the growing season (Figure 3.5A; $F_{3,24} = 1.7$, $P = 0.194$), but *R. pipiens* juveniles remained largest in the clearcuts (Figure 3.5B; $F_{3,24} = 38.8$, $P < 0.001$; Table 3.2 – Stage effect, Stage × Treatment effect, and Stage × Species effect). Additionally, higher canopy cover was associated with reduced mass of *R. pipiens* juveniles at the end of the activity season (Table 3.1; $r^2 = 0.73$; $F_{1,26} = 71.3$, $P < 0.001$).

Discussion

Removal of forest canopy changes the thermal regime, moisture regime, solar exposure (Geiger 1965), and availability of food for anurans (i.e., periphyton, Morin 1983; invertebrate abundance, Wyman 1998). These environmental variables are important factors governing the behavior and performance of anurans (Tracy 1976), and amphibians change their abundance in response to the environmental changes induced by forest harvesting (deMaynadier and Hunter 1995; Debinski and Holt 2000; Russell et al. 2002). My predictions about the response of each species to the harvesting treatments were generally based on Tracy's (1976) classic model of anuran interaction with the

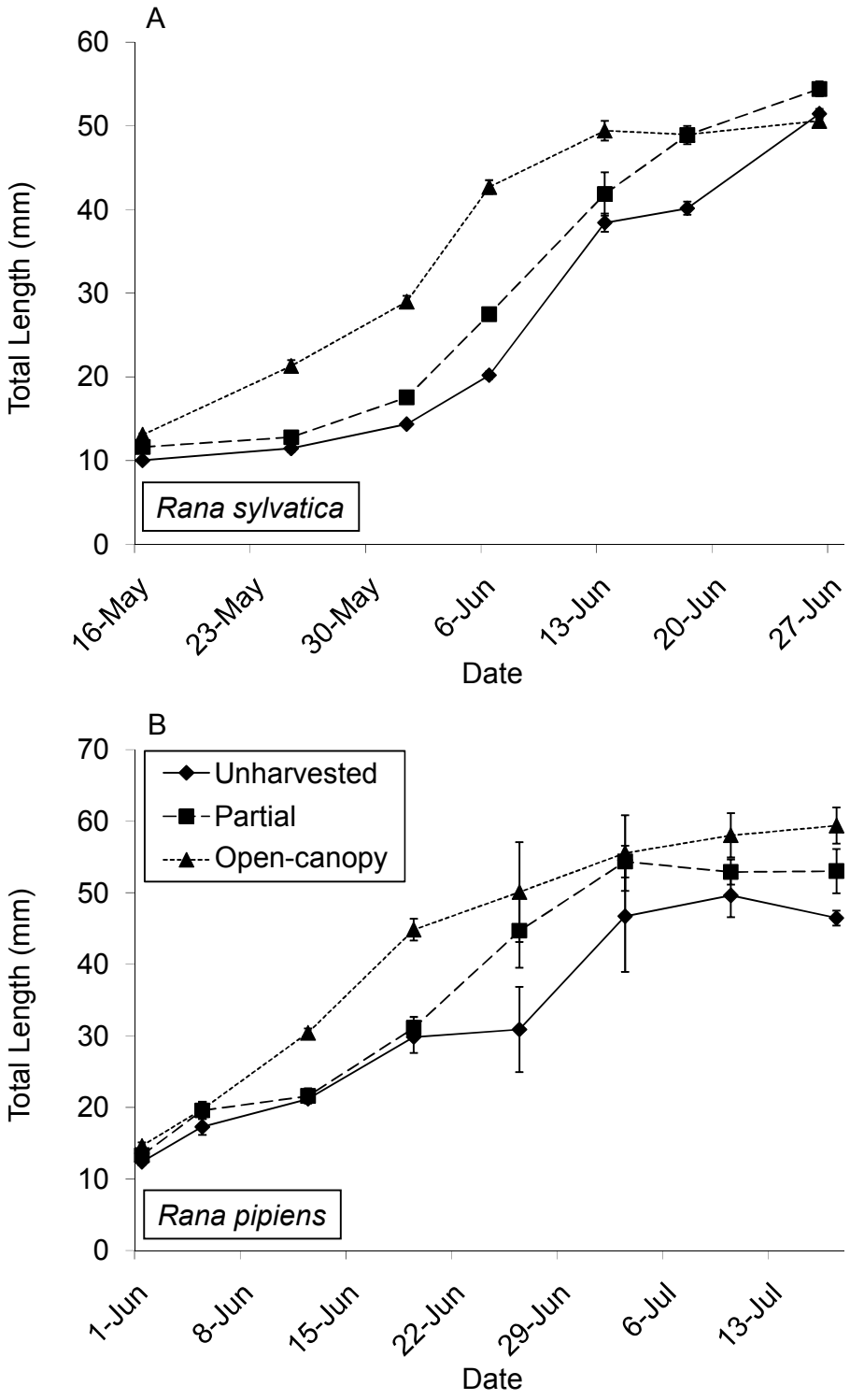

Figure 3.4. The total length (± 1 SE) of *Rana sylvatica* (A: top panel) and *R. pipiens* (B: bottom panel) larvae in the unharvested forest (Unharvested), 50% partial harvest (Partial), and open-canopy (Open-canopy) treatments. The growth curves differed for each species and varied with treatment.

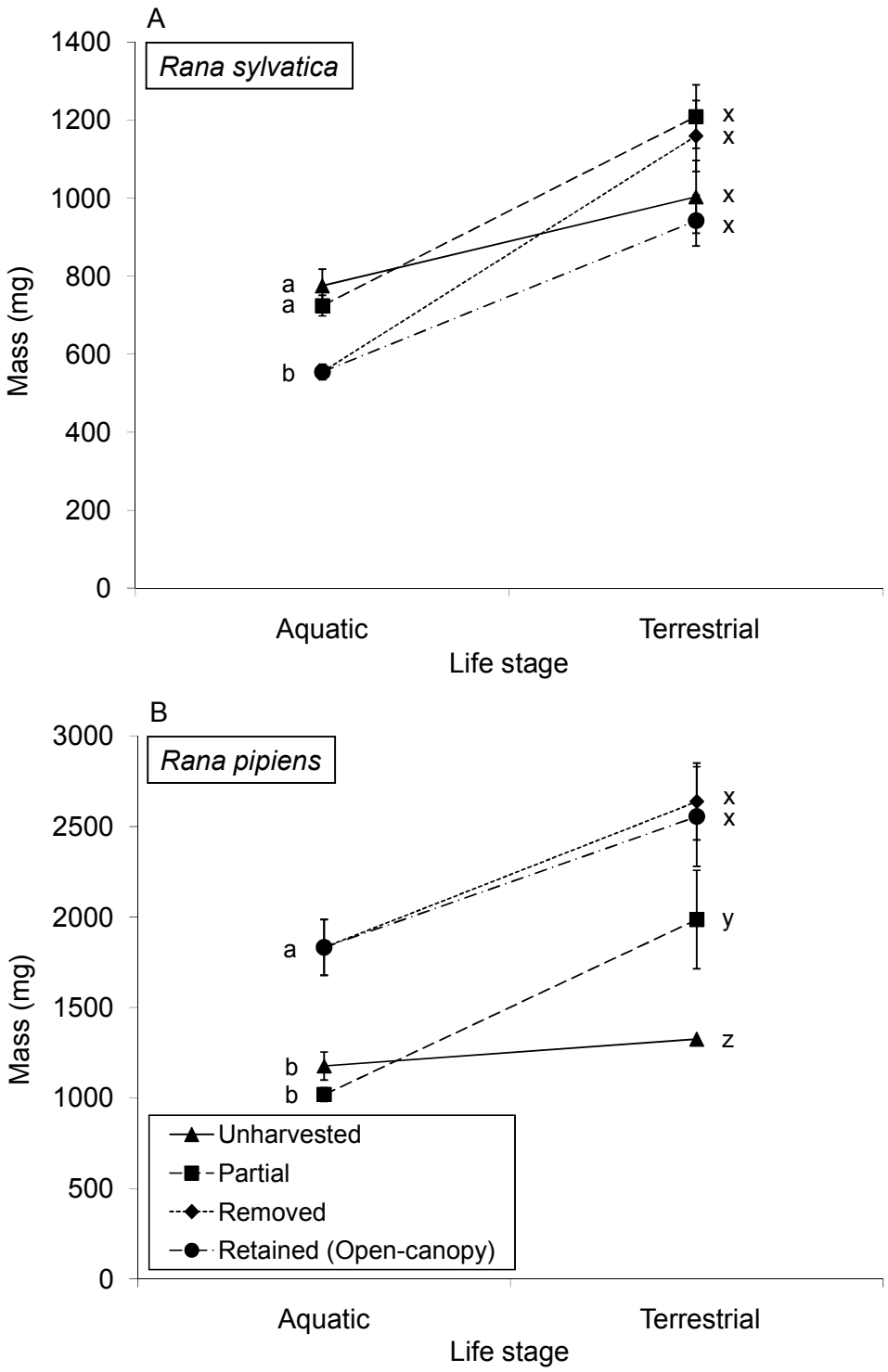

Figure 3.5. The mass (± 1 SE) of *Rana sylvatica* (A: top panel) and *R. pipiens* (B: bottom panel) at metamorphosis (aquatic) and at the end of the first active season (terrestrial) in the unharvested forest (Unharvested), 50% partial harvest (Partial), clearcut with coarse woody debris (CWD) retained (Retained), and clearcut with CWD removed (Removed) treatments. Letters indicate significant differences based on Bonferonni post-hoc pairwise comparisons.

environment, the tolerances of each species to thermal and hydric conditions, and previous work with these species (Werner and Glennemeier 1999; Skelly et al. 2002). As expected, the environmental changes induced by forest harvesting affected *R. pipiens* and *R. sylvatica* differently. I predicted *R. sylvatica* larvae to perform equally well in open-, partial-, and full-canopy environments with regards to survival, but have depressed growth rates in the two forested treatments; juveniles were expected to emerge later and grow and survive at a lower rate in the two clearcut treatments. I predicted *R. pipiens* larvae and juveniles to perform better in the open-canopy environments. The response of both species to the harvesting treatments largely fit with my predictions, but I found some unexpected differences.

My predictions were only partially correct for larval *R. pipiens*. I expected larvae to perform better in the open-canopy treatment, primarily based on previous work in Michigan (Werner and Glennemeier 1999), but larvae in the open-canopy and partial treatments survived equally well; survival was about 34 ± 9% higher than in the unharvested treatment (Figure 3.2B). Larvae in the open-canopy treatment attained the highest mass at the end of the aquatic stage (Figure 3.5B), perhaps because the open-canopy environment was similar to the canopy cover, thermal regime, and food available in breeding ponds used by *R. pipiens* in Maine (Guerry and Hunter 2002). Although the high survival in the partial treatment was unexpected, the regression that predicted (r^2 = 0.36) survival of *R. pipiens* larvae to decrease with decreasing minimum temperature and food availability corroborates previous work (Werner and Glennemeier 1999). Minimum temperature reflected increasing shade from forest cover during the larval period (May-

August), and this result was not surprising given the relatively cold temperatures in Maine and the necessity of larvae and juveniles to grow quickly to overwinter successfully (Hassinger 1970; Werner and Glennemeier 1999).

I expected juvenile *R. pipiens* to perform better in the clearcut treatments, and they did attain higher mass in the clearcuts (Figure 3.5B); however, they survived equally well in the partial and clearcut treatments (Fig 2B). Juvenile *R. pipiens* are found in highest abundance in meadows and other nonforested environments, and the reduction to 50% canopy closure in my partial harvest may have allowed regeneration of a dense understory which could provide the cover preferred by *R. pipiens* (Whitaker 1961; Merrell 1977; Chapter 5). It is noteworthy that both juvenile and adult *R. pipiens* were captured in pitfall traps at my study sites in higher numbers in the forested treatments than in clearcut treatments (Patrick et al. 2006). These disparate results probably reflect the generalist nature of juvenile *R. pipiens* (Dole 1971, 1972a,b). Overall, the forest harvesting treatments had consistent effects on the fitness components of *R. pipiens* across both life stages with animals in the open-canopy treatments emerging earliest and attaining the highest mass.

For *R. sylvatica*, my predictions were partially correct for larvae and correct for juveniles. I expected *R. sylvatica* larvae to perform equally well in open-, partial-, and full-canopy environments with regards to survival, but have depressed growth rates in the two forested treatments; they had the highest survival to metamorphosis in the partial-canopy treatment. My partial-canopy treatment had canopy cover similar to natural ponds that are successfully used for breeding by wild *R. sylvatica* in Maine (> 25% forest cover, DiMauro 1998). On the other hand, animals in the partial-canopy treatment

metamorphosed 13 ± 1 days later than open-canopy individuals (Figure 3.1A) and were 173 ± 35 mg smaller than animals from the unharvested treatment. These results conflict with previous work; the survival of *R. sylvatica* varied little with canopy conditions over the pond (Werner and Glennemeier 1999; Skelly et al 2002). The growth of larvae in the open-canopy treatment was faster than in other treatments, but these animals reached a minimum size and metamorphosed (Figure 3.4A). This increased growth and development rate in open-canopy ponds has been found in similar experiments with *R. sylvatica* larvae in Connecticut, although these studies did not report size at metamorphosis or time to metamorphosis (Skelly et al. 2002; Skelly et al. 2005). Growth to the minimum size for metamorphosis is a well-documented strategy for larvae dealing with a stressful environment (Rose 2005; Teplitsky et al. 2007), and this response has been predicted by theoretical models also (Day and Rowe 2002). This pattern of growth, the abundance of food in the open-canopy treatment (Table 3.1), and the strong negative relationships of maximum temperature with time to metamorphosis ($r^2 = 0.92$) and size at metamorphosis ($r^2 = 0.61$) indicate that *R. sylvatica* larvae in the open-canopy treatment were probably stressed by high temperatures. Survival and growth rates in the unharvested treatment likely were lower because the high canopy cover reduced food availability and temperature. These results support previous work indicating that ponds with high levels of canopy cover may have reduced food availability (Skelly et al. 2002). Additionally, ponds with ~50% canopy cover may increase the overall performance of larval *R. sylvatica* because food is more available and temperatures warmer than in pools in heavily forested environments (Table 3.1).

I expected juvenile *R. sylvatica* to perform better in the forested treatments, but juveniles attained the same mass in all four treatments at the end of the growing season (Figure 3.5A). I detected positive latent effects from the larval to juvenile stages; earlier emerging recently metamorphosed *R. sylvatica* from the open-canopy treatment compensated for smaller size with increased growth in the terrestrial environment (Figure 3.1A and Figure 3.5A). However, the two clearcut treatments had 35 ± 2% fewer juvenile *R. sylvatica* surviving than in the forested treatments (unharvested and partial; Figure 3.2A). If my mortality curves for PIT-tagged *R. pipiens* (Figure 3.3) are similar to mortality patterns in *R. sylvatica*, the density in the pens changed more rapidly in the clearcut than in the forested treatments. Consequently, the surviving animals in the pens may have been able to grow more rapidly and had a better chance of surviving because density is an important factor regulating the growth and survival of amphibians at the juvenile stage (Harper and Semelitch 2007). Although not statistically significant, decreased survival in the clearcut treatments supports my prediction and indicates that *R. sylvatica* from clearcut environments probably have lower lifetime fitness than those from forested environments because fewer animals survive to reproduce. Additionally, I measured fitness correlates only through the end of the first activity season, and the negative latent effect of the thermal stress experienced by larvae from the open-canopy treatment may manifest itself later in life (e.g., Pahkala et al. 2001; De Block and Stoks 2005). Short-term, positive latent effects, such as the compensatory growth I saw in *R. sylvatica*, can have negative consequences later in life (reviewed by Metcalfe and Monaghan 2001), and I would have been unable to detect these negative effects. Overall, the forest harvesting treatments induced opposing changes in the fitness correlates of *R.*

sylvatica at the larval and juvenile life stages, and *R. sylvatica* from the partial treatment were most fit through the end of their first active season.

The different reactions of each species to the harvesting treatments are probably related to differences in behavior and physiological tolerances. Although both *R. pipiens* and *R. sylvatica* regularly use the terrestrial environment during the activity season, they differ in their maximum and minimum lethal temperatures, capacity to withstand dehydration, locomotor ability, habitat preferences, and body size (Hinshaw 1999; Knox 1999; Redmer and Trauth 2005; Rorabaugh 2005). For example, *R. sylvatica* larvae metamorphose after 65-130 days, juveniles disperse up to 1.5 km, hibernate terrestrially, can withstand subfreezing temperatures, and emerge to breed during snowmelt (Redmer and Trauth 2005), whereas *R. pipiens* metamorphose after 90-180 days, juveniles disperse up to 5.2 km, hibernate in ponds and streams, are freeze intolerant, and do not become active until water temperatures reach 7-10°C (Rorabaugh 2005).

Environmental gradients (e.g., canopy cover, hydroperiod) influence amphibian community composition and population dynamics (deMaynadier and Hunter 1995; Skelly et al. 1999; Snodgrass et al. 2000; Werner et al. 2007a,b), and the selective pressure that some of these environmental gradients exert is beginning to be appreciated and formalized into theory (Relyea 2002a; Rudolf and Rödel 2007). The terrestrial environment is used for dispersal, foraging, and overwintering in many amphibian species (e.g., Semlitsch and Bodie 2003), and variation in the terrestrial environment may be an important selective pressure to maintain plasticity in fitness correlates in amphibians. Both species are distributed across the mid- and northern latitudes of North America, and both species encounter a variety of aquatic and terrestrial conditions

(Redmer and Trauth 2005; Rorabaugh 2005). It is likely that the variation in terrestrial conditions experienced by these amphibian species is as important as the aquatic conditions for structuring life history trade-offs. Additionally, phenotypic plasticity at the terrestrial stage, such as that that I have shown for *R. pipiens* and *R. sylvatica*, is likely to exist in other species that exhibit such an ontogenetic niche shift. However, environmental variation at the terrestrial stage has largely been ignored in theoretical models and is an avenue for future research.

Phenotypic plasticity is likely to be more prevalent in species that exploit unpredictable environments. In particular, recent models predict that amphibians inhabiting ephemeral aquatic environments should show plasticity (Roff 1996; Day and Rowe 2002; Rudolf and Rödel 2007). The ephemeral, fish-free ponds *R. sylvatica* uses for breeding are inherently unpredictable given their variable hydroperiods, food resources, and population densities (Pfennig et al. 1991; Rudolf and Rödel 2007). Plasticity in time to metamorphosis should be advantageous in unpredictable environments where costs to remaining in the larval environment can be high (Richter-Boix et al. 2006). In contrast, *R. pipiens* breeds in ponds with longer hydroperiods and their larvae are less likely to experience the high degree of environmental stochasticity experienced by larval *R. sylvatica*. *Rana pipiens* generally fits with the predictions of the classic models of Wilbur and Collins (1973), Werner and Gilliam (1984), and Werner (1986; i.e., that an animal should grow to an optimal body size rather than metamorphosing into an unknown terrestrial environment). Hence, the differences in plasticity I observed at the larval stage are likely to be a product of the different selective pressures that have acted on these two species.

In summary, the forest harvesting treatments induced opposing changes in the fitness correlates of larval and juvenile *R. sylvatica* but not *R. pipiens*, and these results were largely predictable using knowledge of the life history of each species. Empirical evidence from other species of amphibians indicates that strong, negative latent effects of size at metamorphosis and timing of metamorphosis are the typical response of amphibians to environmental stochasticity (e.g., Altwegg and Reyer 2003; Capellán and Nicieza 2007), but I did not detect these negative effects. Instead, *R. sylvatica* compensated for sub-optimal growth and a shorter larval stage with a longer juvenile duration and attained the same final mass at the end of their first active season. Given the recent development of models including threshold effects and costs to prolonging larval duration (Day and Rowe 2002; Rudolf and Rödel 2007), predicting and testing how different species react to different forms of unpredictable environments should be a productive avenue for future research.

CHAPTER 4

FOREST MANAGEMENT ALTERS MULTI-SCALE HABITAT SELECTION AND BREEDING SUCCESS OF WOOD FROGS (*RANA SYLVATICA*)

Abstract

Animals select habitats that maximize their individual lifetime fitness, and the fitness potential of a habitat is the effect of this habitat on an individual's survival and reproduction. To understand the mechanisms underlying fitness potential of a habitat, I conducted two studies of *Rana sylvatica* at key points in its life history. First, I used radio-telemetry data collected on 72 adult frogs and logistic regression modeling to assess habitat selection at three scales (seasonal home range, weekly activity center, daily microhabitat) in multiple seasons in response to an unharvested control and three forest management strategies: clearcutting (with removal of all merchantable timber > 10 cm diameter), clearcutting with coarse woody debris retention, and partial harvesting with removal of < 25% canopy cover. Second, I used observations of adults in two populations and a logistic regression model to assess the breeding success of individuals captured in each treatment in this managed forest. Over the course of two tracking periods, radio-transmittered frogs selected the partially harvested treatment, tended to select the unharvested treatment, and spent 5 ± 2 days longer in these forested treatments than in the clearcut treatments (with and without coarse woody debris retained). The best supported model indicated frogs were more likely to occupy weekly activity centers with more complex ground structure. Daily microhabitats selected by individual frogs varied greatly, but frogs selected microhabitats with higher canopy cover, more complex ground

structure, and moist but not wet substrates. Of the 180 frogs that I captured entering two breeding ponds, 61 bred successfully, and larger frogs and frogs from the forested treatments were more likely to breed. My data suggest that *R. sylvatica* respond to habitat at multiple scales and that their habitat selection may influence their fitness. In particular, the fitness potential of the clearcut treatments is lower than that of the forested treatments. Furthermore, coarse woody debris retention, especially in clearcuts, should ameliorate some of the effects of harvesting, and partial harvesting with removal of < 25% canopy cover is a forest management strategy that may not adversely influence the abundance or fitness of *R. sylvatica*.

Introduction

A keystone of ecological theory is that animals select habitats that maximize their individual lifetime fitness (Fretwell and Lucas 1970) through their effect on reproduction and survival (Fisher 1930). Further, the fitness potential of a habitat is the effect of this habitat on an individual's survival and reproduction (Weins 1989). Factors influencing habitat selection include all components that constitute the animal's realized niche, such as interactions with conspecifics, predators, and prey, and avoidance of physiological stress (Hutchinson 1957; Leibold 1995). Any of these factors can lead organisms to make choices leading to sub-optimal fitness.

The mechanisms underlying fitness potential of a habitat are tied to the ways in which the habitat affects the physiology and morphology of an animal at key points in its life (van Noordwijk 1989; Lauck 2005). Animals that move to exploit transient habitats (e.g., ephemeral ponds) typically have a high degree of phenotypic plasticity in correlates

of fitness (e.g., body size, timing to key developmental points; Rudolf and Rodel 2007). Although this plasticity may allow an individual to survive in multiple habitats, plasticity can have costs. For example, among wood frog (*Rana sylvatica*) tadpoles living in the absence of *Anax* sp. dragonfly predators, individuals with greater plasticity for muscle depth and muscle width had lower survival, whereas individuals with greater plasticity for tail length, body depth, and activity had higher survival (Relyea 2002). Measuring fitness in individuals with different phenotypes in multiple habitats can contribute toward an understanding of the mechanisms underlying habitat selection and the costs associated with plasticity.

Selection of different resources might be one mechanism for maximizing fitness. For example, small bluegill (*Lepomis macrochirus*) living in the presence of largemouth bass (*Micropterus salmoides*) reduced predation risk by selecting highly vegetated areas (Werner et al. 1983). Habitat selection can be thought of as a hierarchical process in which habitat relationships can be measured along a continuum of spatial scale (Johnson 1980; Addicott et al. 1987; Hobbs 2003; Boyce 2006). For example, a habitat component that is highly selected at a fine scale might be unused if it is located in an environment without all other requirements for that organism (Ciarniello et al. 2007). Additionally, different individuals can value resources differently. An individual's valuation of a resource (measured through use) depends partly on the availability of resources to that individual and partly on the perceived risks of negative interactions with conspecifics and predators. This individual variation can allow some animals to exploit sub-optimal environments, although theoretical models and empirical results indicate that this

behavior should incur fitness costs (Fretwell and Lucas 1970; Werner and Hall 1988; DeBlock and Stoks 2005).

Amphibian populations are declining globally, and these declines are due primarily to habitat loss and alteration, which in some cases results from logging forests (Blaustein et al. 1994; Semlitsch 2000; Stuart et al. 2004). Amphibians are sensitive to local environmental changes because they have the following traits: ectothermy; moist, permeable skin, eggs, and gills; exposure to aquatic and terrestrial environments; a high degree of philopatry; and relatively small home ranges and limited dispersal ability (Blaustein et al. 1994; deMaynadier and Hunter 1995; Lauck 2005). Natural changes in forested environments, such as loss and regeneration of canopy trees, alter amphibian habitat in ways that change the amphibian community (Skelly et al. 1999; Werner et al. 2007), and similarly, forest management for timber production can affect amphibian species because logging results in decreased canopy cover and an altered forest floor environment (deMaynadier and Hunter 1995; Patrick et al. 2006). For example, clearcut areas typically have increased soil temperatures, decreased amounts of leaf litter, and different soil moisture characteristics (Hatchell et al. 1970; Gent et al. 1983; Johnson et al. 1985; Pough et al. 1987; Dahlgren and Driscoll 1994; Ash 1995). These habitat changes can result in reductions in abundance of many, but not all, amphibian populations (Pough et al. 1987; DeMaynadier and Hunter 1999), and habitat changes can lead to suboptimal fitness in some amphibian species. For example, components of fitness (i.e., survival and reproductive output) in the newts *Triturus cristatus* and *T. marmoratus* can be lower in fragmented landscapes (Jehle 2000).

Linking measures of the fitness potential of a habitat to responses of amphibians to habitat changes may be complicated because habitat quality for amphibians may be weather-dependent. For example, the movements of red-legged frogs (*Rana aurora*) through clearcuts were influenced by the presence of 3-m wide streams, temperature, and precipitation (Chan-McLoed 2003), and an inter-annual increase in abundance of western red-backed salamanders (*Plethodon vehiculum*) in a thinned area was attributed to increased annual precipitation (Grialou et al. 2000). These examples and other results indicate that the changes in habitat quality resulting from forest harvesting are likely to be mediated by weather patterns and local landscape attributes (Waldick et al. 1999; Russell et al. 2002; Fogarty and Vilella 2003; Jansen and Healey 2003; Rothermel 2004; Timm et al. 2007).

Many of the documented declines of amphibian populations in different habitats are based on relative abundance data (e.g., captures per trap night). However, measures of relative abundance may misrepresent differences in habitat quality for many reasons (e.g., social factors; van Horne 1983), and the relationship between habitat quality and weather variables (e.g., temperature and precipitation) may invalidate such indirect measures of habitat quality (MacKenzie and Kendall 2002). Measuring the response of individuals, rather than a population, can alleviate some of these problems by creating a direct link between an individual's correlates of fitness and the habitat characteristics and weather conditions experienced by that individual at a specific time. Additionally, it is preferable to measure habitat selection for individuals to incorporate individual variation in resource use and availability (Aebischer et al. 1993).

I conducted two studies to link habitat relationships to reproductive success in *Rana sylvatica* (Wood Frog) within a forested environment managed for timber production. First, I used radio-telemetry data to assess habitat selection by adults at three scales in response to three forest management strategies: clearcutting, clearcutting with coarse woody debris retention, and partial harvesting with 50% canopy retention. Second, I used observations of adults in two different populations to assess the breeding success of individuals in these managed forests.

Materials and Methods

Experimental forest harvesting arrays

I used forest-harvesting arrays that incorporated an unharvested control (unharvested forest stand; hereafter "unharvested") and three common forest management strategies (clearcut with coarse woody debris [CWD] removed ["removed"], clearcut with CWD retained [actual retention 45.6 ± 21.6 m^3/ha {mean ± SE}; "retained"], and partial harvest with 50% canopy closure [actual 53.0 ± 33.5%; "partial"]). The experimental arrays were located on the University of Maine Dwight B. Demeritt and Penobscot Experimental Forests (Penobscot County, Maine, USA, 44° 50' N, 68° 35' W) and replicated four times. Each array was a 164-m radius circle centered on a ~ 80 – 530 m^2 vernal pool with the treatments constituting four 2.1 ha sectors around the pool. The hydroperiod of the vernal pools was lengthened to ensure adequate reproduction of focal species by adding pond liner in one case and deepening the three others to 25 – 40 cm with a backhoe. The four treatments were randomly placed with the exception that the partial was always across the pool from the unharvested treatment (see

Patrick et al. 2006 for a complete description of the arrays and harvests). Forest harvesting was completed in April 2004.

Wood frog habitat relationships

Rana sylvatica inhabits tundra, subalpine woodlands, willow thickets, marshes, bogs, and coniferous and deciduous temperate forests (Redmer and Trauth 2005; Lee-Yaw et al. 2008). Its habitat needs vary with season (e.g., Baldwin et al. 2006; Rittenhouse and Semlitsch 2007), and the active season is normally April to November in the northeastern United States (Regosin et al. 2003; Regosin et al. 2005; Redmer and Trauth 2005). Breeding habitat typically is vernal pools, but also includes other still, fish-free waters such as natural backwater stream pools and anthropogenic road-side ditches (Knox 1999; Redmer and Trauth 2005). In late spring and early summer, adults disperse from breeding sites into moist habitats such as marshes, bogs, stream drainages, and forested wetlands (Heatwole 1961; Herreid and Kinney 1967; Vasconcelos and Calhoun 2004), and the distance and timing of post-breeding dispersal depends on availability of such habitats (Roberts and Lewin 1979; Baldwin et al. 2006; Rittenhouse and Semlitsch 2007). Adults are philopatric to the pond where they first breed (Berven and Grudzien 1990), and tend to remain in a restricted area (Bellis 1965). Warmer temperatures, high relative humidity, and prey availability stimulate summertime movement and activity (Bellis 1962; Heatwole 1961). For example, *R. sylvatica's* mean distance moved was 11.2 m (N = 298) between captures with home range sizes from 2.9 – 368.3 m^2 (mean = 64.5 m^2) during the post-breeding season in Minnesota (Bellis 1965). *Rana sylvatica* can tolerate freezing (Layne and Lee 1986), and hibernacula generally are in upland forests

with moist or dry soils under decomposing logs, stumps, leaf litter, rocks, and thick accumulations of moss (Heatwole 1961; Bellis 1961a; Roberts and Lewin 1979; Schmid 1982; Layne et al. 1990; Licht 1991; Pinder et al. 1992). Hibernating *R. sylvatica* have been found at densities of 0.75 ± 0.5 frogs / 100 m^2 (mean ± SD; Regosin et al. 2005).

Post-breeding habitat selection of *R. sylvatica* has been studied in the wild and experimentally (e.g., Licht 1991; Baldwin et al. 2006; Rittenhouse and Semlitsch 2007). These frogs selected for land over water at all temperatures in experimental trials (Licht 1991). Presence of *R. sylvatica* was correlated with deciduous leaf litter, extensive ground cover (e.g., tall herbs/shrubs/grasses), and moist soil in the boreal forest of Alberta, Canada (Constible et al. 2001) and ephemeral drainages in Missouri (Rittenhouse and Semlitsch 2007). During the nonbreeding season in southern Maine, *R. sylvatica* selected moist *Sphagnum*-dominated hummocks and leaf litter retreats on the margins of pools, and summer refugia were shaded, moist, *Sphagnum*-dominated microhabitats (Baldwin et al. 2006).

All life stages of *R. sylvatica* are sensitive to the edges and reduced canopy cover created by forest harvesting in the eastern United States (deMaynadier and Hunter 1998; Gibbs 1998a,b; Werner and Glennemeier 1999; Guerry and Hunter 2002; Patrick et al. 2006). In my experiment, I expected *R. sylvatica* to avoid both clearcuts because of their low thermal tolerance and preference for forested environments (e.g., Heatwole 1961; Bellis 1962, 1965; Brattstrom 1968). Additionally, I expected frogs to select for areas with higher percent canopy cover within the forested treatments (Baldwin et al. 2006).

Wood frog breeding system

Breeding by *R. sylvatica* is explosive with all breeding activity occurring in as few as 3 days, usually in April or May in Maine (Knox 1999; Redmer and Trauth 2005). Males mature 1 – 2 years after metamorphosis, and females mature in 2 – 3 years (Bellis 1961b; Howard 1980; Berven 1990), but age at maturity and maximum age vary with geography (e.g., temperature, growing season, elevation) (Berven 1982a,b). Age may be more variable in males than females with earlier maturity reducing the life span of males (Bastien and LeClair 1992). The estimated maximum age of males is 3 – 4 years and 4 – 5 years for females (Bellis 1961; 1965; Berven 1982a; Bastien and LeClair 1992; Sagor et al. 1998; Redmer and Trauth 2005).

Mate choice in *R. sylvatica* occurs by male-male competition for females in the breeding aggregation, and female choice is not known to occur (Berven 1981; Howard and Kluge 1985). Males change mating strategy from stationary calling to active searching and calling with increased density of males at the breeding aggregation (Phillips and Wade 1990; Woolbright et al. 1990). Although overall male breeding success is largely a function of the sex ratio at the breeding pool (Howard 1980; Howard and Kluge 1985), large males can have greater reproductive success in some populations, and the offspring of large males have higher fitness in some other amphibian species (Elmberg 1990; Woodward 1987). Males of all sizes prefer large females, sometimes ignoring the smallest females, potentially because a size mismatch may lead to lower fertilization (see review by Krupa 1988) or because of the fitness advantage gained by selecting a large female (see review by Krupa 1995). The number of ova produced increases with body size in female *R. sylvatica* (Howard and Kluge 1985), and older

females produce larger ova (Berven 1988). Fitness also may be higher in anuran offspring from larger clutches or eggs (Kaplan 1980).

I expected to see differences in the size and body condition of *R. sylvatica* among the four treatments at reproductive maturity in the following pattern: removed < retained < partial < unharvested treatments. Because male *R. sylvatica* prefer large females and larger males have higher reproductive success, this expected size difference should make males of all treatments prefer "unharvested" females, and "unharvested" males should show the highest reproductive success.

Habitat selection study

I tracked 40 adult *R. sylvatica* during 3 May – 7 June 2005 and 32 adults during 30 September – 7 November 2006. Additionally, I tracked 10 adults during 24 September – 13 October 2004 in a pilot study to determine habitat variables with substantial variability and to determine general movement patterns. I tracked individuals only early and late in the activity season because this allowed us to assess migrations to summer habitat and hibernacula (Baldwin et al. 2006). In the spring, I captured these individuals as they emerged from the breeding pools; in the fall, captures were in or near the experimental arrays (< ~ 300 m from the central breeding pool; Baldwin et al. 2006), and I used only animals that were of known breeding size (> 40 mm SVL). I fit each individual with a radio-transmitter (BD-2 model, 0.9-g, 14-cm external whip antennae, 40-day battery life; Holohil Systems, Carp, Ontario, Canada) with elastic thread beaded with glass beads snug enough to prevent slippage over the rear legs when extended but not so snug as to constrict the skin (Muths 2003; Weick et al. 2005; Blomquist and

Hunter 2007). I released individuals within each treatment approximately 10 m from the edge of the pool and equidistant from adjacent treatments, and I located each frog daily by homing during daylight hours with a R-1000 receiver (Communications Specialists, Orange, California, USA) and yagi antenna. I placed a pin flag next to the frog's location to ease subsequent relocations and marked all movements > 15 cm with a flag. If a frog could not be located visually for five consecutive days, I triangulated its position and confirmed the location and condition of the frog. I mapped each movement with a compass and tape measure from known locations in each experimental array.

I used ArcGIS 9 (Environmental Systems Research Institute, Redlands, California, USA) and Hawth's Analysis Tools (available at http://www.spatialecology.com/htools) to calculate 100% minimum convex polygon (MCP) home ranges, use, and availability of habitat to evaluate 2nd-order resource selection over the duration of the fall and spring tracking periods. I calculated a 100% MCP rather than a 95% MCP to estimate home range size for each frog that moved to at least three unique locations because it is assumed that by removing 5% of the points from a sample of locations will remove outlying points that reflect movements unusual movements (e.g., mate-searching, foraging on a specific resource) from the area calculated; this assumption is not necessary for *R. sylvatica* during distinct portions of their active season (Baldwin et al. 2006). I refer to the minimum convex polygon I estimated for the spring and fall studies as home ranges. These home ranges possibly exclude summer habitat and are more accurately referred to as seasonal home ranges because these minimum convex polygons may represent only two portions (post-breeding and overwintering habitat) of the annual home range required for the survival of *R.*

sylvatica (Baldwin et al. 2006). I used this simple home range estimator in preference to probabilistic estimators because the number of relocations I could obtain on each frog (ca. 30) was unlikely to accurate estimation of home range size with these estimators (e.g., Worton 1995; Seaman and Powell 1996). I calculated availability of habitat for each frog by simulating ten home ranges within the experimental array. I assumed the entire experimental array was available to the frogs over the duration of the fall and spring tracking periods. Each home range was defined by the number of relocations for a given frog and the number of points in each harvest treatment was extracted and averaged across the ten home ranges to yield the availability of habitat for that frog.

I collected data at paired frog and random locations to assess post-breeding habitat selection at two smaller scales that differ temporally and spatially, daily microhabitat and weekly activity centers (Heatwole 1961; Bellis 1965). I attempted to control for spatial and temporal independence of locations by quantifying movement patterns in the 2004 pilot study and using the estimated distances moved and timing of movement during this pilot study as well as existing information on behavior of *R. sylvatica* to design my habitat sampling. Twenty-six and 310 m were the outer quartile of the distribution of daily movements and longest movement respectively made by *R. sylvatica* in the 2004 pilot study, and thus the random points at these distances were assumed to be available to the frogs on a daily and weekly basis respectively. Additionally, I estimated that frogs moved to new locations every 6 – 90 h (mean 34 h) in the 2004 pilot study. However, *R. sylvatica* was primarily nocturnal and most movements occurred at night (see also Baldwin et al. 2006; Rittenhouse and Semlitsch 2007; R. Baldwin and T. Rittenhouse, personal communication). I assumed daily locations were

independent and that remaining in the same location on successive days represented choice. If this assumption is invalid, my sampling procedure would overestimate the importance of variables that were characteristic of locations where frogs remained for multiple relocations (Erickson et al. 2001).

For both the daily microhabitat and weekly activity centers scales, I evaluated habitat use and availability using 14 variables (Table 4.1) collected at the center of a 1-m^2 hexagonal plot centered on the frog's or random point's location. I chose these variables based on previous work on habitat relationships, the ecology and physiology of *R. sylvatica* and other anurans, and the 2004 pilot study (Thorson 1955; Jorgensen 1997). I measured percent cover variables because other species of amphibians selected habitat based forest, vegetation, or ground structure (Griffin and Case 2001; Bartelt 2000; Seebacher and Alford 2002), and temperature and moisture variables may be important because of the permeable skin and poiklothermic nature of amphibians (Heatwole 1961; Licht 1991; Feder and Burggren 1992). For each daily frog location, I gathered the same data at a random point 1 – 26 m from the frog's location, located by choosing a compass bearing and distance from a random number table and pacing the selected distance. Data at each random daily point were collected < 15 minutes after collecting data for the frog's location. To assess habitat availability at the weekly activity center scale, every 6^{th} day I collected data from five random points within a 26-m radius circle positioned 50 – 310 m from the frog's location. I chose the centers of each circle in ArcGIS 9, and if random activity centers overlapped, I reselected new locations.

Table 4.1. Habitat variables collected in 1-m^2 plots to quantify habitat use and availability in *Rana sylvatica*. I collected each variable at the frog's location and at a random location each day (daily microhabitat) and at a set of random points every five days (weekly activity centers). Variables were collected at the center of each plot unless otherwise specified. Percent cover variables were estimated to the nearest 5%.

Variable	Code	Description
% canopy	CC	Percent canopy cover above plot measured with a GSR vertical densiometer
% litter	LI	Percent cover of leaf litter
% standing water	SW	Percent cover of standing water
% *Sphagnum* spp.	SP	Percent cover of *Sphagnum* mosses
% vegetation	VC	Percent cover of vegetation < 0.5 m
% slash	SL	Percent cover of woody debris 2 - 10 cm diameter
Litter moisture	LM	Moisture of leaf litter (1 - dry, 2 - moist, 3 - wet)
Soil moisture	SM	Volumetric water content of soil (Field Scout TDR 200 with 12-cm probes)
Litter depth	LD	Depth (mm) of the litter layer
CWD present	CP	Presence of downed wood > 10 cm diameter
CWD decayed	CD	Coarse woody debris decayed > class 1 (Maser et al. 1979)
Temperature	TE	Temperature (degrees C) at ground surface collected with a Oakton 35612 thermohygrometer (daily microhabitat) or mean daytime (0630-1830 h) temperature from HOBO dataloggers in each treatment (weekly activity centers)
Relative humidity	RH	Relative humidity measured with a Oakton 35612 thermohygrometer (daily microhabitat only)
Dominant cover	DC	Ground cover type in 15 cm circle at center of plot (daily microhabitat only) (0 - bare soil/rock, 1 - wood, 2 - grasses/forbs, 3 - leaf litter, 4 - *Sphagnum* spp., 5 - water)

Breeding success study

I captured (drift fences and by hand) adult *R. sylvatica* returning to breed in April 2007 at the Gilman and Smith experimental arrays (see Patrick et al. 2006 for a description of the drift fence arrangement). Each vernal pool at these sites is ~ 80-m^2 and had little woody vegetation, which allowed for relatively easy observation of courtship behavior and oviposition. Wild frogs at these arrays should have spent the majority of their life span in the experimental array, and I assumed that if a frog was captured in a given treatment that it spent a large portion of its life in that treatment (at least a portion of the previous season and then hibernated there). If this assumption is wrong, my assessment of the effect of harvest treatment on breeding success becomes more conservative because the additional variation should reduce any treatment effect. I tagged all frogs with a sterile 12-mm passive integrated transponder (PIT tag; 134.2 kHz ISO tag; Model TX1411SST, Digital Angel Co., St. Paul, Minnesota, USA) following the scapula insertion technique (Blomquist et al., in press), and I removed the distal and second phalange from the fifth toe of the right rear foot (i.e., the 50 toe of the Martof [1953] system; Heyer et al. 1994) for skeletochronology. Frogs were held in captivity for < 9 h prior to release at ~ 1 h before sunset. Nightly during 22 April – 2 May I visually located amplexing pairs with a spotlight and by scanning the surface of the water with a custom-designed transceiver and antenna system (PIT-pack; Hill et al. 2006; Kurth et al. 2006; Blomquist et al., in press). I identified both members of each located pair with the PIT-pack without disturbing the frogs. I relocated the pair visually and with the PIT-pack until the female oviposited. I defined successful pairs as those that were observed to

oviposit and assumed that breeding success and egg laying were indicative of reproductive success (Howard 1979).

The University of Maine's Veterinary Diagnostic Laboratory prepared toes for skeletochronology following well-established protocols (e.g., LeClair and Castanet 1987; Bastien and Leclair 1992). Toes were placed in Cal-EX™ II decalcifying/fixing agent (Thermo Fisher Scientific, Worcester, Massachusetts, USA) for 24 h, rinsed in tap water for 1 h, and fixed in 10% buffered formalin fixative until processed. Water was removed from each toe over 16.5 h by serially rinsing in de-ionized water, 70% ethanol, 95% ethanol, 100% absolute ethanol, and xylene, and embedded in paraffin for sectioning. The diaphyseal portion of the distal and second phalange was cross-sectioned at a thickness of 5 μm, and a series of cross-sections were de-paraffinized over 28 min by serially rinsing in xylene, 100% ethanol, 95% ethanol, 70% ethanol, and tap water, and stained for ~ 30 min in Ehrlich's hematoxylin. Stained sections were rinsed in tap water, placed in ammonia bluing for 1 min, and rinsed in tap water again. Each section was examined on a slide and re-stained or de-stained as needed before mounting in Flo-texx mounting media (Lerner Laboratories, Pittsburgh, Pennsylvania, USA).

I examined at least five mid-diaphyseal sections from each frog for lines of arrested growth (LAGs) at 400× magnification with a compound microscope. I added one additional LAG to all counts to represent the new LAG being formed at the outer perimeter of the phalange because *R. sylvatica* caught during the breeding season had not formed new bone after emerging from hibernation. In a temperate region such as Maine, LAGs should represent distinct activity seasons and be an adequate reflection of age in a

short-lived species, such as *R. sylvatica*, which has little time to reabsorb LAGs (see review by Halliday and Verrell 1988).

Statistical analyses

I analyzed habitat selection at three spatiotemporal scales: 2nd-order habitat selection at the scale of the home range over the entire duration of the spring and fall studies, 3rd-order selection of weekly activity centers, and 4th-order selection of daily microhabitats (Johnson 1980). The home range sizes and number of relocations for each animal were not normal based on histograms, skewness, and kurtosis of each variable, and therefore I transformed home range sizes with natural logs to meet the assumptions of normality. I used analysis of variance (ANOVA; PROC GLM) to test if home range size varied with season, experimental array, or sex. I calculated a selection index for each treatment by dividing the number of relocations for each frog by the number of random points from simulated home ranges that fell in that treatment (i.e., use divided by availability; Manly et al. 2002). I centered this selection index on zero by calculating the natural log (Manly et al. 2002). To test if this selection index varied among the harvest treatments, I used a Kruskal-Wallis nonparametric ANOVA (WILCOXON option in PROC NPAR1WAY). I used a sign test (PROC UNIVARIATE) to test if the mean selection index from each treatment deviated from zero. I did not use a proportional habitat selection analysis (e.g., compositional analysis) at this scale because 58% (160 of 276) of the cells in the matrix were zeros, and replacing these with a small non-zero proportion (0.0001) would inflate the Type I error rate (Aebischer et al. 1993; Bingham

and Brennan 2004). I conducted all statistical analyses in SAS (version 9.1, SAS Institute, Cary, North Carolina, USA) with $\alpha = 0.05$ unless otherwise specified.

I used conditional logistic regression to compare the mean microhabitat conditions at the frog locations over a 5-day period to the mean of the five points collected at the randomly positioned activity center to assess habitat selection in weekly activity centers (PROC PHREG). I used two strata (week [N = 12] and experimental array [N = 4]) in this analysis to incorporate variability associated with the structure of my habitat sampling. Prior to constructing my models, I screened the 13 possible variables by checking each variable for linearity, univariate significance, and correlation with other variables (Hosmer and Lemeshow 2000). I linearized the logit by defining a threshold for canopy cover at 60% for the activity center analysis based on a univariable plot of the lowess-smoothed logit (Hosmer and Lemeshow 2000). Canopy cover was incorporated into the models as a categorical variable. All other variables were linear. No variables were highly correlated (all $r < 0.6$), but I incorporated variables that were non-significant individually only as modifiers of other variables in candidate models. I constructed 16 candidate models that incorporated possible combinations of temperature, moisture, and forest structure variables (Table 4.2) and used AIC_c and Akaike weights (ω_i) to rank these models and select which model(s) best described *R. sylvatica* activity center selection (Burnham and Anderson 2002). I considered models with $\Delta AIC_c < 2$ to be equally supported. After selecting the best model(s), I incorporated 15 plausible, second-order interactions (CP×ST, LD×LM, LD×ST, LI×LM, LI×SL, LI×SM, LI×ST, SL×ST, CP×SM, LD×SM, SW×SM, ST×SM, VC×LM, VC×SM, VC×ST) individually into the top models(s) and reassessed support for these models including the interactions

Table 4.2. Groupings of habitat variables used in construction of models describing activity center habitat selection by *Rana sylvatica*. Variable codes and descriptions are presented in Table 4.1.

Group name	*K*	Variables
Moisture	4	SW, SP, LM, SM
Low cover	7	SP, VC, LI, SL, LD, CP, CD
High cover	1	CC
Treatment	6	CC, LI, SL, LD, CP
Temp	1	TE

relative to the best model(s) without interactions. I again ranked models using AIC_c and incorporated all interactions that had a lower AIC_c value than the best model without interactions into the final model. If more than one model was supported ($\Delta AIC_c < 2$), I used model averaging to derive parameter estimates (Burnham and Anderson 2002). I used this step-by-step approach because the number of coefficients to be estimated and models run are large if plausible interaction terms are included (28 possible coefficients and > 100 models), even though my data set is also large. Philosophically, this approach is similar to path analysis, in which interactions between particular species are either included or excluded at different stages in the analysis (e.g., Wootton 1994; Ives et al. 1999).

To assess daily microhabitat selection, I modeled each frog individually. I used paired logistic regression (PROC LOGISTIC) to compare the relative selection made by individuals based on differences between the frog location and the paired random location (e.g., Compton et al. 2002; Moore and Gillingham 2007). To make the logit linear, I defined thresholds for vegetation cover at 30%, standing water cover at 40%, slash cover at 30%, and litter depth at 80 mm for the daily microhabitat analysis based on univariable plots of the lowess-smoothed logit (Hosmer and Lemeshow 2000). These

variables were incorporated into the candidate models as categorical variables. All other variables were linear.

I modified my process for development of candidate models for weekly activity centers by adding a variable screening process to account for the relatively small sample size for each individual (N = 20 – 32). I used stepwise model selection with entry and exit criteria of one to narrow the range of model sizes (i.e., number of variables) to include in my candidate model set for each frog (Shtatland et al. 2001; Campbell 2007). This process uses the sequential models built by stepwise model selection to build successively larger models until all variables are entered. The AIC_c values are then plotted and candidate models within a chosen range of the model size with the lowest AIC_c value are built. Shtatland et al. (2001) recommend this procedure as a method for automated model selection from large data sets. However, this automated process follows an "all subsets" procedure that violates the spirit of the information-theoretic approach, and, hence, I used this procedure only as an additional variable screening process (Anderson and Burnham 2002). I considered model sizes with $\Delta AIC_c < 4$ and built ten candidate models for each frog within the range of model sizes. This liberal cutoff allowed models with less support than the typical cutoff of $\Delta AIC_c < 2$ to be included in my candidate model building process and allowed us to include groups of variables that may be important to *R. sylvatica* habitat selection (e.g., Table 4.2).

I used the standardized parameter estimates (β_s) for each variable and frog to draw inferences about how habitat selection varied among individuals in the population. I used the standardized parameter estimates for each variable as the measure of habitat selection. These measures were replicated by using each frog as an independent unit and the sample

size is the number of frogs whose top model(s) included a given variable (e.g., Marzluff et al. 2004). The standardized parameter estimates for most variables were normal based on histograms, skewness, and kurtosis of each variable, but I transformed percent canopy cover, percent leaf litter cover, and percent *Sphagnum* spp. cover, leaf litter moisture, and coarse woody debris decay. I used multiple linear regression (PROC GLM) to test if habitat selection varied with the harvest treatment in which the frog spent the most amount of time, experimental array, season, or sex across each variable. I used a Bonferonni correction to control for Type I error inflation ($\alpha = 0.005$) across variables.

I investigated the frequency distribution of the sexes, age classes, and size classes among the harvest treatments with a Fisher's exact test with a Bonferonni correction ($\alpha = 0.017$). I built a logistic regression model to examine if breeding success was influenced by age, body size (SVL, mass), harvest treatment, or experimental array. Mass was highly correlated with length ($r = 0.90$), so I removed mass from modeling. All other variables were not highly correlated ($r < 0.70$).

Results

Home range estimation and use of harvest treatments

I estimated home range size for 59 of the 72 *R. sylvatica*, excluding 13 frogs that slipped out of their transmitter belt within the first 14 days of tracking. Mean (± SE) 100% minimum convex polygon home range size was 751 ± 228 m^2 (range 3–10745 m^2; Appendix 1), and home range size was not correlated with the number of times the frogs were relocated ($r = 0.1$, $P = 0.468$; Kernohan et al. 2001). Home range size varied with season and experimental array ($F_{5,53} = 7.6$, $P < 0.001$), but not sex. Males (663 ± 254 m^2)

and females (856 ± 401 m^2) had similar size home ranges ($F_{1,53} = 0.1$, $P = 0.825$), but mean home range size in spring (285 ± 94 m^2) was smaller than in fall (1317 ± 501 m^2) ($F_{1,53} = 19.8$, $P < 0.001$). Additionally , the frogs at the North Chemo (70 ± 25 m^2) experimental array had smaller home ranges than the Smith (1094 ± 497 m^2) and South Chemo (1020 ± 364 m^2) arrays ($F_{3,53} = 6.1$, $P = 0.001$; Appendix 2).

On average, frogs spent 14 ± 2, 16 ± 2, 10 ± 1, and 10 ± 1 days in the unharvested, partial, retained, and removed treatments, respectively. Frogs selected the partial treatment ($G_1 = 9.5$, $P < 0.001$) and tended to select the unharvested treatment ($G_1 = 4.5$, $P = 0.162$) more than the other harvest treatments (Kruskal-Wallis $\chi^2_3 = 8.7$, $P = 0.032$) (Figure 4.1). Only two frogs (Frog ID = 35 and 52; Appendix 2) extended their home ranges beyond the edge of the experimental array, but they both were < 25 m beyond the edge of the array; the movements occurred late in each study and were likely migratory movements from breeding habitat to summer habitat (Frog ID = 35) and movements to hibernacula (Frog ID = 52) (Baldwin et al. 2006). This indicates that my definition of available habitat as the experimental array was acceptable. The eight locations (of 1452) of these two frogs that were outside the array were grouped with the unharvested treatment.

Weekly activity center selection

I collected data at 334 *R. sylvatica* weekly activity centers (spring: 207 and fall: 127) plus 309 random activity centers (spring: 196 and fall: 113); 25 random activity centers were removed because they overlapped frog activity centers. Frogs responded to

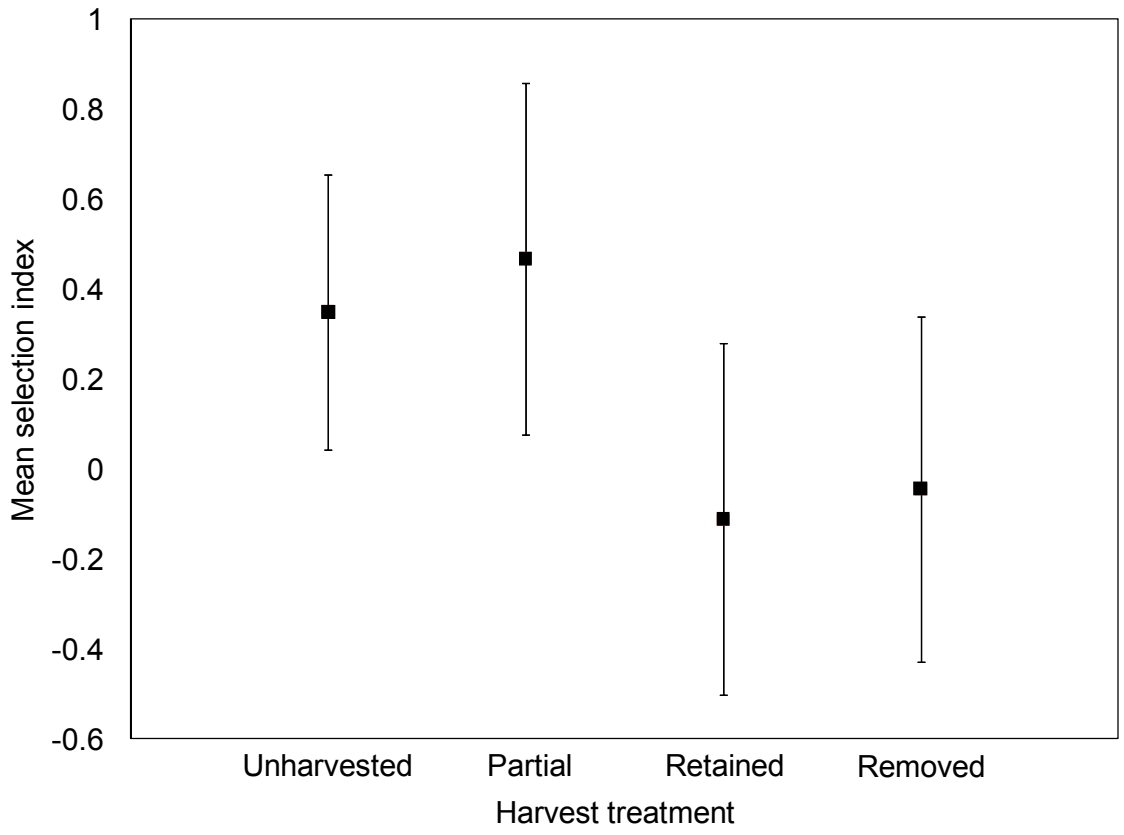

Figure 4.1. Mean (± 95% confidence intervals) selection index calculated from selection indices (natural log of [# of locations in a treatment / random locations in the same treatment]) for all *Rana sylvatica* that used each harvest treatment. Frogs selected the partially harvested treatment and tended to select the unharvested treatment more than expected based on their availability.

all the habitat variables I measured with the top two models having equal support (Table 4.3). These two models had ~ 20 and 11 times the support as the next best model and comprised 100% of the weight for the candidate model set. The top model focused on cover items close to the ground, moisture, and temperature, and the second ranked model was the global model (Table 4.4). Canopy cover was the only variable that did not overlap between these two models. The global model fit my data (Hosmer and Lemeshow $\chi^2_8 = 10.0$, $P = 0.268$; Cox and Snell $r^2 = 0.39$ for both the top models; Cox and Snell

1989). Unlike at the home range scale, I did not find support for the variables that were manipulated by the harvest treatments (Table 4.4).

Table 4.3. Models of weekly activity center habitat selection in *Rana sylvatica*. Model subsets are defined in Table 4.2.

Rank	Model	*K*	log(ℒ)	AIC_c	ΔAIC_c	ω
1	Low cover, moisture, temp	12	-332.61	689.72	0.00	0.72
2	Global model	13	-332.52	691.62	1.89	0.28
3	Treatment, moisture, temp	9	-345.71	709.69	19.97	0
4	Low cover, moisture	11	-346.26	714.93	25.21	0
5	Low cover, temp	9	-359.66	737.61	47.89	0
6	Treatment, moisture	9	-361.20	738.68	48.95	0
7	Low cover	8	-364.82	745.87	56.14	0
8	Treatment, temp	7	-370.33	754.83	65.10	0
9	Treatment	7	-376.41	765.00	75.27	0
10	Moisture, temp	6	-402.20	816.52	126.80	0
11	High cover, moisture, temp	8	-402.14	818.51	128.78	0
12	Moisture	5	-427.67	865.43	175.71	0
13	Temp	2	-430.74	865.50	175.78	0
14	High cover, moisture	6	-427.35	866.84	177.11	0
15	High cover, temp	3	-430.65	867.34	177.61	0
16	High cover	2	-444.93	893.89	204.16	0

Frogs were 7.5 times more likely to occupy activity centers with coarse woody debris present, but only if this coarse woody debris had started to decay and lose its bark (i.e., decayed > class 1) (Table 4.5). Additionally, frogs were more likely to occupy activity centers with higher amounts of slash. The combination of these three variables (CP, CD, SL) indicates that woody debris > 2 cm creates ground structure that is important to frogs regardless of other environmental conditions. Activity centers with deeper leaf litter and higher percent cover of *Sphagnum* mosses were also more likely to be occupied regardless of other environmental conditions. Canopy cover and percent cover of standing water were not useful for describing *R. sylvatica* habitat selection in weekly activity centers; the odds ratios for these variables overlapped one.

Table 4.4. Model-averaged parameter estimates (β) and mean values for each variable for frog (N = 334) and random (N = 309) activity centers from the top two models of weekly activity center habitat selection in *Rana sylvatica*.

Variable	β	SE_{β}	Wald χ^2	*P*	Random Activity Center	SE_{Random}	Frog Activity Center	SE_{Frog}
Intercept	0.477	2.753	0.030	0.863				
% standing water	0.008	0.011	0.533	0.466	7	1	10	1
% *Sphagnum* spp.	0.027	0.009	8.337	0.004	6	1	9	1
% vegetation	-0.049	0.023	4.690	0.030	23	1	25	1
% litter	0.124	0.035	12.868	0.000	59	1	50	1
% slash	0.028	0.009	11.087	0.001	16	1	21	1
Litter depth	0.040	0.006	45.983	<.0001	30	1	46	2
CWD present	2.004	0.503	15.852	<.0001	0.20	0.01	0.26	0.02
CWD decayed	-1.114	0.308	13.077	0.000	0.39	0.03	0.31	0.03
Litter moisture	2.271	0.769	8.731	0.003	1.81	0.04	2.08	0.03
Soil moisture	-3.457	1.220	8.033	0.005	19	1	21	1
Temperature	-0.713	0.131	29.427	<.0001	13.1	0.4	15.5	0.3
Soil moisture × Temperature	0.346	0.057	36.642	<.0001				
% litter × Soil moisture	-0.036	0.015	6.076	0.014				
% litter × Litter moisture	-0.026	0.010	6.766	0.009				
% vegetation × Litter moisture	0.023	0.011	4.489	0.034				
% canopy *	0.006	0.012	0.252	0.616	37	2	30	2

*estimated from global model only

Table 4.5. Odds ratios from top two models of weekly activity center habitat selection in *Rana sylvatica*. CI = confidence interval.

Variable	Odds ratio	Upper CI	Lower CI
% standing water	1.01	0.988	1.032
% *Sphagnum* spp.	1.028	1.01	1.047
% slash	1.029	1.012	1.047
Litter depth	1.04	1.028	1.052
CWD present	7.586	2.831	20.327
CWD decayed	0.325	0.178	0.595
% canopy*	1.006	0.983	1.029

*estimated from global model

Four of the 15 interactions I considered were supported by model selection and were added to the top model, multiplicative effects between: ground surface temperature and soil moisture, percent cover of leaf litter and soil moisture, percent cover of leaf litter and leaf litter moisture, and percent cover of vegetation and leaf litter moisture (Figure 4.2). The probability of a frog occupying an activity center was greatest if the activity center had ground surface temperatures between 8 – 13°C (Figure 4.2A). Additionally, *R. sylvatica* were unlikely to occupy wet activity centers at temperatures less than 6°C and greater than 19°C. The probability of a frog occupying an activity center increased with leaf litter cover > 60%, especially if the activity center had soil moisture > 40% volumetric water content (i.e., wet soils; Figure 4.2B). Frogs were much more likely to occupy activity centers with < 20% cover of leaf litter (Figure 4.2C) and vegetation cover (Figure 4.2D) if the leaf litter present in the area was moist.

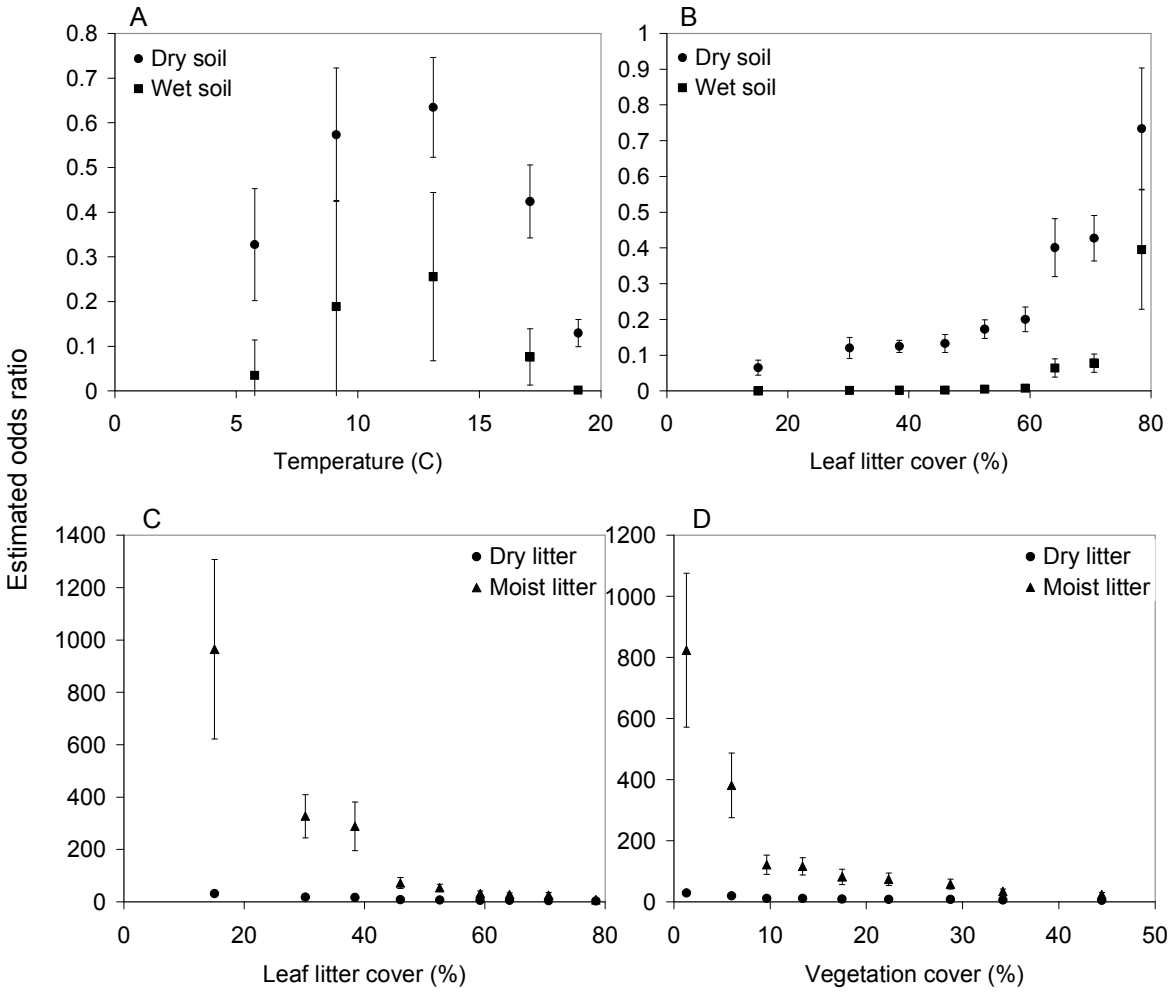

Figure 4.2. Change in odds ratios at two moisture levels for changes in ground surface temperature (A), leaf litter cover (B,C), and vegetation cover (D) for weekly activity center selection.

Daily microhabitat selection

I collected data at 1452 paired *R. sylvatica* and random locations (spring: 831; fall: 621; 2904 total 1-m^2 plots) on 47 frogs (spring: 28 and fall: 19). The best models for individual frogs included only 1 – 3 variables (Appendix 2). Overall, frogs responded to ten of the 14 habitat variables I measured (i.e., those variables were included in at least one frog's best model[s]; Table 4.6). Generally, frogs selected locations with more

canopy cover, more ground structure, and more moisture. However, the range of standardized parameter estimates (β_s) for all of these variables included estimates above and below zero thus indicating that the effect of each variable varied with the individual and the larger context of habitats that individuals experienced during the study. In particular, much of the variation in β_s can be explained by differences in season, experimental array, harvest treatment, and sex (Table 4.6).

Male *R. sylvatica* were more likely to occupy locations with a higher percentage of canopy cover relative to paired random locations (odds ratio = 169.4 ± 7.7), whereas females were 2.6 ± 2.3 times more likely to avoid them (Table 4.6). Frogs at all four experimental arrays were more likely to occupy locations with a higher percentage of canopy cover. However, frogs in the clearcut (removed and retained) treatments appeared to avoid locations with higher percent canopy cover because many of the locations in these treatments were near the vernal pool. Given the location of the vernal pool at the center of the circular array, this density of locations near the pool probably created a bias where the 26-m radius random sampling area contained the edges of the other harvest treatments (Appendix 2).

Frogs selected locations with more woody structure and leaf litter relative to random locations (Table 4.6). The presence of coarse woody debris increased the probability that a frog would occupy a location 3.9 ± 1.5 times. However, this effect varied with harvest treatment, as frogs in the unharvested treatment avoided coarse woody debris (odds ratio to avoid = 8.9 ± 1.1). Decay of coarse woody debris, if present, may increase the probability that a frog would occupy a location, although the variation in this parameter was large (odds ratio = 2.2 ± 2.3). Frogs were 3.8 ± 2.1 times more

Table 4.6. Standardized parameter estimates (β_s) and mean values for frog and random daily locations from the supported model(s) of daily microhabitat selection in *Rana sylvatica* (Appendix 3). N indicates the number of frogs. I show only variation across sex, harvest treatment, experimental array, or season with some statistical support ($P < 0.05$) from multiple linear regression. If < 20 frogs had a variable in their top model set, I tested only for differences among sex and treatment due to inadequate degrees of freedom. I report raw *P*-values, but assess significance using a Bonferonni correction ($\alpha = 0.005$).

Variable		N	Mean β_s	SE β_s	Random Microhabitat	SE_{Random}	Frog Microhabitat	SE_{Frog}
% canopy ($F_{8,22} = 6.2$, $P < 0.001$)		31	2.97	1.44	29	4	44	8
Sex ($F_{1,22} = 11.5$, $P = 0.003$)	F	11	-0.95	0.84	27	5	42	11
	M	20	5.13	2.04	32	6	47	12
Treatment ($F_{3,22} = 6.9$, $P = 0.002$)	Unharvested	13	6.06	2.60	41	3	72	3
	Partial	12	3.03	1.83	28	6	49	7
	Retained	5	-3.74	0.84	17	10	4	4
	Removed	1	-4.28		13		0	
Array ($F_{3,22} = 10.1$, $P < 0.001$)	Gilman	10	8.54	3.94	29	7	51	15
	North Chemo	8	0.51	0.79	33	15	47	24
	Smith	11	0.14	0.45	25	5	36	12
	South Chemo	2	0.59	0.04	41	2	51	2
CWD present ($F_{8,21} = 3.0$, $P = 0.021$)		30	1.37	0.43	0.22	0.04	0.29	0.09
Treatment ($F_{3,21} = 7.2$, $P < 0.001$)	Unharvested	4	-2.19	0.06	0.12	0.12	0.00	0.00
	Partial	16	1.74	0.46	0.24	0.04	0.28	0.14
	Retained	8	2.61	0.87	0.25	0.25	0.46	0.34
	Removed	2	0.48	1.25	0.18	0.05	0.29	0.14
Litter depth ($F_{8,19} = 4.2$, $P = 0.005$)		28	2.31	0.54	30	3	51	7
Treatment ($F_{3,19} = 9.9$, $P < 0.001$)	Unharvested	3	0.19	0.98	28	7	52	15
	Partial	15	1.68	0.59	29	5	48	8
	Retained	1	-1.38		29		29	
	Removed	9	4.47	0.94	32	6	61	17
% leaf litter ($F_{4,8} = 6.8$, $P = 0.011$)		13	2.98	1.22	39	3	52	5
Sex ($F_{1,8} = 17.9$, $P = 0.003$)	F	6	1.22	0.53	41	4	58	6

Table 4.6 Continued.

	M	7	4.49	2.11	37	5	45	7
Soil moisture ($F_{8,14} = 3.0$, $P = 0.036$)		23	1.68	0.92	31	2	35	2
Treatment ($F_{3,14} = 4.0$, $P = 0.031$)	Unharvested	5	0.20	0.45	30	2	39	2
	Partial	7	3.67	2.22	32	1	35	1
	Retained	4	-2.14	2.59	27	6	30	6
	Removed	7	2.95	0.76	33	2	34	5
Array ($F_{3,14} = 3.9$, $P = 0.033$)	Gilman	11	3.93	1.39	33	2	39	1
	North Chemo	3	-2.82	3.62	34	1	36	1
	Smith	8	0.40	0.13	27	3	31	4
	South Chemo	1	0.74		32		35	
% *Sphagnum* spp. ($F_{7,14} = 2.1$, $P = 0.117$)		22	4.05	1.10	4	1	15	4
Treatment ($F_{3,14} = 3.4$, $P = 0.049$)	Unharvested	7	8.52	2.54	6	2	24	5
	Partial	4	-0.07	0.81	2	1	3	2
	Retained	3	1.14	0.45	2	2	8	0
	Removed	8	3.29	0.82	6	3	21	12
% standing water ($F_{4,10} = 0.3$, $P = 0.858$)		15	-1.21	0.33	30	5	17	4
CWD decayed ($F_{7,18} = 0.5$, $P = 0.841$)		26	0.81	0.85	0.59	0.10	1.14	0.26
Litter moisture ($F_{3,8} = 2.5$, $P = 0.137$)		12	1.54	0.96	2.06	0.09	2.25	0.13
% slash ($F_{4,9} = 1.1$, $P = 0.420$)		14	1.34	0.76	20	2	27	3

likely to be found in locations with > 30% percent cover of slash. Frogs were more likely to occupy locations with a greater percent cover of leaf litter and > 80 mm of leaf litter depth, especially in the removed treatment, although the degree to which they exhibited selection varied with sex and harvest treatment respectively.

Rana sylvatica generally selected moister, but not wet, locations relative to random locations (Table 4.6). Frogs were more likely to occupy locations with greater percent cover of *Sphagnum* mosses (odds ratio = 57.3 ± 3.0) and higher soil moisture (odds ratio = 5.4 ± 2.5) except at North Chemo and in the retained treatments. These exceptions may have occurred because North Chemo is a very wet site and the retained treatments at three of the experimental arrays are wet and frogs in this context may be seeking drier locations. *Rana sylvatica* were 4.7 ± 2.6 times more likely to occupy locations with moist or wet leaf litter relative to random locations regardless of season, experimental array, harvest treatment, and sex. However, frogs were 3.4 ± 1.4 times more likely to avoid locations with > 40% percent cover of standing water.

Breeding age distribution and success

I captured 180 *R. sylvatica* (106 males, 74 females) entering the breeding pond at the Gilman (139 frogs) and Smith (41 frogs) experimental arrays. Females were 50.2 ± 0.3 mm and males were 46.1 ± 0.3 mm, and frogs were 1 – 5 years old. Most males were 2-years old and most females were 3-years old, and the oldest male and female were 4- and 5-years old respectively. Females were older than males overall ($\chi^2_4 = 28.2$, Fisher's exact $P < 0.001$). I failed to detect a difference in the age distribution ($\chi^2_{12} = 5.6$, Fisher's

exact $P = 0.935$; Figure 4.3A) or size distribution ($\chi^2_{12} = 11.9$, Fisher's exact $P = 0.513$; Figure 4.3B) of frogs entering the pond from the four harvest treatments.

I observed 31 pairs of frogs successfully breed, and one male mated successfully with two females. A model including age, harvest treatment, body length, and experimental array fit my data (Hosmer and Lemeshow $\chi^2_8 = 11.1$, $P = 0.195$). Body length (Wald $\chi^2_1 = 21.5$, $P < 0.001$) and treatment (Wald $\chi^2_1 = 5.6$, $P = 0.017$) were related to breeding success of these 61 frogs, but age (Wald $\chi^2_1 = 0.1$, $P = 0.740$) and experimental array (Wald $\chi^2_1 = 0.1$, $P = 0.760$) were not.

Larger frogs were 1.3 ± 1.0 times more likely to successfully breed than smaller frogs (Figure 4.4A), and successful breeders were 3 mm larger than unsuccessful frogs (49 ± 0.5 vs. 46 ± 0.3 mm). Additionally, frogs from the unharvested and partial treatments were 1.5 ± 1.2 times more likely to breed successfully than frogs from the retained and removed treatments (Figure 4.4B).

Discussion

I found support for the predictions of Fisher (1930), Fretwell and Lucas (1970), and others that animals should select habitats that maximize their individual lifetime fitness (Weins 1989; Howard 1979; Morris 1989). The fitness potential of the clearcut treatments (removed and retained) was lower than that of the forested treatments for *R. sylvatica* because individuals from those treatments had lower reproductive success. *Rana sylvatica* shifted their distribution in the experimental arrays to select the forested treatments and responded to differences in the habitat conditions in the experimental arrays at all three scales.

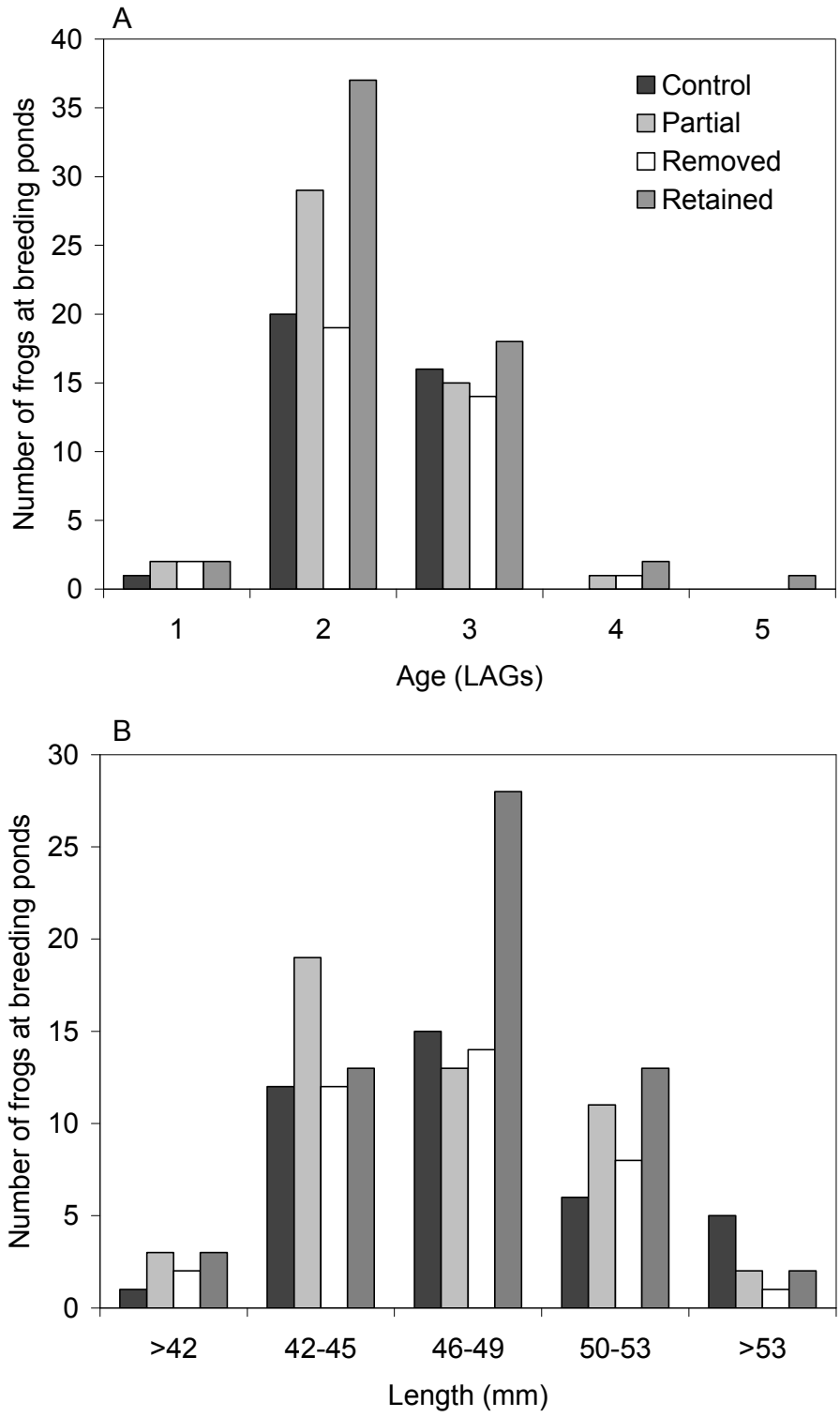

Figure 4.3. Frequency of age (A) and size (B) classes of breeding *Rana sylvatica* at the Gilman and Smith experimental arrays categorized by the harvest treatment in which they were initially captured.

Habitat selection by *R. sylvatica* varied with the scale of measurement. At the seasonal home range scale, frogs selected forested treatments during both spring and fall studies (Figure 4.1). This result is not surprising based on previous research (Constible et al. 2001; Patrick et al. 2006; Baldwin et al. 2006), but it is noteworthy that I did not find a difference between the partial and unharvested treatments. Most studies on amphibians and partial harvesting (typically using species richness or abundance data) report no difference between the partially harvested and unharvested treatments (Pearman 1997; Fredericksen and Fredericksen 2004; Vallan et al. 2004), although there are exceptions (e.g., decrease in richness – Vesely and McComb 2002; increase in richness – Lemckert 1999). It is important to note that the partially harvested areas vary greatly in the amount of timber removed from the site. The partial harvesting I studied removed little standing timber and does not resemble commercial partial harvests (e.g., Robinson 2006); canopy cover was reduced from 73.8 ± 22.7% to 53.0 ± 33.5% (Patrick et al. 2006). Partial harvesting with removal of < 25% of basal area was expected to have minimal impacts on forest-dependent species such as *Ambytsoma maculatum* and *R. sylvatica* (deMaynadier and Hunter 1995), and my results support the recommendation that partial harvesting with removal of < 25% canopy cover or basal area is a viable forest management strategy in ecologically sensitive areas, such as those surrounding vernal pools (Calhoun and deMaynadier 2004; deMaynadier and Houlahan 2007).

Rana sylvatica exhibited a seasonal change in habitat use: home ranges were smaller in spring than in the fall tracking period. This difference has not previously been documented, although earlier work has shown that frogs may move closer to breeding ponds late in the season (Regosin et al. 2003) and move farther away when moving to a

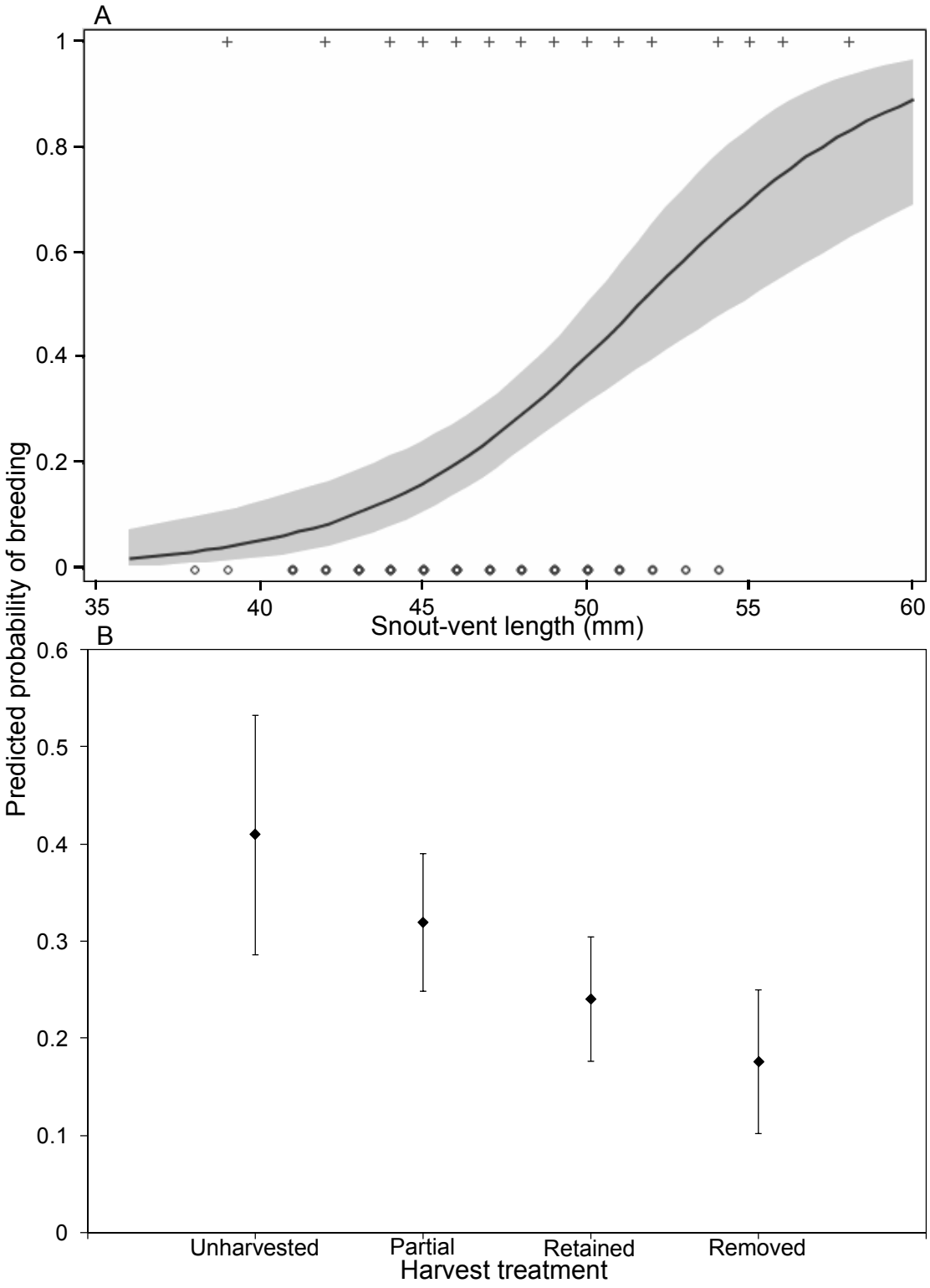

Figure 4.4. Predicted probabilities of breeding success (black line) for *Rana sylvatica* based on a logistic regression model of size (A) and harvest treatment (B). Gray clouds (A) or error bars (B) indicate 95% confidence intervals.

more distant seasonal resource (e.g., forested wetlands in Maine [Baldwin 2005] or ephemeral stream drainages in Missouri [Rittenhouse and Semlitsch 2007]). Frogs may move more in the fall because of increased foraging to increase fat reserves for during hibernation and breeding. Alternatively, lack of cover from little deciduous vegetation in spring may make movement more risky because of predation (Martin et al. 2005).

At the scale of the weekly activity center, canopy cover was not an important habitat component; it was included in the best model set but was not a good predictor (95% confidence interval for the odds ratio overlapped one). Instead, areas with more complex ground structure including locations with higher cover of *Sphagnum* mosses, vegetation, and slash, coarse woody debris present, and deeper leaf litter were more likely to be occupied by frogs. Variables indicating complex ground structure (e.g., deciduous leaf litter; willow, alder, and herbaceous cover) also were important to populations of *R. sylvatica* in Alberta, Canada based on distributional data in managed forests (Constible et al. 2001). I observed that moisture in the leaf litter and soil increased the probability of occupation for activity centers with lower complexity ground structure (Fig 2). Soil moisture also interacted with temperature such that frogs sought out a different optimal temperature at different soil moistures. These results indicate that the activity centers available to frogs may change over time based on precipitation and temperature. For example, recent clearcuts with low complexity of ground structure could be inhabited by frogs for a short period after a rainfall event until the ground dried and temperatures increased. This interaction between temperature and moisture is important for determining the timing of breeding migrations and dispersal from natal ponds in *R.*

sylvatica (Timm et al. 2007), and may also be important in determining the habitats selected by other amphibian species (Chan-McLeod 2003; Fogarty and Vilella 2003; Rittenhouse and Semlitsch 2007).

Similar to my findings for weekly activity centers, frogs select daily microhabitats with more complex ground structure (i.e., more slash and coarse woody debris present) and moisture (Table 4.6). However, the importance of coarse woody debris interacted with canopy cover; frogs were more likely to occupy locations with coarse woody debris in the clearcuts, but this relationship did not exist in the unharvested treatment. Likewise, northern red-backed salamanders (*Plethodon cinereus*) in Maine were more likely to occupy locations in small (~0.2 ha) harvest-created, forest gaps with larger diameter coarse woody debris, but coarse woody debris had no effect in nearby unharvested forest plots (Strojny 2004). Moisture was an important variable in daily microhabitat selection, and *R. sylvatica* generally selected moist daily microhabitats (greater cover of *Sphagnum* mosses, higher soil moisture, and wetter leaf litter) while avoiding the wettest locations (greater cover of standing water; Table 4.6). Other populations of *R. sylvatica* in southern Maine had a similar pattern of selecting moist microhabitats and selection for moisture varied with spatial scale (Baldwin et al. 2006).

Rana sylvatica selected daily microhabitats with more canopy and leaf litter cover, but these relationships varied with the sexes (Table 4.6). Females showed little selection for canopy cover, whereas males strongly selected areas with higher canopy cover. The relative difference between frog locations and random locations, however, was similar for both sexes, and thus we did not reanalyze data at other scales for each sex independently. Differences among the sexes in habitat selection was reported for arroyo

toads (*Bufo microscaphus californicus*; Griffin and Case 2001). Although female *R. sylvatica* are known to hibernate farther from the breeding pool than males (Regosin et al. 2003, 2005), differences between the sexes have not been reported in this species previously. Sex-specific differences in habitat selection in adult amphibians deserve further investigation.

It is noteworthy that the relative importance of three variables varied with the scale examined. Percent cover of vegetation was not included in the best model set describing microhabitat selection of any frog. Apparently, dead ground structure was more important at the microhabitat scale in my experimental arrays, but live vegetation was important at larger scales (weekly activity centers in this study; Constible et al. 2001). Further, ground surface temperature and relative humidity were not supported in the best models describing daily microhabitat selection for any individual frog, but an optimal temperature was an important characteristic of weekly activity centers. In Missouri, *R. sylvatica* used warmer microhabitats with lower humidity (Rittenhouse and Semlitsch 2007), but previous work in Maine indicates *R. sylvatica* select cooler, more humid microhabitats (Baldwin et al. 2006). These differences may be due to genetic differences across the range of *R. sylvatica* (Lee-Yaw et al. 2008), and the ecological currency determining *R. sylvatica* habitat quality is an avenue for future research.

Size was a more important factor determining breeding success than was age in my logistic regression model (Figure 4.4A). This result is further evidence for the prediction that growing fast throughout an amphibian's life and reaching reproductive maturity earlier will lead to increased fitness (Wilbur and Collins 1973; Werner 1986; Semlitsch et al. 1988). The age and size distributions in my two study populations were

similar to other studies; females were generally older and larger than males (Figure 4.3; Bellis 1961b; Howard 1980; Berven 1990; Bastien and LeClair 1992).

Although I did not detect a difference in body size among the harvest treatments, the predicted breeding success of frogs from each of the harvest treatments still followed my expectations; frogs in the unharvested and partial treatments had approximately double the predicted breeding success of those from the clearcut treatments (Figure 4.4B). This result indicates that *R. sylvatica* from clearcut environments probably have lower lifetime fitness than those from forested environments, and thus the fitness potential of clearcut environments may be lower than forested environments for this species. The habitat experienced during one period in an animal's life can have positive or negative effects on the organism's fitness at subsequent times (i.e., latent effects, *sensu* Pechenik 2006; see review by Gimenez 2006). Thus, frogs captured in the clearcut treatments may have experienced a stressful habitat earlier in their life, and the reduced breeding success of these frogs may be a negative consequence of this cumulative stress (reviewed by Metcalfe and Monaghan 2001; Pahkala et al. 2001; De Block and Stoks 2005). Male competition for females in the breeding aggregation is thought to be dictated by size alone (Berven 1981; Howard and Kluge 1985), but these results indicate that other measures of body condition also may be important.

In summary, my data suggest that *R. sylvatica* respond to habitat at multiple scales and that habitat selection may influence their fitness. These results support my initial prediction that the fitness potential of the clearcut treatments is lower than that of the forested treatments. Additionally, I found support for the two forest management strategies tested in my experimental harvesting arrays. Coarse woody debris was a

relatively more important resource in the two clearcut treatments than in the forested treatments. Also, partial harvesting with removal of < 25% canopy cover is a management strategy that may not adversely influence the abundance or fitness of *R. sylvatica*.

CHAPTER 5

A MULTI-SCALE ASSESSMENT OF HABITAT SELECTION AND MOVEMENT PATTERNS OF NORTHERN LEOPARD FROGS (*RANA PIPIENS*) IN A MANAGED FOREST

Abstract

Habitat loss and degradation are two of the most important factors leading to the imperilment of species worldwide including amphibians. Amphibian communities and populations often change in response to changes in the terrestrial landscape surrounding breeding ponds, but mechanisms are poorly understood. I conducted a radio-telemetry study of 40 adult *Rana pipiens* to investigate mechanisms behind changes in abundance due one form of habitat change, forest harvesting. First, I assessed habitat selection at three scales during the post-breeding season (home range, weekly activity center, and daily microhabitat) in response to three forest management strategies: clearcutting, clearcutting with coarse woody debris retention, and partial harvesting with 50% canopy cover. Second, I assessed how the frequency of movement and distances moved varied with these forest harvesting techniques. Habitat selection was most strongly influenced by canopy cover at the scales of home ranges and weekly activity centers. For home ranges, frogs selected the ponds and tended to select the clearcut treatments, and they were 1.5 times more likely to occupy weekly activity centers with less canopy cover (mean = 15% vs. 42% cover). Additionally, frogs selected weekly activity centers with more standing water (mean = 46% vs. 5% cover), greater moist soil moisture (mean = 44% vs. 32% volumetric water content), and 4.7ºC warmer temperatures than random

activity centers, but at higher temperatures they were less likely to occupy activity centers with moist soils. In contrast to the coarser scales, ground structure was more important at the daily microhabitat scale: frogs selected daily microhabitats with live vegetation, little leaf litter cover, moist litter and soil, standing water, and higher temperatures. There was a trend for frogs to make shorter movements while in the ponds and longer movements while in the unharvested controls. Amphibian community composition and landscape distribution are linked to environmental gradients, such as forest disturbance and regeneration, and my results suggest that *R. pipiens* and species with similar habitat requirements may use clearcut areas during the spring and summer that are within migration distance of breeding and overwintering habitats if dense ground vegetation has regenerated.

Introduction

Habitat loss and degradation are two of the most important factors that have led to the imperilment of many species worldwide (Baillie et al. 2004). The mechanisms by which anthropogenic changes to landscapes can negatively affect species include reduced quantity and quality of habitats, increased isolation of key habitats for different life stages, and edge effects (Semlitsch 2000; Stuart et al. 2004; Becker et al. 2007; Gardner et al. 2007).

Most pond-breeding amphibians depend on both aquatic and terrestrial habitat conditions (Wilbur 1980); successful reproduction relies on appropriate aquatic conditions for eggs and larvae and juveniles and adults rely on appropriate conditions in the terrestrial landscape surrounding the breeding pond (Semlitsch 2000). Recent work on

pond-breeding amphibians has highlighted the importance of terrestrial habitat during the nonbreeding season (e.g., Regosin et al. 2005; Sztatecsny and Schabetsberger 2005; Baldwin et al. 2006; Rittenhouse and Semlitsch 2007; Patrick et al. in press). The terrestrial habitat surrounding the breeding pond must be adequate (e.g., quantity, quality, and connectivity) to support animals as they move through the surrounding landscape to forage and overwinter (Semlitsch 2002; Semlitsch and Bodie 2003; Porej et al. 2004). Movements of individuals among different habitats types can affect the growth, survival and reproduction of individuals (De Block and Stoks 2005; Rudolf and Rödel 2007; Becker et al. 2007; Chapter 4) and the age structure, sex ratio, and genetic diversity of populations (Hanski 1998; Squire and Newman 2002). Human-altered environments can have different permeability (i.e., the ability and willingness of an organism to move through a given environment) than unmanipulated environments (Reh and Seitz 1990; Sinsch 1997; Hitchings and Beebee 1997; Rothermel 2004), but empirical data on the effects of human-altered environments on the movements of many species of amphibians are rare (reviewed by Cushman 2006).

Human alterations may be essentially permanent (e.g., suburban development; Egan and Paton 2004; Gagne and Fahrig 2007) or relatively short-term (Skelly et al. 1999; Mazerolle 2001). For example, forest harvesting practices that remove much of the canopy cover and ground structure (e.g., clearcut timber harvesting with removal of coarse woody debris) can decrease the abundance of forest-associated amphibians such as Wood Frogs (*Rana sylvatica*), Spotted Salamanders (*Ambystoma maculatum*), and Northern Red-backed Salamanders (*Plethodon cinereus*) until forest regeneration restores their habitat (Gibbs 1998a,b; Herbeck and Larsen 1999). Clearcutting also can change the

relative composition of the amphibian community by favoring species that prefer open habitats (Skelly et al. 1999; Skelly et al. 2003). Less is known about the influences of more subtle landscape changes, such as partial harvesting, on the distribution and persistence of amphibian populations. For example, light partial harvesting (partial harvesting with removal of < 25% of basal area) and retention of coarse woody debris in clearcut areas are postulated to mitigate for the effects of tree removal for forest-associated amphibian species (deMaynadier and Hunter 1995; Chapter 4), but these hypotheses have not been experimentally tested for many species.

I studied how timber harvesting affected habitat relationships and movement patterns of Northern Leopard Frogs (*Rana pipiens*). I used radio-telemetry to assess habitat selection at three scales, post-breeding season home range, weekly activity center, and daily microhabitat, in response to three forest management treatments: clearcutting, clearcutting with coarse woody debris retention, and partial harvesting with 50% canopy retention. Further, I assessed how the frequency of movement and distances moved varied across these forest harvesting treatments.

Materials and Methods

Experimental forest harvesting arrays

The four experimental arrays were located on the University of Maine's Dwight B. Demeritt and Penobscot Experimental Forests (Penobscot County, Maine, USA, 44° 50' N, 68° 35' W). Each array was a 164-m radius circle centered on a ~ 80 – 530 m^2 pond surrounded by four sectors that constituted 2.1 ha treatments: an unharvested control (unharvested forest stand; hereafter "unharvested") and three forest management

strategies (clearcut with coarse woody debris [CWD] removed ["removed"], clearcut with CWD retained ["retained"], and partial harvest with 50% canopy closure ["partial"]). These four treatments were randomly position around the pond with the caveat that the partial was never adjacent to the unharvested treatment (see Patrick et al. 2006 for a complete description of the arrays). Forest harvesting was completed in April 2004. The clearcuts in my experimental arrays created openings in an otherwise forested landscape; >70% of the landscape within 1 km of my four experimental arrays was forested (Charles Crockett, personal communication).

Habitat requirements and movement phenology

The range of *R. pipiens* extends across continental North America, although the species has disappeared from historic locations in much of western North America (e.g., Clarkson and Rorabaugh 1989; Corn 1994) and some locations in the northeast (Hinshaw 1999; Longcore et al. 2007). Its habitat needs vary with season, and the active season normally is April to November in the northeastern United States (Hinshaw 1999). In the northeastern United States, *R. pipiens* uses emergent marshes and forested wetlands in summer (Dole 1965a,b; Hinshaw 1999; Rorabaugh 2005). Frogs breed and hibernate in aquatic sites; migration to breeding locations follows emergence from hibernation where breeding and hibernacula are separate (Dole 1968; Rorabaugh 2005). Breeding occurs at night, usually starting in early May in Maine (Hinshaw 1999). *Rana pipiens* breed in lentic or slow-moving lotic habitats that are often fishless (Collins and Wilbur 1979; Hecnar 1997, Werner and Glennemeier 1999; Rorabaugh 2005). Ephemeral habitat can be used for breeding, but *R. pipiens* in Maine typically use permanent ponds (A. Calhoun,

personal communication). Hibernacula are deep, permanent bodies of water that do not freeze solid (Rorabaugh 2005). These frogs used terrestrial habitats more than other pond-breeding ranids, and selected for land over water at all temperatures in experimental trials (Licht 1991). Daily movements of adults are usually < 10 m but range up to 53 m in wet pastures and marsh and movement increases with precipitation (Dole 1965a,b, 1971). Home ranges may include breeding sites, hibernacula, and upland foraging areas (Rorabaugh 2005).

Rana pipiens are sensitive to the edges and reduced canopy cover created by forest harvesting in the eastern United States (Werner and Glennemeier 1999; Guerry and Hunter 2002; Patrick et al. 2006). Populations of *R. pipiens* are less likely to be present in ponds surrounded by a landscape with extensive forest cover (Guerry and Hunter 2002). This distribution may primarily be driven by performance of the pre-metamorphic stages; high canopy cover at breeding ponds decreased growth and survivorship of *R. pipiens* larvae (Werner and Glennemeier 1999). Although the evidence is not as clear for post-metamorphic *Rana pipiens* (e.g., Patrick et al. 2006), I expected individuals to move towards and select for my clearcut treatments (retained and removed; Whitaker 1961; Dole 1967, 1971, 1972a,b; Merrell 1977; Pope et al. 2000).

Radio-telemetry and habitat sampling

I tracked 40 adult *R. pipiens* from 16 May – 18 June 2006 after capturing individuals as they emerged from breeding ponds. I generally followed the methods described in Chapter 4, which are summarized here. I fit individuals with a radio-transmitter (BD-2 model, 0.9-g, 14-cm external whip antennae, 40-day battery life;

Holohil Systems, Carp, Ontario, Canada; Muths 2003; Weick et al. 2005; Blomquist and Hunter 2007), and released two (unharvested and partial treatments) or three individuals (retained and removed treatments) within each treatment approximately 10 m from the edge of the pond and equidistant from adjacent treatments (N = 10 per array). I located each frog daily and mapped each movement with a compass and tape measure from known locations in each experimental array.

I used Hawth's Analysis Tools (http://www.spatialecology.com/htools) in ArcGIS 9 (Environmental Systems Research Institute, Redlands, California, USA) to calculate 100% minimum convex polygon home range size, movement paths, use, and availability of habitat to evaluate 2nd-order resource selection over the duration of the tracking period. I calculated a 100% MCP rather than a 95% MCP to estimate home range size for each frog that moved to at least three unique locations because it is assumed that by removing 5% of the points from a sample of locations will remove outlying points that reflect movements unusual movements (e.g., mate-searching, foraging on a specific resource) from the area calculated; this assumption is not necessary for *R. pipiens* during distinct portions of their active season (Dole 1965a,b; Hinshaw 1999; Rorabaugh 2005). I refer to the minimum convex polygons I estimated for the spring and early summer as home ranges. These home ranges probably exclude summer habitat and are more accurately referred to as seasonal home ranges because these minimum convex polygons may represent only one portion (post-breeding) of the annual home range required for survival. I used this simple home range estimator in preference to probabilistic estimators because the number of relocations I could obtain on each frog (ca. 30) was unlikely to accurate estimation of home range size with these estimators (e.g., Worton 1995; Seaman

and Powell 1996). I calculated availability of habitat for each frog by simulating ten home ranges within the experimental array. I assumed the entire experimental array was available to the frogs over the duration of the fall and spring tracking periods. Each home range was defined by the number of relocations for a given frog and the number of points in each harvest treatment was extracted and averaged across the ten home ranges to yield the availability of habitat for that frog.

I assessed post-breeding habitat selection at two smaller scales that differed temporally and spatially, daily microhabitats and weekly activity centers. I attempted to control for spatial and temporal independence of locations by using movement patterns of *R. pipiens* and other terrestrial anurans in the literature and movements of individuals tracked in summer 2005 to design my habitat sampling. Thirty and 300 m were the approximate outer quartile of the distribution of daily movements and the longest movement expected based on movements of another terrestrial anuran, *R. sylvatica*, in my experimental arrays (Chapter 4), and thus the random points at these distances were assumed to be available to the frogs on a daily and weekly basis respectively. Most movements by *R. pipiens* occurred at night (Dole 1965). I assumed daily locations were independent and that remaining in the same location on successive days represented choice. If this assumption is invalid, my sampling procedure would overestimate the importance of variables that were characteristic of locations where frogs remained for multiple relocations (Erickson et al. 2001).

I evaluated habitat use and availability using 14 variables (Table 5.1) chosen based on the habitat relationships, ecology, and physiology of *R. pipiens* and other

Table 5.1. Habitat variables collected in 1-m^2 plots to quantify habitat use and availability in *Rana pipiens*. I collected each variable at the frog's location and at a random location each day (daily microhabitat) and at a set of random points every five days (weekly activity centers). Variables were collected at the center of each plot unless otherwise specified. Percent cover variables were estimated to the nearest 5%.

Variable	Code	Description
% canopy	CC	Percent canopy cover above plot measured with a GSR vertical densiometer
% litter	LI	Percent cover of leaf litter
% standing water	SW	Percent cover of standing water
% *Sphagnum* spp.	SP	Percent cover of *Sphagnum* spp. mosses
% vegetation	VC	Percent cover of vegetation < 0.5 m
% slash	SL	Percent cover of woody debris 2 - 10 cm diameter
Litter moisture	LM	Moisture of leaf litter (1 - dry, 2 - moist, 3 - wet)
Soil moisture	SM	Volumetric water content of soil (Field Scout TDR 200 with 12-cm probes)
Litter depth	LD	Depth (mm) of the litter layer
CWD present	CP	Presence of downed wood > 10 cm diameter
CWD decayed	CD	Coarse woody debris decayed > class 1 (Maser et al. 1979)
Temperature	TE	Temperature (degrees C) at ground surface collected with a Oakton 35612 thermohygrometer (daily microhabitat) or mean daytime (0630-1830 h) temperature from HOBO dataloggers in each treatment (weekly activity centers)
Relative humidity	RH	Relative humidity measured with a Oakton 35612 thermohygrometer (daily microhabitat only)
Dominant cover	DC	Ground cover type in 15 cm circle at center of plot (daily microhabitat only) (0 - bare soil/rock, 1 – dead ground structure, 2 – live ground structure, 3 - water)

anurans (Thorson 1955; Jorgensen 1997) Each variable was measured at the center of a 1-m^2 hexagonal plot centered on the frog's or a random point's location. For each daily frog location, I gathered the same data at a random point 1 – 30 m from the frog's location, selected by choosing a compass bearing and distance from a random number table. I assessed habitat availability at the weekly activity center scale by collecting five random points within a 30-m radius circle positioned 50 – 300 m from the frog's location every 6^{th} day, and these random activity centers were not allowed to overlap each week. Thirty-meter and 300-m radius circles were assumed to be available to the frogs on a daily and weekly basis respectively based on the movements of other anurans in temperate forests in the eastern United States.

Statistical analyses

I analyzed habitat selection at three scales: 2^{nd} order habitat selection of home range over the entire duration of the study, 3^{rd} order selection of weekly activity centers, and 4^{th} order selection of daily microhabitats (Johnson 1980). I estimated 100% minimum convex polygon home range size for frogs that moved to at least three unique locations during the study as a measure of use (i.e., summer home range size). The summer home range sizes and number of locations per treatment for each animal were not normal based on histograms, skewness, and kurtosis of each variable, and therefore I transformed home range sizes and number of locations per treatment using natural logs. I used analysis of variance (ANOVA; PROC GLM) to test if home range size varied with experimental array or sex. I assessed if the distance moved and frequency of movement differed among the harvest treatments using nonparametric ANOVA (WILCOXON option in PROC

NPAR1WAY). I calculated a selection index for each frog as follows: (ln [$\{u_i / u_t\}/\{a_i / a_t\}$]), where for each frog u_i = number of locations in a treatment, u_t = total number of locations, a_i = number of random locations in a treatment, a_t = total number of random locations (Manly et al. 2002). I used a sign test (PROC UNIVARIATE) to test if the mean selection index from each treatment deviated from zero. I did not use a proportional habitat selection analysis (e.g., compositional analysis) at this scale because 45% (72 of 160) of the cells in the matrix were zeros, and replacing these with a small non-zero proportion (0.0001) would inflate the Type I error rate (Aebischer et al. 1993; Bingham and Brennan 2004). I conducted all statistical analyses in SAS (version 9.1, SAS Institute, Cary, North Carolina, USA) with $\alpha = 0.05$ unless otherwise specified. I conducted all statistical analyses in SAS (version 9.1, SAS Institute, Cary, North Carolina, USA) with $\alpha = 0.05$ unless otherwise specified.

To assess habitat selection in weekly activity centers, I used conditional logistic regression to compare the mean microhabitat conditions at the frog locations over a 5-day period to the mean of the five points collected at the randomly positioned activity center (PROC PHREG). I used two strata (week [N = 6] and experimental array [N = 4]) in this analysis to incorporate variability associated with the structure of my habitat sampling. Prior to constructing my models, I screened the 14 possible variables by fitting a model with each variable individually and found all variables were linear (Hosmer and Lemeshow 2000). I incorporated highly correlated variables ($r > 0.7$) variables and those that were non-significant individually only as modifiers of other variables in candidate models. I constructed 16 candidate models that incorporated possible combinations of temperature, moisture, and forest structure variables (Table 5.2)

Table 5.2. Groupings of habitat variables used in construction of models describing activity center habitat selection by *Rana pipiens*. Variable codes and descriptions are presented in Table 5.1.

Group name	*K*	Variables
Moisture	4	SW, SP, LM, SM
Low cover	7	SP, VC, LI, SL, LD, CP, CD
High cover	1	CC
Treatment	6	CC, LI, SL, LD, CP
Temp	1	TE

and used AIC_c and Akaike weights (ω_i) to rank these models and select which model(s) best described selection of activity centers by *R. pipiens* (Burnham and Anderson 2002). I considered models with $\Delta AIC_c < 2$ to be equally supported. After selecting the best model(s), I incorporated 15 plausible interactions (CP×ST, LD×LM, LD×ST, LI×LM, LI×SL, LI×SM, LI×ST, SW×ST, CP×SM, LD×SM, SL×SM, ST×SM, VC×LM, VC×SM, VC×ST) individually into the top models(s) and reassessed support for these models including the interactions relative to the best model(s) without interactions. I again ranked models using AIC_c and incorporated all interactions that had a lower AIC_c value than the best model without interactions into the final model. If more than one model was supported ($\Delta AIC_c < 2$), I used model averaging to derive parameter estimates (Burnham and Anderson 2002). I used this step-by-step approach because the number of coefficients to be estimated and models run are large if plausible interaction terms are included (28 possible coefficients and > 100 models), even though my data set is also large. Philosophically, this approach is similar to path analysis, in which interactions between particular species are either included or excluded at different stages in the analysis (e.g., Wootton 1994; Ives et al. 1999)

To assess daily microhabitat selection, I modeled each frog individually. I used paired logistic regression (PROC LOGISTIC) to compare the relative selection made by

individuals based on differences between the frog location and the paired random location (e.g., Compton et al. 2002; Moore and Gillingham 2007). All variables were linear, and I followed an identical process for development of candidate models as for weekly activity centers with one modification, an additional variable screening process. I modeled only frogs that were tracked for ≥ 20 days. I used stepwise model selection with entry and exit criteria of one to narrow the range of model sizes (i.e., number of variables) to include in my candidate model set for each frog (Shtatland et al. 2001; Campbell 2007; Anderson and Burnham 2002). This process uses the sequential models built by stepwise model selection to build successively larger models until all variables are entered. I considered model sizes with $\Delta AIC_c < 4$ and built ten candidate models for each frog within the range of model sizes.

Results

Home ranges and movement patterns

I estimated home range sizes for 35 of the 40 *R. pipiens* (Figure 5.1; Appendix 4); 5 frogs slipped out of their transmitter belt in the first 3 days of tracking. Mean (± SE) 100% minimum convex polygon home range size was 1096 ± 310 m^2 (range 13–8425 m^2), and home range size was not correlated with the number of times the frogs were relocated ($r = 0.2$, $P = 0.354$). Home range size did not vary with sex or experimental array ($F_{3,34} = 1.3$, $P = 0.300$).

Frogs selected ponds ($G_1 = 7.5$, $P < 0.001$) and tended to select removed treatments ($G_1 = 4$, $P = 0.152$) more than the other harvest treatments (Kruskal-Wallis $\chi^2_4 = 43.5$, $P < 0.001$; Figure 5.2). Only two frogs (Frog ID = 1 and 8; Figure 5.1A) extended

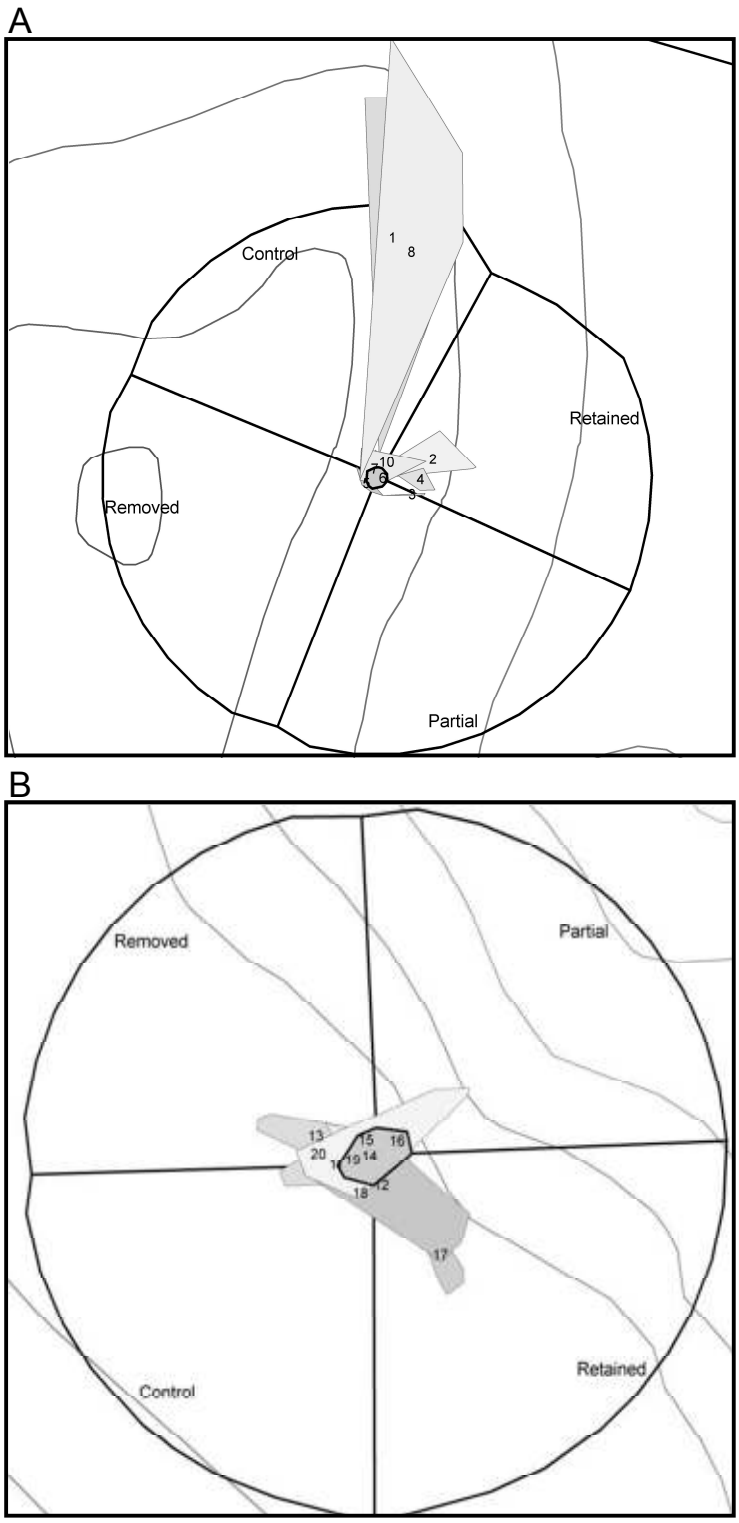

Figure 5.1. Summer home ranges (100% minimum convex polygon) of 35 *Rana pipiens* at the Gilman (A), North Chemo (B), Smith (C), and South Chemo (D) experimental harvesting arrays. Arrays have a 164-m radius, and north is the top of the figure.

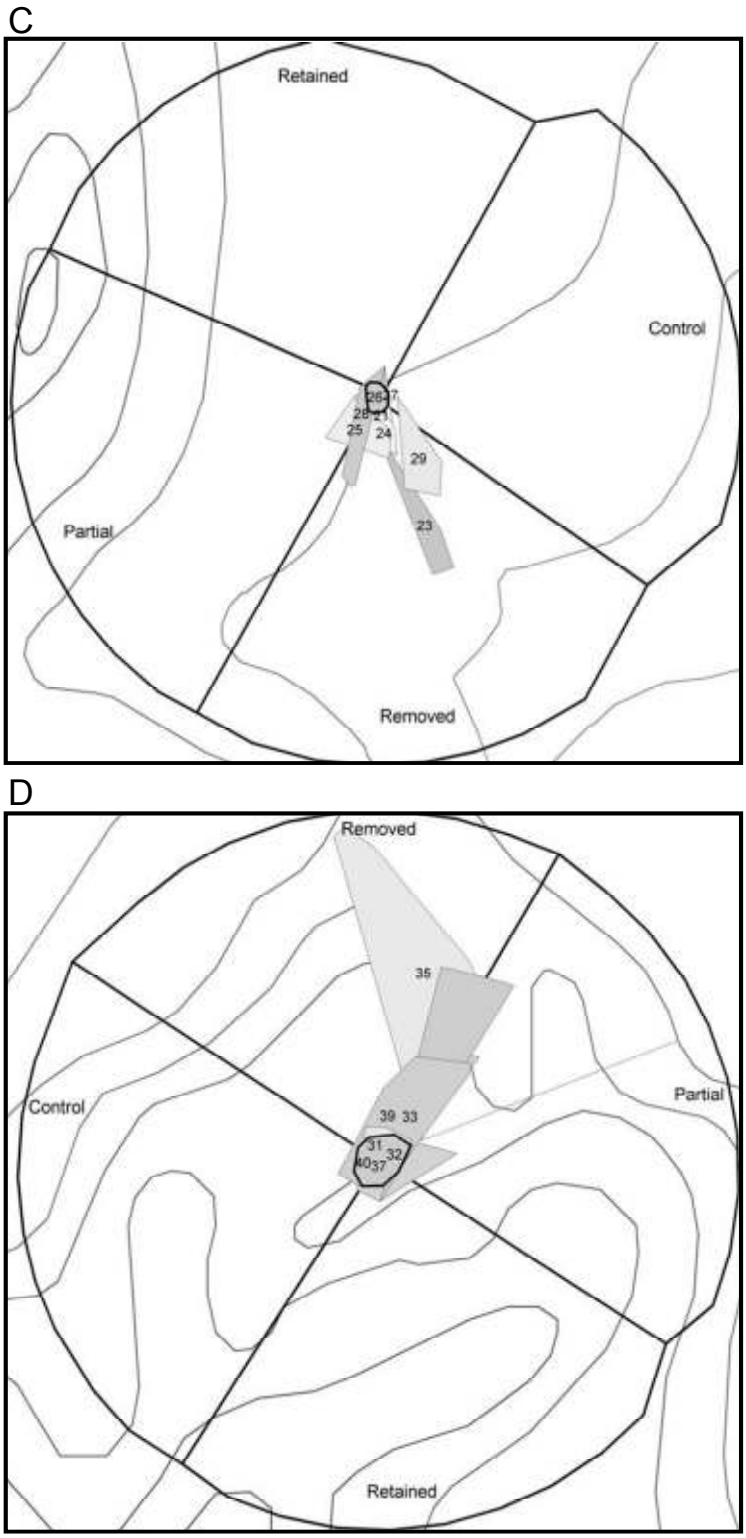

Figure 5.1 Continued.

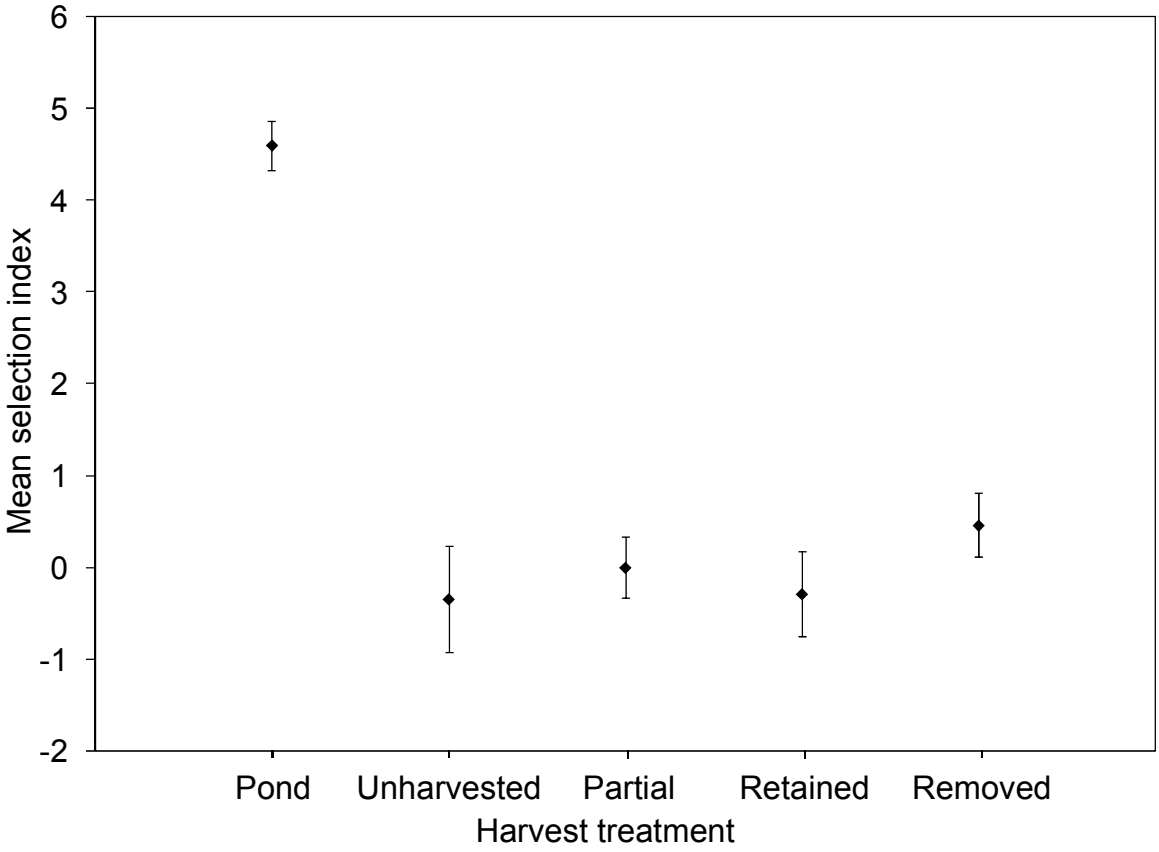

Figure 5.2. Mean selection index (95% confidence interval) calculated from selection indices (natural log [{# of frog locations in a treatment/# total locations for that frog}/{# of random locations in that treatment/# total locations for that frog}]) for each for *Rana pipiens* in the four harvest treatments and the four ponds. A positive selection index means the frogs used that treatment more than expected, and frogs used the ponds and tended to use the removed harvest treatments more than expected.

their home ranges beyond the edge of the experimental array. This indicates that my definition of available habitat as the experimental array was acceptable. These individuals moved beyond the edge of the one array (102 m and 67 m respectively) to the same forested wetland. The portion of forest occupied by each individual was unharvested, and the nine locations (of 643) that were outside the array were grouped into the unharvested treatment.

There was a strong trend for frogs to make shorter movements while in the ponds (G_1 = -51.5, $P < 0.001$) and longer movements while in the unharvested treatments (G_1 = -10.5, $P = 0.028$) compared to the other harvest treatments (Kruskal-Wallis $\chi^2_4 = 9.0$, $P = 0.061$; Figure 5.3). Mean (± SD) total distance move by *R. pipiens* over the study was 134.3 ± 83.0 m, and the longest distance moved in a single day was 159.8 m (Appendix 4). Frogs moved on average 65 ± 24% of the days they were tracked. Movement frequency did not differ among the harvest treatments (Kruskal-Wallis $\chi^2_4 = 4.2$, $P = 0.381$).

Weekly activity center selection

I collected data at 151 and 147 *R. pipiens* and random activity centers respectively; 4 random activity centers were removed because they overlapped frog activity centers. The best supported model incorporated high cover, moisture, and temperature variables (Table 5.3), and although the fit of the global model to my data (Hosmer and Lemeshow $\chi^2_8 = 12.8$, $P = 0.118$) is questionable, the best supported model fit my data (Hosmer and Lemeshow $\chi^2_8 = 6.4$, $P = 0.606$). The best supported model had > 2 times the support as the next best model and comprised 56% of the weight for the candidate model set (Cox and Snell $r^2 = 0.61$; Cox and Snell 1989).

Similar to my results at the home range scale, frogs were 1.5 times more likely to occupy activity centers with less canopy cover, and frog activity centers had less canopy cover (15%) than did random activity centers (42%; Table 5.4). The odds ratios for all other variables in the top model overlapped one, which indicates that these variables are not useful for describing *R. pipiens* habitat selection in weekly activity centers.

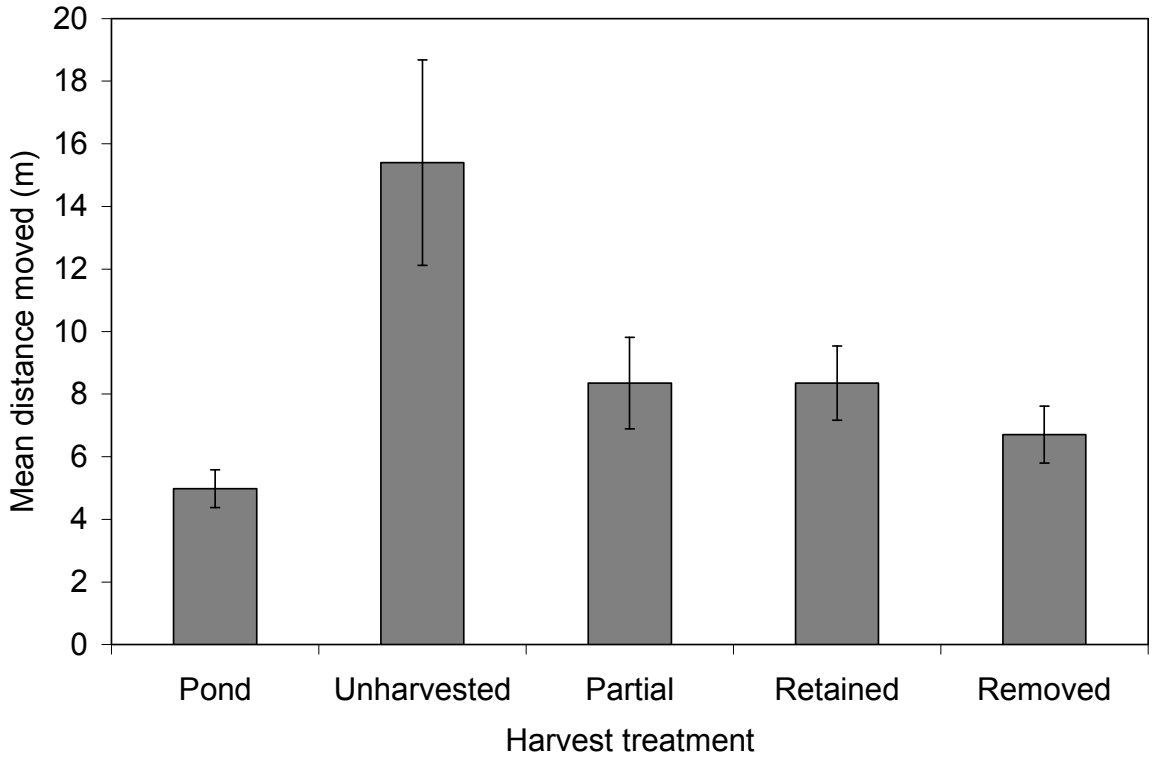

Figure 5.3. Mean movement distance (± 1 SE) of radio-tracked *Rana pipiens* during May and June 2006 in the harvesting treatments.

Frogs selected weekly activity centers with more standing water (mean = 46% vs. 5% cover), greater soil moisture (mean = 44% vs. 32% volumetric water content), and 4.7ºC warmer temperatures (Table 5.4). Two of the 15 interactions were supported: between percent cover of standing water and ground surface temperature and between soil moisture and ground surface temperature. The interaction pattern was the same: i.e., frogs were less likely to occupy activity centers with more moisture at higher temperatures. At a given soil moisture, the probability of a frog occupying an activity center decreased as surface temperature increased from 10.9–32.0°C. This pattern was the same at all soil

Table 5.3. Models of weekly activity center habitat selection in *Rana pipiens*. Model subsets are defined in Table 5.2.

Rank	Model	K	$\log(\mathcal{L})$	AIC_c	ΔAIC_c	ω
1	High cover, Moisture, Temp	8	-33.60	79.70	0.00	0.56
2	Moisture, Temp	6	-35.78	81.84	2.15	0.19
3	Low cover, Moisture, Temp	12	-29.55	82.19	2.49	0.16
4	Global model	13	-29.19	83.65	3.96	0.08
5	Treatment, Moisture, Temp	9	-35.29	87.20	7.50	0.01
6	Treatment, Temp	7	-62.11	136.60	56.91	0
7	Low cover, Temp	9	-60.33	137.28	57.58	0
8	Low cover, Moisture	11	-65.41	151.74	72.05	0
9	High cover, Moisture	6	-72.57	155.42	75.72	0
10	Temp	2	-80.65	163.34	83.65	0
11	High cover, Temp	3	-80.27	164.61	84.92	0
12	Moisture	5	-86.55	181.31	101.62	0
13	Treatment, Moisture	8	-85.55	185.60	105.91	0
14	Treatment	6	-106.10	222.48	142.78	0
15	Low cover	8	-104.63	223.75	144.05	0
16	High cover	2	-147.88	297.80	218.10	0

Table 5.4. Variables describing weekly activity center habitat selection for the population of 37 *Rana pipiens*. Parameter estimates (β) and mean values for each variable were estimated from the best supported model describing differences between 151 frog and 147 random activity centers. Interaction patterns for odds ratios (OR) are described in the text. SE = standard error.

Variable	β	SE_β	OR	SE_{OR}	Random Activity Center	SE_R	Frog Activity Center	SE_F
Intercept	-4.532	5.578						
% standing water	-0.120	0.108			5	1	46	2
% *Sphagnum* spp.	0.008	0.016	1.01	0.02	11	1	12	1
% canopy	-0.022	0.008	0.98	0.01	42	3	15	2
Litter moisture	0.423	0.474	1.53	0.46	1.83	0.07	2.59	0.04
Soil moisture	-0.110	0.157	0.90	0.12	32	1	44	1
Temperature	0.069	0.266			17.4	0.3	22.1	0.3
% standing water × Temperature	0.011	0.006						
Soil moisture × Temperature	0.007	0.008						

moistures in the range that I measured (10–50% volumetric water content), but the decrease was less rapid at lower soil moistures.

Daily microhabitat selection

I collected data at 643 paired *R. pipiens* and random locations (1286 total 1-m^2 plots). The best model(s) varied greatly for individual frogs, and included from one to six variables (Appendix 5). Frogs responded to 11 of the 14 habitat variables I measured (i.e., those variables were included in at least one frog's best model[s]), although the standard error of five of the variables overlapped zero, which indicates that these variables were not useful for describing *R. pipiens* habitat selection at daily locations (Table 5.5).

Table 5.5. Variables describing daily microhabitat selection in *Rana pipiens*. Mean standardized parameter estimates (β_s) and mean values for frog and random daily locations were calculated from the supported model(s) for each frog that used that variable (Appendix 4). N indicates the number of frogs. Dominant cover variables are interpreted as likelihood to be selected relative to bare soil. SE = standard error.

Variable	N	Mean β_s	SE β_s	Random Microhabitat	SE_R	Frog Microhabitat	SE_F
% canopy	10	-0.32	1.97	28	6	23	7
Dominant cover - vegetation	11	4.81	1.39	0.23	0.04	0.23	0.04
Dominant cover - water	9	-1.74	3.28	0.42	0.07	0.60	0.09
Leaf litter depth	10	0.28	2.37	23	3	18	3
Leaf litter moisture	11	2.65	1.54	2.32	0.11	2.78	0.07
% leaf litter	8	-5.77	3.61	27	4	17	4
% slash	7	-3.48	5.94	19	2	11	3
Soil moisture	9	6.34	1.84	27	2	37	2
% standing water	7	8.44	5.09	26	11	50	12
Relative humidity	10	-2.58	2.86	65	1	64	1
Temperature	10	2.22	1.87	21.8	0.5	22.1	0.5
% vegetation	12	0.56	2.16	25	2	30	4

Frogs selected daily locations with greater leaf litter moisture and greater soil moisture, more standing water, less leaf litter cover, and higher temperatures relative to random locations (Table 5.5). In addition, frogs were more likely to be found in locations with vegetation as the dominant cover item. Frogs were 14.2 ± 4.7 times more likely to occupy locations with moist or wet leaf litter, and were 9.3 ± 6.5 times more likely to occupy locations with warmer temperatures (22.1ºC vs. 21.8 ºC). Frogs occupied locations with greater cover of standing water (50% vs. 26%), more saturated soils (37% vs. 27%), and less leaf litter cover (17% vs. 27%) relative to random locations.

Discussion

The clearcuts in my experimental arrays created openings in an otherwise forested landscape thus providing new habitat for species that favor open-canopy environments (Skelly et al. 2002; Werner et al. 2007a,b). Radio-transmittered adult *R. pipiens* shifted their distribution in the experimental arrays to select open-canopy habitat during late spring and early summer and responded to the habitat conditions in my experimental arrays at all three spatial scales. My work supports the importance of open-canopy, terrestrial environments for *R. pipiens* (Werner and Glennmeier 1999; Pope et al. 2000; Guerry and Hunter 2002).

Open-canopy conditions were most important at the coarse scales; *R. pipiens* home ranges within the experimental arrays were centered in the ponds and removed treatments (Figure 5.2), and they selected open canopy activity centers (Table 5.4). Post-breeding, terrestrial habitat for this species includes open-canopy habitats (e.g., meadows, emergent marshes), and these coarse-scale habitat relationships are true in Maine as well.

Additionally, it is noteworthy that my frogs remained in or near the ponds (Figure 5.2). This result contrasts with earlier work in which most locations in the post-breeding season were in terrestrial habitats (McAlpine and Dilworth 1989). Two characteristics of my ponds may have promoted selection for the ponds: the canopy conditions above my ponds were relatively open (< 30%), and my ponds contained some topography that could have allowed frogs to find resting and basking locations out of the water. In the late spring and early summer after breeding, my frogs may be able to forage effectively in or near the ponds, and this behavior could allow them to regain adequate energy reserves before migrating to summer habitat.

This association with open-canopy habitats probably is related to poor performance of juveniles (Werner and Glennmeier 1999; Chapter 3) in areas with high levels of canopy cover. Juvenile *R. pipiens* typically are found in greatest abundance in open-canopy habitats (Whitaker 1961; Merrell 1977), and they may be unable to forage, thermoregulate, or maintain a balanced water budget effectively in closed-canopy environments. My frogs selected weekly activity centers with more standing water, greater soil moisture, and warmer temperatures than random activity centers (Table 5.4). However, the interaction between moisture (both percent cover of standing water and litter moisture) and temperature in the weekly activity center model indicated that frogs were less likely to occupy activity centers with greater soil moisture at warmer temperatures. This interaction may exist because frogs moved to upland areas to forage when prey is more available and digestion is more efficient (i.e., at warmer temperatures; Feder and Burggren 1992; Sztatecsny and Schabetsberger 2005).

Contrasting to this general habitat association with open canopy, juvenile and adult *R. pipiens* were captured with pitfall traps at my experimental arrays in greater numbers in the forested treatments (unharvested and partial) than in clearcut (removed and retained) treatments (Patrick et al. 2006). This study included captures throughout the active season and may have captured animals as they migrated through rather than used habitat within the experimental arrays. These results also may reflect the variation across scales of habitat selection (e.g., selection for microhabitats within the larger treatments) and variation in forest conditions within the experimental arrays (e.g., presence of understory vegetation in forested treatments; Dole 1971, 1972a,b; Chapter 3). Additionally, adults tended to move longer distances in the unharvested treatment (Figure 5.3). Increased movement in the unharvested treatments has been observed in closely related, Southern Leopard Frogs (*Rana sphenocephala*) in identical experimental harvesting arrays in South Carolina (Graeter et al. 2008), and such increased movement may increase the probability that frogs are captured in pitfall traps when they do move. It is noteworthy, however, that the frequency of movement did not differ among the treatments.

Frogs selected daily microhabitats with live vegetation, little leaf litter cover, moist litter and soil, standing water, and higher temperatures (Table 5.5). Previous work on microhabitat relationships during the post-breeding season indicates that *R. pipiens* avoid areas with barren ground, sandy or cultivated soils, and vegetation of low height and density (Dole 1965a,b; Rittschof 1975; Merrell 1977; Beauregard and Leclair 1988; McAlpine and Dilworth 1989), and my results generally support this earlier work. However, microhabitat relationships were consistent across treatments, and I did not find

evidence to support the previous suggestion that microhabitat use may differ between the forested and open-canopy treatments (Table 5.5; Dole 1965a,b).

Selection for structural variables at the microhabitat scale was different than at coarser scales. Frogs selected for open canopy conditions at larger scales and for variables that described ground structure at the daily microhabitat scales. This habitat selection of free-ranging adults helps to corroborate and explain observed growth and survival for juvenile *R. pipiens* held captive in terrestrial pens (14.4 m^2 fenced enclosures) within the experimental arrays (Chapter 3). Individuals in this experiment performed well in the open-canopy treatments because canopy may allow the dense vegetation preferred by *R. pipiens* (Whitaker 1961; Merrell 1977; Prevost and Pothier 2003).

Amphibian community composition and distribution on the landscape and amphibian population dynamics are linked to environmental gradients (e.g., hydroperiod, wetland size; Snodgrass et al. 2000), including those created by forest dynamics (e.g., disturbance and succession; deMaynadier and Hunter 1995; Skelly et al. 1999; Werner et al. 2007a,b). Additionally, connectivity of breeding, summer, and overwintering habitat may be more important than the simple abundance of these habitats (Pope et al. 2000; Gibbs et al. 2005; Becker et al. 2007). My results suggest that *R. pipiens* may use clearcut areas during the spring and summer that are within migration distance of breeding and overwintering habitats if dense ground vegetation has regenerated.

Other amphibian species associated with open-canopy habitats, such as *R. sphenocephala*, may benefit from clearcutting in extensively forested landscapes (Butterfield et al. 2005; Graeter et al. 2008). Having open-canopy, terrestrial habitats with

dense regenerating vegetation within migration distance of breeding ponds and hibernacula and breeding ponds with reduced canopy should favor these species (Werner and Glennmeier 1999; Halverson et al. 2003; Hocking and Semlitsch 2007). However, some species with open-canopy associations may benefit from nearby forest. For example, in northern Maine *R. pipiens* living in landscapes with little forest cover were more likely to be found in ponds adjacent to a forest edge than in ponds isolated from forests (Guerry and Hunter 2002). Although open-canopy associated species may benefit from clearcutting in extensively forested landscapes, forest-specialists, such as *R. sylvatica, A. maculatum*, and *P. cinerius*, may decline in abundance (Gibbs 1998a,b; Herbeck and Larsen 1999).

Forest cover in eastern North America has changed continually over at least the past 1500 years, and in the northeastern United States it has increased in the last century as farms have reverted to forests (Whitney 1994; Foster 1995). Species with open-canopy habitat associations may benefit from natural disturbance agents that create open-canopy habitat and management that mimics natural disturbance regimes to maintain open-canopy conditions. For example, beaver (*Castor canadensis*) colonization of Acadia National Park, Maine resulted in increased emergent wetland habitat and open water habitat (Cunningham et al. 2006). Further, beaver activity and connectivity of wetlands were useful predictors of high species richness for pond-breeding amphibians in the park, and beaver created favorable breeding habitat for species that require permanent and ephemeral wetlands (Cunningham 2003). Amphibian species richness will be greater in landscapes with diverse habitats across many environmental gradients (e.g., hydroperiod,

wetland size, canopy cover; Pope et al. 2000; Snodgrass et al. 2000; Skelly et al. 2002; Gagne and Fahrig 2007).

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APPENDIX 1

Table A1. Characteristics and home ranges of 82 radio-telemetered *Rana sylvatica*. Frogs 73-82 were tracked during a pilot study in 2004 and not used in analyses of habitat selection. Snout-vent length (SVL) and mass were measured at the beginning of each study.

Frog ID	Sex	SVL (mm)	Mass (g)	# of relocations	Home range (m^2)
1	M	44	7.5	2	N/A
2	M	44	7.5	27	8
3	M	45	7.8	13	N/A
4	M	44	6.7	21	6
5	M	45	7.5	27	9
6	M	47	7.1	27	11
7	F	46	7.0	25	24
8	F	51	10.6	11	39
9	F	52	8.4	22	57
10	F	58	14.0	27	267
11	M	46	7.5	27	25
12	M	45	8.0	27	191
13	M	46	7.8	27	441
14	F	55	12.4	6	N/A
15	M	44	6.4	7	6
16	F	49	8.1	27	29
17	F	50	13.6	4	N/A
18	M	43	6.5	27	47
19	M	46	7.7	27	11
20	M	46	9.4	14	N/A
21	M	45	7.4	27	73
22	F	55	10.0	27	162
23	F	51	8.8	27	761
24	F	50	8.3	27	177
25	F	48	9.6	26	28
26	F	52	10.8	14	7
27	F	49	8.6	9	3
28	M	46	8.2	27	246
29	M	45	7.9	6	N/A
30	M	48	8.2	26	115
31	M	45	6.6	26	161
32	M	47	6.7	26	328
33	M	48	7.7	27	128
34	F	58	12.3	13	N/A
35	M	44	7.9	27	2116
36	M	45	6.8	18	91
37	F	53	10.0	27	2804
38	F	49	7.6	27	931
39	F	50	9.3	17	101

Table A1 Continued.

40	M	47	8.3	27	1506
41	F	49	8.1	27	480
42	M	45	12.2	32	106
43	F	51	20.9	32	284
44	M	42	10.5	32	247
45	F	41	10.3	2	N/A
46	F	46	16.1	32	127
47	M	43	11.8	5	6
48	M	43	11.4	12	252
49	F	45	12.8	33	480
50	F	46	14.8	32	297
51	F	49	15.7	1	N/A
52	M	43	11.1	32	7912
53	M	45	12.3	1	N/A
54	F	48	17.1	12	29
55	F	49	17.1	32	568
56	M	46	13.7	7	9
57	M	41	9.7	32	1485
58	F	48	15.5	24	117
59	F	50	19.4	2	N/A
60	M	42	10.6	32	801
61	M	45	13.1	32	683
62	F	51	19.5	32	1880
63	M	46	13.7	3	N/A
64	M	44	12.1	22	1251
65	F	46	15.1	32	1426
66	M	46	12.8	18	1501
67	F	55	24.5	20	10745
68	F	50	12.5	10	904
69	M	43	11.1	32	427
70	F	47	14.7	32	382
71	M	43	10.7	32	1029
72	M	43	10.5	1	N/A
73	M	48	10.5	18	56
74	F	50	14.5	16	161
75	M	47	11.0	10	29
76	F	61	19.9	18	6570
77	M	45	10.7	13	287
78	M	45	9.7	10	936
79	M	47	11.0	15	4064
80	F	44	9.8	14	217
81	M	45	10.7	2	N/A
82	M	46	10.8	14	344

APPENDIX 2

Figure A2. Home ranges (100% minimum convex polygon) of 59 *Rana sylvatica* at the Gilman (A), North Chemo (B), Smith (C), and South Chemo (D) experimental arrays in spring and the Gilman (E) and Smith (F) arrays in fall. Home range sizes were smaller in spring than in fall and smaller at the North Chemo experimental array than other sites.

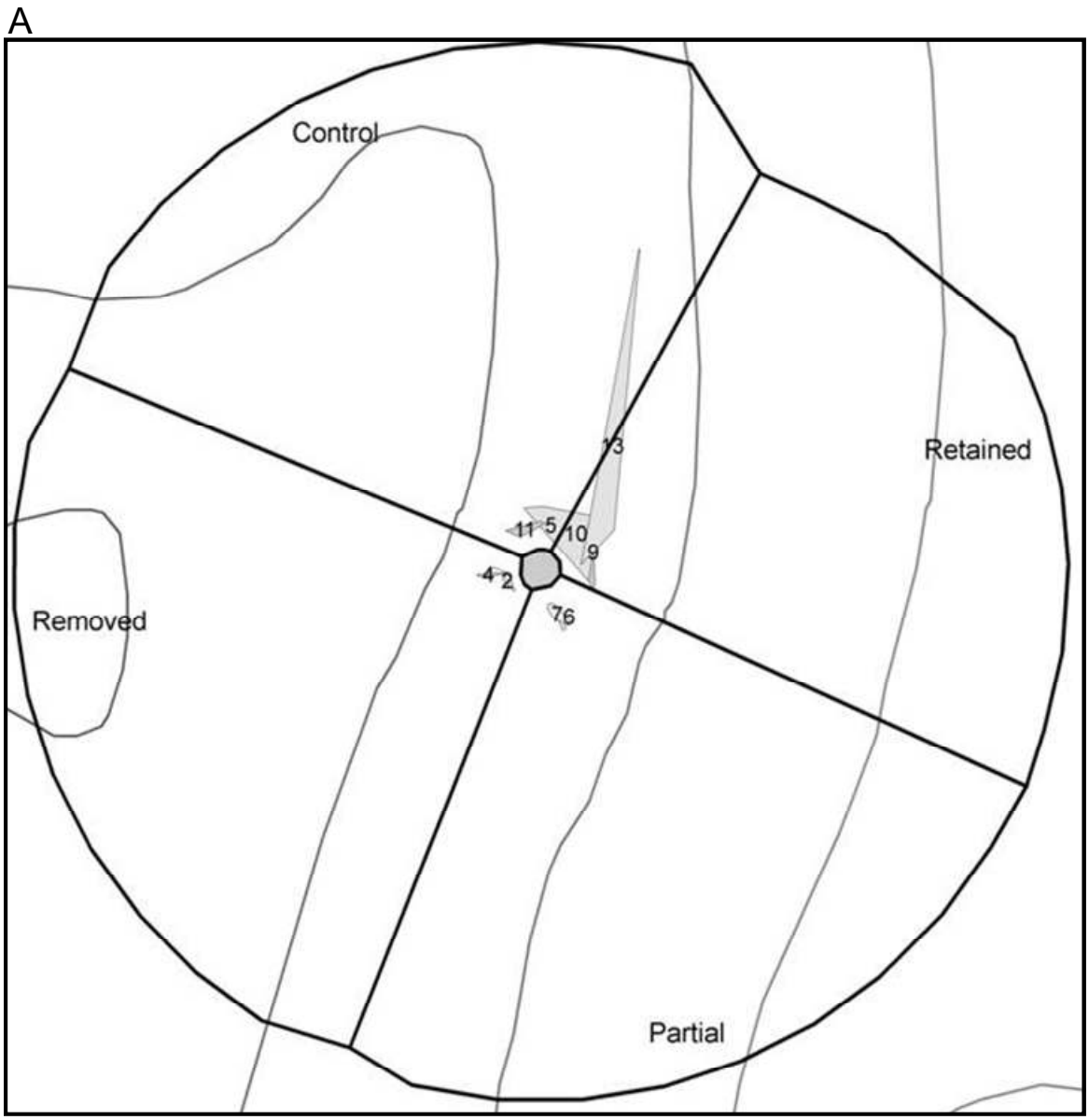


Figure A2 Continued.

B

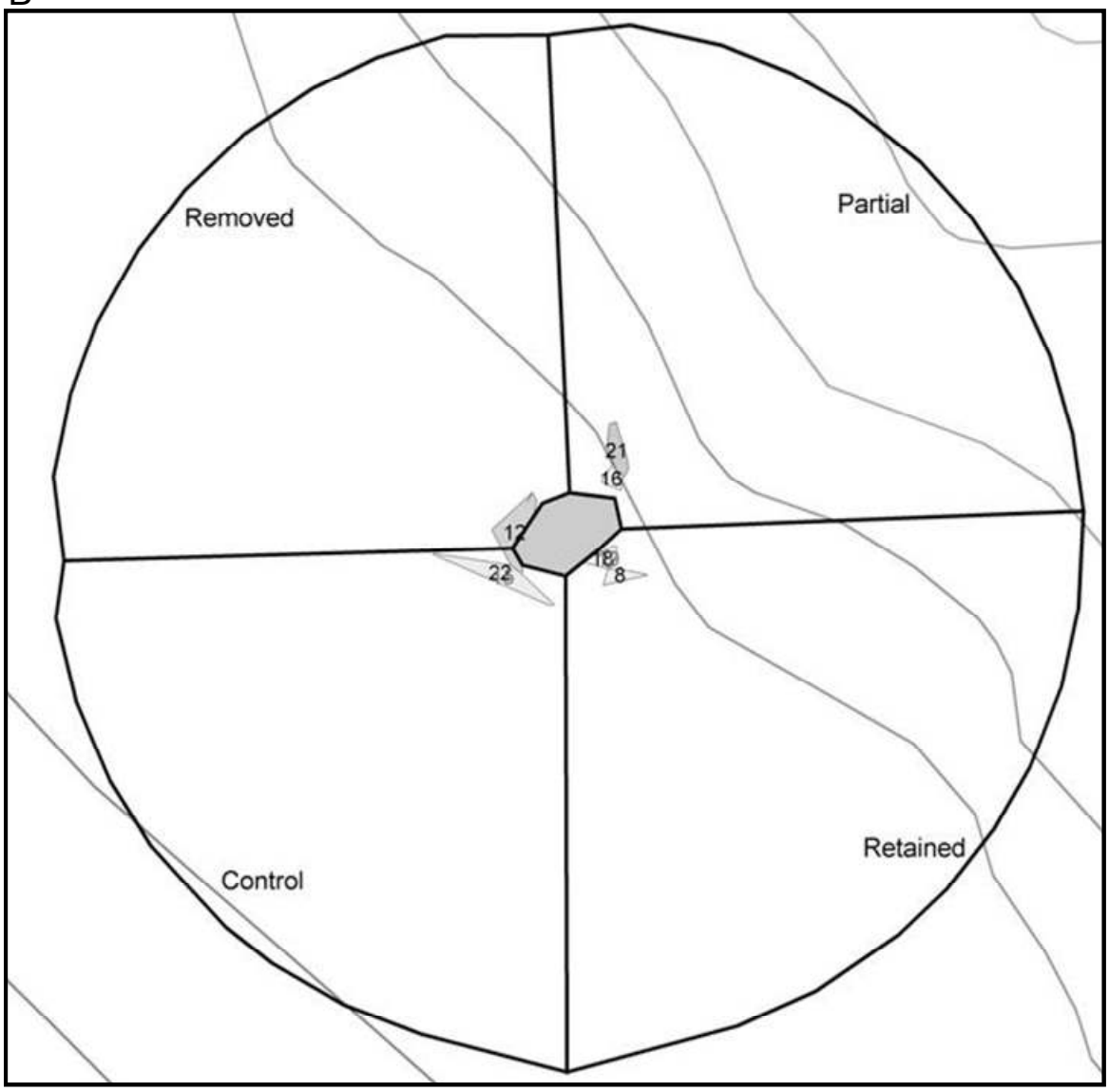


Figure A2 Continued.

C

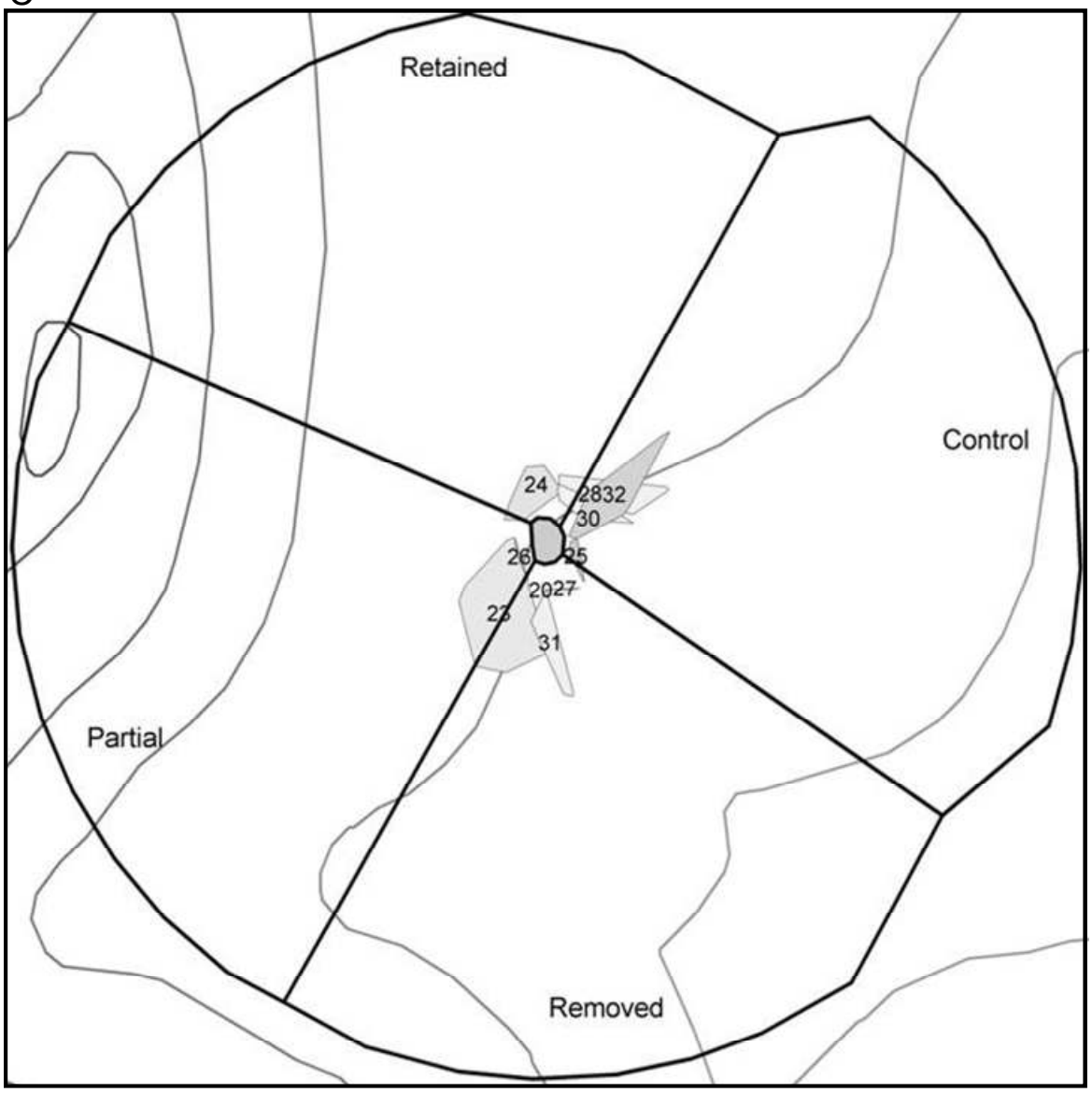


Figure A2 Continued.

D

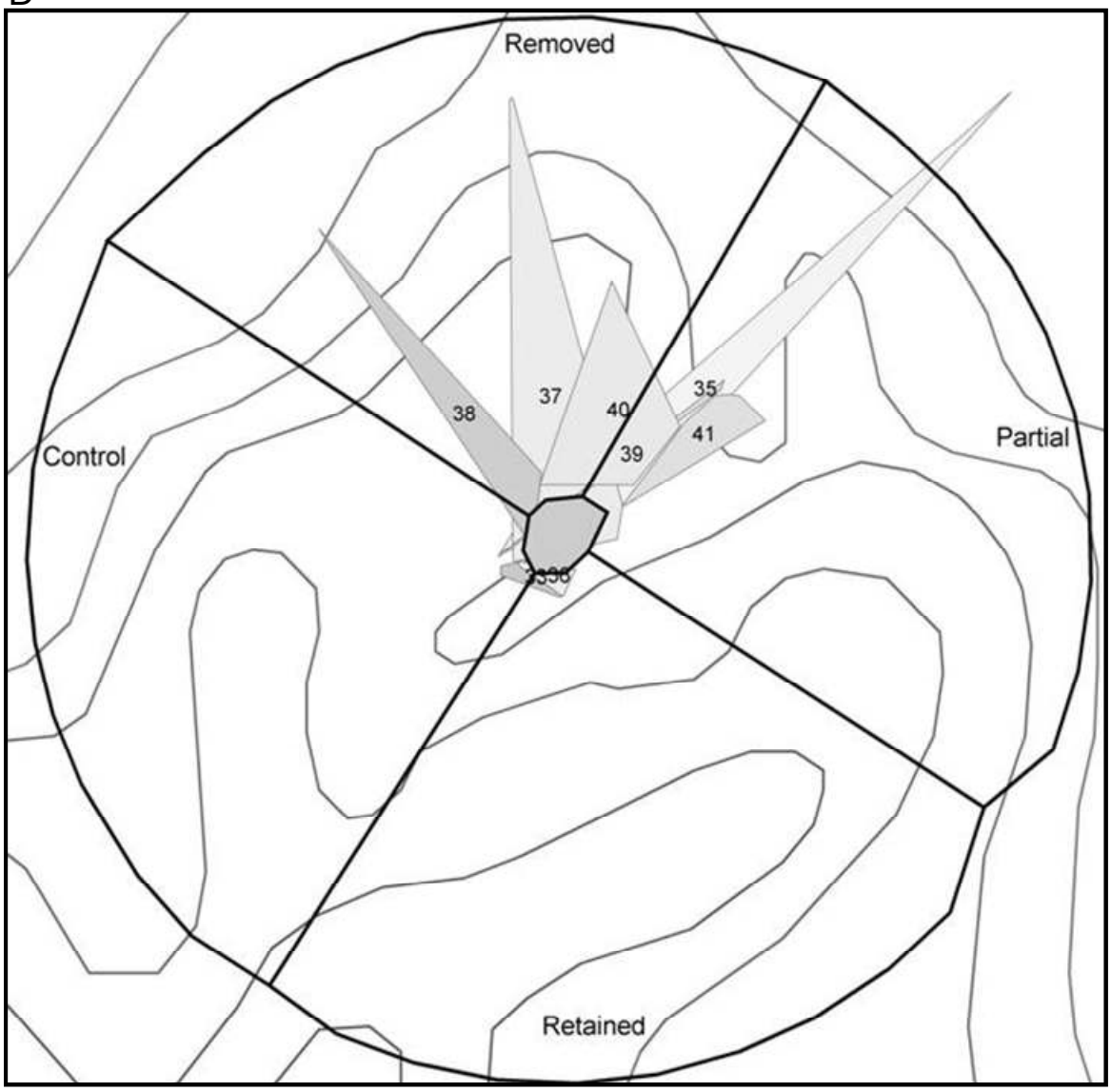
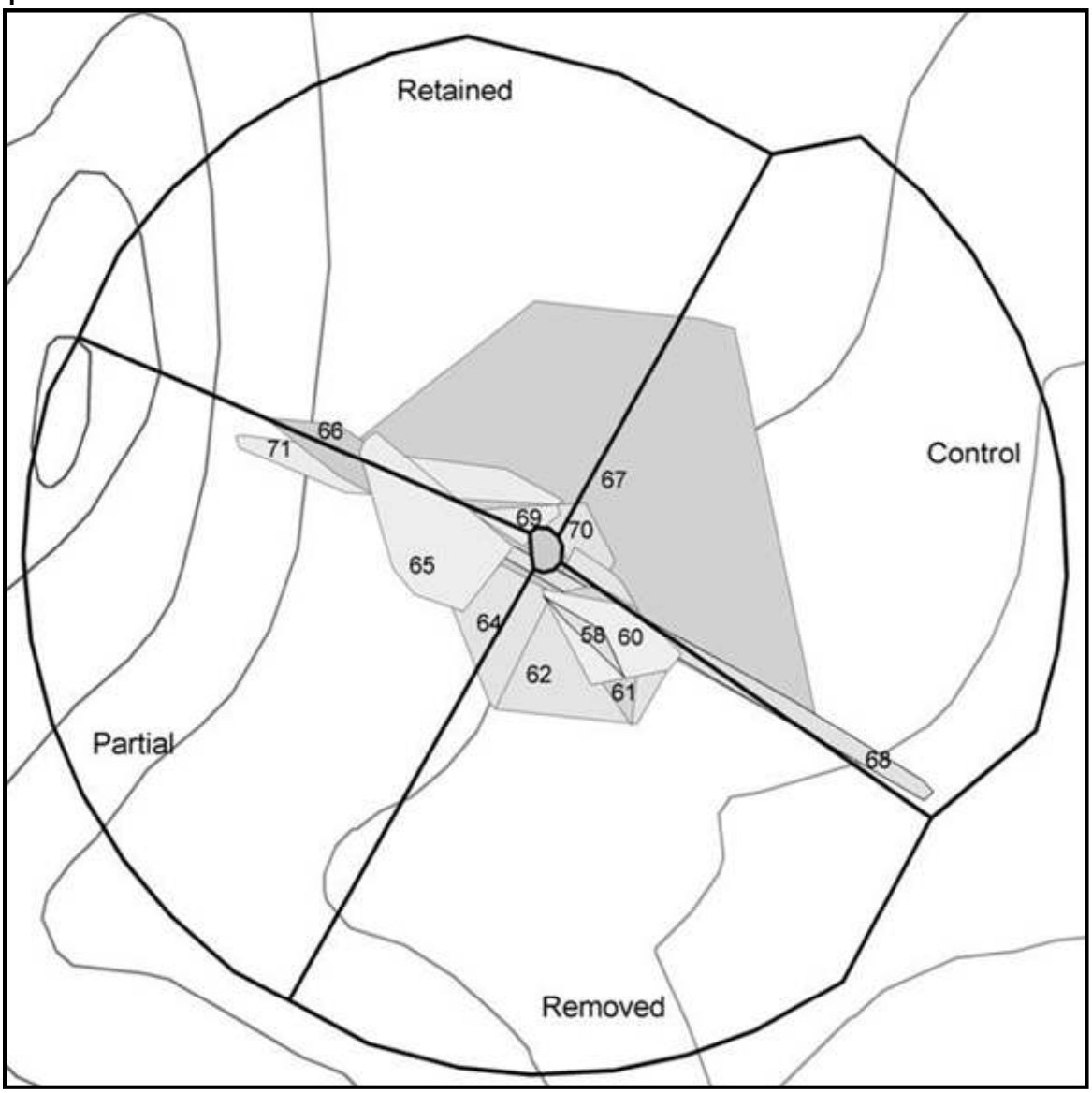


Figure A2 Continued.

E

Figure A2 Continued.

F



APPENDIX 3

Table A3. Top five models of daily microhabitat selection for individual *Rana sylvatica*. I only used frogs with ≥ 20 locations for this analysis. Variable codes are shown in Table 4.1.

Frog ID	Rank	Model	*K*	log(ℒ)	AIC_c	ΔAIC_c	ω
2	1	SP, SL, CP	3	-6.70	20.50	0.00	0.16
2	2	SP, SM, CP	3	-6.90	20.90	0.40	0.13
2	3	SP, SM, LI	3	-7.05	21.18	0.69	0.11
2	4	SP, CP	2	-8.36	21.25	0.75	0.11
2	5	SP, SM, LD	3	-7.19	21.48	0.98	0.09
4	1	SW, SM, LD	3	-2.08	11.66	0.00	0.23
4	2	SL, LD, CP	3	-2.77	13.05	1.39	0.12
4	3	SW, LD, CP	3	-2.77	13.05	1.39	0.12
4	4	SL, LD, CP	3	-2.78	13.05	1.39	0.12
4	5	SM, LD, CP	3	-2.78	13.05	1.39	0.12
5	1	SP, CC	2	-0.79	6.10	0.00	0.27
5	2	SP, CC, LI	3	-0.09	7.27	1.17	0.15
5	3	SP, CC, SM	3	-0.11	7.30	1.20	0.15
5	4	SP, CC, LM	3	-0.29	7.67	1.57	0.12
5	5	SW, SP, CC	3	-0.53	8.16	2.06	0.10
6	1	LI, SM, LD	3	-0.03	7.14	0.00	0.64
6	2	CC, LI, SM	3	-0.92	8.94	1.79	0.26
6	3	CC, SM, SL	3	-2.61	12.30	5.16	0.05
6	4	CC, SM, CP	3	-3.48	14.05	6.91	0.02
6	5	SP, CC, SM	3	-4.45	15.99	8.84	0.01
7	1	CC, SL, LD	3	-6.21	19.62	0.00	0.34
7	2	CC, SL, SM	3	-7.46	22.13	2.51	0.10
7	3	CC, SL, CP	3	-7.63	22.46	2.84	0.08
7	4	CC, LD	2	-9.25	23.07	3.45	0.06
7	5	CC, SL	2	-9.31	23.18	3.56	0.06
9	1	CC, CP	2	-4.77	14.24	0.00	0.23
9	2	CC, CP, CD	3	-4.28	16.06	1.82	0.09
9	3	CC, CP, LM	3	-4.36	16.21	1.98	0.09
9	4	CC, LD, CP	3	-4.66	16.82	2.58	0.06
9	5	CC, LI, CP	3	-4.70	16.90	2.66	0.06
10	1	LD	1	-16.64	35.44	0.00	0.21
10	2	SP	1	-16.83	35.82	0.38	0.17
10	3	SL	1	-17.06	36.28	0.84	0.14
10	4	SW	1	-17.36	36.88	1.44	0.10
10	5	SM	1	-17.61	37.38	1.94	0.08
11	1	SP, LI	2	-0.06	4.64	0.00	0.35
11	2	SP, CC, LI	3	-0.03	7.15	2.51	0.10
11	3	SP, LI, SM	3	-0.04	7.18	2.53	0.10
11	4	SP, LI, CP	3	-0.05	7.20	2.55	0.10
11	5	SP, LI, SW	3	-0.05	7.20	2.55	0.10

Table A3 Continued

12	1	SW	1	-12.54	27.24	0.00	0.76
12	2	SL	1	-14.34	30.85	3.61	0.13
12	3	LM	1	-15.50	33.16	5.92	0.04
12	4	LI	1	-15.57	33.31	6.07	0.04
12	5	LD	1	-16.64	35.44	8.20	0.01
13	1	SL	1	-11.78	25.74	0.00	0.79
13	2	CC	1	-13.80	29.76	4.02	0.11
13	3	CP	1	-14.06	30.29	4.55	0.08
13	4	LI	1	-16.64	35.44	9.70	0.01
13	5	SW	1	-16.64	35.44	9.70	0.01
16	1	LI, LD, CP	3	-0.71	8.51	0.00	0.13
16	2	LD, CP	2	-2.08	8.69	0.18	0.12
16	3	LD, CP, CD	3	-2.09	8.70	0.19	0.12
16	4	SW, LD, CP	3	-1.39	9.88	1.36	0.07
16	5	SM, LD, CP	3	-1.39	9.88	1.37	0.07
18	1	SW, SP, CC	3	-7.17	21.43	0.00	0.35
18	2	SW, SP, LI	3	-7.55	22.20	0.77	0.24
18	3	SW, SP	2	-9.97	24.46	3.03	0.08
18	4	SP, CC	2	-10.15	24.83	3.40	0.06
18	5	SW, SP, SM	3	-9.23	25.56	4.12	0.04
19	1	SW, LI, CP	3	-6.76	20.62	0.00	0.19
19	2	SM, CP, LM	3	-6.93	20.96	0.34	0.16
19	3	SW, CP, LM	3	-7.19	21.48	0.86	0.12
19	4	SW, LI, CP	3	-7.92	22.94	2.32	0.06
19	5	SP, CP, LM	3	-7.97	23.03	2.42	0.06
21	1	CC, CP	2	-7.86	20.23	0.00	0.17
21	2	CC, LD, CP	3	-6.90	20.89	0.66	0.12
21	3	CC, CP, CD	3	-7.03	21.15	0.92	0.11
21	4	SP, CC, CP	3	-7.11	21.31	1.08	0.10
21	5	CC, SM, CP	3	-7.28	21.65	1.42	0.08
22	1	LI	1	-14.97	32.11	0.00	0.29
22	2	CC	1	-15.01	32.19	0.08	0.28
22	3	LD	1	-15.94	34.05	1.95	0.11
22	4	SM	1	-16.04	34.25	2.14	0.10
22	5	LM	1	-16.60	35.38	3.27	0.06
23	1	SM	1	-14.34	30.85	0.00	0.30
23	2	CP	1	-14.34	30.85	0.00	0.30
23	3	CP, CD	2	-14.89	31.95	1.11	0.17
23	4	CC	1	-15.19	32.56	1.71	0.13
23	5	SL	1	-16.45	35.07	4.22	0.04
24	1	SM	1	-14.17	30.50	0.00	0.42
24	2	LM	1	-14.58	31.33	0.83	0.28
24	3	LI	1	-15.44	33.04	2.54	0.12
24	4	SW	1	-15.94	34.05	3.55	0.07

Table A3 Continued

24	5	CC	1	-16.53	35.24	4.73	0.04
25	1	SW	1	-13.86	29.90	0.00	0.68
25	2	LM	1	-16.22	34.61	4.71	0.06
25	3	LI	1	-16.48	35.13	5.23	0.05
25	4	SP	1	-16.62	35.41	5.51	0.04
25	5	SL	1	-16.64	35.45	5.54	0.04
28	1	SP	1	-10.62	23.41	0.00	0.90
28	2	CC	1	-13.13	28.42	5.00	0.07
28	3	LI	1	-15.37	32.91	9.49	0.01
28	4	SL	1	-16.04	34.25	10.83	0.00
28	5	CP	1	-16.11	34.39	10.97	0.00
30	1	SW	1	-14.56	31.29	0.00	0.48
30	2	LD	1	-15.25	32.67	1.39	0.24
30	3	CC	1	-16.93	36.03	4.74	0.04
30	4	SP	1	-17.02	36.21	4.92	0.04
30	5	CP	1	-17.16	36.49	5.20	0.04
31	1	SP, SL, LD	3	-2.10	11.33	0.00	0.93
31	2	SP, LD, CP	3	-6.38	19.90	8.57	0.01
31	3	SP, LD	2	-7.77	20.08	8.75	0.01
31	4	SP, CC, LD	3	-6.47	20.08	8.75	0.01
31	5	SP, LI, LD	3	-6.87	20.89	9.56	0.01
32	1	CC, CP, LM	3	-9.25	25.65	0.00	0.14
32	2	CC, SM	2	-10.94	26.43	0.78	0.09
32	3	CC, LM	2	-11.07	26.68	1.03	0.08
32	4	CC, SM, CP	3	-9.91	26.97	1.32	0.07
32	5	CC, CP	2	-11.24	27.03	1.38	0.07
33	1	LM	1	-16.26	34.68	0.00	0.28
33	2	SW	1	-16.57	35.30	0.62	0.21
33	3	LD	1	-17.33	36.82	2.14	0.10
33	4	SL	1	-17.36	36.88	2.20	0.09
33	5	LI	1	-17.40	36.97	2.28	0.09
35	1	SL	1	-2.78	7.73	0.00	0.80
35	2	CP	1	-4.16	10.49	2.76	0.20
35	3	SP	1	-16.33	34.82	27.09	0.00
35	4	LI	1	-16.51	35.18	27.45	0.00
35	5	SM	1	-16.55	35.27	27.54	0.00
37	1	LI	1	-10.19	22.56	0.00	0.94
37	2	SM	1	-13.15	28.46	5.90	0.05
37	3	CP	1	-15.64	33.44	10.88	0.00
37	4	CC	1	-15.77	33.70	11.14	0.00
37	5	LM	1	-16.09	34.35	11.80	0.00
38	1	SL	1	-13.75	29.66	0.00	0.50
38	2	CP, CD	2	-15.01	32.19	2.53	0.14
38	3	CP	1	-15.13	32.43	2.76	0.12
38	4	LI	1	-15.27	32.71	3.05	0.11

Table A3 Continued

38	5	LM	1	-15.41	32.98	3.32	0.09
40	1	LD	1	-16.04	34.25	0.00	0.36
40	2	SL	1	-17.20	36.56	2.32	0.11
40	3	SP	1	-17.33	36.82	2.58	0.10
40	4	CC	1	-17.61	37.40	3.15	0.08
40	5	CP	1	-17.77	37.70	3.46	0.06
41	1	SM, CP, CD	3	-11.22	29.53	0.00	0.14
41	2	CC, CP, LM	3	-11.71	30.52	0.99	0.08
41	3	CC, LD, CP	3	-11.80	30.70	1.17	0.08
41	4	CP, LM	2	-13.22	30.96	1.43	0.07
41	5	CP, CD, LM	3	-11.99	31.06	1.53	0.06
42	1	SM	1	-11.68	25.50	0.00	0.98
42	2	CC	1	-15.71	33.56	8.06	0.02
42	3	LI	1	-19.42	40.97	15.48	0.00
42	4	CP, CD	2	-19.42	40.98	15.49	0.00
42	5	CP	1	-19.51	41.15	15.65	0.00
43	1	LD	1	-17.53	37.19	0.00	0.52
43	2	SM	1	-18.63	39.40	2.21	0.17
43	3	SW	1	-19.41	40.95	3.77	0.08
43	4	SL	1	-19.50	41.14	3.95	0.07
43	5	CC	1	-19.79	41.71	4.52	0.05
44	1	CP	1	-18.96	40.05	0.00	0.31
44	2	CP, CD	2	-19.46	41.06	1.01	0.19
44	3	SW	1	-19.51	41.15	1.10	0.18
44	4	CC	1	-20.04	42.21	2.16	0.10
44	5	LI	1	-20.18	42.50	2.45	0.09
46	1	SP	1	-11.40	24.94	0.00	0.99
46	2	SW	1	-16.64	35.41	10.47	0.01
46	3	CP, CD	2	-17.11	36.36	11.42	0.00
46	4	SM	1	-17.28	36.70	11.76	0.00
46	5	CP	1	-18.12	38.37	13.44	0.00
49	1	CC	1	-9.28	20.70	0.00	1.00
49	2	LI	1	-15.98	34.09	13.39	0.00
49	3	SW	1	-19.41	40.95	20.25	0.00
49	4	LM	1	-20.02	42.17	21.47	0.00
49	5	SP	1	-21.07	44.28	23.58	0.00
50	1	LI	1	-16.42	34.98	0.00	0.83
50	2	SM	1	-18.78	39.69	4.71	0.08
50	3	SL	1	-20.10	42.34	7.36	0.02
50	3	SW	1	-20.10	42.34	7.36	0.02
50	5	CP	1	-20.74	43.62	8.64	0.01
52	1	SP	1	-18.02	38.18	0.00	0.60
52	2	LI	1	-19.67	41.48	3.30	0.12
52	3	CD	1	-20.44	43.01	4.83	0.05
52	4	SM	1	-20.51	43.16	4.98	0.05

Table A3 Continued

52	5	CC	1	-20.51	43.17	4.98	0.05
55	1	SP	1	-11.21	24.57	0.00	1.00
55	2	SW	1	-18.02	38.18	13.62	0.00
55	3	CP	1	-18.58	39.29	14.73	0.00
55	4	CC	1	-18.78	39.70	15.13	0.00
55	5	CD	1	-20.47	43.07	18.50	0.00
57	1	SL	1	-18.72	39.57	0.00	0.52
57	2	SW	1	-20.10	42.34	2.77	0.13
57	3	SP	1	-20.38	42.91	3.34	0.10
57	4	CC	1	-21.27	44.68	5.11	0.04
57	5	LD	1	-21.32	44.77	5.20	0.04
58	1	SW	1	-11.78	25.76	0.00	0.27
58	2	LD	1	-11.98	26.15	0.39	0.22
58	3	CD	1	-12.17	26.54	0.78	0.18
58	4	CC	1	-12.48	27.15	1.39	0.14
58	5	CP	1	-12.84	27.88	2.12	0.09
60	1	SL	1	-18.72	39.57	0.00	0.31
60	2	SM	1	-18.89	39.92	0.35	0.26
60	3	CP	1	-19.56	41.26	1.69	0.13
60	4	SP	1	-19.99	42.13	2.56	0.09
60	5	CD	1	-20.20	42.53	2.96	0.07
61	1	SM	1	-17.19	36.53	0.00	0.81
61	2	SW	1	-20.10	42.34	5.81	0.04
61	3	SP	1	-20.39	42.91	6.38	0.03
61	4	LM	1	-20.44	43.02	6.49	0.03
61	5	CC	1	-20.82	43.78	7.25	0.02
62	1	LI	1	-19.19	40.52	0.00	0.35
62	2	SM	1	-20.19	42.53	2.01	0.13
62	3	LM	1	-20.36	42.85	2.33	0.11
62	4	CD	1	-20.69	43.52	3.00	0.08
62	5	LD	1	-20.79	43.73	3.21	0.07
64	1	LD	1	-13.10	28.41	0.00	0.22
64	2	CC	1	-13.54	29.28	0.87	0.14
64	3	CD	1	-13.58	29.37	0.96	0.14
64	4	SP	1	-13.86	29.94	1.52	0.10
64	5	SL	1	-13.89	29.99	1.58	0.10
65	1	LI	1	-18.18	38.50	0.00	0.64
65	2	SW	1	-20.10	42.34	3.84	0.09
65	3	CC	1	-20.68	43.50	5.00	0.05
65	4	SP	1	-20.81	43.75	5.25	0.05
65	5	SL	1	-21.07	44.28	5.79	0.04
69	1	SL	1	-16.08	34.30	0.00	0.84
69	2	CD	1	-18.51	39.16	4.86	0.07
69	3	SM	1	-19.33	40.79	6.50	0.03
69	4	CP	1	-19.56	41.26	6.96	0.03

Table A3 Continued

69	5	LD	1	-20.79	43.73	9.43	0.01
70	1	CC	1	-11.33	24.79	0.00	1.00
70	2	SP	1	-17.55	37.23	12.44	0.00
70	3	CP	1	-18.72	39.57	14.77	0.00
70	4	LD	1	-19.41	40.95	16.16	0.00
70	5	LI	1	-19.73	41.60	16.80	0.00
71	1	CP	1	-18.72	39.57	0.00	0.28
71	2	CD	1	-18.72	39.57	0.00	0.28
71	3	SM	1	-19.55	41.23	1.66	0.12
71	4	LI	1	-19.62	41.39	1.82	0.11
71	5	CC	1	-19.66	41.46	1.89	0.11

APPENDIX 4

Table A4. Characteristics and home ranges of 40 radio-telemetered *Rana pipiens* that were tracked during May-June 2006. Snout-vent length (SVL) and mass were taken at the beginning of the study. SD = standard deviation.

Frog ID	Sex	SVL (mm)	Mass (g)	# of relocations	% days moved	Mean move (m)	Move SD	Total move (m)	Home range (m^2)
1	M	72	31.1	20	70	19.0	37.8	380.4	8425
2	F	80	54.8	4	75	26.3	33.5	105.2	922
3	M	73	32.1	27	74	5.3	5.4	142.0	788
4	F	77	32.8	27	81	7.0	9.1	188.0	754
5	F	77	33.6	9	56	3.2	8.5	28.6	13
6	F	86	52.4	17	59	3.0	4.7	50.8	161
7	F	73	35.8	10	80	5.3	7.3	52.5	70
8	M	79	50.7	27	56	4.3	11.4	116.1	594
9	M	72	30.4	2	0				
10	M	83	49.6	10	70	2.9	3.4	28.6	85
11	F	87	66.0	14	71	6.1	5.9	85.9	159
12	M	80	41.5	27	81	7.1	9.3	192.6	468
13	M	75	33.2	7	71	38.4	59.0	269.0	6832
14	F	75	36.4	20	40	4.4	9.2	88.9	216
15	M	73	33.3	27	81	4.8	5.4	129.0	469
16	F	85	64.7	27	70	6.2	12.0	166.8	425
17	F	79	41.9	4	100	12.0	7.9	47.9	274
18	M	77	35.0	22	77	14.5	17.2	320.0	2068
19	M	73	29.8	2	50	7.6	10.7	15.2	
20	F	85	54.2	13	62	9.9	11.0	128.6	426
21	F	78	36.7	24	88	8.5	14.8	205.1	1823
22	F	79	42.1	11	45	9.6	17.2	105.2	489
23	F	73	34.7	10	50	6.4	6.8	63.6	205
24	F	86	64.4	6	83	11.3	10.6	68.0	461
25	M	77	39.0	12	83	5.6	4.7	66.6	131
26	M	71	26.7	14	71	10.0	13.4	139.6	519
27	M	79	43.3	5	80	8.9	8.4	44.7	54
28	M	68	25.7	24	75	6.9	7.5	165.8	403
29	M	76	36.0	12	67	8.5	13.8	102.1	397
30	F	79	41.5	2	0				
31	F	77	42.2	14	21	4.6	12.4	65.0	518
32	M	70	30.0	27	89	6.0	6.7	162.4	452
33	F	76	39.3	24	71	8.9	16.9	212.6	850
34	F	86	56.5	2	50	64.6	91.4	129.3	
35	F	79	41.1	27	59	9.7	20.1	261.7	4203
36	M	79	47.9	2	0				
37	M	70	30.0	23	91	6.7	6.0	153.6	735
38	M	71	30.0	27	67	6.5	19.1	176.5	2005

Table A4 Continued

39	F	86	58.2	27	81	7.2	7.3	194.1	1729
40	M	66	24.6	9	89	12.9	12.0	116.1	249

APPENDIX 5

Table A5. Supported models ($\Delta AIC_c < 2$) of daily microhabitat selection for individual *Rana pipiens*. I only used frogs with ≥ 20 locations for this analysis. Variable codes are shown in Table 5.1.

Frog ID	Rank	Model	*K*	log(ℒ)	AIC_c	ΔAIC_c	ω
1	1	SW, VC, CC	3	-6.22	19.71	0.00	0.08
1	2	SW, VC, CC, LD	4	-5.18	20.58	0.87	0.05
1	3	LD	1	-9.36	20.91	1.20	0.04
1	4	VC, LD	2	-8.16	20.91	1.20	0.04
1	5	VC, CC, LD, DC3	4	-5.43	21.08	1.37	0.04
1	6	CC, LD, LM, DC3	4	-5.51	21.24	1.53	0.04
1	7	LD, TE	2	-8.41	21.41	1.70	0.03
1	8	LI, LD	2	-8.48	21.56	1.85	0.03
2	1	VC, LM, DC3, TE	4	-4.04	17.90	0.00	0.14
2	2	VC, CC,LM, DC3, TE	5	-2.61	18.07	0.17	0.13
2	3	VC, CC,LM, DC3	4	-4.86	19.53	1.63	0.06
2	4	VC, CC,LM, DC3, RH	5	-3.41	19.67	1.77	0.06
2	5	VC, CC,SM, DC3, RH	5	-3.41	19.68	1.78	0.06
2	6	VC, LM, DC3	3	-6.37	19.79	1.89	0.06
3	1	CC, SM, DC1	3	-8.32	23.69	0.00	0.07
3	2	CC, SM	2	-9.71	23.92	0.23	0.07
3	3	CC, SM, DC1, RH	4	-7.45	24.72	1.03	0.04
3	4	CC, SL, SM	3	-8.87	24.78	1.09	0.04
3	5	CC, SL, SM, DC1	4	-7.57	24.95	1.26	0.04
3	6	CC, SM, DC1, DC3	4	-7.63	25.08	1.39	0.04
3	7	CC, SM, LM	3	-9.02	25.08	1.39	0.04
3	8	CC, LD, SM, DC1	4	-7.81	25.44	1.75	0.03
3	9	CC, SM, RH	3	-9.24	25.53	1.84	0.03
3	10	CC, LI, SM	3	-9.32	25.69	2.00	0.03
8	1	SW, VC, SL, SM, DC1	5	-1.39	15.63	0.00	0.48
8	2	SW, VC, SL, LD, DC1	5	-1.98	16.82	1.19	0.27
12	1	VC, CC, LM, DC1, DC3, TE	6	-6.81	29.82	0.00	0.10
12	2	VC, CC, LM, DC1, DC3	5	-8.71	30.29	0.47	0.08
12	3	SW, CC, SM, LM	4	-10.44	30.69	0.87	0.07
12	4	SW, SM, LM	3	-11.83	30.70	0.88	0.06
12	5	SW, CC, LM	3	-12.31	31.67	1.85	0.04
12	6	VC, CC, SM, LM, DC1, DC3	6	-7.75	31.70	1.88	0.04
14	1	CC, LI, LD	3	-3.73	14.97	0.00	0.11
14	2	VC, CC, LI, TE, RH	5	-0.44	15.17	0.20	0.10
14	3	CC, LI, DC1, TE, RH	5	-0.83	15.95	0.98	0.07
14	4	CC, LI	2	-5.71	16.13	1.16	0.06
14	5	SW, CC, LM, DC3	4	-2.80	16.27	1.30	0.06
14	6	CC, LM, TE	3	-4.45	16.41	1.44	0.05
14	7	SW, VC, CC, LM	4	-3.13	16.93	1.96	0.04
15	1	VC, LM, DC1, DC3	4	-8.49	26.79	0.00	0.12

Table A5 Continued

15	2	VC, LI, LD, LM, DC1, DC3	6	-5.73	27.67	0.88	0.07
15	3	VC, LD, LM, DC1, DC3	5	-7.60	28.06	1.27	0.06
15	4	SW, VC, LM, DC1, DC3	5	-7.67	28.20	1.41	0.06
15	5	VC, LI, LM, DC1, DC3	5	-7.74	28.33	1.54	0.05
15	6	VC, LM, DC1, DC3, TE	5	-7.83	28.51	1.72	0.05
15	7	VC, LM, DC3	3	-10.79	28.63	1.84	0.05
16	1	SW, SL, SM, TE	4	-0.12	10.07	0.00	0.86
18	1	LI, SL, LD	3	-0.72	8.78	0.00	0.14
18	2	VC, LI, DC3	3	-0.73	8.80	0.02	0.14
18	3	LI, LM	2	-2.11	8.85	0.07	0.14
18	4	VC, LI, DC1	3	-0.77	8.88	0.10	0.14
21	1	SM, RH	2	-8.90	22.38	0.00	0.14
21	2	SM	1	-10.63	23.44	1.06	0.08
21	3	CC, SM, RH	3	-8.38	23.96	1.58	0.06
21	4	VC, SM, RH	3	-8.53	24.26	1.89	0.05
21	5	SM, TE, RH	3	-8.54	24.28	1.90	0.05
21	6	VC, SM	2	-9.87	24.31	1.93	0.05
28	1	RH	1	-9.11	20.41	0.00	0.16
28	2	VC, RH	2	-8.69	21.96	1.55	0.07
28	3	DC1, RH	2	-8.70	21.97	1.56	0.07
32	1	SM, LM, DC1	3	-5.48	18.00	0.00	0.25
32	2	SM, LM, DC1, RH	4	-4.89	19.59	1.60	0.11
33	1	VC, CC, SL, LD, DC1, RH	6	-0.70	18.35	0.00	0.46
35	1	LD, SM, TE	3	-1.40	9.84	0.00	0.21
35	2	LD, SM, TE, RH	4	-0.19	10.19	0.35	0.17
35	3	LI, LD, SM, TE	4	-0.80	11.41	1.57	0.09
35	4	LD, SM, DC1, TE	4	-0.95	11.71	1.87	0.08
37	1	CC, LD, LM, RH	4	-0.04	10.30	0.00	0.16
37	2	CC, LD, LM, TE	4	-0.09	10.40	0.11	0.15
37	3	CC, LD, LM	3	-2.17	11.60	1.30	0.08
37	4	CC, SL, LD, LM	4	-0.71	11.63	1.34	0.08
37	5	CC, SL, LM, DC3	4	-0.72	11.65	1.36	0.08
37	6	VC, CC, LD, LM	4	-0.99	12.20	1.90	0.06
38	1	SW, VC, DC1	3	-11.78	30.60	0.00	0.06
38	2	VC, DC1	2	-13.11	30.71	0.11	0.06
38	3	VC, LM, DC1	3	-11.85	30.75	0.14	0.06
38	4	VC, LD, DC1	3	-11.87	30.78	0.17	0.05
38	5	SW, VC, LD, DC1	4	-10.56	30.93	0.33	0.05
38	6	VC, LI, DC1	3	-12.19	31.41	0.81	0.04
38	7	VC, DC1, DC3	3	-12.33	31.71	1.11	0.03
38	8	SW, VC, LI, DC1	4	-10.95	31.73	1.12	0.03
38	9	SW, VC, SL, LD, DC1	5	-9.49	31.84	1.23	0.03
39	1	SM, LM	2	-9.76	24.03	0.00	0.11
39	2	SM	1	-11.13	24.41	0.39	0.09
39	3	LI, SM	2	-10.41	25.32	1.30	0.06

Table A5 Continued

39	4	SM, TE	2	-10.46	25.41	1.39	0.06
39	5	LI, SM, TE	3	-9.19	25.43	1.40	0.05
39	6	CC, SM	2	-10.74	25.98	1.95	0.04
39	7	SM, RH	2	-10.76	26.01	1.98	0.04

BIOGRAPHY OF THE AUTHOR

Sean Michael Blomquist was born in Chicago, Illinois on July 12, 1975. He grew up in Lexington, Kentucky and graduated from Lafayette High School in 1993. After traveling and spending time in Stockholm, Sweden, he attended and received his Bachelor of Science from Denison University. During his undergraduate research, he investigated the homing behavior of spotted salamanders under the guidance of Lynn Zimmerman and Walter Shriner. He completed his Masters of Science in 2000 at the University of Nevada, Reno where he worked with Jack Hayes, Kent Hatch, and Dick Tracy. He studied the life history of Columbia spotted frogs in the Toiyabe Range, Nevada for his Masters thesis. Sean worked for Mike Sredl at the Arizona Game and Fish Department as an Amphibians and Reptiles Biologist for three years where he helped manage and conserve Arizona's native leopard frogs.

Sean entered the Department of Wildlife Ecology at the University of Maine in 2003 to work with Mac Hunter. He was awarded a University Graduate Research Assistantship in 2007. In 2008, Sean was recognized by the Maine Agricultural and Forest Experimentation Station with a Dow and Griffee Award for student research, and was recognized as the Outstanding Graduate Student in Wildlife Ecology. Sean is a candidate for the Doctor of Philosophy degree in Wildlife Ecology from the University of Maine in May, 2008.