

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

SEAN M. BLOMQUIST^{1,2} AND MALCOLM L. HUNTER JR.¹

¹Department of Wildlife Ecology, 5755 Nutting Hall, University of Maine, Orono, Maine 04469-5755, USA

²Corresponding author's e-mail: seanblomquist@yahoo.com

Abstract.—Amphibian communities and populations respond to changes in the terrestrial landscape surrounding breeding ponds, but mechanisms are poorly understood. We radio-tracked 40 adult *Lithobates [Rana] pipiens* to assess habitat selection and movements at three scales (home range, weekly activity center, and daily microhabitat) in response to a control and three forest management strategies: clearcutting, clearcutting with coarse woody debris retention, and partial harvesting (50% canopy cover retained). At the home range scale, frogs selected the ponds as opposed to the surrounding terrestrial environment; whereas, weekly activity centers were 1.5 times more likely to have little canopy cover (mean = 15% vs. 42% cover at random sites). Weekly activity centers also had more standing water (mean = 46% vs. 5% cover), greater soil moisture (mean = 44% vs. 32% volumetric water content), and 4.7°C warmer temperatures than random activity centers. Frogs selected daily microhabitats dominated by live vegetation with moister litter and soil, more standing water, and 0.3°C warmer temperatures than random. Frog movements were on average almost twice as long in the unharvested control as the other treatments and the pond. Moisture appeared to be a dominant driver of habitat selection at all three scales. Selection for forested areas was strongest at the weekly activity center scale and seemed to be linked to thermoregulation and possibly cover from predator. Our results suggest that *L. 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.

Key Words.— amphibian; anuran; coarse woody debris; fluctuating resource availability; home range; niche; timber harvest

INTRODUCTION

Most pond-breeding amphibians depend on both aquatic and terrestrial habitats (Semlitsch 2000). 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. Recent work on pond-breeding amphibians has highlighted the importance of the terrestrial environment during the nonbreeding season for foraging, thermoregulation, hydroregulation, dispersal, migration, and overwintering (e.g., Regosin et al. 2005; Sztatecsny and Schabetsberger 2005; Baldwin et al. 2006; Rittenhouse et al. 2009). Human-alteration of the terrestrial environment can affect the ability and willingness of amphibians to move overland (i.e., permeability is reduced; e.g., Rothermel 2004), but empirical data on this are uncommon (reviewed by Cushman 2006).

Timber harvesting is one form of human alteration that differs in its intensity and effects on different amphibian species. Logging that removes much of the canopy cover and microhabitat structure (e.g., clearcut timber harvesting without retention of coarse woody debris; CWD) can decrease the abundance of forest-associated amphibian species, such as Wood Frogs (*Lithobates*

[Rana] sylvaticus), Spotted Salamanders (*Ambystoma maculatum*), and Northern Red-backed Salamanders (*Plethodon cinereus*) until forest regeneration restores essential components of their habitat (deMaynadier and Hunter 1995; Ash 1997; Herbeck and Larsen 1999). Most of this research has focused on forest-associated amphibian species, but clearcutting also can change the relative composition of the amphibian community by increasing the abundance of species that prefer open-canopy habitats, such as American Toads (*Anaxyrus [Bufo] americanus*) and Southern Leopard Frogs (*Lithobates [Rana] sphenocephala*). For example, *A. americanus* increased in abundance in 6 ha clearcuts after harvesting occurred in headwater riparian areas (Perkins and Hunter 2006).

Less is known about the influences of less intense timber harvesting practices, such as partial harvesting (i.e., commercial thinning, selection harvesting), on the distribution and persistence of amphibian populations. Light partial harvesting (partial harvesting with removal of < 25% of basal area; approximately equivalent to > 50% canopy retention in the northeastern United States) and retention of CWD in clearcut areas are postulated to mitigate the effects of tree removal on forest-associated amphibian species (deMaynadier and Hunter 1995), but empirical evidence supporting these hypotheses is mixed. For example, Western Red-backed Salamanders



FIGURE 1. Aerial photograph taken in June 2004 of an experimental timber harvesting array at the Dwight B. Demeritt Experimental Forest, Maine, USA. (Photographed by Malcolm L. Hunter Jr.)

(*Plethodon vehiculum*) decreased in abundance after partial harvesting with 16% reduction in basal area (Grialou et al. 2000), but the abundance of *P. cinereus* was no different between unharvested controls and partial harvesting with 23% reduction in basal area (Patrick et al. 2006). Further, anuran abundances were greater in unmanipulated 55-year old forests in Georgia than similar forested areas where all CWD was removed (Owens et al. 2008), but anuran abundances in Maine were not different in clearcuts with CWD retained and removed (Patrick et al. 2006). The “partial harvesting” and “CWD” hypotheses have not been experimentally tested for many species, and the mechanisms driving changes in abundance are poorly known.

We studied how timber harvesting affected habitat relationships and movement patterns of Northern Leopard Frogs (*L. pipiens*), an open-canopy associated species that has disappeared from many historical locations throughout its range (e.g., Clarkson and Rorabaugh 1989; Longcore et al. 2007). We used radio-telemetry to assess habitat selection at three scales, post-

breeding season home range, weekly activity center, and daily microhabitat, in response to a control and three timber harvesting practices: clearcutting, clearcutting with CWD retention, and partial harvesting with 50% overstory canopy retention. Further, we assessed how the frequency of movement and distances moved varied across these treatments.

MATERIALS AND METHODS

Experimental timber harvesting arrays.—The four experimental plots (hereafter, “experimental arrays” *sensu* Patrick et al. 2006) 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 pond ranging in size from 80–530 m² surrounded by four terrestrial sectors that constituted approximately 2.1 ha treatments: an unharvested control (unharvested forest stand; hereafter, “unharvested”) and three forest management practices: clearcut with coarse



FIGURE 2. Northern Leopard Frog (*Lithobates pipiens*) with a radio-transmitter in the unharvested control treatment of the North Chemo experimental array at the Penobscot Experimental Forest, Maine, USA. (Photographed by Sean M. Blomquist)

woody debris (CWD) removed (hereafter, “CWD removed”), clearcut with CWD retained (hereafter, “CWD retained”), and partial harvest with 50% overstory canopy retention (approximately equal to removal of 25% basal area; hereafter, “partial”). These four treatments were randomly positioned around the pond with the caveat that the partial treatment was never adjacent to the unharvested treatment (Fig. 1; see also Patrick et al. 2006). The forest in each array had not been harvested for ≥ 40 y, and timber harvesting was completed in April 2004.

The forests were predominately mixed coniferous-deciduous forests with dominant tree species including Balsam Fir (*Abies balsamea*), Eastern White Pine (*Pinus strobus*), Northern White Cedar (*Thuja occidentalis*), Red Maple (*Acer rubrum*), Eastern Hemlock (*Tsuga canadensis*), Red Oak (*Quercus rubra*), and Paper Birch (*Betula papyrifera*). Understory included American Beech (*Fagus grandifolia*), Bigtooth Aspen (*Populus grandidentata*), Quaking Aspen (*P. tremuloides*), and Balsam Poplar (*P. balsamifera*). The clearcuts in our experimental arrays created openings in an otherwise forested landscape; $> 70\%$ of the landscape within 1 km of the four experimental arrays was forested.

Habitat requirements and movement phenology of *Lithobates pipiens*.—The habitat requirements of *L. pipiens* vary with season (Rorabaugh 2005). This species breeds in semi-permanent or permanent ponds and hibernates in deep ponds that do not freeze solid, but uses the terrestrial environment more than other pond-breeding ranids during the remainder of the year. For

example, adults selected the terrestrial environment when given a choice of aquatic and terrestrial environments in a laboratory experiment (Licht 1991). *Lithobates pipiens* use emergent marshes and forested wetlands in the non-breeding season (Dole 1965a,b; Rorabaugh 2005). 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).

Breeding populations of adult *L. pipiens* are less likely to be present in ponds surrounded by a landscape with extensive forest cover (Guerry and Hunter 2002; Eigenbrod et al. 2008), and the presence of “summer” habitats (marsh, old fields, hay fields, scrub) within 1 km is an important component of predicting the presence of breeding populations (Pope et al. 2000). However, the habitat relationships in the terrestrial environment and details of why these coarse-scale relationships exist for populations are less clear. For example, adult *L. pipiens* typically spend the majority of time spent in marshes, pastures, scrub, and other open-canopy habitats in the non-breeding, active season (Dole 1965a,b; Merrell 1977), but Patrick et al. (2006) documented higher abundance of adults in unharvested and partially harvested forests than < 2 -y old clearcuts. We expected that 3-y old clearcuts would serve as summer habitat for adults because they had regenerated adequate vegetative cover, and that *L. pipiens* would select for the CWD retained and CWD removed treatments.

Radio-telemetry technique.—We evaluated habitat selection at three scales: habitat selection of home range over the entire duration of the study (2nd order), selection of weekly activity centers (3rd order), and selection of daily microhabitats (4th order; following Johnson 1980). We tracked 40 adult *L. pipiens* from 16 May–18 June 2006. We captured individuals after completion of breeding activity at the breeding pond or in the terrestrial environment nearby (Appendix 1), and held them for ≤ 8 d in terrestrial enclosures until release. We fit individuals with a radio-transmitter (BD-2 model, 0.9-g, 14-cm external whip antenna, 40-day battery life; Holohil Systems, Carp, Ontario, Canada) attached with a beaded chain (Blomquist and Hunter 2007; Fig. 2). We released two individuals into each unharvested and partial treatments and three individuals into each CWD retained and CWD removed treatments (N = 10 per array, 40 total) because we wanted to bias individuals to move out of the 3-y old clearcuts if they were still unsuitable habitat. All individuals were released on 16 May approximately 10 m from the edge of their respective pond, and we located each frog daily thereafter during daylight hours. We mapped each movement with a compass and tape measure from known locations in each experimental array, and took great care to avoid disturbing the frogs when collecting

Herpetological Conservation and Biology

TABLE 1. Habitat variables collected in 1-m² plots to quantify habitat use and availability in *Lithobates pipiens*. We collected each variable at the frog's location and at a random location each day (daily microhabitat) and at a set of random points for each 5-day period (weekly activity center) from 16 May to 18 June 2006. Variables were collected at the center of each plot unless otherwise specified. Percentage cover variables were estimated to the nearest 5%.

Variable	Code	Description
% canopy	CC	Percentage canopy cover above plot measured with a GSR vertical densiometer
% litter	LI	Percentage cover of leaf litter
% standing water	SW	Percentage cover of standing water
% <i>Sphagnum</i> spp.	SP	Percentage cover of <i>Sphagnum</i> spp. mosses
% vegetation	VC	Percentage cover of vegetation < 0.5 m
% slash	SL	Percentage 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 center)
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)

movement and habitat data. Coordinates for known locations were obtained using a Trimble GeoExplorer GPS unit (post-corrected accuracy of generally < 1 m).

Home range selection and movement patterns.—We used Hawth's Analysis Tools (Available from <http://www.spatial ecology.com/htools> [Accessed 18 February 2006]) in ArcGIS (Environmental Systems Research Institute, Redlands, California, USA) to calculate 100% minimum convex polygon size, movement path length, and simulated home ranges to evaluate habitat selection and movement patterns over the duration of tracking period. We used a minimum convex polygon to estimate home range size in preference to probabilistic estimators because the number of relocations we could obtain on each frog (~30) was unlikely to estimate accurately home range size with these estimators (e.g., Seaman and Powell 1996). We calculated a 100% MCP rather than a 95% MCP to estimate home range size for each frog because removing 5% of the sampled points was not necessary for *L. pipiens* during distinct portions of the active season. We estimated a home range for all frogs that moved to at least three unique locations but excluded frogs with < 10 locations (e.g., the smallest sample size considered by Seaman and Powell 1996) from further analysis. We calculated availability of habitat for each frog by simulating ten randomly positioned home ranges within the experimental array. Each simulated home range was identical in area and number of relocations to the observed home range for each frog. The number of simulated relocations in the simulated home range were extracted from each harvest treatment and averaged across the ten simulated home ranges to yield an

estimate of possible habitat use (i.e., availability of habitat) for each individual.

The observed home range sizes, number of locations per treatment, distance moved, and frequency of movement (number of days that an animal moved) for each animal were not normal based on histograms, skewness, and kurtosis of each variable, and therefore we natural log-transformed home range sizes and number of locations per treatment to correct this problem; data met all other assumptions of analysis of variance (ANOVA). We used ANOVA or t-test to examine if home range size varied with experimental array or sex, respectively. We assessed whether the distance moved and frequency of movement differed among the harvest treatments using nonparametric Kruskal-Wallis test because we could not correct problems with normality. We investigated if individuals exhibited homing behavior (Dole 1972a,b) using a Mann-Whitney test to compare the dominant direction moved over the course of the study to the direction the individual was collected.

We used a selection index to investigate if frogs selected major habitat categories (i.e., breeding pond and 4 harvest treatments) over the course of the study. We calculated a zero-centered selection index for each frog in each treatment,

$$(1) \quad si_{tf} = \ln \left(\frac{\frac{u_{tf}}{u_f}}{\frac{a_{tf}}{a_f}} \right),$$

where u_{tf} is the number of relocations for frog f in treatment t and u_f is the total number of relocations for

frog f , a_{ft} is the number of locations from the 10 simulated home ranges for frog f that fell in treatment t , a_f = total number of random locations from the 10 simulated home ranges for frog f that fell in treatment t (i.e., use divided by availability; Manly et al. 2002). We used a sign test to determine if the mean selection index for each treatment differed from zero. We conducted all statistical analyses in SAS (Version 9.1, SAS Institute, Cary, North Carolina, USA) with $\alpha = 0.05$ and report means \pm standard error unless otherwise specified.

Selection of weekly activity centers.—We attempted to control for spatial and temporal dependence of weekly activity centers by using movement patterns of *L. pipiens* and other terrestrial anurans to design our habitat sampling based on literature and pilot data. We assumed that 30-m and 300-m radius circles were available to the frogs on a daily and weekly basis respectively based on the movements of *L. pipiens* and other anurans in temperate forests in the eastern United States (Dole 1965a,b, 1971; Merrell 1977; Sean Blomquist and Malcolm Hunter, unpubl. data). We evaluated habitat use and availability using 12 variables (Table 1) chosen based on the habitat relationships, ecology, and physiology of *L. pipiens* and other anurans (Thorson 1955; Jorgensen 1997) and measured at the center of a 1-m² hexagonal plot. We measured each variable at five locations in a frog activity center over the span of five days for each frog. On the 6th day, we chose each random activity center as a non-overlapping, 30-m radius circle positioned 50–300 m from the center of the frog's activity center (Hawth's Analysis Tools *op. cit.*), and we measured each variable at five locations within each random activity center by randomly selecting a compass azimuth and distance 1–30 m from the center of the random activity center.

We used conditional logistic regression to compare the mean habitat conditions at frog activity centers over a 5-d period (hereafter, "week") to the mean habitat conditions at random activity centers. We used two strata (week [N = 6] and experimental array [N = 4]) in this analysis to incorporate variability associated with the structure of our habitat sampling. Additionally, this analytical strategy allowed us to incorporate the variation in sample size because eight frogs lost their transmitters prior to 18 June (Appendix 1). We used a sequential approach to build our candidate model set. First, we defined plausible combinations of variables and second-order interactions describing the relationship among temperature, moisture, and forest structure variables based on the biology of *L. pipiens* and other anurans and our treatments, and we constructed 16 candidate models based on these groupings of habitat variables (Table 2; Burnham and Anderson 2002). Second, we checked each of the possible variables for linearity and correlation with other variables to meet the

assumptions of logistic regression (Hosmer and Lemeshow 2000). We linearized the logit by defining a threshold for canopy cover at 60% for the activity center analysis based on a univariate plot of the lowess-smoothed logit (Hosmer and Lemeshow 2000). Canopy cover was incorporated into the models as a binary variable (i.e., canopy > 60% and canopy \leq 60%). All other variables were linear, and no variables were highly correlated (all $r < 0.7$). Third, we used AIC_c and Akaike weights (ω_i) to rank the 16 candidate models and select which model(s) best described *L. pipiens* activity center selection (Burnham and Anderson 2002). We considered models with Δ AIC_c < 2 to be equally supported. Fourth, we incorporated each second-order interaction individually into the best model(s) (Table 2) and reassessed support for these models including the interactions relative to the best model(s) without interactions. We ranked models using AIC_c and incorporated all interactions that had a lower AIC_c value than the best model(s) without interactions into the final model. Finally, if more than one model was supported, we used model averaging to derive parameter estimates (Burnham and Anderson 2002).

Daily microhabitat selection.—We evaluated habitat use and availability of daily microhabitats using 14 variables (Table 1). Daily when we located each frog, we measured these 14 variables at the center of a 1-m² hexagonal plot and a microhabitat 1–30 m from the frog chosen by randomly selecting a compass azimuth and distance.

We used case-control logistic regression to compare the relative selection made by each individual based on the difference between the frog microhabitat variables and the paired-random microhabitat variables (e.g., Compton et al. 2002; Moore and Gillingham 2006). We modeled only frogs that were tracked for ≥ 20 d, and all variables were linear. To develop candidate models for daily microhabitat selection, we modified our process for development of candidate models from that used for weekly activity centers by adding a model size constraint to account for the relatively small sample size for each individual (N < 30). We 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 our candidate model set for each frog (Shtatland et al. 2001; Campbell et al. 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) recommended 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

TABLE 2. Groupings of habitat variables used in construction of models describing activity center habitat selection by *Lithobates pipiens*. Variable codes and descriptions are presented in Table 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
Temperature	1	TE
Temperature interactions	6	CP×ST, LD×ST, SL×ST, VC×ST, SW×ST, SM×ST
Litter moisture interactions	4	LD×LM, LI×LM, SL×LM, VC×LM
Soil moisture interactions	5	VC×SM, LI×SM, LD×SM, CP×SM, SW×SM

approach, and, hence, we used this procedure only to constrain the possible model sizes included in the candidate set (Anderson and Burnham 2002). We considered model sizes with $\Delta AIC_c < 4$, and built 10 candidate models for each frog within this optimal range of model sizes. This liberal cutoff allowed model sizes with less support than the typical cutoff of $\Delta AIC_c < 2$ to be included in our candidate model building process and allowed us to include groups of variables (e.g., Table 2) that may be important to *L. pipiens* habitat selection.

We used the standardized parameter estimates (β_s) for each variable to draw inferences about how habitat selection varied among individuals in the population. We transformed β_s for percentage canopy cover, percentage leaf litter cover, and percentage *Sphagnum* spp. cover using an arcsine square root transformation and transformed leaf litter moisture by lumping the moist and wet categories and CWD decay by lumping categories two to five (Table 1; Maser et al. 1979) to correct issues with non-normality. β_s for remaining variables were normal based on histograms, skewness, and kurtosis of each variable. We used multiple linear regression to examine if habitat selection varied with experimental array, sex, or the harvest treatment in which the frog spent the greatest amount of time (hereafter, “dominant treatment”). We tested each variable independently. Thus, β_s for each frog are independent units of replication, and the sample size was the number of frogs whose top model(s) included a given variable (e.g., Marzluff et al. 2004).

RESULTS

Home range selection and movement patterns.—Frogs at the Gilman ($1347 \pm 1181 \text{ m}^2$) and South Chemo ($1328 \pm 468 \text{ m}^2$) experimental arrays tended to have larger home ranges than frogs at the Smith ($348 \pm 77 \text{ m}^2$) and North Chemo ($803 \pm 198 \text{ m}^2$) experimental arrays ($F = 2.6$, $df = 3,26$, $P = 0.073$; Fig. 3), but home range size did not vary with sex ($t = -0.88$, $df = 33$, $P = 0.386$). Mean home range size was $1096 \pm 310 \text{ m}^2$ (range 13–

8425 m^2), and home range size was not correlated with the number of times a frog was relocated ($r = 0.2$, $P = 0.354$; Appendix 2). Frogs exhibited no evidence of homing (i.e., no relationship between movement angle and angle to collection location; $U = 0.5$, $df = 1$, $P = 0.833$), and home range size (Spearman $r = -0.1$, $P = 0.527$) and total movement distance (Spearman $r = -0.1$, $P = 0.621$) were not correlated with distance to collection location. We analyzed home range sizes for 30 of the 40 *L. pipiens*; five frogs slipped out of their transmitter belts, two were predated, one died of unknown causes, and two are suspected to have died of chytridiomycosis in the first 10 days of tracking (Appendix 1; Sean Blomquist, unpubl. data).

On average, frogs spent $8 \pm 1 \text{ d}$ in the pond, $5 \pm 1 \text{ d}$ in the unharvested, $5 \pm 1 \text{ d}$ in the partial, $6 \pm 1 \text{ d}$ in the CWD retained, and $7 \pm 1 \text{ d}$ in the CWD removed treatments. Frogs selected ponds ($G = 7.5$, $df = 1$, $P < 0.001$) over terrestrial habitat, and tended to select CWD removed treatments ($G = 4.0$, $df = 1$, $P = 0.152$) more than the other harvest treatments (Kruskal-Wallis $\chi^2 = 43.5$, $df = 4$, $P < 0.001$; Fig. 4). Eighteen of the 40 frogs entered the pond during the study and two frogs (Frogs 1 and 8; Fig. 3A) extended their home ranges beyond the edge of the experimental array; this indicates that our definition of the experimental array as available habitat was acceptable. These two individuals moved 102 m and 67 m, respectively, beyond the edge of the Gilman experimental array to the same forested wetland. The nine locations that these two frogs spent in the unharvested forest beyond the edge of experimental arrays were grouped with the unharvested treatment.

Frogs made $3.8 \pm 0.9 \text{ m}$ shorter movements while in the ponds (max. daily movement = 63.1 m; $G = -51.5$, $df = 1$, $P < 0.001$) and $6.6 \pm 1.8 \text{ m}$ longer movements while in the unharvested treatments (max. daily movement = 159.8 m; $G = -10.5$, $df = 1$, $P = 0.028$) relative to movement in the CWD removed (max. daily movement = 84.8 m), CWD retained (max. daily movement = 71.8 m), and partial (max. daily movement = 99.0 m) treatments. However, the treatments only tended to

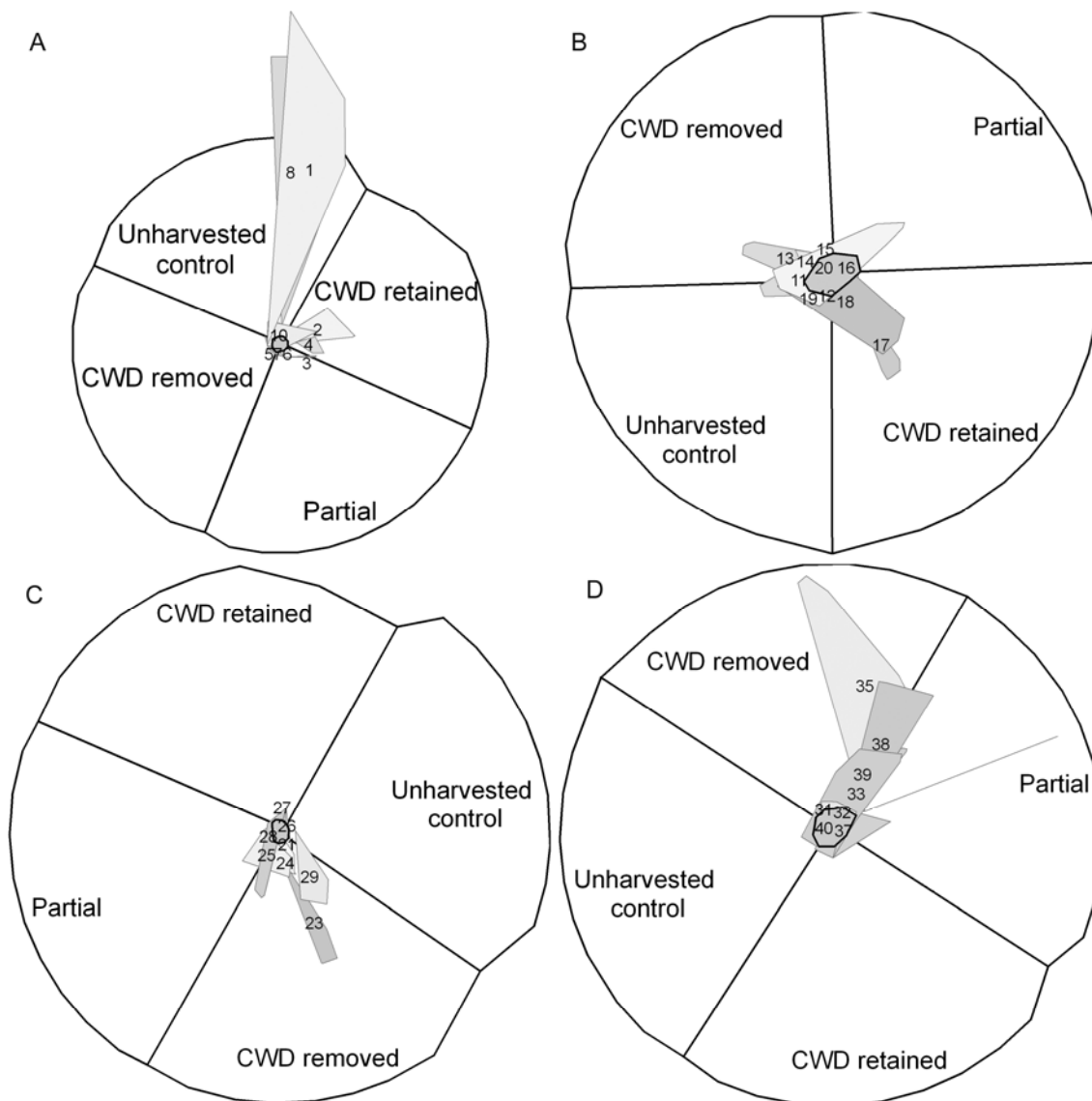


FIGURE 3. Home ranges (100% minimum convex polygon) of 35 *Lithobates pipiens* tracked during May and June 2006 in Maine, USA at the Gilman (A), North Chemo (B), Smith (C), and South Chemo (D) experimental arrays. Experimental arrays have a 164-m radius, and north is the top of each map. Small deviations from the 164-m radius were required at the Gilman and Smith sites because adjacent landowners did not want timber harvesting to occur on their property.

differ from each other overall (Kruskal-Wallis $\chi^2 = 9.0$, $df = 4$, $P = 0.061$; Fig. 5). Four of the five longest movements occurred in the unharvested treatment, and nine of the 10 longest movements occurred in forested areas (unharvested and partial treatments or outside of the experimental array); these 10 longest movements were made by six different frogs. Mean total distance moved by *L. pipiens* over the study was 134.3 ± 15.0 m (Appendix 1). Frogs moved $71 \pm 5\%$ of the days during the study, and moved on average 8.8 ± 1.5 m when they moved. Movement frequency did not differ among the harvest treatments (Kruskal-Wallis $\chi^2 = 4.2$, $df = 4$, $P = 0.381$).

Selection of weekly activity centers.—Similar to our 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 average canopy cover (15%) than did random activity centers (42%; Tables 3 and 4). Additionally, frogs selected weekly activity centers with an optimum balance of moisture and temperature. 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 4.7°C warmer temperatures than random activity centers (Table 4). These three variables interacted in two ways: between percentage cover of

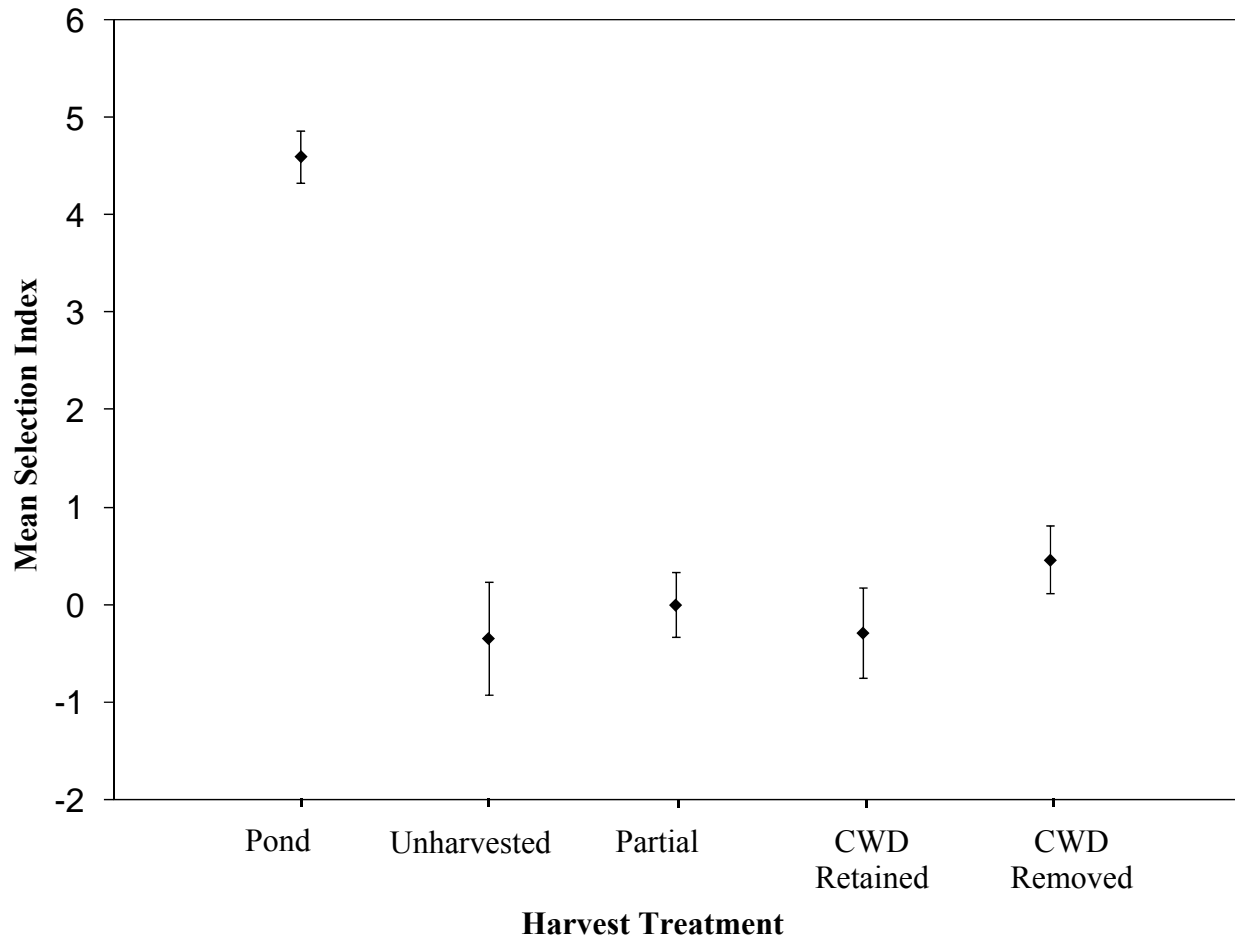


FIGURE 4. Mean selection index (\pm 95% confidence interval) calculated from selection indices for each of 30 *Lithobates pipiens* in the four harvest treatments and the four ponds tracked during May and June 2006 in Maine, USA. A positive selection index means the frogs used that treatment more than expected.

standing water and ground surface temperature and between soil moisture and ground surface temperature. The interaction pattern was the same: 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 moistures in the range that we measured (10–50% volumetric water content), but the decrease in probability of occupancy was less rapid at lower soil moistures. Percentage cover of *Sphagnum* spp. mosses and litter moisture were included in the best model, but the 95% confidence intervals for odds ratios of these variables overlapped one; thus, these variables are not useful for describing *L. pipiens* habitat selection in weekly activity centers.

The best supported model incorporated high cover, moisture, and temperature variables (Table 3), and it had

> 2 times the support as the next best model and comprised 56% of the weight for the candidate model set (Score $\chi^2 = 200.5$, $df = 8$, $P < 0.001$; Cox and Snell $r^2 = 0.61$; Cox and Snell 1989). Although the fit of the global model to our data (Hosmer and Lemeshow $\chi^2 = 12.8$, $df = 8$, $P = 0.118$) is questionable, the best supported model fit our data (Hosmer and Lemeshow $\chi^2 = 6.4$, $df = 8$, $P = 0.606$).

Daily microhabitat selection.—Frogs selected daily microhabitats with greater leaf litter moisture, greater soil moisture, more standing water, less leaf litter cover, and higher temperatures relative to random microhabitats (Table 5). Additionally, frogs were more likely to be found in microhabitats with live vegetation as the dominant cover item. Frogs were 14.2 ± 4.7 (\pm 95% CI) times more likely to occupy microhabitats with moist or wet leaf litter, and were 9.3 ± 6.5 (\pm 95% CI) times more likely to occupy microhabitats with slightly

TABLE 3. Models of weekly activity center habitat selection in *Lithobates pipiens*. Model subsets are defined in Table 2.

Rank	Model	K	log(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

warmer temperatures (22.1°C vs. 21.8°C). Frogs occupied microhabitats 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 microhabitats.

The best model(s) varied greatly for individual frogs, included from one to six variables, and were significant (Appendix 3). Frogs responded to 11 of the 14 habitat variables we measured (i.e., those variables were included in at least one frog's best model[s]). However, the standard error of six of 11 variables included in the top models overlapped zero, which indicates that these variables were not useful for describing daily microhabitat selection (Table 5). We found no evidence that habitat selection varied with experimental array, sex, or dominant treatment.

DISCUSSION

Habitat selection at three scales.—The *L. pipiens* complex has been associated with forests (e.g., Enge and Marion 1986; Patrick et al. 2006) as well as open-canopy areas or edges (e.g., Skelly et al. 1999; Werner and Glennemeier 1999; Guerry and Hunter 2002; Russell et al. 2002; Eigenbrod et al. 2008). The relative importance of canopy cover, temperature, ground cover, and moisture described in this study may help clarify the association of the *L. pipiens* complex with forested habitat. Our frogs may have selected the ponds because the canopy conditions above our ponds were relatively open (< 30% canopy cover) and frogs could easily thermoregulate and maintain their water balance. However, selection for open-canopy conditions was strongest at the weekly activity center scale, and adults were 1.5 times more likely to occupy weekly activity centers with little canopy cover (mean = 15% vs. 42% cover at random sites). Additionally, evidence of thermoregulatory behavior was strongest at the weekly

activity center scale (i.e., frogs selected activity centers with 4.7°C warmer temperatures than random); however, some thermoregulation may occur at the daily microhabitat scale, but again frogs selected for microhabitats with 0.3°C warmer temperatures than random. The method of thermoregulation is likely the same at both scales; frogs selected for activity centers and microhabitat with less canopy cover than random. These results indicate that canopy cover is an important variable for thermoregulation in *L. pipiens*, and thermoregulation occurs primarily at the weekly activity center scale.

Selection for cover at the microhabitat scale was different than at the two coarser scales; *L. pipiens* selected daily microhabitats dominated by live vegetation < 0.5 m in height (e.g., cattails; *Typha* sp., grasses, forbs, and saplings). Previous work on microhabitat relationships during the post-breeding season generally agree with our results (e.g., Dole 1965a,b; Rittschof 1975; Merrell 1977; Beauregard and Leclair 1988; McAlpine and Dilworth 1989). Live ground vegetation is probably important cover from predators and may work in conjunction with the cryptic coloration of *L. pipiens* against visually oriented predators (Heinen and Hammond 1997). Use of such vegetated refuges may be a common strategy to avoid predation among anurans that use open-canopy habitats. For example, the Western Toad (*Bufo boreas*) used open-canopy habitats only when adequate ground cover was available (Bartelt et al. 2004; Bull 2006). Additionally, our frogs may have been able to select the ponds because they had dense stands of cattails (*Typha* sp.) and other ground vegetation for cover. Microhabitat relationships were consistent across treatments; in particular we did not find evidence to support previous suggestions that microhabitat use may differ between forested and open-canopy habitats (Dole 1965a,b).

TABLE 4. Variables describing weekly activity center habitat selection for *Lithobates 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. Four random activity centers were removed because they overlapped frog activity centers. Interaction patterns for odds ratios (OR) are described in the text. SE = standard error; CI = 95% confidence interval.

Variable	β	SE $_{\beta}$	OR	CI $_{OR}$	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
% <i>Sphagnum</i> spp.	0.008	0.016	1.01	0.04	11	1	12	1
% canopy	-0.022	0.008	0.98	0.02	42	3	15	2
Litter moisture	0.423	0.474	1.53	0.92	1.83	0.07	2.59	0.04
Soil moisture	-0.110	0.157	0.90	0.24	32	1	44	1
Temperature	0.069	0.266			17.4	0.3	22.1	0.3
% standing water \times Temperature	0.011	0.006						
Soil moisture \times Temperature	0.007	0.008						

Moisture was important at all three scales, and our results suggest moisture is a dominant factor influencing habitat selection for *L. pipiens*. Adults selected home ranges that included the ponds, weekly activity centers with more standing water and greater soil moisture than random activity centers, and daily microhabitats with greater litter and soil moisture and greater cover of standing water than random locations. Maintenance of an optimum water balance has been hypothesized as a primary motivator of behavior in amphibians (Thorson 1955; Jorgensen 1997). Somewhat surprisingly, frogs were less likely to occupy areas with greater soil moisture at warmer temperatures. This may have occurred because most frogs moved to upland areas to forage when prey are more available and digestion is more efficient (i.e., at warmer temperatures; Feder and Burggren 1992; Sztatecsny and Schabetsberger 2005). *Lithobates pipiens* typically disperse after breeding from ponds to forage, and summer habitats include grasslands, meadows, fields, peat bogs, and pastureland (Rorabaugh 2005), but use of these habitats varies based on moisture (e.g., Pope et al. 2000; Mazzerole 2001).

Movement patterns.—*Lithobates pipiens* tended to move longer distances in the unharvested treatment, and there are at least three plausible explanations for this pattern. First, they may have used the path of least resistance for travel given that our unharvested treatments lacked a dense understory (Patrick et al. 2006). Similar results were observed in the closely related Southern Leopard Frog (*L. sphenoccephala*) in nearly identical experimental harvesting arrays in South Carolina (Graeter et al. 2008), and such behavior is common in other frogs. For example, Green Frogs (*L. clamitans*) on a golf course used short, grass habitat that allowed fast movement (Birchfield and Deters 2005).

Second, cover is an important variable in the risk perception of frogs (e.g., Martin et al. 2005), and *L. pipiens* may have tended to move more in forested areas because of reduced predation risk from avian predators. Alternatively, *L. pipiens* may have tended to move more in our unharvested treatments because they lacked a dense understory that provided cover from mammalian and other ground predators.

Third, it is noteworthy that nine of the 10 longest movements observed in this study occurred in forested

TABLE 5. Variables describing daily microhabitat selection in *Lithobates pipiens*. Mean standardized parameter estimates (β_s) and mean parameter values were calculated from the supported model(s) for each frog that used that variable (Appendix 1) based on data collected daily at 643 paired frog and random 1-m² plots (1286 total). Dominant cover variables are interpreted as likelihood to be selected relative to bare soil. N indicates the number of frogs that selected a variable. 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

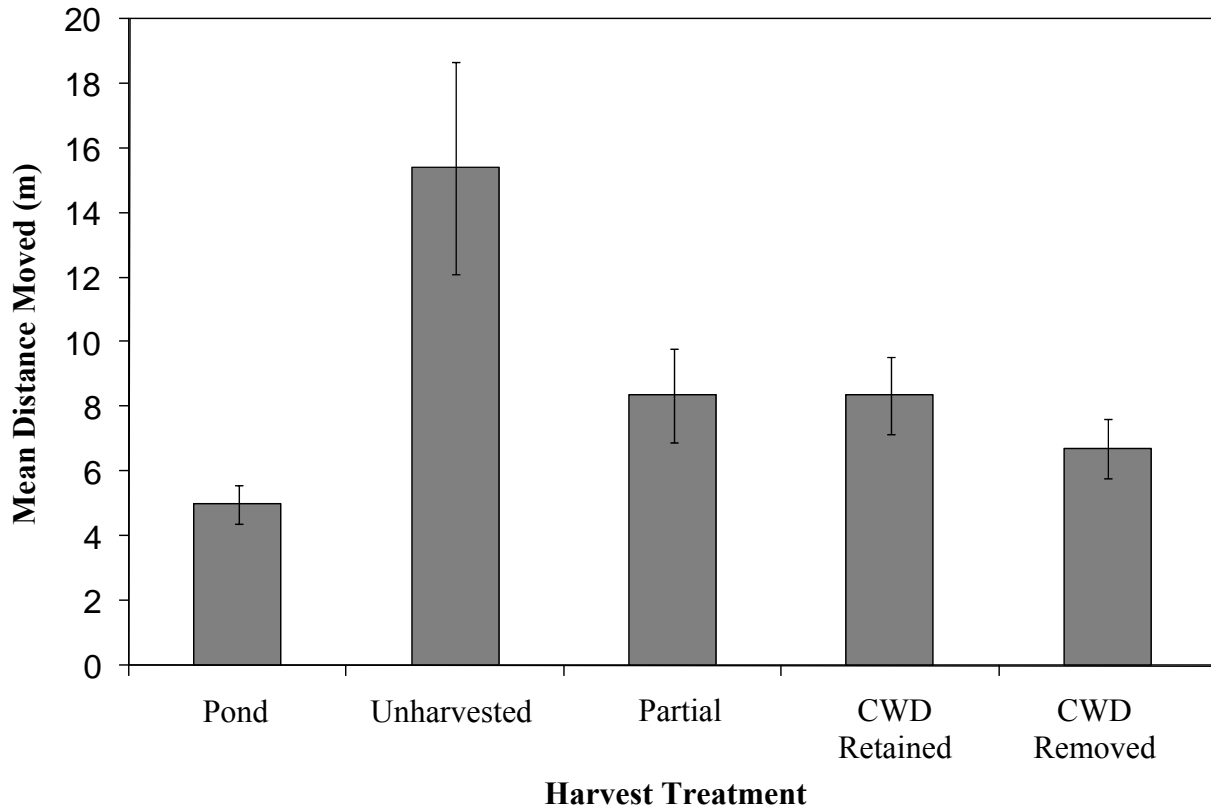


FIGURE 5. Mean movement distance (± 1 standard error) of radio-tracked *Lithobates pipiens* by harvesting treatments during May and June 2006 in Maine, USA.

(unharvested and partial) treatments, and forest cover may be important during migration for thermo- and hydro-regulation. Amphibian migrations are often timed to co-occur with rain events or optimal temperatures (e.g., Todd and Winne 2006). Additionally, habitat can be an important factor in determining success during migration (Patrick et al. 2008), and the suitability of a habitat for migration is possibly a trade-off among risk of predation, resistance to movement, and physiological constraints (Rittenhouse et al. 2009).

Conservation implications.—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 (i.e., spatial arrangement) among breeding, summer, and overwintering habitat may be more important than the simple abundance of these habitats (Pope et al. 2000; Gibbs et al. 2005; Eigenbrod et al. 2008). Our results may help explain the patterns of pond occupancy observed in this previous research. The clearcuts in our

experimental arrays created small patches of open-canopy habitat in an otherwise forested landscape, and our results indicate that *L. pipiens* used these during the spring and early summer because they were within migration distance of breeding and overwintering habitats and they had dense ground vegetation.

Open-canopy, terrestrial habitats with dense regenerating vegetation within migration distance of breeding ponds and hibernacula and breeding ponds with reduced canopy should also favor other amphibian species associated with open-canopy habitats, such as *L. sphenoccephala* (Graeter et al. 2008). Small-scale active habitat management may be appropriate for species of concern in some situations, but it would be unwise to extrapolate our results to support large-scale clearcutting to create habitat for such species. Managers should interpret our results with caution for at least three reasons. First, species with open-canopy habitat associations may benefit from natural disturbances that create open-canopy habitat, and any active management should attempt to mimic natural disturbance regimes (i.e., size and position on the landscape) that create open-canopy conditions in the study region. Our clearcuts created 2.1 ha patches of open-canopy habitat, and if active habitat management is determined to be an

appropriate strategy for species of concern in the Acadian forests of northern New England and Atlantic Canada, clearcuts of this size may provide habitat after adequate ground cover has regenerated (e.g., after two growing seasons in Maine). Second, landscape context is important because a species may need different habitat types for different portions of its life cycle and the habitats needed for the entire life cycle of the species of concern should be considered before implementing any active management. For example, in northeastern Maine *L. pipiens* living in agricultural 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), and this may be because *L. pipiens* use forested corridors for longer movements. Our clearcuts occurred near breeding ponds in an extensively forested area landscape with many wetlands. Third, management practices that favor species that prefer open-canopy may negatively impact forest specialists, such as plethodontid salamanders (Herbeck and Larsen 1999), and active habitat management should take into account the whole species assemblage before implementing actions. For example, we found no evidence that partial harvesting or retention of CWD was beneficial for *L. pipiens*, but *Ambystoma maculatum* was found in higher abundances in these treatments relative to the clearcut with CWD-removed within the same experimental arrays (Patrick et al. 2006).

Lithobates pipiens has declined throughout its range for a variety of reasons including habitat loss (e.g., Rorabaugh 2005). This species depends on a landscape that includes breeding ponds, upland foraging areas, overwintering aquatic habitats, and connectivity that allow movement among these habitats. Reliance on multiple habitats throughout the annual cycle makes this species especially susceptible to loss, alteration, and fragmentation of habitats (Becker et al. 2007). The loss of wetlands in the United States (e.g., Dahl 2006) and increase in forest cover (Whitney 1994) have probably contributed to the decline of this species. In summary, our research can help inform conservation strategies for this species in two ways. First, *L. pipiens* selected activity centers in the late spring and summer that focused on open-canopy areas with ample moisture and standing water. These areas are likely important for foraging to regain mass after the breeding season. Second, *L. pipiens* used unharvested forest for longer movements. Connecting forest between different habitats used during the annual cycle may be important to the persistence of populations because of genetic and demographic processes. Future research should identify the possible fitness consequences of habitat selection during different life history stages and during migration versus other parts of the annual cycle.

Acknowledgments.—We thank Brian Shaw and Rebecca Dionne for their tireless help in the field and lab. We collected frogs under Maine Department of Inland Fisheries and Wildlife Permit 06-377, and conducted experiments under University of Maine IACUC Permit A2006-03-03. The LEAP project (Land-use Effects on Amphibian Populations – National Science Foundation Grant No. 0239915) and University of Maine supported this research. We thank Aram Calhoun, Daniel Harrison, Nancy Karraker, Cynthia Loftin, Stephen Mullin, and Alan White for improving the manuscript. This is Maine Agricultural and Forest Experiment Station Paper 3049.

LITERATURE CITED

- Anderson, D.R., and K.P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. *Journal of Wildlife Management* 66:912–918.
- Ash, A.N. 1997. Disappearance and return of Plethodontid salamanders to clearcut plots in the southern Blue Ridge Mountains. *Conservation Biology* 11:983–989.
- Baldwin, R.F., A.J.K. Calhoun, and P.G. deMaynadier. 2006. Conservation planning for amphibian species with complex habitat requirements: a case study using movements and habitat selection of the Wood Frog *Rana sylvaticus*. *Journal of Herpetology* 40:443–454.
- Bartelt, P.E., C.R. Peterson, and R.W. Klaver. 2004. Sexual differences in the post-breeding movements and habitats selected by Western Toads (*Bufo boreas*) in southeastern Idaho. *Herpetologica* 60:455–467.
- Beauregard, N., and R. Leclair. 1988. Multivariate analysis of the summer habitat structure of *Rana pipiens* Schreber, in Lac Saint Pierre (Quebec, Canada). Pp. 129–143 *In* Management of Amphibians, Reptiles and Small Mammals in North America. Szaro, R.C., K.E. Severson, and D.R. Patton (eds.), U.S. Forest Service, General Technical Report RM-166.
- Becker, C.G., C.R. Fonseca, C.F.B. Haddad, R.F. Batista, and P.I. Prado. 2007. Habitat split and the global decline of amphibians. *Science* 318:1775–1777.
- Birchfield, G.L., and J.E. Deters. 2005. Movement paths of displaced northern Green Frogs (*Rana clamitans melanota*). *Southeastern Naturalist* 4:63–76.
- Blomquist, S.M., and M.L. Hunter Jr. 2007. An externally attached radio-transmitter effects limited changes in the antipredator behavior and vagility of *Rana pipiens* and *Rana sylvaticus*. *Journal of Herpetology* 41:430–438.
- Bull, E. 2006. Sexual differences in the ecology and habitat selection of Western Toads (*Bufo boreas*) in northeastern Oregon. *Herpetological Conservation and Biology* 1:27–38.

Blomquist and Hunter.—Northern Leopard Frog movements in managed forest.

- Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Inference: A Practical Information Theoretic Approach. 2nd Edition. Springer-Verlag, New York, New York, USA.
- Campbell, S.P., J.W. Witham, and M.L. Hunter Jr. 2007. The long-term effects of a group-selection timber harvest on abundance of forest birds. *Conservation Biology* 21:1218–1229.
- Clarkson, R.W., and J.C. Rorabaugh. 1989. Status of leopard frogs (*Rana pipiens* complex: Ranidae) in Arizona and southeastern California. *Southwestern Naturalist* 34:531–538.
- Compton, B.W., J.M. Rhymer, and M. McCollough. 2002. Habitat selection by Wood Turtles (*Clemmys insculpta*): an application of paired logistic regression. *Ecology* 83:833–843.
- Cox, D.R., and E.J. Snell. 1989. *The Analysis of Binary Data*. 2nd Edition. Chapman and Hall, London, England.
- Cushman, S. 2006. Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation* 128:231–240.
- Dahl, T.E. 2006. Status and Trends of Wetlands in the Conterminous United States 1998 to 2004. U.S. Fish and Wildlife Service, Washington, D.C., USA. 116 p.
- deMaynadier, P.G., and M.L. Hunter, Jr. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. *Environmental Reviews* 3:230–261.
- Dole, J.W. 1965a. Spatial relations in natural populations of the Leopard Frog, *Rana pipiens* Schreber, in northern Michigan. *American Midland Naturalist* 74:464–478.
- Dole, J.W. 1965b. Summer movement of adult Leopard Frogs, *Rana pipiens* Schreber, in northern Michigan. *Ecology* 46:236–255.
- Dole, J.W. 1971. Dispersal of recently metamorphosed Leopard Frogs, *Rana pipiens*. *Copeia* 1971:221–228.
- Dole, J.W. 1972a. Evidence of celestial orientation in newly-metamorphosed *Rana pipiens*. *Herpetologica* 28:273–276.
- Dole, J.W. 1972b. The role of olfaction and audition in the orientation of Leopard Frogs, *Rana pipiens*. *Herpetologica* 28:258–260.
- Eigenbrod, F., S.J. Hecnar, and L. Fahrig. 2008. The relative effects of road traffic and forest cover on anuran populations. *Biological Conservation* 141:35–46.
- Enge, K.M., and W.R. Marion. 1986. Effects of clearcutting and site preparation on herpetofauna of a North Florida flatwoods. *Forest Ecology and Management* 14:177–192.
- Feder, M.E., and W.W. Burggren. 1992. *Environmental Physiology of the Amphibians*. University of Chicago Press, Chicago, Illinois, USA.
- Gibbs, J.P., K.K. Whiteleather, and F.W. Schueler. 2005. Changes in frog and toad populations over 30 years in New York State. *Ecological Applications* 15:1148–1157.
- Graeter, G.J., B.B. Rothermel, and J.W. Gibbons. 2008. Habitat selection and movement of pond-breeding amphibians in experimentally fragmented pine forests. *Journal of Wildlife Management* 72:473–482.
- Grialou, J.A., S.D. West, and R.N. Wilkins. 2000. The effects of forest clearcut harvesting and thinning on terrestrial salamanders. *Journal of Wildlife Management* 64:105–113.
- Guerry, A.D., and M.L. Hunter, Jr. 2002. Amphibian distributions in a landscape of forests and agriculture: an examination of landscape composition and configuration. *Conservation Biology* 16:945–754.
- Heinen, J.T., and G. Hammond. 1997. Antipredator behaviors of newly metamorphosed Green Frogs (*Rana clamitans*) and Leopard Frogs (*R. pipiens*) in encounters with Eastern Garter Snakes (*Thamnophis s. sirtalis*). *American Midland Naturalist* 137:136–144.
- Herbeck, L.A., and D.R. Larsen. 1999. Plethodontid salamander response to silvicultural practices in Missouri Ozark forests. *Conservation Biology* 13:623–632.
- Hosmer, D.W., and S. Lemeshow. 2000. *Applied Logistic Regression*. 2nd Edition. Wiley, New York, New York, USA.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Jorgensen, B.C. 1997. 200 years of amphibian water economy: from Robert Townson to the present. *Biological Review* 1997:153–237.
- Licht, L.L. 1991. Habitat selection of *Rana pipiens* and *Rana sylvaticus* during exposure to warm and cold temperatures. *American Midland Naturalist* 125:259–268.
- Longcore J.R., J.E. Longcore, A.P. Pessier, and W.A. Halteman. 2007. Chytridiomycosis widespread in anurans of northeastern United States. *Journal of Wildlife Management* 71:435–444.
- Manly, B.F. J., L.L. McDonald, D.L. Thomas, T.L. McDonald, and W.P. Erickson. 2002. *Resource Selection by Animals*, 2nd Edition. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Martin, J., J.J. Luque-Larena, and P. Lopez. 2005. Factors affecting escape behavior of Iberian Green Frogs (*Rana perezi*). *Canadian Journal of Zoology* 83:1189–1194.
- Marzluff, J.M., J.J. Millspaugh, P. Hurvitz, and M.S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. *Ecology* 85:1411–1427.
- Maser, C.R., G. Anderson, and J.K. Cromack. 1979. Dead and down woody material. Pp. 78–95 *In* *Wildlife*

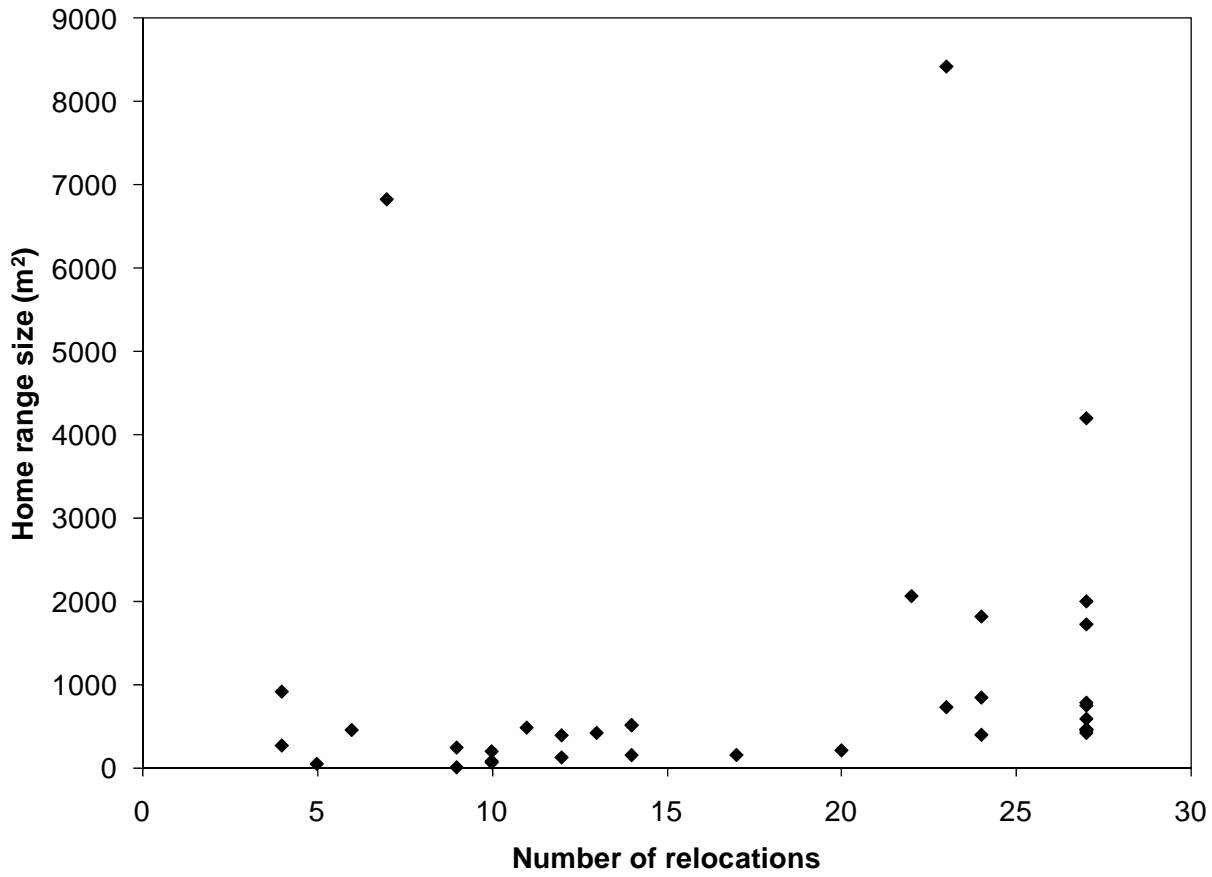
- Habitats in Managed Forests: The Blue Mountains of Oregon and Washington. Thomas, J.W. (Ed.). U.S. Forest Service Agricultural Handbook.
- Mazerolle, M.J. 2001. Amphibian activity, movement patterns, and body size in fragmented peat bogs. *Journal of Herpetology* 35:13–20.
- McAlpine, D.F., and T.G. Dilworth. 1989. Microhabitat and prey size among three species of *Rana* (Anura: Ranidae) sympatric in eastern Canada. *Canadian Journal of Zoology* 67:2244–2252.
- Merrell, D.J. 1977. Life History of the Leopard Frog, *Rana pipiens*, in Minnesota. Occasional Paper Number 15. Bell Museum of Natural History. University of Minnesota, Minneapolis, USA.
- Moore, J.A., and J.C. Gillingham. 2006. Spatial ecology and multi-scale habitat selection by a threatened rattlesnake: the Eastern Massasauga (*Sistrurus catenatus catenatus*) *Copeia* 2006:742–751.
- Patrick, D.A., M.L. Hunter Jr., and A.J.K. Calhoun. 2006. Effects of experimental forestry treatments on a Maine amphibian community. *Forest Ecology and Management* 234:323–332.
- Patrick, D.A., E.B. Harper, M.L. Hunter Jr., and A.J.K. Calhoun. 2008. Terrestrial habitat selection and strong density-dependent mortality in recently metamorphosed amphibians. *Ecology* 89:2563–2574.
- Perkins, D.W., and M.L. Hunter, Jr. 2006. Effects of riparian timber management on amphibian communities in Maine. *Journal of Wildlife Management* 70:657–670.
- Pope, S.E., L. Fahrig, and H.G. Merriam. 2000. Landscape complementation and metapopulation effects on Leopard Frog populations. *Ecology* 81:2498–2508.
- Regosin, J.V., B.S. Windmiller, R.N. Howman, and J.M. Reed. 2005. Variation in terrestrial habitat use by four pool-breeding amphibian species. *Journal of Wildlife Management* 69:1481–1493.
- Rittenhouse, T.A.G., R.D. Semlitsch, and F.R. Thompson, III. 2009. Survival costs associated with Wood Frog breeding migrations: effects of timber harvest and drought. *Ecology*.
- Rittschof, D. 1975. Some aspects of the natural history and ecology of the Leopard Frog, *Rana pipiens*. Ph.D. Dissertation, University of Michigan, Ann Arbor, Michigan, USA. 212 p.
- Rorabaugh, J.C. 2005. *Rana pipiens*, Northern Leopard Frog. Pp. 570–577 *In* *Declining Amphibians: A United States' Response to the Global Problem*. Lannoo, M.J. (Ed.). University of California Press, Berkeley, California, USA.
- Rothermel, B.B. 2004. Migratory success of juveniles: a potential constraint on connectivity for pond-breeding amphibians. *Ecological Applications* 14:1535–1546.
- Russell, K.R., H.G. Hanlin, T.B. Wigley, and D.C. Guynn. 2002. Responses of isolated wetland herpetofauna to upland forest management. *Journal of Wildlife Management* 66:603–617.
- Seaman, D.E., and R.A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075–2085.
- Semlitsch, R.D. 2000. Principles for management of aquatic-breeding amphibians. *Journal of Wildlife Management* 64:615–631.
- Shtatland E.S., E. Cain, and M.B. Barton. 2001. The perils of stepwise logistic regression and how to escape them using information criteria and the output delivery system. Paper 222–26 *In* SUGI 26 Proceedings. Fry, F. (Ed.). Long Beach, California, USA. Available at <http://www2.sas.com/proceedings/sugi26/proceed.pdf>.
- Skelly D.K., E.E. Werner, and S.A. Cortwright. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. *Ecology* 80:2326–2337.
- Snodgrass, J.W., M.J. Komorowski, A.L. Bryan, Jr., and R.B. Cunningham. 2000. Relationships among isolated wetland size, hydroperiod, and amphibian species richness: implications for wetland regulations. *Conservation Biology* 14:414–419.
- Sztatecsny, M., and R. Schabetsberger. 2005. Into thin air: vertical migration, body condition, and quality of terrestrial habitats of Alpine Common Toads, *Bufo bufo*. *Canadian Journal of Zoology* 83:788–796.
- Thorson, T.B. 1955. The relationship of water economy to terrestriality in amphibians. *Ecology* 36:100–116.
- Todd, B.D., and C.T. Winne. 2006. Ontogenetic and interspecific variation in timing of movement and responses to climatic factors during migrations by pond-breeding amphibians. *Canadian Journal of Zoology* 84:715–722.
- Werner, E.E., and K.S. Glennemeier. 1999. Influence of forest canopy cover on the breeding pond distributions of several amphibian species. *Copeia* 1999:1–12.
- Werner, E.E., D.K. Skelly, R.A. Relyea, and K.L. Yurewicz. 2007a. Amphibian species richness across environmental gradients. *Oikos* 116:1697–1712.
- Werner, E.E., K.L. Yurewicz, D.K. Skelly, and R.A. Relyea. 2007b. Turnover in an amphibian metacommunity: the role of local and regional factors. *Oikos* 116:1713–1725.
- Whitney, G.G. 1994. *From Coastal Wilderness to Fruited Plain: A History of Environmental Change in Temperate North America 1500 to the Present*. Cambridge University Press, Cambridge, England.

Blomquist and Hunter.—Northern Leopard Frog movements in managed forest.

APPENDIX 1. Characteristics and home ranges of 40 radio-telemetered *Lithobates [Rana] pipiens* that were tracked during May-June 2006 in Maine, USA. Snout-vent length (SVL) and mass were taken at the beginning of the study. Collection distance is the distance from the breeding pond that the individual was captured if that individual was captured in the terrestrial environment. SD = standard deviation.

Frog	Sex	SVL (mm)	Mass (g)	Collection distance (m)	# 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	7260	4	75	26.3	33.5	105.2	922
3	M	73	32.1	120	27	74	5.3	5.4	142.0	788
4	F	77	32.8	120	27	81	7.0	9.1	188.0	754
5	F	77	33.6	7256	9	56	3.2	8.5	28.6	13
6	F	86	52.4	6922	17	59	3.0	4.7	50.8	161
7	F	73	35.8	6933	10	80	5.3	7.3	52.5	70
8	M	79	50.7	42	27	56	4.3	11.4	116.1	594
9	M	72	30.4		2	0				
10	M	83	49.6	1257	10	70	2.9	3.4	28.6	85
11	F	87	66.0	6081	14	71	6.1	5.9	85.9	159
12	M	80	41.5	42	27	81	7.1	9.3	192.6	468
13	M	75	33.2	26	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	665	27	70	6.2	12.0	166.8	425
17	F	79	41.9	1995	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	249	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	637	24	88	8.5	14.8	205.1	1823
22	F	79	42.1	1093	11	45	9.6	17.2	105.2	489
23	F	73	34.7	1093	10	50	6.4	6.8	63.6	205
24	F	86	64.4	199	6	83	11.3	10.6	68.0	461
25	M	77	39.0	1976	12	83	5.6	4.7	66.6	131
26	M	71	26.7	1215	14	71	10.0	13.4	139.6	519
27	M	79	43.3	1995	5	80	8.9	8.4	44.7	54
28	M	68	25.7	1094	24	75	6.9	7.5	165.8	403
29	M	76	36.0	33	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	649	24	71	8.9	16.9	212.6	850
34	F	86	56.5	676	2	50	64.6	91.4	129.3	
35	F	79	41.1	412	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	405	27	67	6.5	19.1	176.5	2005
39	F	86	58.2	1106	27	81	7.2	7.3	194.1	1729
40	M	66	24.6	1106	9	89	12.9	12.0	116.1	249

APPENDIX 2. Area-observation curve for home ranges of 35 radio-telemetered *Lithobates [Rana] pipiens* that were tracked during May-June 2006 in Maine, USA. Home range size was not correlated with the number of times a frog was relocated.



Blomquist and Hunter.—Northern Leopard Frog movements in managed forest.

APPENDIX 3. Supported models ($\Delta AIC_c < 2$) of daily microhabitat selection for individual *Lithobates pipiens* that were tracked during May-June 2006 in Maine, USA. We only used frogs with ≥ 20 locations for this analysis. Variable codes are shown in Table 1.

Frog	Rank	Model	K	log(L)	AIC _c	ΔAIC_c	ω	r ²	χ^2	df	P
1	1	SW, VC, CC	3	-6.22	19.71	0.00	0.08	0.76	19.4	3	<0.001
1	2	SW, VC, CC, LD	4	-5.18	20.58	0.87	0.05	0.81	21.5	4	<0.001
1	3	LD	1	-9.36	20.91	1.20	0.04	0.45	11.2	1	<0.001
1	4	VC, LD	2	-8.16	20.91	1.20	0.04	0.66	15.6	2	<0.001
1	5	VC, CC, LD, DC3	4	-5.43	21.08	1.37	0.04	0.79	20.5	4	<0.001
1	6	CC, LD, LM, DC3	4	-5.51	21.24	1.53	0.04	0.71	17.4	4	0.001
1	7	LD, TE	2	-8.41	21.41	1.70	0.03	0.63	14.6	2	0.001
1	8	LI, LD	2	-8.48	21.56	1.85	0.03	0.64	14.9	2	0.001
2	1	VC, LM, DC3, TE	4	-4.04	17.90	0.00	0.14	0.78	23.6	4	<0.001
2	2	VC, CC, LM, DC3, TE	5	-2.61	18.07	0.17	0.13	0.83	26.5	5	<0.001
2	3	VC, CC, LM, DC3	4	-4.86	19.53	1.63	0.06	0.68	19.4	4	0.001
2	4	VC, CC, LM, DC3, RH	5	-3.41	19.67	1.77	0.06	0.78	23.8	5	0.000
2	5	VC, CC, SM, DC3, RH	5	-3.41	19.68	1.78	0.06	0.70	20.3	5	0.001
2	6	VC, LM, DC3	3	-6.37	19.79	1.89	0.06	0.68	19.1	3	<0.001
3	1	CC, SM, DC1	3	-8.32	23.69	0.00	0.07	0.66	18.2	3	<0.001
3	2	CC, SM	2	-9.71	23.92	0.23	0.07	0.65	18.0	2	<0.001
3	3	CC, SM, DC1, RH	4	-7.45	24.72	1.03	0.04	0.71	20.7	4	<0.001
3	4	CC, SL, SM	3	-8.87	24.78	1.09	0.04	0.69	19.7	3	<0.001
3	5	CC, SL, SM, DC1	4	-7.57	24.95	1.26	0.04	0.70	20.0	4	0.001
3	6	CC, SM, DC1, DC3	4	-7.63	25.08	1.39	0.04	0.67	18.8	3	<0.001
3	7	CC, SM, LM	3	-9.02	25.08	1.39	0.04	0.61	16.4	3	0.001
3	8	CC, LD, SM, DC1	4	-7.81	25.44	1.75	0.03	0.69	19.7	4	0.001
3	9	CC, SM, RH	3	-9.24	25.53	1.84	0.03	0.68	19.4	3	<0.001
3	10	CC, LI, SM	3	-9.32	25.69	2.00	0.03	0.59	15.9	3	0.001
8	1	SW, VC, SL, SM, DC1	5	-1.39	15.63	0.00	0.48	0.92	31.8	5	<0.001
8	2	SW, VC, SL, LD, DC1 VC, CC, LM, DC1, DC3,	5	-1.98	16.82	1.19	0.27	0.91	31.0	5	<0.001
12	1	TE	6	-6.81	29.82	0.00	0.10	0.78	23.6	6	0.001
12	2	VC, CC, LM, DC1, DC3	5	-8.71	30.29	0.47	0.08	0.72	21.1	5	0.001
12	3	SW, CC, SM, LM	4	-10.44	30.69	0.87	0.07	0.61	16.6	4	0.002
12	4	SW, SM, LM	3	-11.83	30.70	0.88	0.06	0.53	13.8	3	0.003
12	5	SW, CC, LM VC, CC, SM, LM, DC1,	3	-12.31	31.67	1.85	0.04	0.50	12.8	3	0.005
12	6	DC3	6	-7.75	31.70	1.88	0.04	0.75	22.1	6	0.001
14	1	CC, LI, LD	3	-3.73	14.97	0.00	0.11	0.78	17.6	3	0.001
14	2	VC, CC, LI, TE, RH	5	-0.44	15.17	0.20	0.10	0.89	22.1	5	0.001
14	3	CC, LI, DC1, TE, RH	5	-0.83	15.95	0.98	0.07	0.89	22.0	5	0.001
14	4	CC, LI	2	-5.71	16.13	1.16	0.06	0.74	16.3	2	<0.001
14	5	SW, CC, LM, DC3	4	-2.80	16.27	1.30	0.06	0.88	21.5	4	<0.001
14	6	CC, LM, TE	3	-4.45	16.41	1.44	0.05	0.77	17.4	3	0.001
14	7	SW, VC, CC, LM	4	-3.13	16.93	1.96	0.04	0.87	21.3	4	<0.001
15	1	VC, LM, DC1, DC3 VC, LI, LD, LM, DC1,	4	-8.49	26.79	0.00	0.12	0.61	16.5	4	0.002
15	2	DC3	6	-5.73	27.67	0.88	0.07	0.71	20.7	6	0.002
15	3	VC, LD, LM, DC1, DC3	5	-7.60	28.06	1.27	0.06	0.65	18.2	5	0.003
15	4	SW, VC, LM, DC1, DC3	5	-7.67	28.20	1.41	0.06	0.64	17.5	5	0.004
15	5	VC, LI, LM, DC1, DC3	5	-7.74	28.33	1.54	0.05	0.64	17.5	5	0.004

Herpetological Conservation and Biology

15	6	VC, LM, DC1, DC3, TE	5	-7.83	28.51	1.72	0.05	0.62	17.1	5	0.004
15	7	VC, LM, DC3	3	-10.79	28.63	1.84	0.05	0.44	10.9	3	0.012
16	1	SW, SL, SM, TE	4	-0.12	10.07	0.00	0.86	0.89	29.7	4	<0.001
18	1	LI, SL, LD	3	-0.72	8.78	0.00	0.14	0.98	29.1	3	<0.001
18	2	VC, LI, DC3	3	-0.73	8.80	0.02	0.14	0.98	29.0	3	<0.001
18	3	LI, LM	2	-2.11	8.85	0.07	0.14	0.93	26.3	2	<0.001
18	4	VC, LI, DC1	3	-0.77	8.88	0.10	0.14	0.97	28.4	3	<0.001
21	1	SM, RH	2	-8.90	22.38	0.00	0.14	0.63	14.2	2	0.001
21	2	SM	1	-10.63	23.44	1.06	0.08	0.48	11.9	1	0.001
21	3	CC, SM, RH	3	-8.38	23.96	1.58	0.06	0.87	23.3	3	<0.001
21	4	VC, SM, RH	3	-8.53	24.26	1.89	0.05	0.86	22.7	3	<0.001
21	5	SM, TE, RH	3	-8.54	24.28	1.90	0.05	0.64	17.8	3	0.001
21	6	VC, SM	2	-9.87	24.31	1.93	0.05	0.61	13.6	2	0.001
28	1	RH	1	-9.11	20.41	0.00	0.16	0.63	17.3	1	<0.001
28	2	VC, RH	2	-8.69	21.96	1.55	0.07	0.64	17.7	2	0.000
28	3	DC1, RH	2	-8.70	21.97	1.56	0.07	0.58	15.5	2	0.000
32	1	SM, LM, DC1	3	-5.48	18.00	0.00	0.25	0.77	23.3	3	<0.001
32	2	SM, LM, DC1, RH VC, CC, SL, LD, DC1,	4	-4.89	19.59	1.60	0.11	0.83	26.1	4	<0.001
33	1	RH	6	-0.70	18.35	0.00	0.46	0.69	17.5	6	0.008
35	1	LD, SM, TE	3	-1.40	9.84	0.00	0.21	0.92	31.7	3	<0.001
35	2	LD, SM, TE, RH	4	-0.19	10.19	0.35	0.17	0.94	33.1	4	<0.001
35	3	LI, LD, SM, TE	4	-0.80	11.41	1.57	0.09	0.94	32.7	4	<0.001
35	4	LD, SM, DC1, TE	4	-0.95	11.71	1.87	0.08	0.93	32.5	4	<0.001
37	1	CC, LD, LM, RH	4	-0.04	10.30	0.00	0.16	0.98	30.5	4	<0.001
37	2	CC, LD, LM, TE	4	-0.09	10.40	0.11	0.15	0.98	30.3	4	<0.001
37	3	CC, LD, LM	3	-2.17	11.60	1.30	0.08	0.93	27.5	3	<0.001
37	4	CC, SL, LD, LM	4	-0.71	11.63	1.34	0.08	0.97	30.1	4	<0.001
37	5	CC, SL, LM, DC3	4	-0.72	11.65	1.36	0.08	0.97	29.9	4	<0.001
37	6	VC, CC, LD, LM	4	-0.99	12.20	1.90	0.06	0.96	29.5	4	<0.001
38	1	SW, VC, DC1	3	-11.78	30.60	0.00	0.06	0.44	10.9	3	0.012
38	2	VC, DC1	2	-13.11	30.71	0.11	0.06	0.39	9.5	2	0.009
38	3	VC, LM, DC1	3	-11.85	30.75	0.14	0.06	0.44	10.9	3	0.012
38	4	VC, LD, DC1	3	-11.87	30.78	0.17	0.05	0.43	10.5	3	0.015
38	5	SW, VC, LD, DC1	4	-10.56	30.93	0.33	0.05	0.49	12.2	4	0.016
38	6	VC, LI, DC1	3	-12.19	31.41	0.81	0.04	0.42	10.4	3	0.016
38	7	VC, DC1, DC3	3	-12.33	31.71	1.11	0.03	0.42	10.4	3	0.016
38	8	SW, VC, LI, DC1	4	-10.95	31.73	1.12	0.03	0.48	12.0	4	0.017
38	9	SW, VC, SL, LD, DC1	5	-9.49	31.84	1.23	0.03	0.69	19.5	5	0.002
39	1	SM, LM	2	-9.76	24.03	0.00	0.11	0.64	17.6	2	<0.001
39	2	SM	1	-11.13	24.41	0.39	0.09	0.45	11.2	1	0.001
39	3	LI, SM	2	-10.41	25.32	1.30	0.06	0.61	16.6	2	<0.001
39	4	SM, TE	2	-10.46	25.41	1.39	0.06	0.60	16.3	2	<0.001
39	5	LI, SM, TE	3	-9.19	25.43	1.40	0.05	0.70	20.3	3	<0.001
39	6	CC, SM	2	-10.74	25.98	1.95	0.04	0.60	16.1	2	<0.001
39	7	SM, RH	2	-10.76	26.01	1.98	0.04	0.58	15.3	2	0.001

Blomquist and Hunter.—Northern Leopard Frog movements in managed forest.



SEAN BLOMQUIST is a postdoctoral associate at Tennessee Technological University and is an Assistant Coordinator for the Science Advisory Committee of the Cumberland Habitat Conservation Plan. He received his B.S. in Biology from Denison University, his M.S. in Biology from University of Nevada, Reno, and his Ph.D. in Wildlife Ecology from University of Maine. Before returning for his Ph.D., Sean worked for the Arizona Game and Fish Department as an Amphibians and Reptiles Biologist. Sean's current research includes modeling the effects of timber harvesting on endangered, threatened, and highly endemic species on the Cumberland Plateau and developing habitat models for *Desmognathus walteri* and *D. abditus*. The research reported here is part of his dissertation research. (Photographed by Valerie Moreau)



MALCOLM "MAC" HUNTER is the Libra Professor of Conservation Biology in the Department of Wildlife Ecology at the University of Maine. He earned his B.S. in Wildlife Science at University of Maine in 1974 and his D.Phil. in Zoology at Oxford University. His research covers a wide range of organisms and ecosystems: amphibians, turtles, birds, plants, mammals, lakes, streams, peatlands, grasslands, and especially forests. (Photographed by Aram Calhoun)