Canadian Journal of Zoology
Revue canadienne de zoologie

**Amphibian terrestrial habitat selection and movement
patterns vary with annual life history period**

Journal:	<i>Canadian Journal of Zoology</i>
Manuscript ID	cjz-2016-0148.R1
Manuscript Type:	Article
Date Submitted by the Author:	05-Jan-2017
Complete List of Authors:	Groff, Luke; University of Maine, Department of Wildlife, Fisheries, and Conservation Biology Calhoun, Aram; University of Maine, Department of Wildlife, Fisheries, and Conservation Biology Loftin, Cynthia; University of Maine, U.S. Geological Survey, Maine Cooperative Fish and Wildlife Research Unit
Keyword:	habitat use, HOME RANGE < Habitat, Lithobates sylvaticus, MIGRATION < Discipline, post breeding, resource selection, wood frog

SCHOLARONE™
Manuscripts

1 **Amphibian terrestrial habitat selection and movement patterns vary with annual life**
2 **history period**

3 Luke A. Groff, Aram J. K. Calhoun, and Cynthia S. Loftin

4

5 **L.A. Groff.** Department of Wildlife, Fisheries, and Conservation Biology, University of Maine,
6 5755 Nutting Hall, Orono, ME 04469, USA (email: luegroff@gmail.com).

7 **A.J.K. Calhoun.** Department of Wildlife, Fisheries, and Conservation Biology, University of
8 Maine, 5755 Nutting Hall, Orono, ME 04469, USA (email: calhoun@maine.edu).

9 **C.S. Loftin.** U.S. Geological Survey, Maine Cooperative Fish and Wildlife Research Unit, 5755
10 Nutting Hall, Orono, ME 04469, USA (email: cynthia.loftin@maine.edu).

11 **Corresponding author:** Luke A. Groff (email: luegroff@gmail.com, phone: 717-979-9543,
12 fax: 207-581-2858).

¹Supplementary Table S1 is available with the article through the journal Web site at:

Amphibian terrestrial habitat selection and movement patterns vary with annual life history period

Luke A. Groff, Aram J. K. Calhoun, and Cynthia S. Loftin

Abstract

Identification of essential habitat is a fundamental component of amphibian conservation; however, species with complex life histories frequently move among habitats. To better understand dynamic habitat use, we evaluated wood frog (*Lithobates sylvaticus* (LeConte, 1825)) habitat selection and movement patterns during the spring migration and foraging periods and described the spatio-temporal variability of habitats used during all annual life history periods. We radio-tracked 71 frogs in Maine during 2011–2013 and evaluated spring migration, foraging activity center (FAC), and within-FAC habitat selection. Telemetered frogs spent the greatest percentage of each field season in hibernacula ($\geq 54.4\%$), followed by FACs ($\geq 25.5\%$), migration habitat ($\geq 16.9\%$), and breeding sites ($\geq 4.5\%$). FACs ranged $49\text{--}1335\text{ m}^2$ ($568.0 \pm 493.4\text{ m}^2$), and annual home ranges spanned $1413\text{--}32\,165\text{ m}^2$ ($11\,780.6 \pm 12\,506.1\text{ m}^2$). During spring migration, wood frogs exhibited different movement patterns (e.g., turn angles), selected different habitat features, and selected habitat features less consistently than while occupying FACs, indicating that the migration and foraging periods are ecologically distinct. Habitat use studies that do not discriminate among annual life history periods may obscure true ecological relationships and fail to identify essential habitat necessary for sustaining amphibian populations.

Key words: Anuran, habitat use, home range, *Lithobates sylvaticus*, migration, post breeding, resource selection, radio telemetry, wood frog.

¹Supplementary Table S1 is available with the article through the journal Web site at:

Introduction

The efficacy of species conservation is dependent on maintaining or improving access to essential habitats throughout the focal species' lifespan. Habitat use, selection, and preference (hereafter simplified as "use") studies, especially when paired with demographic data, identify essential habitats; however, because ecological relationships and processes are dynamic, it is critical to know how species use habitats both throughout their lifespans and across geographies (Schooley 1994). Variation in habitat use is driven by the respective species' life history, broadly defined as a sequence of biological events from birth through reproduction to death (Campbell et al. 1997). For example, Chinook Salmon (*Oncorhynchus tshawytscha* (Walbaum in Artedi, 1792)) use stream pools and margins associated with bank cover as fry (Lister and Genoe 1970), coastal ocean habitats as adults (Hinke et al. 2005), and third- or higher order streams for spawning during the terminal period of their life (Bjornn and Reiser 1991). By better understanding how species use and move among habitats and across landscapes during different seasons or life stages, resource managers and conservationists can design more informed and effective management plans and conservation strategies.

A species' life history includes its *annual* life history, which we define as a sequence of biological events (e.g., breeding) within a given year that are characteristic of the species. Some amphibians, such as the wandering salamander (*Aneides vagrans* Wake and Jackman, 1999) (Spickler et al. 2006), may breed, forage, and overwinter in a single habitat (e.g., tree crown), whereas others, such as pool-breeding species, migrate among habitats or habitat patches. The terms breeding period and hibernal (or overwintering) period are explicit and informative, because they describe the primary activity performed during the respective period. In contrast, the non-migratory period between breeding and hibernation, which is used for self-maintenance

¹Supplementary Table S1 is available with the article through the journal Web site at:

(e.g., foraging, recovering from injury, avoiding predators), typically is vaguely referred to as the post-breeding or non-breeding period. We prefer the term foraging period, because it clearly describes one of the primary activities being performed. Generally, amphibian habitat use during the foraging and hibernal periods has been understudied relative to the breeding period.

Amphibian habitat use has been evaluated with varied techniques (e.g., drift fencing and pitfall traps), with individuals commonly captured at breeding sites, marked (e.g., toe-clipped) or outfitted with a radio transmitter, and subsequently relocated. Researchers typically consider all relocations collected after the breeding period to represent foraging habitat use (Baldwin et al. 2006a; Rittenhouse and Semlitsch 2007). This approach, however, mixes migration (from breeding sites to foraging habitats) and foraging activity center (FAC) habitat use and activity pattern data. Migrations are round-trip movements toward and away from breeding sites (Semlitsch 2008), and activity centers are localized areas where individuals subsist for prolonged periods (Semlitsch 1981). Many reptile species, for example, occupy restricted seasonal activity centers during summer and fall months (Fitch and Achen 1977; Compton et al. 2002), suggesting they select specific habitats, habitat features, or environmental conditions during this period. Seasonal activity centers rarely have been described for amphibians (but see Semlitsch 1981; Baldwin et al. 2006a), which may reflect aspects of their life history (e.g., short-lived, high mortality rates) and morphology (e.g., small size, slick and delicate epidermis) that hinder extended tracking periods and radio transmitter retention. Failing to discriminate among annual life history periods when evaluating amphibian habitat selection may conceal important ecological relationships and, thus, potentially facilitate ineffective conservation.

We used radio telemetry to track wood frogs (*Lithobates sylvaticus* (LeConte, 1825)) in north-central Maine during all annual life history periods between May 2011 and May 2013. The

¹Supplementary Table S1 is available with the article through the journal Web site at:

species has several distinct annual life history periods (breeding, migration [spring and fall], foraging, hibernation) and uses different habitats during each. Wood frogs breed primarily in non-permanent, fish-free wetlands during late winter and early spring (Guerry and Hunter 2002; Herrmann et al. 2005); occupy forested uplands and wetlands with closed canopies during summer and early fall (Baldwin et al. 2006a; Rittenhouse and Semlitsch 2007; Blomquist and Hunter 2010); and hibernate in forested uplands with open canopies during winter (Groff et al. 2016). Our first objective was to evaluate spring migration and FAC habitat selection at micro (2 m) and macro (10 m) spatial scales. We predicted that the habitat features selected during migration from breeding sites to foraging habitats (hereafter simplified as “spring migration”) would differ and be more variable between years and scales than those selected while occupying FACs. More specifically, we predicted frogs would migrate along streams and riparian areas and select foraging habitat with closed canopies, abundant ground structure (e.g., logs), and located near water sources. Our second objective was to describe the spatio-temporal dynamics of habitats used during the breeding, migration (spring and fall), foraging, and hibernation annual life history periods. Generally, we predicted frogs would migrate from breeding sites to foraging habitat in late spring, make return migrations in late fall, and hibernate near breeding sites.

Materials and methods

Study area

We conducted this research at Turtle Ridge in the Nahmakanta Public Reserved Land (NPRL), Maine, USA (Fig. 1). The NPRL is in the Quebec/New England Boundary Mountains ecoregion, characterized by numerous waterbodies, low mountains with moderately broad valleys, dense forests, shallow loamy to coarse-loamy soils, granite bedrock, and one of the

¹Supplementary Table S1 is available with the article through the journal Web site at:

coldest climates in New England (Griffith et al. 2009). Our study area includes coniferous and mixed coniferous-deciduous forest dominated by spruce (*Picea* spp.), Balsam Fir (*Abies balsamea*), Northern White Cedar (*Thuja occidentalis*), Red Maple (*Acer rubrum*), aspen (*Populus* spp.), and birch (*Betula* spp.). Elevations at Turtle Ridge range 378–518 m AMSL. Mean monthly precipitation during 1944–2014 in Kokadjo, Maine, 27 km east of our study area, ranged 55–103 mm, and monthly mean high and low temperatures ranged –5–25 °C and –17–12 °C, respectively (Canty 2014).

Terrestrial habitat selection

We radio-tracked 71 adult wood frogs at Turtle Ridge during 12 May 2011–05 May 2013. Radio transmitters (models R1614 and R1625, Advanced Telemetry Systems, Isanti, Minnesota, USA) were affixed to 29 females (2011: $n = 14$, 2012: $n = 20$) and 42 males (2011: $n = 28$, 2012: $n = 20$) with waistbands (see Groff et al. 2015); 11 of these frogs (female: $n = 5$, male: $n = 6$) were tracked in both 2011 and 2012, but only one was tracked from the starting to the ending date. We initially captured 20 frogs with dip nets in mid-May 2011 at breeding sites, subsequently found new frogs to replace those we lost (e.g., slipped waistband, transmitter failure), and ceased tracking after all frogs had entered their hibernacula and were poised for hibernation (Groff et al. 2016). Each field season began and ended with the onset of breeding. We tracked as many as 20 frogs simultaneously, relocated each one to three times per week, and replaced transmitters 5–10 days before battery failure. Relocation coordinates were recorded with a global positioning system (DeLorme, model PN-60, Yarmouth, Maine, USA) and imported into a geographic information system (ArcGIS, version 10.0, Esri, Redlands, California, USA).

¹Supplementary Table S1 is available with the article through the journal Web site at:

We classified each frog relocation as breeding, spring migration, FAC, fall migration, or hibernaculum. Breeding relocations were collected in May and early June ≤ 5 m from breeding sites. Spring migration relocations corresponded with movements from breeding to foraging habitat, and fall migration relocations corresponded with movements from foraging to hibernaculum. Migration movements typically were long and unidirectional, whereas movements during the foraging period were shorter and varied widely in direction. Therefore, we delineated foraging habitat by identifying where one segment of a frog's path first crossed another segment and using all succeeding relocations prior to fall migration to generate 100% minimum convex polygons (MCPs; Fig. 2). Three frogs, which did not migrate in the fall, hibernated in their foraging habitat, so we generated their MCPs with all successive relocations prior to hibernation. We classified all relocations within the MCPs as FAC relocations but included in our analyses only those frogs with four or more FAC relocations that spanned a period > 20 days. We estimated FAC area for frogs tracked from spring migration through fall migration or hibernation and home range size for frogs tracked from breeding through hibernation by generating 95% isopleths from kernel density estimates (kernel type: Gaussian) in Geospatial Modelling Environment (GME, version 0.7.2.0, <http://www.spatialecology.com/gme>, accessed on April 2014). Bandwidths were adjusted until the area of the 95% kernels equaled the area of the corresponding MCP (Row and Blouin-Demers 2006).

We evaluated wood frog terrestrial habitat selection three ways with a use-availability design that discriminated between spring migration and FAC relocations. Breeding, fall migration, and hibernaculum relocations were excluded from all habitat selection analyses. First, we evaluated spring migration habitat selection by comparing spring migration relocations to paired (i.e., available) locations. Paired locations were sited from the frog's previous relocation

¹Supplementary Table S1 is available with the article through the journal Web site at:

with a random compass bearing and a random distance > 2 m but less than the Euclidean distance between the previous and current relocation. The 2 m minimum distance was selected so that the paired location microhabitat plots did not overlap the corresponding frog relocation plots. Our approach to siting paired locations assumes all habitats between a frog's previous and current relocation were available. In 2012 we restricted all random compass bearings associated with spring migration relocations to $\pm 90^\circ$ of the frog's movement trajectory. This restriction was implemented after observing in 2011 that frogs typically migrated in a single direction from breeding sites to FACs; thus, we refined our interpretation of available habitat. Second, we evaluated FAC selection by comparing FAC relocations to spring migration relocations. Although habitat and habitat features encountered by frogs during spring migration were available as FAC habitat, they were not used for prolonged periods. Third, we evaluated within-FAC habitat selection by comparing FAC relocations to paired locations, which were sited with the same technique used to site spring migration paired locations. In 2012, we ceased restricting compass bearings after the frogs selected FACs, wherein they exhibited an erratic rather than linear movement pattern.

We characterized habitat features surrounding frog relocations and paired locations with 15 field measured and four derived covariates that described habitat (1–11) and landscape features (12–15), microclimate (16–17), and distance to aquatic resources (18–19; Table 1). All habitat feature covariates except percent canopy cover, leaf litter depth, and percent soil moisture were quantified within 2 m (microhabitat) and 10 m (macrohabitat) diameter circular plots; covariates that described landscape features, microclimate, and distance to resources did not vary between these scales. We quantified habitat features at two spatial scales because, while wood frog terrestrial habitat selection has been evaluated at 1–2 m spatial scales (Baldwin et al. 2006a;

¹Supplementary Table S1 is available with the article through the journal Web site at:

Rittenhouse and Semlitsch 2007; Blomquist and Hunter 2010), we wanted to determine if selection varied across scales. We excluded eight FAC and four spring migration relocations that corresponded with movements ≤ 1 m by eight frogs, because the coinciding microhabitat plots overlapped those of the previous relocations.

Data analyses

We evaluated wood frog spring migration and within-FAC habitat selection with conditional logistic regression models (function: `coxph`; package: `survival`) and FAC habitat selection with mixed effects logistic regression models (function: `glmer`; package: `lme4`). We included frog ID as a cluster term in the `coxph` models and a random effect in the mixed models to account for data non-independence within frogs and unequal sample sizes among frogs. We defined 30 *a priori* candidate models that represented alternative habitat selection hypotheses (Table 2). Fourteen models incorporated habitat covariates, six incorporated landscape covariates, three incorporated microclimate covariates, three incorporated distance covariates, and four were composite models. We applied each model to both the 2011 and 2012 datasets and independently incorporated habitat features measured at micro (2 m plots) and macro (10 m plots) spatial scales.

We standardized all covariates, calculated the Pearson correlation coefficient (r) for each covariate pair, and determined no pairs were strongly correlated at $r \geq |0.7|$. We evaluated support for all competing models and ranked them by Akaike Information Criterion corrected for small sample size (AICc) and Akaike weights of evidence (w_i) (functions: `AICc`, `aictab`; package: `AICcmodavg`). We considered models with ΔAICc units < 2.0 equally supported and derived model-averaged parameter estimates (function: `modavg`; package: `AICcmodavg`) from candidate

¹Supplementary Table S1 is available with the article through the journal Web site at:

model confidence sets delimited by a cumulative w_i of 0.95 (Burnham and Anderson 2002). Important predictors of wood frog terrestrial habitat included those covariates with 95% confidence intervals around the odds ratio that did not include 1.0. Estimated coefficients (β_i) are interpreted similarly for conditional and classic logistic regression models: an n -unit increase in a covariate results in a $e^{n\beta_i}$ increase in the odds ratio. However, the former model is interpreted in terms of habitat differences between animal relocations and paired locations (Compton et al. 2002). We calculated the percent agreement of important predictors between scales and years by dividing the number of observed matches by the number of possible matches. For example, if X_1 and X_2 were important microscale predictors in 2011 and X_2 and X_3 were important macroscale predictors in the same year, then the percent agreement between scales in 2011 would be 33% ($1/3 = 0.33$). Statistical analyses were conducted with R (R Development Core Team, 2012).

We compared spring migration and FAC turn angles and step lengths (i.e., distance between successive relocations) with mixed-effects models that included frog ID as a random effect (function: lmer; package: lme4). Turn angles were estimated with the movement.pathmetrics tool in GME, then rescaled to 0–180° by ‘folding’ about the north-south axis (e.g., E = W, SE = SW; McCune and Keon 2002) so that 0° corresponded with a forward linear movement, and 180° corresponded with a direction reversal movement.

Results

We tracked 42 wood frogs for 1–232 days (mean $\pm$ 1 s.d. = 64.5 ± 67.5 days) in 2011 and 40 frogs for 1–365 days (64.6 ± 82.2 days) in 2012; 11 of these frogs were tracked for 68–691 days (337.8 ± 152.8 days) during 2011–2013 (supplementary Table S1)¹. Each frog was relocated 1–56 times (10.4 ± 10.8 relocations, $n = 71$). We incorporated 407 of 741 relocations in

¹Supplementary Table S1 is available with the article through the journal Web site at:

our analyses (spring migration: 54 [2011] and 90 [2012] relocations; FAC: 121 [2011] and 142 [2012] relocations) (Fig. 1). Thirty frogs were lost due to undetected radio signals (e.g., transmitter failure, unobserved predation), 15 were tracked through hibernation, 20 shed their transmitters, nine were intentionally released (e.g., injury, time constraints), three died, and five were depredated. We report 82 fates for 71 frogs, because 11 frogs were tracked across years and were assigned two fates. Waistband injuries are detailed in Groff et al. (2015).

Spatial variation in habitat use and movements

The total distance traveled by telemetered frogs ranged 7–1210 m (315.5 ± 301.2 , $n = 71$), and the maximum travel rate ranged 0.9–144.6 m/day (26.3 ± 27.0 , $n = 71$; supplementary Table S1)¹. Euclidean distances ranged 0–569 m (206.4 ± 167.8 m, $n = 25$) between FACs and the nearest breeding site, 0–550 m (192.7 ± 220.6 m, $n = 11$) between FACs and the respective frog's hibernaculum, and 8–317 m (126.2 ± 84.1 m, $n = 15$) between hibernacula and the nearest breeding site. We estimated Euclidean distances from FACs and hibernacula to nearest breeding site, because we were unable to identify the true breeding site of every frog. We had too few relocations to define FACs for four frogs tracked through hibernation. Three frogs hibernated within their FACs.

Step length ($\chi^2 = 90.44$, $P < 0.001$) and turn angle ($\chi^2 = 118.58$, $P < 0.001$) were statistically different during spring migration and the foraging period, with movements being longer and straighter during migration. Step lengths ranged 0–454 m (68.7 ± 78.2 m) during spring migration and 0–155 m (16.0 ± 17.4 m) within FACs, while turn angles ranged 0.7–172.6° ($50.9 \pm 42.9^\circ$) during spring migration and 0.3–180.0° ($113.7 \pm 51.6^\circ$) within FACs. These differences were not artifacts of our telemetry protocol, as the number of days between

¹Supplementary Table S1 is available with the article through the journal Web site at:

successive relocations did not differ significantly ($\chi^2 = 0.64$, $P = 0.42$) between spring migration (5.5 $\pm$ 2.1 days) and FAC relocations (5.5 $\pm$ 2.2 days). The maximum travel rate between successive relocations was 144.6 m/day during spring migration and 42.7 m/day within a FAC.

FAC area ranged 49–1335 m² (568.0 $\pm$ 493.4 m², $n = 10$), and home range area ranged 1413–32 165 m² (11 780.6 $\pm$ 12 506.1 m², $n = 5$). Fourteen of the 25 FACs included an aquatic resource (e.g., seep, stream) that was not used for breeding. Two of the 11 frogs tracked in both years maintained FACs in 2012 that overlapped their 2011 FAC. A third frog also migrated in 2012 to its 2011 FAC; however, we had too few relocations to define its 2012 FAC. The remaining eight frogs tracked in both years were lost in 2012 during breeding or spring migration. Of the 15 frogs monitored during hibernation, one was monitored during both the 2011/12 and 2012/13 winters. This frog selected a hibernaculum in 2012 located 3.5 m from its 2011 hibernaculum.

Temporal variation in habitat use and movements

Wood frogs spent the greatest percentage of each field season in hibernacula (2011/12: 54.4%, 2012/13: 56.2%), followed by FACs (2011/12: 25.5%, 2012/13: 26.1%), spring and fall migration habitat (2011/12: 18.5%, 2012/13: 16.9%), and breeding sites (2011/12: 4.5%, 2012/13: 5.7%); these percentages are based on the mean number of days spent in each habitat (Table 3). Frogs used migration, foraging, and hibernational habitats during $\geq 90.4\%$ of the 2011/12 field season and $\geq 90.7\%$ of the 2012/13 field season; these percentages are based on the maximum number of days spent at breeding sites during the respective year (Table 3).

Terrestrial habitat selection

¹Supplementary Table S1 is available with the article through the journal Web site at:

Top-ranked models varied with habitat, spatial scale, and year (Table 4). With one exception (2011 within-FAC analysis), top-ranked macrohabitat models were better or equally supported relative to top-ranked microhabitat models. We identified 11 covariates that were important predictors of wood frog spring migration, FAC, or within-FAC habitats (Table 5). The only predictor consistently important across the three analyses was distance to nearest breeding site (Breed). Frogs selected habitats nearer to breeding sites than paired locations during spring migration and the foraging period, with FAC relocations being further from breeding sites than spring migration relocations. Distance to nearest aquatic resource (Aquatic), leaf litter depth (Depth), number of logs and stumps (Logs), and percent soil moisture (Moisture) were important predictors in both the spring migration and within-FAC analyses. Generally, frogs selected spring migration and foraging habitat nearer to aquatic resources and with deeper leaf litter, more logs and stumps (except 2011 spring migration macro analysis), and greater soil moisture than paired locations. Notably, the odds ratios indicate that every additional centimeter of leaf litter depth resulted in a 114% increase in the odds of a locale being selected during spring migration in 2011 (micro) and a 68–95% increase when occupying FACs in either year (micro, macro) (Table 5).

Wood frog habitat selection was more consistent across spatial scales than between years and, with one exception (between years: micro), habitat selection was more consistent during the foraging period than during spring migration (Table 6). During spring migration, there was 33% (2011) and 29% (2012) agreement between scales and 17% (micro) and 20% (macro) agreement between years. Across FACs, there was 100% agreement between scales (2011, 2012) and 0% agreement between years (micro, macro). Within FACs, there was 40% (2011) and 57% (2012) agreement between scales and 14% (micro) and 25% (macro) agreement between years.

¹Supplementary Table S1 is available with the article through the journal Web site at:

Discussion

Habitat selection is a dynamic process that varies not only with biological events (e.g., life history periods) but also among spatial scales and years. Wood frogs in north-central Maine selected habitat features differently and more consistently when occupying FACs than during spring migration. For example, habitat feature (i.e., Canopy, Depth), distance to aquatic resource (i.e., Aquatic, Breed), and microclimate covariates (i.e., Temperature) were consistently selected within FACs across scales or years, whereas only distance to aquatic resource covariates (i.e., Aquatic, Breed) were consistently selected during spring migration. Wood frog habitat selection varied more between years than scales, which likely is owing to environmental stochasticity (e.g., precipitation) (Campbell et al. 2010). For instance, five covariates (i.e., Aquatic, Breed, Canopy, Depth, Temperature) were selected within FACs across scales, but only a single covariate (i.e., Depth) was selected across years. FAC fidelity and relatively straight migration paths further suggest that spring migration and foraging habitat use are not arbitrary or random processes. Differences in movement patterns and habitat selection during the spring migration and foraging periods emphasize the importance of evaluating habitat use data with respect to annual life history period.

There exists tremendous variability in reported movement distances among and within amphibian species (Smith and Green 2005, Constible et al. 2010), and this likely is at least partially attributable to context (i.e., environmental effects). For example, the maximum total distance traveled by a telemetered frog in our study area (1210 m) is > 2.5 times greater than that estimated in Maine, Missouri, Minnesota, and Massachusetts (Bellis 1965; Rittenhouse and Semlitsch 2007; Semlitsch and Skelly 2008). In eastern Missouri, wood frogs migrated from

¹Supplementary Table S1 is available with the article through the journal Web site at:

artificial breeding sites on ridge tops to moist, lower elevation drainages (Rittenhouse and Semlitsch 2007). This spatial arrangement of habitats contrasts with that in our study area, where frogs migrated between low elevation breeding sites and higher and drier foraging habitat. Desiccation and predator avoidance were reported as mechanisms of migration in Missouri (Rittenhouse et al. 2009); however, relatively cool temperatures and frequent precipitation events likely discount the role of desiccation in our study area. Amphibians have flexible ecologies (Berven 1982*a, b*; Morrison and Hero 2003) and, therefore, the efficacy of species conservation programs may be improved by incorporating, or at least considering, contextual variation (e.g. habitat arrangement) among geographies.

Riparian zones function as both migration and dispersal corridors for many taxa, including amphibians (Burbrink et al. 1998, Anderson et al. 2015). Across scales and years, wood frogs in north-central Maine selected spring migration habitat nearer to aquatic resources and breeding sites than paired locations; many frogs migrated away from breeding sites via non-permanent streams and riparian zones before moving upslope to occupy FACs. It is possible that frogs selected spring migration habitat at spatial scales larger than those we evaluated. For example, juvenile wood frogs in central Maine selected habitat patches at a coarse spatial scale (2.2 ha) during emigration and did not respond to small scale (4 m² and 100 m²) habitat differences until settled in post-emigration habitats (Patrick et al. 2008). This research, however, was conducted within a study area manipulated with four forest harvest treatments (e.g., partial cut), whereas ours was conducted in a relatively intact, homogeneously forested study area that had not been recently harvested. Therefore, wood frog spring migration habitat use at Turtle Ridge may be driven by innate movement rules, such as migrating along environmental

¹Supplementary Table S1 is available with the article through the journal Web site at:

thresholds (e.g., moisture) and gradients (e.g., elevation), rather than specific habitat preferences (Ousterhout et al. 2014).

Generally, wood frog spring migration and foraging habitat were similar. Only two covariates, distance to nearest breeding site and percent canopy cover, were determined important predictors of FAC habitat. Frogs consistently migrated to FACs that were farther from breeding sites (2011) and had greater canopy cover (2012) than spring migration habitat. Amphibians may move away from breeding sites to avoid desiccation (though not likely in our study area) and predators (Toledo 2000; Rittenhouse et al. 2009) and select for increased canopy cover to facilitate thermoregulation and potentially improve foraging success (Walton 2013).

Within FACs, wood frogs selected habitats across scales or years that were located nearer to aquatic resources and had deeper leaf litter, greater canopy cover, and cooler ground temperatures than paired locations. FACs contained diverse non-breeding aquatic habitats, including seeps, semi-permanent streams, ephemeral wetlands, cedar-dominated floodplains, and inundated depressions ringing boulders. The species' affinity for relatively deep litter has been documented in varied landscapes (Rittenhouse and Semlitsch 2007; Blomquist and Hunter 2010) and during different life history and annual life history periods (Earl and Semlitsch 2015; Groff et al. 2016). Increased litter provides increased foraging opportunities (Walton 2013), as well as refuge from extreme temperatures (Parajulee et al. 1997; Groff et al. 2016), desiccation (Seebacher and Alford 2002), and predators (Rittenhouse et al. 2009). Although the wood frog has been described as a canopy cover generalist (Schiesari 2006), such variation likely is specific to the breeding period. To our knowledge, the literature ubiquitously demonstrates that wood frogs select closed canopy habitats during the foraging period (Baldwin et al. 2006a, b; Rittenhouse and Semlitsch 2007; Blomquist and Hunter 2010).

¹Supplementary Table S1 is available with the article through the journal Web site at:

Few studies have documented the use of seasonal activity centers by amphibians (but see Semlitsch, 1981; Baldwin et al., 2006a) despite being commonly reported for other ectotherms (Fitch and Achen 1977; Compton et al. 2002). This may be an artifact of short tracking periods that provide an incomplete assessment of the respective species' habitat use. Abbreviated tracking periods may not capture seasonal or life history dynamics, may bias habitat selection and movement pattern inferences, and cannot reveal habitat fidelity. Tracking periods can be extended with a radio transmitter attachment technique that minimizes injury while maximizing transmitter retention (Groff et al. 2015).

Wood frogs traveled longer, straighter distances at faster rates, selected different habitat features, and selected habitat features more variably during spring migration than while occupying FACs. These results indicate that spring migration and the foraging period are ecologically distinct. Consequently, true ecological relationships and essential habitat necessary for sustaining populations may not be identified when habitat use studies do not discriminate among annual life history periods.

Terrestrial habitat surrounding breeding sites is critical for the persistence of semi-aquatic amphibian populations; however, amphibian conservation and management efforts typically protect little, if any, terrestrial habitat. For example, Maine's Natural Resources Protection Act conserves exemplary vernal pools and surrounding terrestrial habitat within < 77 m, yet 72% (18/25) of FACs and 60% (9/15) of hibernacula selected by wood frogs in our study area were located > 100 m from the nearest breeding site. The relative importance of terrestrial habitats especially is evident when quantified temporally, rather than spatially; wood frogs spent > 90% (> 330 days) of 2011 and 2012 in migration, FAC, and hibernatal habitats. Conservation efforts

¹Supplementary Table S1 is available with the article through the journal Web site at:

that reflect species' diverse and dynamic habitat needs across life histories ultimately will be more effective for long-term population persistence.

Acknowledgements

Permits were obtained from the Maine Department of Inland Fisheries and Wildlife (2011–2014). This project was supported by Maine's Sustainability Solutions Initiative through National Science Foundation award EPS-0904155 to the Experimental Program to Stimulate Competitive Research at the University of Maine; the University of Maine and the Maine Department of Inland Fisheries and Wildlife through their Cooperative Agreement with the U.S. Geological Survey Maine Cooperative Fish and Wildlife Research Unit; the U.S. Department of Agriculture National Institute of Food and Agriculture through Hatch project number ME0-H-6-00509-13; and the Department of Wildlife, Fisheries, and Conservation Biology at the University of Maine. We thank V. Popescu for reviewing an early draft of this manuscript; V. Popescu, B. Hossack, and Z. Loman for providing statistical support; L. Hecker and J. Armstrong for assisting with fieldwork; and two anonymous reviewers for making suggestions that improved this manuscript. At the time of publication, the datasets had not been released by the sponsoring agencies. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This is Maine Agricultural and Forest Experiment Station publication no. 3522.

¹Supplementary Table S1 is available with the article through the journal Web site at:

<https://mc06.manuscriptcentral.com/cjz-pubs>

References

- Anderson, N.L., Paszkowski, C.A., and Hood, G.A. 2015. Linking aquatic and terrestrial environments: can beaver canals serve as movement corridors for pond-breeding amphibians? *Anim. Conserv.* **18**: 287–294. doi:10.1111/acv.12170.
- Baldwin, R.F., Calhoun, A.J.K., and deMaynadier, P.G. 2006a. Conservation planning for amphibian species with complex habitat requirements: a case study using movements and habitat selection of the wood frog *Rana sylvatica*. *J. Herpetol.* **40**: 442–453. doi:10.1670/0022-1511(2006)40[442:CPFASW]2.0.CO;2.
- Baldwin, R.F., Calhoun, A.J.K., and deMaynadier, P.G. 2006b. The significance of hydroperiod and stand maturity for pool-breeding amphibians in forested landscapes. *Can. J. Zool.* **84**: 1604–1615. doi:10.1139/z06-146.
- Bellis, E.D. 1965. Home range and movements of the wood frog in a northern bog. *Ecology*, **46**: 90–98. doi:10.2307/1935261.
- Berven, K.A. 1982a. The genetic basis of altitudinal variation in the wood frog *Rana sylvatica* I. An experimental analysis of life history traits. *Evolution*, 36:962–983. doi: 10.2307/2408075.
- Berven, K.A. 1982b. The genetic basis of altitudinal variation in the wood frog *Rana sylvatica* II. An experimental analysis of larval development. *Oecologia*, 52:360–369. doi: 10.1007/BF00367960.
- Bjornn, T.C., and Reiser, D.W. 1991. Habitat requirements of salmonids in streams. *In* Influences of forest and rangeland management on salmonid fishes and their habitats. Edited by W.R Meehan. Am. Fish. Soc. Spec. Publ. No. 19. pp. 83–138.
- Blomquist, S.M., and Hunter Jr., M.L. 2010. A multi-scale assessment of amphibian habitat

¹Supplementary Table S1 is available with the article through the journal Web site at:

selection: wood frog response to timber harvesting. *Ecoscience*, **17**: 251–264.

doi:10.2980/17-3-3316.

Burbrink, F.T., Phillips, C.A., and Heske, E.J. 1998. A riparian zone in southern Illinois as a potential dispersal corridor for reptiles and amphibians. *Biol. Conserv.* **86**: 107–115. doi: 10.1016/S0006-3207(98)00054-8.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, N.Y.

Campbell, S.P., Witham, J.W., and Hunter, M.L. 2010. Stochasticity as an alternative to deterministic explanations for patterns of habitat use by birds. *Ecol. Monogr.* **80**: 287–302. doi: 10.1890/08-2366.1.

Campbell, N.A., Mitchell, L.G., and Reece, J.B. 1997. Biology: concepts and connections.

Benjamin/Cummings Publishing Company, Menlo Park, C.A.

Canty, J.L. 2014. Weatherbase. Available from: <http://www.weatherbase.com>. Archived by WebCite at <http://www.webcitation.org/6hTv5Rqev> on 13 May 2016.

Compton, B.W., Rhymer, J.M., and McCollough, M. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. *Ecology*, **83**: 833–843. doi:10.1890/0012-9658(2002)083[0833:HSBWTC]2.0.CO;2.

Constible, J.M., Gregory P.T., and Larsen K.W. 2010. The pitfalls of extrapolation in conservation: movements and habitat use of a threatened toad are different in the boreal forest. *Anim. Conserv.* **13**: 43–52. doi: 10.1111/j.1469-1795.2009.00291.x

Earl, J.E., and Semlitsch, R.D. 2015. Importance of forestry practices relative to microhabitat and microclimate changes for juvenile pond-breeding amphibians. *For. Ecol. Manage.* **357**: 151–160. doi:10.1016/j.foreco.2015.08.023.

¹Supplementary Table S1 is available with the article through the journal Web site at:

- 444 Fitch, H.S., and von Achen, P.L. 1977. Spatial relationships and seasonality in the skinks
445 *Eumeces fasciatus* and *Scincella laterale* in northeastern Kansas. *Herpetologica*, **33**: 303–
446 313. Available from http://www.jstor.org/stable/3891946?seq=1#page_scan_tab_contents
447 [accessed 18 June 2016].
- 448 Griffith, G.E., Omernik, J.M., Bryce, S.A., Royte, J., Hoar, W.D., Homer, J.W., Keirstead, D.,
449 Metzler, K.J., and Hellyer, G. 2009. Ecoregions of New England. U.S. Geological Survey,
450 Reston, V.A. Available from
451 https://archive.epa.gov/wed/ecoregions/web/html/new_eng_eco.html [accessed 18 June
452 2016].
- 453 Groff, L.A., Calhoun, A.J.K., and Loftin, C.S. 2016. Hibernial habitat selection by wood frogs
454 (*Lithobates sylvaticus*) in a northern New England landscape. *J. Herpetol.* **50**:559–569.
- 455 Groff, L.A., Pitt, A.L., Baldwin, R.F., Calhoun, A.J.K., and Loftin, C.S. 2015. Evaluation of a
456 waistband for attaching external radiotransmitters to anurans. *Wildl. Soc. Bull.* **39**: 610–
457 615. doi:10.1002/wsb.554.
- 458 Guerry, A.D., and Hunter, M.L. 2002. Amphibian distributions in a landscape of forests and
459 agriculture: an examination of landscape composition and configuration. *Conserv. Biol.* **16**:
460 745–754. doi:10.1046/j.1523-1739.2002.00557.x.
- 461 Herrmann, H.L., Babbitt, K.J., Baber, M.J., and Congalton, R.G. 2005. Effects of landscape
462 characteristics on amphibian distribution in a forest-dominated landscape. *Biol. Conserv.*
463 **123**: 139–149. doi:10.1016/j.biocon.2004.05.025.
- 464 Hinke, J.T., Foley, D.G., Wilson, C., and Watters, G.M. 2005. Persistent habitat use by Chinook
465 salmon *Oncorhynchus tshawytscha* in the coastal ocean. *Mar. Ecol. Prog. Ser.* **304**: 207–
466 220. doi:10.3354/meps304207.

¹Supplementary Table S1 is available with the article through the journal Web site at:

- 467 Lister, D.B., and Genoe, H.S. 1970. Stream habitat utilization by cohabiting underyearlings of
468 chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Big Qualicum
469 River, British Columbia. J.Fish. Res. Board Can. **27**: 1215–1224. doi:10.1139/f70-144.
- 470 McCune, B., and Keon, D. 2002. Equations for potential annual direct incident radiation and heat
471 load. J.Veg. Sci. **13**: 603–606. doi:10.1111/j.1654-1103.2002.tb02087.x.
- 472 Ousterhout, B.H., Luhning, T.M., and Semlitsch, R.D. 2014. No evidence of natal habitat
473 preference induction in juveniles with complex life histories. Anim. Behav. **93**: 237–242.
474 doi:10.1016/j.anbehav.2014.04.035.
- 475 Parajulee, M.N., Wilson, L.T., Rummel, D.R., Carroll, S.C., Trichilo, P.J., Slosser, J.E., and
476 Fuchs, T.W. 1997. Relationship between ambient and leaf litter temperatures in
477 overwintering habitats of boll weevil (Coleoptera: Curculionidae). Environ. Entomol. **26**:
478 135–141. doi:http://dx.doi.org.prxy4.ursus.maine.edu/10.1093/ee/26.2.135.
- 479 Patrick, D.A., Harper, E.B., Hunter, M.L., and Calhoun, A.J.K. 2008. Terrestrial habitat selection
480 and strong density-dependent mortality in recently metamorphosed amphibians. Ecology,
481 **89**: 2563–2574. doi:10.1890/07-0906.1.
- 482 R Development Core Team. 2008. R: A language and environment for statistical computing. R
483 Foundation for Statistical Computing. Available from: <http://www.R-project.org>. [accessed
484 18 June 2016].
- 485 Rittenhouse, T.A.G., Semlitsch, R.D., and Thompson III, F.R. 2009. Survival costs associated
486 with wood frog breeding migrations: effects of timber harvest and drought. Ecology, **90**:
487 1620–1630. doi:10.1890/08-0326.1.
- 488 Rittenhouse, T.A.G., and Semlitsch, R.D. 2007. Postbreeding habitat use of wood frogs in a
489 Missouri oak-hickory forest. J. Herpetol. **41**: 645–653. doi:10.1670/07-015.1.

¹Supplementary Table S1 is available with the article through the journal Web site at:

- 490 Row, J.R., and Blouin-Demers, G. 2006. Kernels are not accurate estimators of home-range size
491 for herpetofauna. *Copeia*, 2006: 797–802. doi:10.1643/0045-
492 8511(2006)6[797:KANAE0]2.0.CO;2.
- 493 Schiesari, L. 2006. Pond canopy cover: a resource gradient for anuran larvae. *Freshw. Biol.* **51**:
494 412–423. doi:10.1111/j.1365-2427.2005.01497.x.
- 495 Schooley, R.L. 1994. Annual variation in habitat selection: patterns concealed by pooled data. *J.*
496 *Wildl. Manage.* **58**: 367–374. doi:10.2307/3809404.
- 497 Seebacher, F., and Alford, R.A. 2002. Shelter microhabitats determine body temperature and
498 dehydration rates of a terrestrial amphibian (*Bufo marinus*). *J. Herpetol.* **36**: 69–75.
499 doi:10.1670/0022-1511(2002)036[0069:SMDBTA]2.0.CO;2.
- 500 Semlitsch, R.D., and Skelly, D.K. 2008. Ecology and conservation of pool-breeding amphibians.
501 *In* Science and conservation of vernal pools in northeastern North America. *Edited by*
502 A.J.K. Calhoun and P.G. deMaynadier. CRC Press, Boca Raton, F.L. pp. 127–148.
- 503 Semlitsch, R.D. 1981. Terrestrial activity and summer home range of the mole salamander
504 (*Ambystoma talpoideum*). *Can. J. Zool.* **59**: 315–322. doi:10.1139/z81-047.
- 505 Semlitsch, R.D. 2008. Differentiating migration and dispersal processes for pond-breeding
506 amphibians. *J. Wildl. Manage.* **72**: 260–267. doi:10.2193/2007-082.
- 507 Smith, A.M., and Green, D.M. 2005. Dispersal and the metapopulation paradigm in amphibian
508 ecology and conservation: are all amphibian populations metapopulations? *Ecography*, **28**:
509 110–128.
- 510 Spickler, J.C., Sillett, S.C., Marks, S.B., and Welsh Jr., H.H. 2006. Evidence of a new niche for a
511 North American salamander: *Aneides vagrans* residing in the canopy of old-growth
512 redwood forest. *Herpetol. Conserv. Biol.* **1**: 16–26. Available from

¹Supplementary Table S1 is available with the article through the journal Web site at:

513 http://www.herpconbio.org/contents_vol1_issue1.html [accessed 18 June 2016].
514 Toledo, L.F. 2000. Predation of juvenile and adult anurans by invertebrates: current knowledge
515 and perspectives. *Herpetol. Rev.* **36**: 395–400. Available from
516 <https://ssarherps.org/publications/journals/herpetological-review/> [accessed 18 June 2016].
517 Walton, B.M. 2013. Top-down regulation of litter invertebrates by a terrestrial salamander.
518 *Herpetologica*, **69**: 127–146. doi:10.1655/HERPETOLOGICA-D-12-00029.
519

Draft

¹Supplementary Table S1 is available with the article through the journal Web site at:

<https://mc06.manuscriptcentral.com/cjz-pubs>

Tables

Table 1. Descriptions and sources for 19 covariates incorporated in *a priori* candidate models used to evaluate wood frog (*Lithobates sylvaticus*) spring migration, foraging activity center (FAC), and within-FAC habitat selection during 2011–2013 in north-central Maine, USA.

No.	Covariate	Description	Method or source
1	Canopy	Percent canopy cover	Sph. densiometer ^a
2	Depth	Leaf litter depth	Ruler
3	Moisture	Percent soil moisture	Moisture meter ^b
4	Leaf	Percent leaf litter cover	Visual estimate ^c
5	Moss	Percent moss cover	Visual estimate
6	Water	Percent water cover	Visual estimate
7	CWD	Percent coarse woody debris with diameter < 10 cm	Visual estimate
8	Tree	Number of trees with diameter > 10 cm	Count
9	Logs	Number of logs and stumps with diameter > 10 cm	Count
10	Rocks	Number of rocks with maximum diameter 0.2–2 m	Count
11	Boulders	Number of boulders with maximum diameter > 2 m	Count
12	Aspect	Aspect converted to linear aspect	Compass ^d
13	Slope	Percent slope	Clinometer ^e
14	Solar	Incident radiation	McCune and Keon (2002) ^f
15	Elevation	Elevation above mean sea level	NED ^g
16	Temperature	Temperature measured at ground level	Weather meter ^h
17	Humidity	Relative humidity measured at ground level	Weather meter
18	Breed	Distance to nearest breeding site	Tape measure, ArcGIS ⁱ
19	Aquatic	Distance to nearest aquatic resource	Tape measure, ArcGIS

^aForest Densiometers, model: Model-A, Bartlesville, Oklahoma, USA
^bSpectrum Technologies Inc., model: FieldScout 100, Aurora, Illinois, USA
^cPercentage classes: < 1, 1–10, 11–25, 26–50, 51–75, 76–90, 90–99, and > 99%; modeled with class midpoints
^dSilva, model: Ranger CL, Racine, Wisconsin, USA
^eSuunto, model: PM-5/360 PC, Vantaa, Finland
^fIncident radiation calculated with latitude, slope, and aspect values using Eq. 3 described in McCune and Keon (2002)
^gNational Elevation Dataset (10 m)
^hKestrel, Model: Wind Meter 3000, Birmingham, Michigan, USA
ⁱDistances ≤ 20 m measured in field with tape measure; distances > 20 m measured with ArcGIS

¹Supplementary Table S1 is available with the article through the journal Web site at:

525 Table 2. Model group, name, and inclusive covariates for 30 *a priori* candidate models used to
 526 evaluate wood frog (*Lithobates sylvaticus*) spring migration, foraging activity center (FAC), and
 527 within-FAC habitat selection during 2011–2013 in north-central Maine, USA.

Group	Name	Inclusive covariates
Habitat	Hab1	Canopy
	Hab2	Moisture
	Hab3	CWD
	Hab4	Canopy+Moisture
	Hab5	Canopy+Depth
	Hab6	Canopy+CWD
	Hab7	Moisture+CWD
	Hab8	Canopy+Moisture+Depth
	Hab9	Canopy+Moisture+CWD
	Hab10	Trees+Logs+Rocks+Boulders ^a
	Hab11	CWD+Logs+Rocks+Boulders ^a
	Hab12	Leaf+Moss+Water+CWD
	Hab13	Canopy+Moisture+Depth+CWD
	HabGlobal	Canopy+Depth+Moisture+Leaf+Moss+Water+CWD+Trees+Logs+Rocks+Boulders ^a
Landscape	Land1	Solar
	Land2	Aspect+Slope
	Land3	Aspect+Elevation
	Land4	Slope+Elevation
	Land5	Solar+Elevation
	LandGlobal	Aspect+Slope+Solar+Elevation
Microclimate	Micro1	Temperature
	Micro2	Humidity
	MicroGlobal	Temperature+Humidity
Distance	Dist1	Breed
	Dist2	Aquatic
	DistGlobal	Breed+Aquatic
Composite	Comp1	Canopy+Moisture+Aspect+Elevation+Temperature+Aquatic
	Comp2	Canopy+Moisture+Solar+Elevation+Temperature+Breed
	Comp3	CWD+Logs+Rocks+Boulders ^a +Aspect+Humidity+Breed
	Comp4	CWD+Logs+Rocks+Boulders ^a +Elevation+Humidity+Aquatic

^aBoulders covariate included only in 2012 models because data were not collected in 2011.

¹Supplementary Table S1 is available with the article through the journal Web site at:

528 Table 3. Temporal variability of habitats used by wood frogs (*Lithobates sylvaticus*) during all annual life history period during 2011–
529 2013 in north-central Maine, USA.

Habitat	Date range		Length of time ^a	
	First relocation (n)	Last relocation (n)	No. of Days (n)	Mean ± 1 s.d.
2011/12				
Breeding	12 May ^b	13 May–16 Jun. (14)	1–35 (14)	16.5 ± 11.2
Spring migration ^c	17 May–23 Jun. (14)	17 May–7 Jul. (5)	11–48 (4)	25.8 ± 17.0
FAC ^d	24 May–12 Jul. (5)	10–31 Aug. (5)	35–134 (4)	93.0 ± 48.9
Fall migration ^{e,f}	17 Aug.–7 Sep. (5)	8 Sep.–6 Oct. (7)	28–49 (4)	41.8 ± 9.7
Hibernaculum ^g	20 Sep.–19 Oct. (10)	13–20 Apr. 2012 (9)	177–213 (9)	198.4 ± 11.4
2012/13				
Breeding	20 Apr. ^a	4–24 May (6)	14–34 (6)	20.8 ± 6.8
Spring migration ^c	9–30 May (6)	9 May–10 Jul. (7)	11, 61 (2)	36.0 ± 35.4
FAC ^d	15 May–12 Jul. (7)	23 Aug.–29 Sep. (8)	75–149 (6)	95.2 ± 27.2
Fall migration ^{e,f}	30 Aug.–5 Oct. (8)	5–14 Oct. (4)	6–36 (3)	25.7 ± 17.0
Hibernaculum ^g	23 Sep.–22 Oct. (5)	28 Apr.–5 May 2013 (5)	188–217 (5)	205.0 ± 11.0

^aLength of time columns calculated only for frogs tracked before, during, and after using the respective habitat.
^bDate that breeding choruses were first detected.
^cSpring migration length based on number of days between respective frog’s last breeding site and first FAC relocation.
^dForaging activity center (FAC) length based on number of days between respective frog’s last spring migration and first fall migration relocation.
^eFall migration length based on number days between respective frog’s last FAC relocation and hibernaculum entry date.
^fFall migration data exclude frogs that hibernated within their FACs.
^gHibernaculum first and last relocation dates correspond with hibernaculum entry and emergence dates, respectively.

Table 4. All models with ΔAICc values < 2 used to evaluate wood frog (*Lithobates sylvaticus*) spring migration, foraging activity center (FAC), and within-FAC habitat selection during 2011–2013 in north-central Maine, USA.

Year	Scale	Model	K ^a	AICc ^b	ΔAICc^c	w_i^d	LL ^e
Spring migration							
2011	Micro	DistGlobal	2	63.86	0.00	0.39	–29.87
^f	-	Dist2	1	65.55	1.69	0.17	–31.76
-	Macro	Comp4	6	60.38	0.00	0.69	–23.77
2012	Micro	Comp2	6	100.95	0.00	0.72	–44.23
-	Macro	Comp2	6	100.95	0.00	0.83	–44.23
FAC							
2011	Micro	Dist1	3	66.69	0.00	0.84	–30.28
-	Macro	Dist1	3	66.69	0.00	0.53	–30.28
-	-	Comp4	8	67.72	1.03	0.32	–25.42
2012	Micro	Comp1	8	126.34	0.00	0.50	–54.85
-	-	Comp2	8	127.58	1.24	0.27	–55.46
-	Macro	Comp1	8	126.34	0.00	0.49	–54.85
-	-	Comp2	8	127.58	1.24	0.27	–55.46
Within-FAC							
2011	Micro	HabGlobal	10	123.42	0.00	0.95	–51.23
-	Macro	HabGlobal	10	134.34	0.00	0.60	–56.69
-	-	Hab13	4	136.23	1.90	0.23	–64.03
2012	Micro	Comp2	6	180.91	0.00	0.30	–84.30
-	-	Hab8	3	181.40	0.49	0.24	–87.66
-	-	Comp1	6	182.10	1.18	0.17	–84.90
-	-	Hab13	4	182.64	1.72	0.13	–87.25
-	Macro	Comp2	6	180.91	0.00	0.25	–84.30
-	-	Hab8	3	181.40	0.49	0.19	–87.66
-	-	Comp4	7	181.75	0.83	0.16	–83.67
-	-	Hab13	4	182.02	1.11	0.14	–86.94
-	-	Comp1	6	182.10	1.18	0.14	–84.90

^aK: number of parameters.

^bAICc: Akaike Information Criterion corrected for small sample size.

^c ΔAICc : difference in AICc values between the top-ranked and respective model.

^d w_i : Akaike weight of evidence.

^eLL: log-likelihood value.

^fShort dashes (-) indicate cell content is the same as the cell above.

¹Supplementary Table S1 is available with the article through the journal Web site at:

<https://mc06.manuscriptcentral.com/cjz-pubs>

533 Table 5. Summary data for all important predictors of wood frog (*Lithobates sylvaticus*) spring migration, foraging activity center
534 (FAC), and within-FAC habitat selection during 2011–2013 in north-central Maine, USA. For the FAC analysis, the Frog relocations
535 column refers to FAC relocations, and the Paired locations column refers to spring migration relocations.

Year	Scale	Covariate	β	Std. error	Odds ratio	95% C.I.		Frog relocations			Paired locations		
						Lower	Upper	Range	Mean	s.d.	Range	Mean	s.d.
Spring migration													
2011	Micro	Aquatic	−2.45	0.78	0.09	0.02	0.40	1–325	78.61	87.81	0–344	101.72	98.81
- ^a	-	Elevation	−2.79	0.85	0.06	0.01	0.33	396–447	413.35	14.11	386–453	419.07	17.60
-	Macro	Aquatic	−2.07	1.01	0.13	0.02	0.92	1–325	78.61	87.81	0–344	101.72	98.81
-	-	Logs	−1.37	0.38	0.25	0.12	0.54	0–25	11.52	5.53	2–35	14.54	6.01
2012	Micro	Aquatic	−2.56	0.78	0.08	0.02	0.36	0–369	94.96	104.67	0–423	95.12	107.23
-	-	Breed	−0.77	0.32	0.46	0.25	0.87	0–946	214.36	246.32	0–998	228.01	256.25
-	-	Depth	0.76	0.30	2.14	1.19	3.85	0–5.8	1.99	1.55	0–5.0	1.85	1.23
-	-	Leaf	−1.22	0.39	0.30	0.14	0.63	0–85.5	35.82	27.18	0–85.5	51.98	25.11
-	-	Logs	0.42	0.16	1.52	1.11	2.08	0–11	1.47	1.68	0–6	0.93	1.17
-	Macro	Aquatic	−2.56	0.78	0.08	0.02	0.36	0–369	94.96	104.67	0–423	95.12	107.23
-	-	Breed	−0.77	0.32	0.46	0.25	0.87	0–946	214.36	246.32	0–998	228.01	256.25
-	-	Moisture	0.45	0.22	1.57	1.02	2.41	1.7–100	28.72	23.72	3.6–77.0	20.43	15.59
-	-	Solar	0.42	0.14	1.52	1.16	2.00	0.7–1.0	0.84	0.08	0.6–1.0	0.81	0.09
FAC													
2011	Micro	Breed	1.81	0.76	6.11	1.38	27.14	0–585	173.62	191.19	0–481	137.87	130.51
-	Macro	Breed	1.67	0.75	5.31	1.22	23.14	0–585	173.62	191.19	0–481	137.87	130.51
2012	Micro	Canopy	1.10	0.55	3.00	1.02	8.84	57.4–99.5	92.17	6.95	0.4–100	83.88	19.18
-	Macro	Canopy	1.10	0.55	3.00	1.02	8.84	57.4–99.5	92.17	6.95	0.4–100	83.88	19.18
Within-FAC													
2011	Micro	Canopy	1.22	0.39	3.39	1.58	7.28	70.4–100	92.01	6.22	75.0–99.5	90.10	5.50
-	-	Depth	0.56	0.20	1.75	1.18	2.59	0–6.9	2.11	1.54	0–4.4	1.90	0.88
-	-	Logs	0.32	0.12	1.38	1.09	1.74	0–7	1.59	1.67	0–5	0.98	1.07
-	Macro	Canopy	1.29	0.42	3.63	1.59	8.28	70.4–100	92.01	6.22	75.0–99.5	90.10	5.50
-	-	Depth	0.67	0.19	1.95	1.35	2.84	0–6.9	2.11	1.54	0–4.4	1.90	0.88
-	-	Moisture	0.69	0.33	1.99	1.04	3.81	2.3–100	24.01	30.17	1.2–100	13.32	13.34
-	-	Water	1.55	0.45	4.71	1.95	11.39	0–63	4.52	10.96	0–15.5	1.06	3.19

¹Supplementary Table S1 is available with the article through the journal Web site at:

2012	Micro	Aquatic	-3.36	1.52	0.03	0.00	0.69	0-182	43.32	51.35	0-265	47.89	54.10
-	-	Breed	-0.61	0.25	0.54	0.33	0.89	0-507	173.63	174.24	0-523	176.92	176.16
-	-	Depth	0.52	0.15	1.68	1.25	2.26	0-15.0	2.62	1.89	0-5.2	2.06	1.17
-	-	Temperature	-1.79	0.54	0.17	0.06	0.48	9.2-31.0	20.29	4.38	9.1-29.9	20.82	4.40
-	-	Water	1.85	0.79	6.36	1.35	29.96	0-15.5	1.43	4.00	0-15.5	0.80	2.94
-	Macro	Aquatic	-3.97	1.70	0.02	0.00	0.53	0-182	43.32	51.35	0-265	47.89	54.10
-	-	Breed	-0.61	0.25	0.54	0.33	0.89	0-507	173.63	174.24	0-523	176.92	176.16
-	-	Depth	0.52	0.14	1.68	1.28	2.21	0-15.0	2.62	1.89	0-5.2	2.06	1.17
-	-	Logs	0.34	0.11	1.40	1.13	1.74	0-41	13.44	8.13	0-40	12.25	7.18
-	-	Moisture	0.37	0.18	1.45	1.02	2.06	0.6-100	18.33	25.90	1.2-74.80	12.85	14.88
-	-	Temperature	-1.79	0.54	0.17	0.06	0.48	9.2-31.0	20.29	4.38	9.1-29.9	20.82	4.40

^aShort dashes (-) indicate cell content is the same as the cell above.

Draft

¹Supplementary Table S1 is available with the article through the journal Web site at:

<https://mc06.manuscriptcentral.com/cjz-pubs>

Table 6. Number of observed (first value) and possible matches (second value) between scales and years for all important predictors of wood frog (*Lithobates sylvaticus*) spring migration, foraging activity center (FAC), and within-FAC habitat selection during 2011–2013 in north-central Maine, USA.

Analysis	2011	2012	Micro (2 m)	Macro (10 m)
Spring migration				
Between scales	1/3	2/7	- ^a	-
Between years	-	-	1/6	1/5
FAC				
Between scales	1/1	1/1	-	-
Between years	-	-	0/2	0/2
Within-FAC				
Between scales	2/5	4/6	-	-
Between years	-	-	1/7	1/8

^aShort dashes (-) indicate no data.

¹Supplementary Table S1 is available with the article through the journal Web site at:

Figure captions

Fig 1. Study area located at Turtle Ridge in the Nahmakanta Public Reserved Land (NPRL), Maine, USA. Map inset: gray shading represents the Quebec/New England Boundary Mountains ecoregion (Boundary Mountains), and black shading represents the NPRL. Primary map: orange circles represent the 407 wood frog (*Lithobates sylvaticus*) spring migration and foraging activity center relocations included in analyses; gray circles represent the 334 breeding, fall migration, and hibernaculum relocations excluded from analyses; contour lines represent 10 m changes in elevation; and blue shading represents all known water sources.

Fig 2. Foraging activity center (FAC) minimum convex polygons and migration routes for seven example wood frogs (*Lithobates sylvaticus*) tracked during 2011–2013 in north-central Maine, USA. The area of the seven FACs shown ranged 76–604 m². Each color represents a unique frog, and the black double arrows indicate migration directionality; arrows pointing towards FACs indicate spring migration, whereas arrows pointing away indicate fall migration. Primary map: gray circles represent migration relocations, black circles represent hibernacula, colored polygons represent FACs, colored lines represent migration routes, light gray contour lines represent 5 m changes in elevation, and blue shading represents all known water sources. Map inset: one frog's FAC with relocations sequentially numbered. The path segment connecting relocation 3 (not shown) and 4 is the first to cross another path segment; thus, all succeeding relocations prior to fall migration (relocation 17) were used to delineate the frog's FAC minimum convex polygon.

¹Supplementary Table S1 is available with the article through the journal Web site at:

Fig 1. Study area located at Turtle Ridge in the Nahmakanta Public Reserved Land (NPRL), Maine, USA. Map inset: gray shading represents the Quebec/New England Boundary Mountains ecoregion (Boundary Mountains), and black shading represents the NPRL. Primary map: orange circles represent the 407 wood frog (*Lithobates sylvaticus*) spring migration and foraging activity center relocations included in analyses; gray circles represent the 334 breeding, fall migration, and hibernaculum relocations excluded from analyses; contour lines represent 10 m changes in elevation; and blue shading represents all known water sources.

Fig. 1
621x471mm (120 x 120 DPI)

Fig 2. Foraging activity center (FAC) minimum convex polygons and migration routes for seven example wood frogs (*Lithobates sylvaticus*) tracked during 2011–2013 in north-central Maine, USA. The area of the seven FACs shown ranged 76–604 m². Each color represents a unique frog, and the black double arrows indicate migration directionality; arrows pointing towards FACs indicate spring migration, whereas arrows pointing away indicate fall migration. Primary map: gray circles represent migration relocations, black circles represent hibernacula, colored polygons represent FACs, colored lines represent migration routes, light gray contour lines represent 5 m changes in elevation, and blue shading represents all known water sources. Map inset: one frog's FAC with relocations sequentially numbered. The path segment connecting relocation 3 (not shown) and 4 is the first to cross another path segment; thus, all succeeding relocations prior to fall migration (relocation 17) were used to delineate the frog's FAC minimum convex polygon.

Fig. 2

635x476mm (120 x 120 DPI)