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A multi-scale assessment of amphibian habitat selection: Wood frog response to timber harvesting

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Abstract: To understand changes in habitat selection in response to timber harvesting, we used radio-telemetry data from 82 adult wood frogs (*Lithobates sylvaticus*, formerly *Rana sylvatica*) and logistic regression modelling to assess habitat selection in response to an unharvested control and 3 forest management techniques: clearcutting (with removal of all merchantable timber > 10 cm diameter), clearcutting with coarse woody debris (CWD) retention, and partial harvesting with retention of ~50% canopy cover. At the home range scale, frogs selected the partially harvested treatment in spring 2005 and avoided the CWD-retained treatment in fall 2006. Frogs spent 5 ± 2 d (mean ± SE) longer in forested treatments than in both clearcut treatments, but certain individuals were able to specialize on the clearcut treatments. At the weekly activity centre scale, the best-supported models indicated that frogs were more likely to occupy locations with more complex ground structure, especially coarse woody debris, warmer temperatures, moister substrates, and greater canopy cover than random. Resource use among frogs overlapped substantially at both the weekly activity centre and daily microhabitat scales. Frogs selected daily microhabitats with more complex ground structure, greater canopy cover, and moister substrates than random. Selection at coarser scales may be mechanistically linked to finer scale resource selection by the physiological processes of thermos and hydro-regulation. Our results support recommendations for minimizing the impact of logging by retaining coarse woody debris in clearcuts and partial harvesting with retention of ~50% canopy cover.

Keywords: changing resource availability, conditional logistic regression, forest, logging, resource selection.

Introduction

A major premise of ecological theory is that animals select habitats that maximize their individual lifetime fitness by influencing reproduction and survival (Fretwell & Lucas, 1970). Further, the quality, or fitness potential, of a habitat is the effect of this habitat on an individual's survival and reproduction (Coulson *et al.*, 2006). Factors that influence fitness potential include behavioral interactions with conspecifics, predators, and prey and avoidance of physiological stress.

The mechanisms underlying fitness potential of a habitat are tied to the ways in which habitat affects the physiology and morphology of an animal at key points in its life (Lauck, 2005). Animals that exploit transient habitats (*e.g.*, ephemeral ponds) typically have a high degree of phenotypic plasticity in correlates of fitness (*e.g.*, body size, timing to key developmental points; Rudolf & Rödel, 2007). Although this plasticity may allow an individual to survive in multiple habitats, plasticity can have costs. For example, among wood frog tadpoles (*Lithobates sylvaticus*, formerly *Rana sylvatica*) living in the absence of *Anax* sp. dragonfly predators, individuals with greater plasticity for muscle depth and muscle width had lower survival, whereas individuals with greater plasticity for tail length, body depth, and activity had greater survival (Relyea, 2002). Measuring plasticity in individuals in multiple habitats can contribute toward an understanding of the mechanisms underlying habitat selection and the costs associated with plasticity.

Individual variation in behaviour is relevant to many evolutionary and ecological processes (Bolnick *et al.*, 2003), and different individuals can value resources differently. Valuation of a resource (measured through use) depends on availability to that individual and on perceived risks of negative interactions with conspecifics, competitors, and predators. Individual variation can allow some animals to exploit sub-optimal environments, although theoretical models and empirical results indicate that this behaviour should incur fitness costs (Fretwell & Lucas, 1970; Bolnick *et al.*, 2003).

Habitat selection can be thought of as a hierarchical process that can be measured along a continuum of spatial scale (Boyce, 2006), and behavioural selection of different resources might be a mechanism for maximizing fitness. For example, small bluegills (*Lepomis macrochirus*) living in the presence of largemouth bass (*Micropterus salmoides*) reduced predation risk by selecting highly vegetated areas (Werner *et al.*, 1983). A habitat component that is highly selected at a fine scale might be unused if it is located in an environment without all other requirements for that organism (*e.g.*, Ciarniello *et al.*, 2007). For measurement purposes, this continuum of spatial scale has been broken into 4 orders of selection corresponding to the spatial habitat use of the study animal. First-order selection occurs at the spatial scale of the geographic range, 2nd-order selection occurs at the home range, 3rd-order selection occurs within the home range, and 4th-order selection is selection for micro-habitats (Johnson, 1980).

Pond-breeding amphibians are ideal for studying the link between changes in habitat and mechanisms underlying habitat selection. Amphibians are sensitive to local environmental changes because they have the following traits: ectothermy; moist, permeable skin, eggs, and gills; a requirement for both aquatic and terrestrial environments; a high degree of philopatry and site fidelity; and relatively small home ranges and limited dispersal ability (reviewed by Lauck, 2005). Habitat changes can modify amphibian community composition and can lead to decreased fitness in some amphibian species (deMaynadier & Hunter, 1995; Patrick, Hunter & Calhoun, 2006; Werner *et al.*, 2007). For example, wood frogs had lower survival in areas harvested for timber compared to unharvested areas (Rittenhouse, Semlitsch & Thompson, 2009). However, the mechanisms causing these community-level changes are poorly understood (Semlitsch *et al.*, 2009), and changes in individual behaviour may be one, albeit poorly explored, mechanism.

Determining mechanistic relationships between behavioural responses of amphibians and habitat changes may be complicated because habitat quality for amphibians may be weather-dependent (Timm, McGarigal & Compton, 2007). For example, movements of red-legged frogs (*Rana aurora*) through clearcuts were influenced by temperature and precipitation (Chan-McLeod, 2003). Also, an inter-annual increase in abundance of western red-backed salamanders (*Plethodon vehiculum*) in a thinned forest was attributed to increased annual precipitation (Grialou, West & Wilkins, 2000). This relationship between habitat quality and weather may invalidate indirect measures of habitat quality (*e.g.*, relative abundance, density; MacKenzie & Kendall, 2002). However, measuring the response of individuals creates a direct link between an individual's behaviour and the habitat characteristics and weather conditions experienced by that individual at a specific time and thus will incorporate individual variation in resource use and availability (Aebischer, Robertson & Kenward, 1993).

We conducted a study to link changes in habitat to changes in individual behaviour in wood frogs within replicated forested environments managed for timber production. We used radio-telemetry data to assess habitat selection by adults at 3 scales in response to an unharvested control and 3 forest management strategies: clearcutting, clearcutting with coarse woody debris retention, and partial harvesting with 50% canopy retention. We tested for selection and individual variation in use of the treatments at the seasonal home range scale. We used an information-theoretic approach to evaluate 26 hypotheses about how frogs would respond to timber harvest and environmental variables at the weekly activity centre scale and 7 hypotheses about how frogs would respond to these variables at the daily micro-habitat scale. Generally, we hypothesized that the selection of the forested treatments would be highest and wood frogs would select for cool, moist locations with canopy cover.

Methods

Study area and experimental timber-harvesting arrays

We used experimental timber-harvesting arrays that incorporated an unharvested control (unharvested forest stand; hereafter “unharvested”) and 3 common forest management strategies (clearcut with coarse woody debris [CWD] removed [“CWD removed”], clearcut with CWD retained [actual retention 45.6 ± 21.6 $m^3 \cdot ha^{-1}$, mean ± Se; “CWD retained”], and partial harvest with 50% canopy closure [actual 53.0 ± 33.5%; “partial”]). For comparison, canopy cover in our control was 73.8 ± 22.7%, and the partial, CWD removed, and unharvested treatments had residual CWD densities of 33.9 ± 7.3, 12.7 ± 7.5, and 22.9 ± 11.8 $m^3 \cdot ha^{-1}$, respectively (Patrick, Hunter & Calhoun, 2006). The experimental arrays were located on the university of Maine Dwight B. Demeritt and Penobscot experimental Forests (Penobscot County, Maine, USA, 44° 50' n, 68° 35' W) and replicated 4 times. Each array was a 164-m radius circle centred on a ~ 80–530-m^2 vernal pool, with the treatments constituting four 2.1-ha sectors around the pool (Figure 1). The 4 treatments were randomly placed with the exception that the partial treatment was always across the pool from the unharvested treatment (see Patrick, Hunter & Calhoun, 2006 for a complete description of the arrays and harvests). Harvesting occurred from November 2003 to April 2004.

The habitat needs of wood frogs vary with season (Baldwin, Calhoun & deMaynadier, 2006; Rittenhouse & Semlitsch, 2007). Breeding habitat typically is vernal pools, but also includes other still, fish-free waters such as backwater stream pools, bog pools, and anthropogenic road-side ditches (Karns, 1992; Redmer & Trauth, 2005). in late spring and early summer, adults disperse from breeding sites into moist habitats such as marshes, bogs, stream drainages, and forested wetlands (Heatwole, 1961; Mazerolle, 2001), and the distance and timing of post-breeding dispersal depends on availability of such habitats (Baldwin, Calhoun & deMaynadier, 2006, Rittenhouse & Semlitsch, 2007). However, adults exhibit breeding site fidelity and tend to remain in a restricted area (Redmer & Trauth, 2005). For example, the mean distance moved was 11.2 m(n = 298) between captures with home range sizes from 2.9 to 368.3 m^2 (mean = 64.5 m^2) during the post-breeding season in Minnesota (Bellis, 1965). During the post-breeding season, presence of wood frogs was positively correlated with deciduous leaf litter, extensive ground cover (*e.g.*, tall herbs/shrubs/grasses), and moist soil in the boreal forest of Alberta, Canada (Constible *et al.*, 2001) and forested, ephemeral drainages in Missouri (Rittenhouse & Semlitsch, 2007). in southern Maine, wood frogs selected moist *Sphagnum*-dominated hummocks and leaf litter retreats on the margins of pools, and summer refugia were shaded, moist, *Sphagnum*-dominated microhabitats (Baldwin, Calhoun & deMaynadier, 2006). Wood frogs can tolerate freezing, and hibernacula generally are in upland forests with moist or dry soils under decomposing logs, stumps, leaf litter, rocks, and thick accumulations of moss (Redmer & Trauth, 2005).

All life stages of wood frogs are sensitive to the edges and reduced canopy cover created by timber harvesting in the eastern united States (deMaynadier & Hunter, 1998; Werner & Glennemeier, 1999; Patrick, Hunter & Calhoun, 2006). in our experiment, we expected wood frogs to avoid both clearcut treatments because of their low thermal tolerance and preference for forested environments (Heatwole, 1961; Bellis, 1965; Feder & Burggren, 1992). Additionally, we expected frogs to select areas with greater percent canopy cover within the forested treatments (Baldwin, Calhoun & deMaynadier, 2006).

Habitat selection study

We collected data and analyzed habitat selection at 3 spatiotemporal scales: 2^{nd}-order selection (seasonal home range), 3^{rd}-order selection (weekly activity centre), and 4^{th}-order selection (daily microhabitat) (Johnson, 1980; Boyce, 2006). We tracked 40 adult wood frogs during 3 May – 7 June 2005 and 32 adults during 30 September – 7 November 2006. Additionally, we tracked 10 adults during 24 September – 13 October 2004 in a pilot study to determine which habitat variables had substantial variability for analysis and to determine general movement patterns. We tracked 3 females and 7 males in fall 2004 (47 ± 5 mm Snout-Vent Lenght, SVL [mean ± SD]; 11.8 ± 3.1 g), 18 females and 22 males in spring 2005 (48 ± 4 mm SVL; 8.6 ± 1.8 g), and 16 females and 16 males in fall 2006 (46 ± 3 mm SVL; 13.8 ± 3.6 g). We tracked individuals only early and late in the activity season because this allowed us to assess migrations to summer habitat and hibernacula (Baldwin, Calhoun & deMaynadier, 2006). in the spring, we captured these individuals as they emerged from breeding pools by hand, dip net, and pitfall trap (see Patrick, Hunter & Calhoun, 2006 for a description of drift fences and pitfall traps). in the fall, frogs were captured by hand, dip net, and pitfall trap in or near experimental arrays (<~300 m from the central breeding pool), and we used only animals that were of known breeding size (> 40 mm SVL). We assumed we would not bias movement patterns of animals by moving them to arrays in the fall because adult frogs will remain within 340 m of the breeding pool during the remainder of the activity season in Maine (Baldwin, Calhoun & deMaynadier, 2006; R. Baldwin, pers. comm.).

We fit each individual with a radio-transmitter (BD-2 model, 0.9-g, 14-cm external whip antennae, 40-d battery life; Holohil Systems, Carp, Ontario, Canada) with elastic thread beaded with glass beads snug enough to prevent slippage over the rear legs when extended but not so snug as to constrict the skin (Blomquist & Hunter, 2007). We released individuals within each treatment ~10 m from the edge of the pool and equidistant from adjacent treatments, and we located each frog daily by homing during daylight hours with an R-1000 receiver (Communications Specialists, orange, California, USA) and yagi antenna. We placed a pin flag next to the frog location to ease subsequent relocations and marked all movements > 15 cm with a flag. if a frog could not be located visually for 5 consecutive days, we triangulated its position and confirmed the location and condition of the frog. if a frog was found dead or the transmitter harness failed, we removed the relocations since the last visual observation of the frog. Dead frogs were collected and frozen for later analysis (S. Blomquist, unpubl. data). We mapped each movement with a compass and tape measure from known locations in each experimental array.

2^{nd}*-order habitat selection* (*seasonal home range*)

We used ArcGIS (version 9.3, environmental Systems Research institute, Redlands, California, USA) and Hawth’s Analysis Tools (available at http://www.spatialecology.com/htools) to calculate 100% minimum convex polygon (MCP) seasonal home ranges, use, and availability of habitat to evaluate selection over the duration of the spring 2005 and fall 2006 tracking periods. We calculated a 100% MCP rather than a 95% MCP to estimate seasonal home range size for each frog that moved to at least 3 unique locations because removing 5% of the sampled points was not necessary for wood frogs during distinct portions of their active season (Baldwin, Calhoun & deMaynadier, 2006). We calculated availability of habitat for each frog by simulating 10 seasonal home ranges within the experimental array. Each simulated seasonal home range was identical in area and number of relocations to the seasonal home ranges for each frog. To yield the availability of habitat, the number of simulated relocations in each harvest treatment was averaged across the 10 simulated seasonal home ranges.

We used analysis of variance (ANOVA) to test if home range size varied with season (spring 2005, fall 2006), experimental array (Gilman, north Chemo, South Chemo, Smith), or sex (male, female). The seasonal home range sizes did not meet the assumption of normality (Kolmogorov-Smirnov test $D = 0.33$, $P = 0.010$), so we transformed them with natural logs to attain normality (Kolmogorov-Smirnov test $D = 0.08$, $P > 0.150$) before conducting the ANOVA. We calculated a zero-centred selection index for each frog in each treatment,

$$si_{tf} = \ln\left(\frac{x_{tf}}{x_{tr}}\right)$$

where x_{tf} is the number of relocations for frog *f* in treatment *t* and x_{tr} is the mean number of random points from the 10 simulated seasonal home ranges that fell in treatment *t* (*i.e.*, use divided by availability; Aebischer, Robertson & Kenward, 1993). To test if this selection index varied among the seasons, experimental arrays, or sexes, we used a Kruskal-Wallis *H* test or Mann-Whitney *U* test because these selection indices typically do not meet parametric assumptions (Manly *et al.*, 2002). We used a sign test to verify if the mean selection index for each treatment deviated from zero.

We tested for individual specialization in use of each treatment following the likelihood approach of Petraitis (1979). Briefly, this approach assumes that we can determine the probability that individual *i*'s resource use (the vector of n_{ij}'s or p_{ij}'s) was drawn randomly from the resource use distribution of the population (the vector of q_j's). This multinomial probability can be compared to the maximum likelihood that the individual and population have the same resource use distribution. We used Petraitis's (1979) correction for small sample sizes,

$$W_i = \left(\left[\frac{q_i}{p_{ij}}\right]^{n_{ij}}\right)^{\frac{1}{n_{ij}}}$$

where n_i is the number of resources used by individual *i*. These metric ranges from 0 for specialists to 1 for generalists. We used the program IndSpec for this analysis (Bolnick *et al.*, 2002). We conducted all other statistical analyses in SAS (version 9.1, SAS institute, Cary, North Carolina, USA) with α = 0.05 and present means ± standard error unless otherwise specified.

3rd-order habitat selection (*weekly activity centre*)

We examined spatial and temporal independence of wood frog locations in a pilot study conducted in 2004. We estimated distances moved and timing of movements during this pilot study and integrated existing information on behaviour of wood frogs to design our habitat sampling. A 26-m-radius circle included 75% of daily movements, and a 310-m-radius circle included the longest movement made by a wood frog in a week. We assumed random points within these distances were available to the frogs on a daily and weekly basis, respectively. Additionally, we estimated that frogs moved to new locations every 6–90 h (mean = 34 h) in the pilot study. However, wood frogs were primarily nocturnal, and most movements occurred at night (see also Heatwole, 1961; Bellis, 1965; Baldwin, Calhoun & deMaynadier, 2006; Rittenhouse & Semlitsch, 2007; T. Rittenhouse, pers. comm.). We assumed daily locations were independent and that remaining in the same location on successive days represented choice. if this assumption is invalid, our sampling procedure would overestimate the importance of variables that were characteristic of locations where frogs remained for multiple relocations (Erickson *et al.*, 2001).

We evaluated habitat use and availability using 12 variables (Table I) collected at the centre of a 1-m^2 hexagonal plot centred on the frog or random location. We chose these variables based on previous work on habitat relationships, the ecology and physiology of wood frogs and other anurans, and the pilot study. We measured percent cover variables because other species of amphibians selected habitat based on surrounding vegetation and ground structure (*e.g.*, Griffin & Case, 2001), and temperature and moisture variables may be important because of the permeable skin and poikilothermic nature of amphibians (Feder & Burggren, 1992). To assess habitat availability at the weekly activity centre scale, **every 6th day** we collected data from 5 random locations within a 26-m-radius circle positioned 50–310 m from the frog location. We chose the centres of each random weekly activity centre in ArcGIS, and if they overlapped, we reselected them to maintain independent samples of available habitat.

To assess habitat selection in weekly activity centres, we used conditional logistic regression to compare the mean habitat conditions at the frog locations over a 5-d period to the mean of the 5 plots collected at the randomly positioned weekly activity centre. We used 2 strata (week [*n* = 12] and experimental array [*n* = 4]) in this analysis to incorporate variability associated with the structure of our habitat sampling.

We used an information-theoretic approach to evaluate competing hypotheses about habitat selection of weekly activity centres. To build our candidate model set, we considered plausible combinations of 12 variables and six 2^{nd}order interactions to form 26 candidate conditional logistic regression models. **We considered models that describe hypotheses about** variation in the relationship among temperature (TE), moisture (SW, SP, LM, SM), and forest structure (CC, LI, SP, VC, SL, LD, CP, CD) variables based on the biology of wood frogs and other anurans. We also considered models that describe the ways our treatments (CC, LI, SL, LD, CP) may influence habitat relationships (Table I).

The six 2^{nd}-order interactions we considered when building our candidate model set (CP×TE, CP×SM, VC×TE, VC×SM, CC×TE, CC×SM) have been postulated by others. The presence of coarse woody debris is thought to provide thermal and hydric refugia for amphibians (deMaynadier & Hunter, 1995). Forest amphibian abundance and presence has been correlated with vegetation and other forms of ground cover (*i.e.*, forest floor and understory structure), and this structure has been postulated to provide the appropriate thermal and hydric environments (Constible *et al.*, 2001). Finally, canopy cover is also thought to provide the appropriate thermal and hydric environments (*e.g.*, Baldwin, Calhoun & deMaynadier, 2006; Rittenhouse & Semlitsch, 2007).

We used Akaike's Information Criterion corrected for small sample size ($\mathrm{AIC_c}$) and Akaike's model weights (ω) rank the 26 candidate models and select which model(s) best described selection of weekly activity centres. We considered models with the change in AIC_c (ΔAIC_c) < 2 to be equally supported (Burnham & Anderson, 2002). **If no model comprised** ≥ 90% of the weight of the candidate model set, we used model averaging to derive parameter estimates from the top models that comprised a 90% confidence set (*i.e.*, **≥ 90%** of the model weight; Burnham & Anderson, 2002). We based our interpretation of the importance of each model on model weights and evidence ratios ($\omega_{\text{top model}}/\omega_i$). We based our interpretation of the importance of each variable on the descriptive ability of each variable (*i.e.*, the 95% confidence intervals for the odds ratio did not overlap one).

Prior to fitting conditional logistic regression models, we checked each of the possible variables for linearity and correlation with other variables to meet the assumptions of logistic regression (Hosmer & Lemeshow, 2000). Because canopy cover was basically a categorical variable based on a univariate plot of the lowess-smoothed logit, we defined a threshold for canopy cover at 60% for the weekly activity centre analysis (Hosmer & Lemeshow, 2000). Canopy cover was incorporated into the models as a categorical variable with 2 levels (< 60% and ≥ 60%). All other variables were linear, and no variables were highly correlated (all $r < 0.6$). We tested the goodness-of-fit of the global model (Burnham & Anderson, 2002). As described for the seasonal home range scale, we tested for individual specialization in habitat use following the likelihood approach of Petraitis (1979; Bolnick *et al.*, 2002).

4th-order resource selection (*daily microhabitat*)

For each daily frog location, we gathered the same habitat data for frog locations and paired locations. These paired locations were chosen based on a random compass bearing and distance between 1 and 26 m from the frog location; a 26-m-radius circle included 75% of daily movements in our pilot data set. Data at each paired location were collected < 15 min after collecting data at the frog location.

To assess daily microhabitat selection, we modelled each frog individually. We only included frogs with ≥ 20 relocations for this analysis to ensure adequate sample size for model selection and parameter estimation. We used case-control logistic regression, a form of conditional logistic regression, to compare the relative selection made by individuals based on differences between the frog location (case) and the paired random location (control; *e.g.*, Compton, Rhymer & McCollough, 2002).

We used an information-theoretic approach to evaluate competing hypotheses about habitat selection of daily microhabitats. We developed 7 candidate models and constrained the maximum model size to 7 variables because of the small number of observations for each frog. The candidate models were based on plausible combinations of 14 variables (Table I). We considered models that describe hypotheses that the relationship among temperature (TE), moisture (SW, SP, LM, SM, RH), and forest structure (CC, LI, SP, VC, SL, LD, CP, CD, DC) variables could vary based on the biology of wood frogs and other anurans. We also considered hypotheses about how variables directly manipulated by our treatments (CC, CP) may influence habitat relationships (Table I). As described for the weekly activity centre scale, we ranked these 7 models using AIC_c and ω, calculated variation in selection of these models, calculated model-averaged parameter estimates, and based our interpretation of the importance of each model to the sample population of frogs based on average model weights and evidence ratios. Unlike at the weekly activity centre scale, we used the standardized parameter estimates (β_s) for each variable and frog to draw inferences about how habitat selection varied among individuals in the population. We calculated model selection uncertainty to investigate the variation in how individuals selected each model. We based our interpretation of the importance of each variable on cumulative model weights, evidence ratios, and the descriptive ability of each variable for frogs in our sample population (Burnham and Anderson, 2002; p. 167).

To meet the assumptions of logistic regression, we defined thresholds for vegetation cover at 30%, standing water cover at 40%, slash cover at 30%, and litter depth at 80 mm for the daily microhabitat analysis based on univariate plots of the lowess-smoothed logit (Hosmer & Lemeshow, 2000). These variables were incorporated into the candidate models as categorical variables with 2 levels each ($<$ and $\geq$ threshold). All other variables were linear. As described for the seasonal home range scale, we tested for individual specialization in habitat use following the likelihood approach of Petraitis (1979; Bolnick *et al.*, 2002).

Results

2nd-order habitat selection (seasonal home range) and use of harvest treatments

Mean (± Se) seasonal home range size in spring 2005 (285 ± 94 m^2) was smaller than in fall 2006 (1317 ± 501 m^2; Figure 2a; $F_{1, 53} = 19.8$, $P < 0.001$, $n = 59$), and frogs at the north Chemo experimental array had smaller seasonal home ranges (70 ± 25 m^2; Figure 1e) than frogs at the Smith (1094 ± 497 m^2; Figure 1c) and South Chemo (1020 ± 364 m^2; Figure 1f) experimental arrays (Figure 2b; $F_{3, 53} = 6.1$, $P < 0.001$, $n = 59$). Males (663 ± 254 m^2) and females (856 ± 401 m^2) had similar size seasonal home ranges ($F_{1, 53} = 0.1$, $P = 0.825$, $n = 59$). Mean seasonal home range size was 751 ± 228 m^2 (range 3–10 745 m^2). These analyses were on log-transformed home range sizes, but we present untransformed means.

On average, frogs spent 14 ± 2, 16 ± 2, 10 ± 1, and 10 ± 1 d in the unharvested, partial, CWD retained, and CWD removed treatments, respectively. **Frogs selected the partial treatment (sign test = 6.0, P < 0.001) in spring** 2005 and avoided the CWD retained (sign test = 4.5, P = 0.023) in fall 2006 (Figure 3; spring 2005: unharvested, sign test = 3.5, P = 0.144; CWD retained, sign test = 3.0, P = 0.180; CWD removed, sign test = 3.0, P = 0.238; fall 2006: unharvested, sign test = 1.0, P = 0.804; partial, sign test = 3.5, P = 0.092; CWD removed, sign test = 1.5, P = 0.549; n = 59). Selection varied by season (Mann-Whitney U_1 = 2673.0, $P <$ 0.001, n = 59) but not by sex (Mann-Whitney U_1 = 3100.5, P = 0.334, n = 59) or experimental array (Kruskal-Wallis H_3 = 2.4, P = 0.486, n = 59).

At the seasonal home range scale, individuals varied greatly in their use of the treatments, and individuals ranged from specialists (W_i = 0.18) to generalists (W_i = 0.84). Most frogs specialized their habitat use (W_i < 0.5 and proportional use > 0.8): 34 of the 59 frogs were specialists on 1 of the 4 treatments (W_i = 0.41; Figure 4a). Proportional use of the forested treatments (unharvested = 0.34; partial = 0.27) was higher than the clearcuts (CWD retained = 0.18; CWD removed = 0.21).

Seasonal home range size was not correlated with the number of times the frogs were relocated in both seasons (Spearman r = 0.1, P = 0.468, n = 59) or the distance from the pond at which they were captured in fall 2006 (Spearman r = 0.2, P = 0.179, n = 34). We estimated seasonal home range size for 59 of the 72 wood frogs (Figure 1), excluding 10 frogs that slipped out of their transmitter belts and 3 frogs that died within the first 14 d of tracking.

3rd-Order habitat selection (Weekly activity centre)

Wood frogs were 4 times more likely to occupy weekly activity centres with coarse woody debris present and wetter leaf litter than random (Table II; Table III). Frogs occupied weekly activity centres that had coarse woody debris 6% more of the time compared to random. Additionally, individuals were 1.01–1.74 times more likely to occupy weekly activity centres with on average 16 mm deeper leaf litter, 3% greater cover of *Sphagnum* mosses, 5% greater cover of slash, and 2.4 °C warmer temperature than random. Additionally, 26% of the weekly activity centres occupied by frogs were forested (≥ 60% canopy cover). Frogs were less likely to occupy weekly activity centres with on average 2% drier soil, 9% greater cover of leaf litter, and less decayed coarse woody debris than random. Percent standing water and vegetation cover were not useful for describing wood frog weekly activity centres; the odds ratios for these variables overlapped 1.

We collected data at 334 wood frog weekly activity centres (spring 2005: 207; fall 2006: 127) plus 309 random weekly activity centres (spring 2005: 196; fall 2006: 113); 25 random weekly activity centres were removed from analysis because they overlapped frog weekly activity centres. Frogs responded to all 12 habitat variables we measured, with the global model having the most support (Table II). Three models comprised ~91% of the weight for the candidate model set. The second-ranked model focused on cover items close to the ground, moisture, and temperature. The third-ranked model focused on variables that would be directly affected by the treatments, moisture, and temperature. The global model fit our data (Hosmer and Lemeshow $\chi^2 = 10.0$, $P = 0.268$). Notably, none of the six 2nd-order 8 interactions were supported by model selection; models containing 2nd-order interactions comprised < 9% of the weight of the candidate model set and received 16 times less support than the global model.

At the weekly activity centre scale, all individuals were generalists (> 0.88, range 0.65–0.99) as measured by the habitat variables included in the top models (Figure 4b). Three variables had consistently high proportional use (> 0.1) across all frogs: percent cover of vegetation, percent cover of leaf litter, and leaf litter depth.

4^{tH}-order resource selection (daily microhabitat)

Generally, wood frogs selected daily microhabitats with more ground structure, more canopy cover, and more coarse woody debris than random locations (Table IV). Frogs were 13 times more likely to occupy microhabitats with coarse woody debris present (Table V), and 26% of the locations occupied by frogs contained coarse woody debris (Table VI). Other important ground structure features included *Sphagnum* mosses, leaf litter, slash, and vegetation. Frogs were 1.02–1.10 times more likely to occupy locations with greater percentage of these cover types. Microhabitats occupied by frogs contained on average 4, 6, 4, and 1% greater of these cover types relative to random microhabitats, respectively. Of all the variables we considered to describe ground structure, coarse woody debris and *Sphagnum* mosses were the most important, with almost twice the amount of support as indicated by cumulative model weight.

Wood frogs were 2.8 times more likely to occupy microhabitats with more canopy cover relative to random microhabitats (Table V). Frogs occupied microhabitats with on average 35% canopy cover. Canopy cover was relatively less important than the ground structure variables (1.3 times less support; Table IV), and coarse woody debris and *Sphagnum* mosses received over twice as much support as canopy cover as indicated by cumulative model weight.

Moisture was also important for predicting the micro-habitats of wood frogs, although less so than ground structure (2.4 times less support) or canopy cover (1.8 times less support). Moisture variables that were useful in describing the microhabitats of wood frogs included leaf litter moisture, relative humidity, and soil moisture. Frogs were 1.01–1.07 times more likely to occupy locations with greater humidity or moisture relative to random microhabitat, although the difference between microhabitats occupied by frogs and random microhabitats was quite small (< 2% difference).

We collected data at 1452 paired wood frog and random daily microhabitats (spring 2005: 831; fall 2006: 621; 2904 total 1-m^2 plots) for 46 frogs (spring 2005: 28; fall 2006: 18). The top model(s) for frogs varied greatly; no single model was the top model for > 18 frogs, and all 7 of the *a priori* models were in the supported model set for ≥ 5 frogs (Table IV). Overall, frogs responded to all 18 habitat variables (13 + 5 dummy variables for dominant cover) included in the 7 *a priori* models (Table V). However, only 9 variables (CP, SP, LI, SL, VC, CC, LM, RH, SM) were useful for prediction; the odds ratios for those variables did not overlap 1 (Table VI). Notably, temperature and dominant cover type received little support from model selection (*i.e.*, average model weight < 10%) and were not useful in describing wood frog daily microhabitats.

At the daily microhabitat scale, all individuals were generalists (> 0.88, range 0.69–0.96) as measured by the habitat variables included in each individual's top models (Figure 4b). Five variables had consistently high proportional use (> 0.1) among all frogs: percent cover of vegetation, leaf litter, and slash as well as soil moisture and leaf litter depth.

Discussion

Three lines of evidence indicate that differences in habitat selection at coarser scales in wood frogs may be mechanistically linked to physiological processes at finer scales: 1) frogs responded to 3 different sets of resources at the 3 scales investigated, 2) resource use changed over time only at the coarse scales, and 3) individuals exhibited variation in resource use. We will consider each of these in turn.

First, at the coarsest scale, wood frogs selected a seasonal home range that provided all the required resources that enable them to successfully balance physiological constraints, and the forested treatments provided the resources for doing so more than the clearcuts. More specifically, at the seasonal home range scale, frogs selected the partially harvested treatment in spring and avoided the CWD retained treatment in fall (Figure 3), and proportional use of the forested treatments was higher than the clearcut treatments. However, the fact that 16 individuals were able to survive in the clearcut treatments indicates there may be resource associations at finer scales that motivate habitat selection (Orians & Wittenberger, 1991), such as cover, moisture, and temperature. At the scale of the weekly activity centre, essential resources for frogs were complex ground structure (cover by *Sphagnum* mosses, vegetation, slash, deep leaf litter, and especially presence of coarse woody debris; Constible *et al.*, 2001), substrate moisture, canopy cover, and temperature (Table III). At the daily microhabitat scale, essential resources were complex ground structure, canopy cover, and substrate moisture (Tables V and VI). Notably, canopy cover played a lesser role than ground structure at the weekly activity centre and daily microhabitat scales.

Second, both the size of seasonal home ranges and selection of variables in weekly activity centres varied temporally, which indicates that frogs were responding to temporal changes in essential resources at these scales. Seasonal home ranges were smaller in spring 2005 than in fall 2006, perhaps because of 2 factors that vary with season: soil moisture is higher in spring than fall because of snowmelt, and lack of cover prior to leaf-out may make spring movements more risky because of predation. Amphibian movements may be constrained by the appropriate temperature and moisture (*e.g.*, Chan-McLeod, 2003; Timm, McGarigal & Compton, 2007), and cover is an important variable in the risk perception of frogs (*e.g.*, Martin, Luque-Larena & Lopez, 2005). Furthermore, wood frogs move close to breeding ponds prior to overwintering and then away from them after breeding to reach distant resources used in the summer (*e.g.*, Regosin, Windmiller & Reed, 2003; Baldwin, Calhoun & deMaynadier, 2006; Rittenhouse & Semlitsch, 2007), and the increased size of home ranges in the fall may be a consequence of such movements. Notably, daily microhabitat relationships did not vary across seasons, indicating resource relationships at this scale may remain relatively constant over time. We must offer a word of caution in interpreting these seasonal results. We were unable to track the same individual in multiple seasons or years. Additionally, we only studied wood frogs in 1 season in 2 different years. Because of this limitation, we attempted to study a large number of animals in each season, but the patterns we observed may be related to annual as well as seasonal variation.

Third, we also observed great individual variation in resource selection (Figures 2b and 4), but less so in selection of coarse woody debris and moisture. This has at least 2 important implications. The importance of coarse woody debris did not vary across the 2 finer scales; frogs were more likely to occupy microhabitats and activity centres with coarse woody debris. Frogs may use different behavioural strategies to meet hydric requirements depending on the availability of moisture and ground cover variables. Frogs generally selected moist weekly activity centres and daily microhabitats, as indicated by greater cover of *Sphagnum* mosses, greater soil moisture, and wetter leaf litter (Tables III, V and VI). Previous research with wood frogs also indicates frogs may use different strategies to maintain their water balance in the terrestrial environment depending on the availability of moisture and ground cover variables (*e.g.*, leaf litter depth; Baldwin, Calhoun & deMaynadier, 2006; Rittenhouse & Semlitsch, 2007).

Together, these 3 lines of evidence indicate that physiological constraints may be important at the finer scales. However, we must offer a word of caution in interpreting these results because our study was limited in the number of relocations we were able to obtain on any given individual (max. 32). We limited the model sizes we considered to less than the number of observations (Hosmer & Lemeshow, 2000), but this small sample size of relocations may have limited our ability to detect some patterns in resource selection.

Scale-dependency in habitat selection indicates that essential resources are available at different spatial and temporal scales, and these differences are linked to different ecological processes (Orians & Wittenberger, 1991; Ciarniello *et al.*, 2007). Amphibians must balance the physiological constraints of thermo- and hydro-regulation with pressures such as predation risk and foraging to meet energetic demands, and these pressures manifest themselves at different scales. At both the weekly activity centre and the daily microhabitat scales, most individuals used locations with complex ground structure, probably because the cover it provides both reduces predation risk and facilitates thermo- and hydro-regulation. Temperature was only useful in describing the location of weekly activity centres, indicating that frogs select an optimal thermal regime at this scale and respond to other constraints including hydro-regulation, cover, and foraging at finer scales. Selection for temperature at the weekly activity centre scale may be one reason why some terrestrial amphibian species use activity centres (Semlitsch, 1981). This result, coupled with consistent daily microhabitat and weekly activity centre selection for substrate moisture, indicates frogs are selecting areas with appropriate temperature on longer temporal scales, while hydro-regulation occurs on daily to weekly temporal scales and may be a more variable process in terrestrial amphibians. This balance between thermoregulation in weekly activity centres and hydro-regulation in both weekly activity centres and daily microhabitats indicates these physiological processes may play an important role in structuring terrestrial habitat selection by wood frogs.

The habitat experienced during one period in an animal's life can have positive or negative effects on its fitness at subsequent times (*i.e.*, latent effects, *sensu* Pechenik, 2006). our results indicate that the fitness potential of forest types may be linked to resource selection at the micro-habitat (*i.e.*, 4th-order) scale because these relationships were 1) more closely dictated by physiological tolerances, 2) relatively consistent among individuals, and 3) did not vary over time. In meso-scale experiments where habitat quality was manipulated, wood frogs experienced density-dependent mortality in high-quality habitat (shade, coarse woody debris, and leaf litter; Patrick *et al.*, 2008), thus indicating that microhabitat selection can regulate population dynamics. Further, animals that do not exhibit density-dependent habitat selection may have compounded costs (*e.g.*, decreased survival in high-quality habitat as well as decreased breeding success in lower-quality habitats) at the population level. This pattern of habitat occupancy and fitness potential may be similar to the ideal-despotic distribution of Fretwell and Lucas (1970).

Habitat relationships at finer scales were apparently dictated by the processes of thermoregulation and hydro-regulation. Thus, some individuals may have been able to survive in the clearcut treatments by finding small patches of habitat that had an adequate thermal and hydric regime and were characterized by complex ground cover, especially coarse woody debris. However, a patchy distribution of weekly activity centres or daily microhabitats may decrease the likelihood of detecting food resources and increase the energetic cost and predation risk associated with moving (Orians & Wittenberger, 1991; Rittenhouse, Semlitsch & Thompson, 2009). Thus, the patchy distribution of essential resources may explain avoidance of the clearcut treatments and may have fitness implications for those individuals that survived in the clearcuts (Berven, 1981; Metcalfe & Monaghan, 2001).

Our results support 2 recommendations for minimizing the impact of timber harvesting. First, partial harvesting with retention of > 50% canopy cover may be a viable forest management strategy in ecologically sensitive areas, such as those surrounding vernal pools and places with endangered species. Canopy cover in our experimental arrays was reduced from 73.8 ± 22.7% to 53.0 ± 33.5% (Patrick, Hunter & Calhoun, 2006), and wood frogs selected these partially harvested treatments in the spring 2005 study. Second, retention of coarse woody debris is probably important following timber harvesting to provide thermal and hydric refuges for amphibians and other ground-dwelling organisms. We retained 2–4 times the volume of coarse woody debris ($45.6 \pm 21.6\ \mathrm{m}^3\cdot\mathrm{ha}^{-1}$) in the CWD retained treatment compared to residual volumes left in other treatments. Retention of coarse woody debris was most important at the weekly activity centre and daily microhabitat scales, and was the single most important variable structuring wood frog habitat selection at these scales.

In summary, wood frogs respond to habitat at multiple scales and exhibited considerable variation in habitat selection across scales and among individuals at the coarser scales. More specifically, selection of the forested treatments at coarser scales may be mechanistically linked to 3rd- and 4th-order resource selection by the physiological processes of thermo- and hydro-regulation. Resources that led to selection of a forested seasonal home range were structural elements that provide ground cover, such as coarse woody debris, but the relative importance of most resources varied with scale. Finally, seasonal home range size and weekly activity centre selection varied over time, but daily microhabitats selected and the resource use of most individuals was consistent at this scale; thus, these microhabitat relationships may be most important for linking habitat relationships to fitness.

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Figures

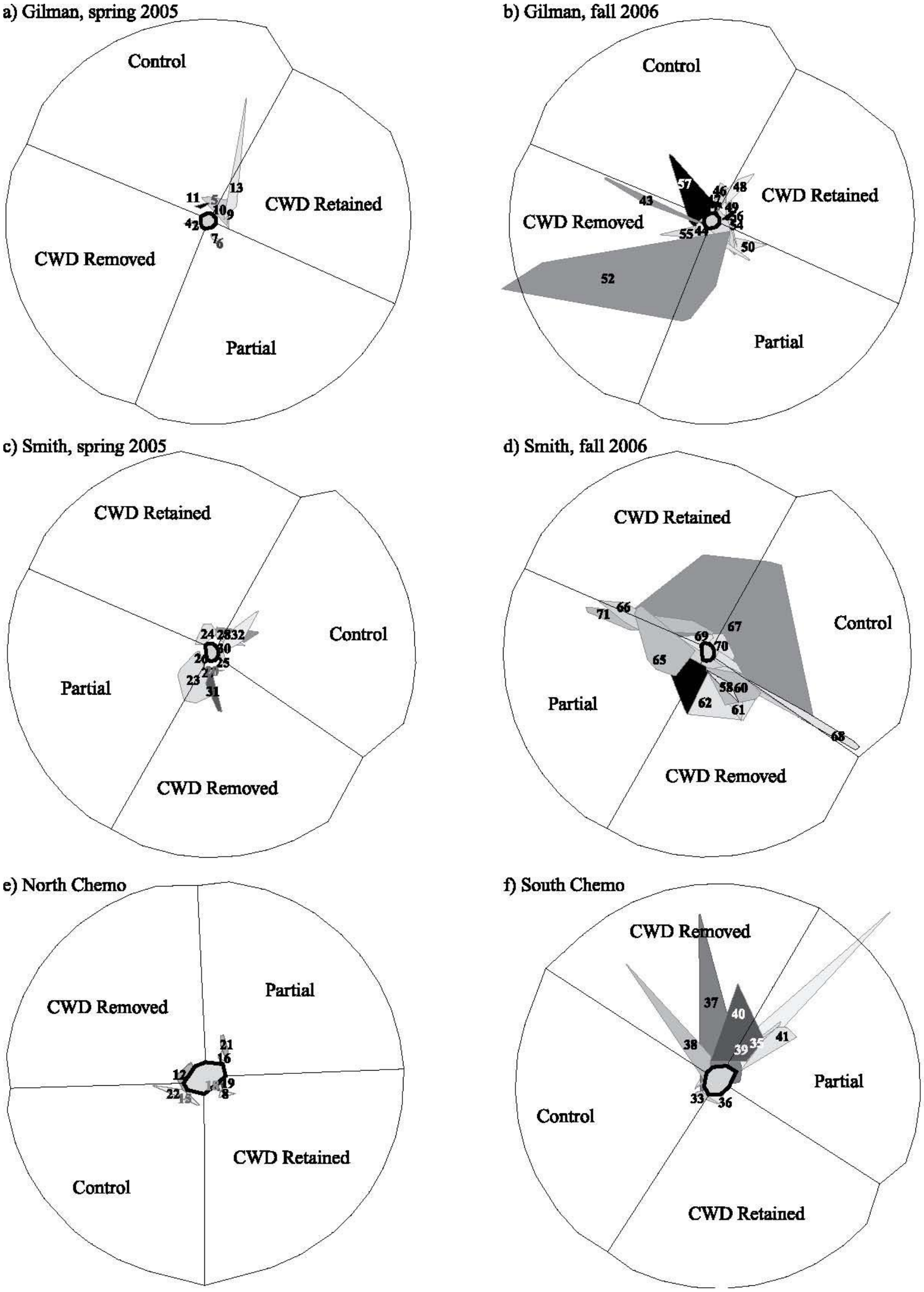

Figure 1. Home ranges (100% minimum convex polygon) of 59 wood frogs at the Gilman (a, spring 2005; b, fall 2006), Smith (c, spring 2005; d, fall 2006), North Chemo (e), and South Chemo (f) experimental arrays. Home range sizes were smaller in spring than in fall 2006 and smaller at the North Chemo experimental array than other sites. Only 2 frogs (Frog 35 in Figure 1b and Frog 52 in Figure 1f) extended their home ranges beyond the edge of the experimental array, and this indicates that our definition of available habitat as the experimental array was acceptable. The 8 locations (of 1452) of these 2 frogs that were outside the array were grouped with the unharvested treatment.

Table I. Habitat variables collected in 1-m^2 plots to quantify habitat use and availability in wood frogs. We collected each variable at the frog location and at a random location each day (4th-order - daily microhabitat) and at a set of random points **every 5 d (3rd-order – weekly activity centre).** Variables were collected at the centre of each plot unless otherwise specified. An initial set of 16 variables was chosen based on literature and field observations. This set of 16 was reduced to 14 based on a pilot study conducted in 2004. The 2 variables removed were percent cover of bare soil and percent cover of rock estimated to the nearest 5%.

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

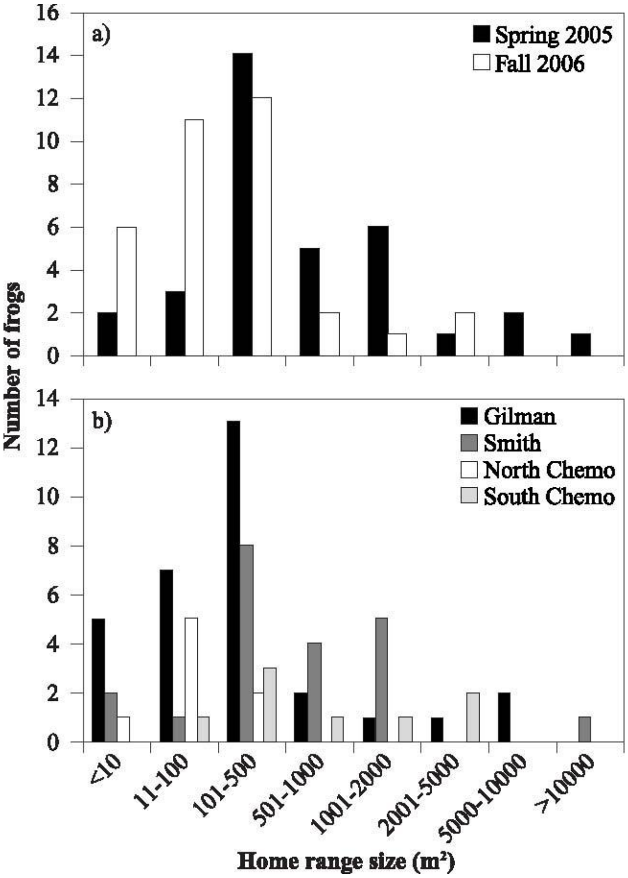

Figure 2. Histograms of variation in home range size in spring 2005 (black) and fall 2006 (white) (a) and across the Gilman (black), North Chemo (white), Smith (dark grey), and South Chemo (light grey) experimental arrays (b) for wood frogs.

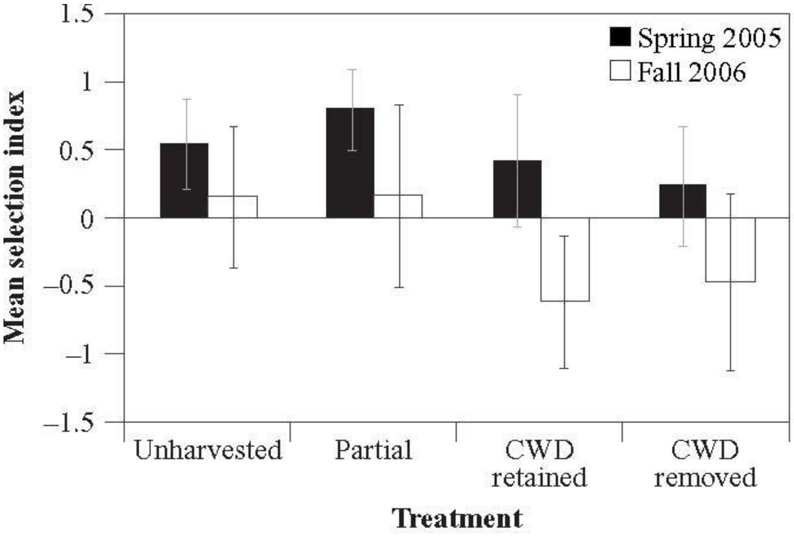

Figure 3. Mean selection index (± 95% confidence intervals) for all wood frogs that used each harvest treatment. Home range selection (2nd order) varied by season, **and frogs selected the forested treatments in spring 2005 (black)** and avoided the CWD retained treatment in the fall 2006 (white).

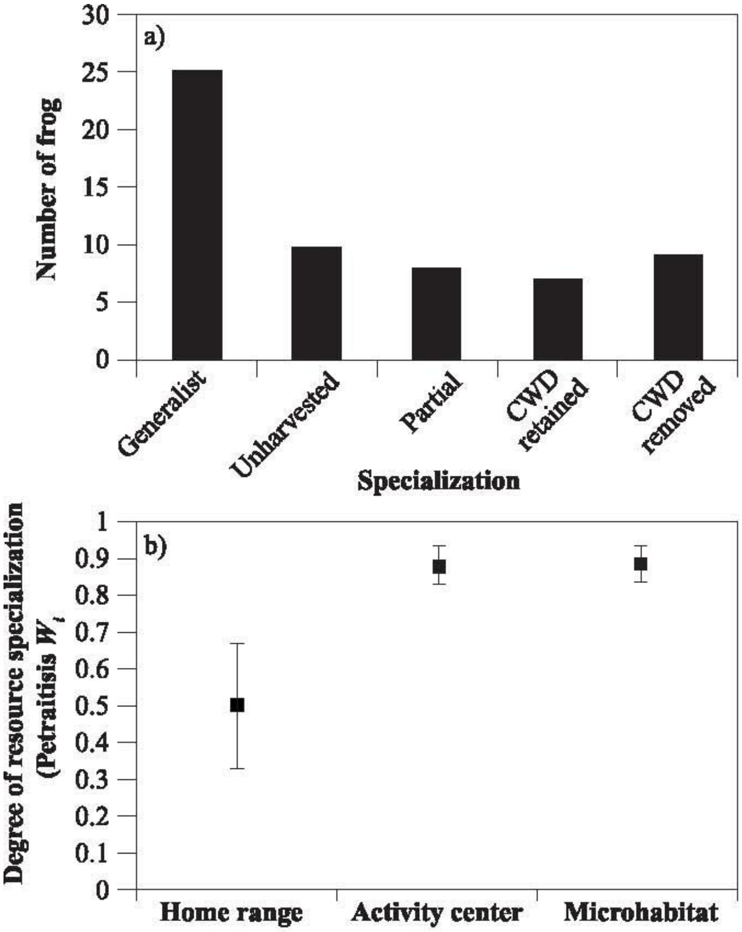

Figure 4. Percent of specialists (Petraitis *Wi* < 0.5; *n* = 59) at the home range scale (a) and mean (± SE) Petraitis *Wi*, a measure of individual specialization in resource use, at the weekly activity centre (3rd order), home range (2nd order), and daily microhabitat (4th order) scales (b) by wood frogs.

Table II. Ranking of *a priori* conditional logistic regression models of 3rd-order habitat selection (weekly activity centre) in wood frogs. Variable codes are defined in Table I, *K* is the number of variables included in the model, and log(*L*) is the log-likelihood of the model. Models were ranked using change in Akaike's Information Criterion corrected for small sample size (ΔAICc) and Akaike's model weights (ω).

Rank	Model	*K*	log(*L*)	AIC_c	ΔAIC_c	ω
1	SW+SP+VC+CC+LI+SL+LD+CP+CD+LM+SM+TE	12	–271.62	567.73	0.00	0.65
2	SW+SP+VC+LI+SL+LD+CP+CD+LM+SM+TE	11	–274.04	570.49	2.75	0.16
3	SW+SP+CC+LI+SL+LD+CP+LM+SM+TE	10	–275.54	571.42	3.69	0.10
4	SW+SP+VC+CC+LI+SL+LD+CP+CD+LM+SM+TE+CP×TE+CP×SM+VC×TE +VC×SM+CC×TE+CC×SM	18	–268.22	573.53	5.80	0.04
6	SW+SP+VC+LI+SL+LD+CP+CD+LM+SM+CP×TE+CP×SM+VC×TE+VC×SM	15	–271.46	573.69	5.96	0.03
7	SW+SP+CC+LI+SL+LD+CP+LM+SM+TE+CP×TE+CP×SM+CC×TE+CC×SM	14	–273.51	575.68	7.95	0.01
8	SW+SP+VC+LI+SL+LD+CP+CD+LM+SM+CP×SM+VC×SM	12	–287.02	598.54	30.81	0.00
9	SW+SP+VC+LI+SL+LD+CP+CD+LM+SM	10	–289.21	598.77	31.03	0.00
10	CC+LI+SL+LD+CP+TE	6	–294.38	600.90	33.16	0.00
11	CC+LI+SL+LD+CP+TE+CP×TE+CC×TE	8	–293.07	602.37	34.64	0.00
12	SW+SP+CC+LI+SL+LD+CP+LM+SM	9	–292.15	602.58	34.85	0.00
13	SP+VC+LI+SL+LD+CP+CD+TE	8	–293.40	603.03	35.30	0.00
14	SW+SP+CC+LI+SL+LD+CP+LM+SM+CP×SM+CC×SM	11	–290.95	604.32	36.59	0.00
15	SP+VC+LI+SL+LD+CP+CD+TE+CP×TE+VC×TE	10	–292.77	605.88	38.15	0.00
16	SP+VC+LI+SL+LD+CP+CD	7	–309.88	633.93	66.20	0.00
17	CC+LI+SL+LD+CP	5	–312.41	634.91	67.17	0.00
18	SW+SP+LM+SM+TE	5	–330.69	671.47	103.73	0.00
19	SW+SP+CC+LM+SM+TE	6	–330.69	673.50	105.77	0.00
20	SW+SP+CC+LM+SM+TE+CC×TE+CC×SM	8	–329.28	674.79	107.06	0.00
21	TE	1	–352.79	707.59	139.85	0.00
22	CC+TE+CC×TE	3	–351.18	708.40	140.66	0.00
23	CC+TE	2	–352.73	709.48	141.75	0.00
24	SW+SP+LM+SM	4	–360.27	728.61	160.87	0.00
25	SW+SP+CC+LM+SM	5	–359.87	729.84	162.11	0.00
26	SW+SP+CC+LM+SM+CC×SM	6	–359.60	731.32	163.59	0.00
	CC	1	–384.03	770.07	202.34	0.00

Table III. Model-averaged parameter estimates (□), odds ratios, and descriptive statistics for each variable for wood frog (*n* = 334) and random (*n* = 309) weekly activity centres (3rd-order habitat selection) from conditional logistic regression models comprising > 90% of the weight of the candidate model set (Table II). Parameter estimates for variables that occurred in models comprising a 90% confidence set were averaged using the model weights to compute a weighted average. Variable codes and units for each variable are defined in Table I, SE = unconditional standard error, Min. = minimum, Max. = maximum, CI = 95% confidence interval

					Random activity centre				Frog activity centre			
Variable	β	Odds ratio	Lower Ci	Upper Ci	Mean	Se	Min.	Max.	Mean	Se	Min.	Max.
CC	0.552	1.737	1.055	2.859	0.24	0.02	0	1	0.26	0.03	0	1
CD	–0.825	0.438	0.237	0.812	0.30	0.03	0	1	0.28	0.02	0	1
CP	1.358	4.021	1.603	10.125	0.20	0.01	0	1	0.26	0.02	0	1
LD	0.039	1.039	1.028	1.051	30.00	1.00	0	210	46.00	2.00	0	199
LI	–0.017	0.983	0.970	0.997	59.00	1.00	0	95	50.00	1.00	0	99
LM	1.420	4.136	2.478	6.904	1.81	0.04	1	3	2.08	0.03	1	3
SL	0.028	1.029	1.012	1.046	16.00	1.00	0	67	21.00	1.00	0	80
SM	–1.018	0.361	0.192	0.679	19.00	1.00	1	50	21.00	1.00	1	50
SP	0.023	1.023	1.005	1.041	6.00	1.00	0	57	9.00	1.00	0	95
SW*	0.016	1.017	0.998	1.036	7.00	1.00	0	100	10.00	1.00	0	80
TE	0.136	1.145	1.088	1.206	13.10	0.40	–2.8	39	15.50	0.30	5.9	30
VC*	0.004	1.004	0.991	1.017	23.00	1.00	0	100	25.00	1.00	0	90

*No inferences were made from these variables because the odds ratio confidence intervals overlapped 1.

Table IV. Model selection uncertainty in change in Akaike's Information Criterion corrected for small sample size (ΔAICc) and Akaike's model weights (ω) for 7 *a priori* conditional logistic regression models of 4th-order resource selection (daily microhabitat) in wood frogs. Because the smallest sample size we considered for this scale was 20 (range 20–32), we constrained the largest models considered to 7 variables. *N*support indicates the number of frogs (out of 46 included in the analysis) with support for that model (ΔAICc < 2). Variable codes are defined in Table I, SE = standard error.

Rank	Model	Mean ΔAICc	$SE_{\Delta AICc}$	Mean ω	SE_{ω}	$N_{support}$
1	SP+VC+LI+SL+LD+CP+CD	6.46	1.01	0.29	0.06	18
2	CC	7.58	1.23	0.22	0.04	14
3	CP	7.82	1.04	0.18	0.04	15
4	SW+SP+RH+SM+LM	8.50	1.04	0.12	0.03	7
5	SW+SP+RH+SM+LM+Te	10.52	1.03	0.06	0.02	3
6	TE	11.11	1.17	0.05	0.01	6
7	DC1+DC2+DC3+DC4+DC5	12.88	1.19	0.09	0.04	5

Table V. Mean and variation in cumulative Akaike's model weight (∑ω) and the number of frogs (*N*support; out of 46 included in the analysis) with support (ΔAICc < 2) for each variable used to describe wood frog and random daily microhabitats (4th-order selection). Parameter estimates for variables that occurred in models comprising a 90% confidence set for each frog were averaged using the model weights to compute a weighted average. The median values of model-averaged, standardized parameter estimates (β*s*) and odds ratios were calculated from frogs with support for that variable (*N*support). Variable codes are defined in Table I, SE = standard error, CI = 95% confidence interval.

Variable	Mean ∑ω	Se $_{\sum\omega}$	N_{support}	Median β_s	Median odds ratio	Median lower CI	Median upper CI
CP	0.47	0.06	27	0.693	12.998	0.003	> 1000
SP	0.46	0.06	26	0.033	1.101	0.329	4.048
CD	0.29	0.06	18	1.725	10.444	< 0.001	> 1000
LD	0.29	0.06	18	–0.009	0.934	0.028	24.519
LI	0.29	0.06	18	0.027	1.028	0.879	1.226
SL	0.29	0.06	18	0.031	1.057	0.125	10.466
VC	0.29	0.06	18	0.039	1.023	0.527	1.600
CC	0.22	0.04	14	1.028	2.796	0.458	28.584
LM	0.18	0.05	8	0.068	1.070	0.090	12.758
RH	0.18	0.05	8	0.018	1.026	0.869	1.167
SM	0.18	0.05	8	0.097	1.006	0.037	1.259
SW	0.18	0.05	8	–0.152	0.859	0.033	21.897
TE	0.11	0.02	9	–0.002	0.998	0.562	2.095
DC1	0.09	0.04	5	0.670	2.004	< 0.001	> 1000
DC2	0.09	0.04	5	10.338	> 1000	< 0.001	> 1000
DC3	0.09	0.04	5	11.151	> 1000	< 0.001	> 1000
DC4	0.09	0.04	5	10.220	> 1000	< 0.001	> 1000
DC5	0.09	0.04	5	12.186	> 1000	< 0.001	> 1000

Table VI. Mean, unconditional standard error (SE), minimum (Min.), and maximum (Max.) value of each variable measured for wood frog and random daily microhabitats (4th-order selection). We calculated these descriptive statistics for all 46 frogs included in this scale of analysis (Overall). We also calculated these statistics only based on frogs for which a variable was useful for describing their habitat (Description), and *N*describe indicates the number of frogs where the odds ratio confidence intervals did not overlap 1. Variable codes and units for each variable are defined in Table I.

	Overall									Description							
	Random microhabitat				Frog microhabitat					Random Microhabitat				Frog microhabitat			
Variable	Mean	Se	Min	Max	Mean	SE	Min.	Max	$N_{describe}$	Mean	SE	Min.	Max.	Mean	SE	Min.	Max.
CP	0.21	0.01	0	1	.27	0.01	0	1	6	.2	.01	0	1	.26	.01	0	1
SP	7	0.00	0	95	10	1.00	0	95	11	6	1	0	90	10	1	0	95
CD	0.61	0.04	0	5	.79	0.04	0	5	0								
LD	28	1.00	0	110	44	1.00	0	110	0								
LI	43	1.00	0	100	48	1.00	0	100	5	44	1	0	100	51	1	0	100
16	16	1.00	0	100	19	1.00	0	95	2	15	1	0	100	19	1	0	90
VC	26	1.00	0	100	28	1.00	0	95	5	26	1	0	100	27	1	0	95
CC	27	1.00	0	100	34	1.00	0	100	11	28	1	0	100	35	1	0	100
LM	2.17	0.02	1	3	2.16	0.02	1	3	2	2.16	.03	1	3	2.17	.03	1	3
RH	44	1.00	2	98	44	1.00	2	95	6	44	1	2	98	44	1	3	95
SM	29	0.00	2	61	31	0.00	3	60	7	28	0	2	58	30	0	3	60
SW	18	1.00	0	100	12	1.00	0	100	0								
TE	15.1	0.20	1	35	15.2	0.20	0.4	36.9	0								
DC1	0.05	0.01	0	1	0.03	0.01	0	1	0								
DC2	0.23	0.01	0	1	0.03	0.01	0	1	0								
DC3	0.38	0.01	0	1	0.47	0.01	0	1	0								
DC4	0.13	0.01	0	1	0.12	0.01	0	1	0								
DC5	0.12	0.01	0	1	0.15	0.01	0	1	0								