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Postbreeding Habitat Use of Wood Frogs in a Missouri Oak-Hickory Forest

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ABSTRACT.—Fitness benefits to individuals from using a particular habitat during the non-breeding season are likely species- and habitat-specific. Our goal was to define the postbreeding habitat use of adult Wood Frogs (*Rana sylvatica*) within continuous oak-hickory forest in Missouri. We used radio-telemetry to determine whether adult Wood Frogs are evenly spaced throughout this forest type or clumped at a particular resource. In addition, we determined microhabitat selection using conditional logistic regression that compares the microhabitat at frog locations to paired points located 2 m from the frog. Adult frogs migrated from breeding sites located on ridgetops into ephemeral, rocky ravines. Use of drainages by Wood Frogs depended on the distance between the breeding site and drainage, and the orientation of drainages relative to the pond edge influenced whether migratory paths of frogs are funneled or spaced apart. The most supported model of microhabitat selection indicated that frogs selected locations with increased leaf litter depth and air temperature and with decreased humidity and light compared to paired points. Persistence of Wood Frog populations along the southwestern edge of their range requires successful annual migrations between breeding sites and forested drainages, which are important nonbreeding habitat for Wood Frogs in a Missouri oak-hickory forest.

Pond-breeding amphibians use aquatic habitat for breeding and extensive amounts of terrestrial habitat during the nonbreeding season to complete their complex life cycle (Semlitsch and Bodie, 2003). Recent work has begun to highlight important habitat requirements of amphibians during the nonbreeding season (e.g., Pilliod et al., 2002; Regosin et al., 2005; Sztatecsny and Schabetsberger, 2005; Baldwin et al., 2006). Fitness potential of habitat, defined as the effect of habitat quality on individual survival and reproduction (Franklin et al., 2000), is essential for predicting the effects of habitat modification on population persistence. However, fitness benefits are likely species- and habitat- specific and behavioral plasticity may occur in wide-ranging species. Detailed studies of microhabitats used by amphibians within a particular vegetation community as well as mechanistic studies that link habitat use to population dynamics are needed to fully understand amphibian habitat requirements (Armstrong, 2005).

The geographic range of Wood Frogs (*Rana sylvatica*) covers the eastern United States and Canada, with relic populations in the U.S. Rocky Mountains and the Ozark region. Wood Frog populations occur within a wide variety of plant communities including deciduous oak-hickory forests, coniferous boreal forests, grassy meadows, aspen groves, and prairies, but they are largely absent from southeast coastal areas (Muths et al., 2005). The wide range indicates that Wood Frogs can live in vegetation communities consisting of either forests or grasslands depending on local weather conditions. As ectotherms, amphibians are inherently linked to the microclimate conditions of their habitat (Feder and Burggren, 1992). Vegetation structure can be as important as vegetation type or species, and habitat selection based on vegetative structure has been confirmed in other species (Griffin and Case, 2001). In addition, habitat selection can change with environmental conditions; for example, Wood Frogs move from humus to leaves as substrate moisture decreases (Heatwole, 1961; Patrick et al., 2006). The availability of refuge sites with moderate temperature and moisture levels is likely an important component of amphibian habitat selection during the nonbreeding season (Bartelt, 2000; Seebacher and Alford, 2002). Identifying the structural features of the habitat that create preferred microclimates may facilitate comparison to other regions and, thus, improve our understanding of Wood Frog habitat use across its broad geographic range.

Our goal was to define the postbreeding habitat use of adult Wood Frogs within continuous oak-hickory forest in Missouri. The first objective was to determine whether adult Wood Frogs are evenly spaced throughout this forest type or clumped at a particular resource. We used movement paths of radio-tagged frogs migrating from breeding sites to identify non-

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breeding habitat within the forest. The second objective was to determine whether frogs select microhabitat during migration. We compared microhabitat variables at frog locations while the frog was present to microhabitat variables at paired points located 2 m from the frog. We develop a set of a priori models that test hypotheses regarding the relative importance of microclimate variation (e.g., soil temperature, relative humidity) and structural features of habitat (e.g., litter depth, percent canopy cover) and the relative importance of temperature and moisture in microhabitats used by Wood Frogs.

MATERIALS AND METHODS

Study Site.—The study was conducted at the Daniel Boone Conservation Area (DBCA), Warren County, Missouri. DBCA is centered within a continuous tract of forest bordered by corn and soybean agriculture about 9 km to the north and by the Missouri River about 6 km to the south. The area contains mature, second-growth oak (*Quercus* spp.) and hickory (*Carya* spp.) overstory, with sugar maple (*Acer saccharum*) beginning to establish in the understory (i.e., Outer Ozark Border Subsection as described by Nigh and Schroeder, 2002). Local relief (i.e., elevation change within 2.59 km^2) ranges from 46–76 m. Small, intermittent streams begin in DBCA and flow south toward the Missouri River, cutting through loess ridge tops and exposing limestone rock. Amphibian breeding sites are ponds that were constructed greater than 30 yr ago on ridge tops as wildlife watering holes and were naturally colonized by a variety of amphibian species. We tracked Wood Frogs as they emigrated from three ponds located 375–1,370 m apart (i.e., Pond 2 a.k.a. LEAP Pond 2, Pond 27 a.k.a. Teacup Pond, and Pond 5 a.k.a. LEAP Pond 5).

Radio-Telemetry.—We captured six female and 36 male Wood Frogs at three ponds during the two-day breeding period using hand captures and minnow traps. If transmitters could not be immediately attached upon capture, frogs were placed in enclosures (1 × 2 × 1 m) at the pond edge and held for less than two days. We attached 1.0-g transmitters (model BD-2 with whip antennae and 1 mm diameter tube; Holohil Systems Inc., Canada) using a belt constructed from 1-mm stretch bead cord (Mainstays Crafts, Sulyn Industries, Inc.; as in Baldwin et al., 2006). Transmitter mass was on average 6.9% of frog body mass. All frogs were fitted with transmitters on 6 or 7 March 2004 and released within 5 m of the pond edge. We relocated frogs during daylight hours for 50 consecutive days using a R2000 ATS receiver and yagi antenna (Advanced Telemetry Systems, Inc., Isanti, Minnesota). Upon homing to the frog, we obtained a visual sighting, carefully pulled out the whip antenna from beneath leaf litter, and placed a wire flag next to the frog. If the antenna was visible next to the flag upon subsequent relocations, we did not disturb the frog by obtaining a visual sighting. All movements greater than 10 cm were marked with a flag. Flags were later mapped with a compass and tape measure or GPS unit with submeter accuracy (Trimble Pathfinder Pro XL) and imported into Arcview (version 3.2; Environmental Systems Research Institute, Redlands, California). For each frog, we calculated total distance traveled, net distance (i.e., straight line distance between first and last relocation), and maximum straight line distance traveled between daily relocations.

We analyzed the spatial distribution of frog locations at each pond using Ripley's K function (Ripley, 1981; Venables and Ripley, 2002) within the ''Spatial'' library of program R (Ihaka and Gentleman, 1996). Ripley's K quantifies spatial dependence between points at a range of spatial scales and is presented as a cumulative distribution function, $K(t)$, of the expected number of points within a given distance of a single point. The $K(t)$ function operates within a region D, the spatial extent of all points. We used $L(t)$, a square-root transformation that linearized $K(t)$ and stabilized variance (Venables and Ripley, 2002). We defined points as all frog locations at each pond. We calculated 95% confidence envelopes by simulating 100 random point distributions where the number of points in each simulation was equivalent to the total number of frog locations at each pond. The domain for the simulated points was equivalent to the smallest dimension of D and was unique for each pond. We tested for nonrandom Wood Frog spatial distributions at each pond by comparing $L(t)$ to the 95% confidence envelopes. We classified the distribution as clumped if $L(t)$ fell above the simulated 95% confidence envelopes, uniform if it fell below the envelopes, and random if it fell within the envelopes.

Microhabitat.—We collected microhabitat data at frog locations while the frog was present by placing probes within refugium as close to the frog as possible without actually touching the frog (i.e., within 8 cm). We also collected microhabitat data at three points paired to each frog location that were located 2 m from the frog. We placed the probes within the leaf litter as if a frog was present within the leaf litter. We chose the spacing of these points to determine whether frogs select microhabitat within the last one to two jumps of migratory movements. One paired point was located 2 m from the frog in the direction from which the frog was pre-

TABLE 1. Fourteen a priori models of Wood Frog microhabitat selection at DBCA in Warren County, Missouri. Models were developed based on eight variables, including litter depth (litter), three categories of course woody debris (CWD), percent canopy cover (canopy), percent of leaf cover (leaves), percent of relative humidity (humidity), air temperature (airtemp), soil temperature (soiltemp), light (light). The global model contained all eight variables.

Model Name	Variables
1. Structure	litter, CWD, canopy, leaves
2. StructureA	litter, CWD, leaves
3. StructureB	canopy
4. Microclimate	humidity, airtemp, soiltemp, light
5. ClimateA	humidity
6. ClimateB	light, airtemp, soiltemp
7. Moisture	litter, leaves, CWD, humidity
8. MoistA	litter, humidity
9. MoistB	leaves, CWD
10. Temperature	canopy, CWD, airtemp, soiltemp, light
11. TempA	canopy, soiltemp, light
12. TempB	CWD, airtemp
13. Literature	litter, humidity, soiltemp, light
14. Global	litter, CWD, canopy, leaves, humidity, airtemp, soiltemp, light

viously located and two additional points were located 2 m from the frog at 90° from the first direction (Cooper and Millspaugh, 1999). We only collected microhabitat data at relocations spaced at least 5 m apart, and we did not collect data at release points even if the frog remained there for several days. In addition, we only collected microhabitat data when frogs settled at a location for several days (i.e., periods without rain when the top layer of leaf litter was dry).

We collected eight microhabitat variables, including soil temperature at 5 cm depth (Taylor Digital Pocket Thermometer), light at the surface of the leaf litter (silicone photovoltaic detector), air temperature and humidity within the refugium or leaf litter (Extech Hygro-Thermometer RH101), litter depth (ruler), canopy cover (spherical crown densiometer), diameter of coarse woody debris within 2 m, and percent ground cover (1 m^2 daubenmire frame). We classified coarse woody debris as no CWD, small CWD (i.e., presence of CWD 10–24 cm in diameter), and large CWD (i.e., presence of CWD greater than 25 cm in diameter). Approximately 85% of all ground cover was deciduous leaf litter with the remaining 15% being split between six other cover types (i.e., forbs/mosses, grass, fine woody debris, coarse woody debris, rock, bare soil); therefore, we used percent leaf litter as the ground cover variable.

We used conditional logistic regression to compare the microhabitat conditions at the frog location to the three paired points (i.e., unused locations); thus, each strata ($N = 100$) was composed of four points. This logistic model uses data collected with a case-control sampling design; and thus we assume that used locations are rare within the habitat, and paired locations were unused by frogs because we would have found frogs at these locations while collecting microhabitat data (Keating and Cherry, 2004). We used an information-theoretic approach to determine support for models representing alternative hypotheses concerning Wood Frog microhabitat use (Burnham and Anderson, 2002). We developed four a priori subglobal models to test whether frog locations were based on structural habitat features, microclimate variables, moisture conditions, or temperature conditions (Table 1). We further split the subglobal models into eight a priori candidate models. In addition, we proposed a candidate model that contained variables suggested as being important within the physiological literature (Thorson, 1955; Feder, 1983; Jorgensen, 1997; Seebacher and Alford, 2002) and included a global model. We ranked the 14 a priori models and selected the best approximating model using the change in Akaike Information Criterion (ΔAIC) and Akaike weights (ω). We calculated odds ratios and 95% confidence limits for parameters in the most supported model to facilitate interpretation (Keating and Cherry, 2004).

RESULTS

Movements.—We tracked 42 Wood Frogs for 42.6 ± 9.76 days. The belt attachment technique was both effective and efficient. None of the transmitters slipped, all frogs were fitted with belts within two days and at the end of the study all transmitters were removed within two days. Abrasions were minimal but did gradually worsen over the 50 days, preventing us

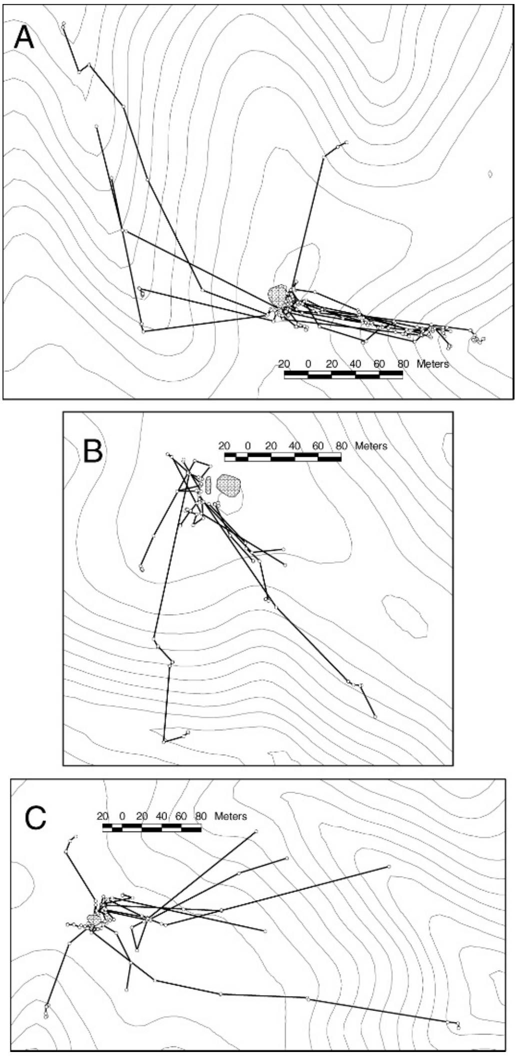

FIG. 1. Movement paths for 17 Wood Frogs at Pond 5 (A), 13 Wood Frogs at Pond 2 (B), and 12 Wood Frogs at Pond 27 (C). Frogs migrated from breeding sites located on ridge tops at the DBCA in Warren County, Missouri and into drainages that were used as nonbreeding habitat. Each black line represents a movement path of one frog and was created by drawing a straight line between daily relocation points (i.e., open circles). Note that frogs did not migrate out ridge tops and that frogs at Pond 5 entered the top of the drainage with one frog migrating into the drainage to the north of the breeding site, four frogs migrating into the drainage to the west, and 12 frogs migrating to the closest drainage to the east.

from replacing the first transmitter on each frog with a second transmitter.

We relocated frogs daily for a total of 1,791 relocations (Appendix 1). Most of our relocations (i.e., 76.4%) verified that frogs did not move between locations (i.e., antenna in the exact same location as previous day). Frogs regularly spent 6–11 days at the same location and the maximum number of days at the same location was 24 days. When movements did occur, 56.5% of movements were less than 5 m and 17.9% of movements were greater than 20 m. Movements greater than 20 m occurred only 3.8% of the time and all corresponded with rain events. Frogs made migratory movements away from ponds on 24 and 25 March 2004 (mean total distance = 76.2 ± 62.3 m; max total distance = 248.9 m) during the first rain event postbreeding (total two-day rainfall = 5.1 cm; mean daily temperature = 16.1°C); therefore, as soon as an evening rainfall occurred frogs emigrated from breeding sites. We did not document any movement between ponds during the study period.

Macrohabitat.—Wood Frogs made linear, directed movements from breeding sites located on ridge tops into ephemeral, rocky ravines (hereafter referred to as drainages; Fig. 1). The $L(t)$ function for each pond fell above the 95% confidence envelopes, indicating that Wood Frogs had a clumped distribution at each pond. Therefore, Wood Frogs were not randomly or evenly spaced throughout the oak-hickory forest but clumped within drainages. Once frogs entered drainages, they did not return to a ridge top or move into different drainages during the 50-day study period. Frogs at Pond 5 directed movements toward the top of drainages (Fig. 1A). Movement paths for frogs at Pond 2 and Pond 27 were also directed toward drainages, but each frog directed its movement toward a slightly different part of the drainage (Fig. 1B and 1C). Notably, 17 frogs at Pond 5 migrated into the drainage to the southeast that begins approximately 30 m from the pond, four frogs migrated into the drainage to the west that begins approximately 70 m from the pond, and only one frog migrated into the drainage to the north that begins approximately 200 m from the pond (Fig. 1A).

Microhabitat.—Prior to collecting microhabitat data, 93% of frogs were completely covered with leaf litter, and we could see an eye or part of the body without moving any leaves for the remaining 7%. When we moved leaves after collecting microhabitat data to verify the location of the pelvic patch, 60% of frogs had their pelvic patch pressed against the soil, and 40% of frogs were located within the leaf layer (i.e., pelvic patch on a leaf).

Clear separation occurred between the global model ($\omega = 0.9993$) and the other candidate models (Table 2), indicating support for the structural, microclimate, moisture, and temperature hypotheses. Frogs used locations with

TABLE 2. Conditional logistic regression models ranked by AICc to test alternative models of Wood Frog microhabitat use in a Missouri oak-hickory forest. Models with low AICc and high Akaike weight (ω) have more substaintial support.

Model	k	AICc	ΔAICc	ω
Global	9	191.649	0.000	0.9993
Literature	4	207.039	15.390	0.0005
Microclimate	4	208.366	16.717	0.0002
MoistA	2	211.647	19.998	0.0000
Moisture	5	215.475	23.827	0.0000
ClimateB	3	216.300	24.651	0.0000
Temperature	6	219.113	27.464	0.0000
TempB	3	227.478	35.829	0.0000
ClimateA	1	229.855	38.207	0.0000
Structure	5	242.888	51.239	0.0000
StructureA	4	244.167	52.519	0.0000
TempA	3	247.109	55.460	0.0000
StructureB	1	253.983	62.335	0.0000
MoistB	3	258.256	66.607	0.0000

increased leaf litter depth and air temperature and with decreased humidity and light compared to paired points located 2 m from frogs (Tables 3, 4). For example, odds ratios of coefficients indicate a 26% increase in the odds of a location being used by frogs for every 1 cm increase in litter depth and every 1°C increase in air temperature (Table 3). In addition, frog locations were positively associated with small coarse woody debris but negatively associated with large coarse woody debris.

DISCUSSION

All areas within oak-hickory forest were not used equally by adult Wood Frogs. Adult frogs migrated from breeding sites located on ridgetops into ephemeral, rocky ravines, indicating that these drainages are important nonbreeding habitat for Wood Frogs in oak-hickory forests. Wood Frogs have previously been shown to use red maple forested wetlands or other wet forests during the summer (Regosin et al., 2005; Baldwin et al., 2006), but this habitat type and the associated sphagnum moss ground cover does not occur at our study site. Wood Frogs in Missouri used deciduous leaf litter. Leaf litter has a complex structure that prevents evaporative water loss (O'Connor et al., 2006) and has previously been shown to prevent water loss better than rock crevices, hollows under trees, or dense ground vegetation (Seebacher and Alford, 2002).

Drainages may have been used by frogs during the spring and summer for a variety of reasons, including the presence of refuge sites with appropriate microclimate conditions and abundant prey. Hydroregulation by frogs in terrestrial habitats involves absorbing water through the pelvic patch while sitting on moist substrates, because frogs constantly lose water across the skin into the air via evaporation (Thorson, 1955; Heatwole and Lim, 1961). Drainages likely facilitate the ability of frogs to regulate water by providing moist soil and cool temperatures. In a related experiment where water loss was measured simultaneously with both soil moisture and temperature, we found that survival of juvenile Wood Frogs held on ridge tops ranged from 7.5–11.8%, whereas survival within drainages ranged from 53.6–59.3%, indicating that mortality caused by desiccation is reduced in drainages (T. A. G. Rittenhouse, E. B. Harper, L. R. Rehard, and R. D. Semlitsch, unpubl. data). In addition, drainages shade frogs from direct sunlight, shelter them from wind, and steep topography creates breaks in the leaf litter. We observed frogs completely covered with leaf litter but sitting in foraging postures when steep slopes created a gap out the side of the leaf litter. Finally, drainages with moist soil conditions may allow for increased invertebrate activity, thus increasing the probability of invertebrates approaching the sit-and-wait predator. Competition for food underlies habitat selection theories for birds and

TABLE 3. Parameter estimates (coefficients and standard error), odds ratios, and 95% confidence limits from the most supported model explaining microhabitat conditions at frog locations in a Missouri oak-hickory forest.

Variable	Estimate	SE	Wald χ^2	P-value	Odds Ratio	95% confidence limit Lower	95% confidence limit Upper
Litter	0.234	0.081	8.428	0.004	1.264	1.079	1.480
Humidity	−0.081	0.025	10.938	0.001	0.922	0.879	0.968
Airtemp	0.237	0.077	9.523	0.002	1.267	1.090	1.473
Light	−27.297	11.789	5.362	0.021	<0.001	<0.001	0.015
Soiltemp	0.227	0.212	1.149	0.284	1.255	0.829	1.900
CWD small	0.405	0.340	1.415	0.234	1.668	0.624	4.455
CWD large	−0.298	0.528	0.318	0.573	0.826	0.153	4.468
% canopy	0.040	0.029	1.844	0.175	1.040	0.983	1.102
Leaves	0.008	0.009	0.825	0.364	1.008	0.990	1.027

TABLE 4. Microhabitat characteristics of locations used by Wood Frogs and paired unused locations.

	Used by frogs				Unused locations			
Variable	Mean	SD	Min	Max	Mean	SD	Min	Max
Litter (cm)	5.94	1.725	1.000	11.000	5.18	2.035	0.000	11.000
Humidity (%)	76.31	14.375	34.200	95.100	80.48	12.366	33.600	96.600
Airtemp (°C)	53.09	11.881	30.800	97.100	51.45	10.661	30.500	85.600
Light	0.32	0.037	0.225	0.388	0.33	0.033	0.244	0.410
Soiltemp (°C)	48.76	4.554	40.500	57.400	48.73	4.602	39.400	59.000
% canopy (%)	88.81	8.305	62.500	100.000	87.62	7.746	62.500	100.000
Leaves (%)	85.90	16.227	20.000	100.000	83.60	20.695	0.000	100.000

mammals (Fretwell and Lucas, 1969; Jones, 2001). Anurans seem to be less tied to food resources (Bartelt et al., 2004) because they are generalists that feed on invertebrates in proportion to their availability (Forstner et al., 1998). However, invertebrate mass within a habitat has been linked to anuran mass, indicating that prey availability can affect habitat quality (Sztatecsny and Schabetsberger, 2005). The importance of prey availability in Wood Frog habitat selection warrants further investigation.

Our data suggest that use of drainages by Wood Frogs depends on the distance between the breeding site and drainage. Migrating between two spatially separated habitats presents a tradeoff between the potential costs of migration and the potential fitness benefits of reaching nonbreeding habitat of high quality. Migration costs include a large expenditure of energy for locomotion and exposure to visual predators. We did not investigate whether some drainages are higher quality habitat for Wood Frogs than other drainages; however, the three drainages at Pond 5 clearly differ in the number of frogs using the drainage. Intraspecific competition may be higher in drainages located near breeding sites compared to those located at greater distances because of the density of frogs within the drainage. Therefore, frogs that migrate to drainages far from breeding sites may experience high migration costs, but benefit from reduced competition during the nonbreeding season.

Our data also suggest that the orientation of drainages relative to the pond edge may influence how much terrestrial habitat is traversed by migrating frogs. When drainages were located at a perpendicular angle to the pond edge, as occurred at Pond 5, the movements of all frogs were directed toward the top of the drainage. In other words, frogs funneled through a small corridor of terrestrial habitat. When drainages were parallel to the pond edge, as occurred at Pond 2 and Pond 27, frogs radiated away from the pond in multiple directions and paths did not overlap as frequently. This pattern has been consistent among years (TAGR, unpubl. data). Therefore, landscape configuration may influence the degree to which habitat modification affects a local population. Small scale timber harvest or development (e.g., one house) that occurs near a Wood Frog breeding site will likely affect adult breeding migrations. When drainages are perpendicular to the breeding site, the placement of the disturbance outside of movement corridors may minimize effects, whereas habitat modification near breeding sites with parallel drainages may affect some proportion of the population regardless of placement.

Much to our surprise Wood Frogs remained in the exact same location for multiple days and did not make any daily foraging movements. We confirmed this result using thread-trailing tracking devices in following years (TAGR, unpubl. data). However, daily telemetry relocations allowed us to observe hydrotactic movements within the leaf litter. Frogs sat high within the layers of leaves following rain events when litter was wet and moved lower within the leaves as the litter dried. By three to four days after a rain when the top of the leaf litter was completely dry, approximately 60% of frogs would be sitting with their pelvic patch pressed against the soil. We observed on 13 occasions a frog sitting completely exposed on top of the leaf litter. All of these observations were on humid mornings immediately following rain. When we relocated these frogs either later the same day or the following day, frogs had moved less than 1 m and were under the litter; thus, they were not migrating during daylight hours even when litter was wet.

Wood Frogs used deciduous leaf litter as microhabitat. Therefore, Wood Frog microhabitat use in a Missouri oak-hickory forest differs greatly compared to microhabitat use in more northern forests that contain sphagnum moss and humus (Baldwin et al., 2006). In addition, we found no indication that frogs choose to sit near shelter objects, such as coarse woody debris, rock outcrops, or any live vegetation. Although frogs did not use coarse woody debris greater than 25 cm in diameter, frog locations were positively associated with small pieces of coarse woody debris (i.e., 10–25 cm diameter). We did not quantify fine woody debris (i.e., $<$ 10 cm diameter), but small sticks may provide important structure within the leaf litter layer.

Our most supported microhabitat model indicated that frogs used locations with increased leaf litter depth; however, we did not observe frogs seeking out the deepest litter in the forest, such as a leaf pile next to a rock or other object. We believe that the relationship between use and litter depth may not be linear, with frogs using moderate litter depths of approximately 6 cm. Frogs used humid locations (mean humidity = 76.3%), but humidity at frog locations was lower than paired locations. Explanations that incorporate the association with increased litter depth and decreased humidity include frogs using locations where leaves are less tightly packed or frogs pushing leaves apart when entering the litter. Space between the leaves may allow for air movement (i.e., reduced humidity levels) and may also increase access to invertebrates moving through the litter. Therefore, microhabitat use may reflect the need to maintain hydration levels while also obtaining foraging opportunities. Increased digestion rates at warmer temperatures along with high evaporation and radiation rates when in direct sunlight likely explain the positive association of frogs using locations with low light levels and yet warm soil temperatures (Feder and Burggren, 1992).

Conservation of pond-breeding amphibian populations requires the maintenance of both breeding and nonbreeding habitat and the successful migration of individuals between these spatially separated habitats (Semlitsch, 2000; Baldwin et al., 2006). Drainages within oak-hickory forest are a landscape feature of the habitat that allows for microclimate conditions within the leaf litter that serve as nonbreeding habitat for Wood Frogs during the spring and summer. Therefore, the persistence of Wood Frog populations along the southwestern edge of their range requires successful annual migrations between breeding sites and drainages. Our data suggest that any attempts to enhance or create Wood Frog breeding sites within this portion of the range should consider the proximity and landscape configuration of breeding sites and forested drainages.

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APPENDIX 1. Summary of Wood Frog movements. We report the number of radio relocations (relocations), number of spatial locations where a frog was relocated (frog locations), total distance traveled (TotDis), straightline distance between first and last frog location (NetDis) and maximum straightline distance traveled in one day (MaxSMov).

ID	Sex	Pond	Mass (g)	SVL (mm)	Relocations	Frog locations	TotDis (m)	NetDis (m)	MaxSMov (m)
1.467	x	2	14.50	61	13	2	0.82	0.82	0.82
1.008	y	2	17.50	59	46	14	275.91	216.01	144.01
1.030	y	2	17.00	61	48	13	134.41	92.24	61.25
1.060	y	2	14.00	53	8	3	0.21	0.21	0.21
1.080	y	2	17.75	57	46	9	253.92	245.12	120.57
1.119	y	2	15.50	59	41	8	74.32	24.44	29.47
1.267	y	2	13.50	55	48	7	181.55	99.63	83.95
1.301	y	2	16.75	56	48	11	53.14	15.66	13.49
1.32	y	2	15.75	55	48	9	28.75	27.83	14.97
1.34	y	2	12.00	51	47	4	87.7	79.74	59.96
1.388	y	2	14.00	55	47	8	103.79	94.41	34.45
1.427	y	2	14.25	54	34	6	60.27	58.63	29.67
1.483a	y	2	11.00	51	27	2	0.24	0.24	0.24
1.100	y	2.5	16.00	57	48	9	320.12	289.29	237.67
1.149	y	2.5	17.00	58	48	9	218.96	194.39	101.62
1.170	y	2.5	13.25	53	47	5	81.29	67.77	33.59
1.189	y	2.5	18.00	60	48	9	118.8	85.71	58.06
1.209	y	2.5	15.50	58	48	8	33.93	31.38	17.77
1.229	y	2.5	15.75	58	48	9	86.98	21.93	32.66
1.483	y	2.5	13.75	55	18	4	171.96	167.24	159.18
1.518	y	2.5	14.50	58	47	12	408.03	393.34	143.11
1.538	y	2.5	18.50	60	38	10	147.84	132.26	79.96
1.559	y	2.5	12.50	51	44	12	130.39	47.50	38.19
1.571	y	2.5	13.25	54	47	14	110.54	103.87	66.14
1.467a	y	2.5	12.75	52	33	8	29.56	10.78	8.06
1.220	x	5	13.25	60	46	12	159.98	107.22	117.76
1.261	x	5	17.50	66	47	16	182.33	165.66	124.15
1.289	x	5	15.00	62	46	16	146.27	135.05	34.37
1.309	x	5	20.50	66	45	13	111.25	97.46	38.81
1.448	x	5	14.00	61	46	14	121.2	90.32	40.79
1.020	y	5	12.50	51	48	17	94.54	1.02	15.29
1.049	y	5	14.50	53	33	12	187.19	120.37	68.01
1.069	y	5	16.75	57	46	13	138.09	120.80	61.78
1.088	y	5	11.75	57	47	11	331.38	297.35	103.82
1.110	y	5	12.00	52	46	6	242.82	173.12	125.03
1.140	y	5	12.75	53	47	14	62.98	13.86	20.24
1.160	y	5	15.25	57	47	6	250.62	223.10	150.28
1.181	y	5	14.00	55	47	13	160.85	131.66	110.2
1.198	y	5	15.50	57	47	7	147.19	140.80	122.04
1.328	y	5	10.50	51	46	19	99.94	79.92	37.96
1.379	y	5	10.50	53	46	14	133.77	113.60	116.18
1.400	y	5	11.75	51	46	14	172.62	149.85	115.15