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Movement Ecology and Habitat Use of Three Sympatric Anuran Species

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***Abstract*.—Studies focused on movement ecology and habitat use allow for the identification and prioritization of critical habitats and movement corridors for species conservation in altered landscapes. We used radio-telemetry to examine the movements and habitat use of three sympatric anuran species in two forested study landscapes with diverse aquatic resources in the drought-prone Piedmont ecoregion of the southeastern USA to identify required habitats and movement corridors. We tracked 15 Wood Frogs (*Lithobates sylvaticus*), 11 Southern Leopard Frogs (*Lithobates sphenocephalus*), and six Green Frogs (*Lithobates clamitans*) between 27 January and 30 June 2012. Wood Frogs and Southern Leopard Frogs moved among ephemeral wetland, marsh, and stream habitats. Green Frogs used ephemeral wetland, swamp, and stream habitats. At the 2-m scale, Wood Frogs and Green Frogs selected areas with ample deciduous leaf ground cover; Southern Leopard Frogs selected areas with ample fern ground cover. At the 20-m scale, Wood Frogs selected areas with high relative humidity; Southern Leopard Frogs and Green Frogs selected aquatic areas. The variation in habitat use by the three species supports the importance of conserving heterogeneous features within a landscape to maintain biodiversity.**

Key Words.—amphibians; biodiversity; Green Frog; habitat selection; *Lithobates*; radio-telemetry; Southern Leopard Frog; Wood Frog

Introduction

For effective biodiversity conservation in increasingly altered landscapes, management plans must ensure that all required habitats and movement corridors be maintained for migration and dispersal of species, geographic shifts in communities, and other ecological processes (Fahrig 2003; Nathan et al. 2008). Studies focused on movement ecology and habitat use allow for effective identification and prioritization of critical habitats and movement corridors for species conservation, which is increasingly important given the logistical constraints (e.g., limited funding and increasing human population and demand for resources) that hinder conservation efforts (Barton et al. 2015). Knowledge of movement ecology for species that move among disparate habitats and ecosystems (i.e., mobile link organisms such as amphibians) can also contribute to conservation of ecosystem function and resilience through time as these species transfer resources and contribute to trophic and nontrophic processes in multiple ecosystems (Lundberg and Moberg 2003).

Movement ecology and habitat use of amphibians are increasingly studied for some species in some portions of their range, but knowledge gaps remain (Pittman et al. 2014). Amphibian movement ecology and habitat use data may allow for the elucidation of specific threats to particular populations and species (Pittman et al. 2014). Such data may also contribute to the development of more accurate models that better predict amphibian population responses to habitat alteration (Semlitsch 2008; Pittman et al. 2014). Whereas the need for such studies on imperiled species or those with limited geographic distributions is readily apparent, investigations on widespread species are also warranted because the consistent or inconsistent use of habitat by these species throughout their ranges may provide insights into how species with greater plasticity will respond to increasingly altered (including by climate change) and fragmented habitats.

Wood Frogs (*Lithobates sylvaticus*), Southern Leopard Frogs (*Lithobates sphenocephalus*), and Green Frogs (*Lithobates clamitans*) are widespread species native to North America. The distribution of Wood Frogs encompasses much of Alaska (USA), Canada, and the northeastern USA, extending southward along the Appalachian Mountains and Piedmont ecoregion to northern Georgia (Dodd 2013). Southern Leopard Frogs are found throughout the southeastern USA, occurring from central Illinois to south Florida, and westward to eastern Texas (Dodd 2013). The Green Frog, with two recognized subspecies, occurs throughout eastern North America from the St. Lawrence River Valley in southeastern Canada to northern Florida and eastern Texas, USA (Dodd 2013).

These three species vary both in their degree of association with aquatic and terrestrial ecosystems and sensitivity to habitat alteration and loss. Wood Frogs are the most terrestrial of the three species and are commonly associated with closed-canopy deciduous and mixed deciduous forests (Guerry and Hunter 2002; Browne et al. 2009; Dodd 2013), often using moist deciduous leaf litter as refugia (Baldwin et al. 2006; Rittenhouse and Semlitsch 2007; Dodd 2013). They typically breed in fishless, ephemeral wetlands (Dodd 2013). Wood Frogs are negatively impacted by alteration and destruction of the ephemeral wetlands in which they breed, and by deforestation and development (including road building) of the adjacent and greater terrestrial habitat in which the pools occur (deMaynadier and Hunter 1999; Egan and Paton 2004; Homan et al. 2004; Skidds et al. 2007). Southern Leopard Frogs are often associated with wetter environments that are typified by herbaceous plant cover and low canopy (e.g., marshes, swamps, floodplain forests), and have been found in a wide variety of waterbodies (Metts et al. 2001; Lichtenberg et al. 2006; Liner et al. 2008). They are relatively tolerant of deforestation and development, as long as wetlands remain available (Delis et al. 1996; Russell et al. 2002; Dodd 2013). Green Frogs are closely associated with waterbodies and have been found in a wide variety of ephemeral, permanent, lentic, and lotic habitats, around which they maintain small home ranges, primarily leaving the water to forage along the banks and in terrestrial habitats with dense vegetation and abundant leaf litter (Martof 1953; Knutson et al. 1999; Lamoureux et al. 2002). Development (including roads) and agriculture negatively impact Green Frogs (deMaynadier and Hunter 2000; Woodford and Meyer 2003; Gray et al. 2007), but they may be somewhat tolerant of or have the capacity to flee from deforestation and development if high quality habitat is available nearby (Woodford and Meyer 2003; Semlitsch et al. 2008). Wood Frogs, Southern Leopard Frogs, and Green Frogs remain poorly studied in the Piedmont ecoregion of the southeastern USA, a drought-prone region that has been impacted by rapid human population growth, urbanization, exurban development, and other land use changes that degrade, fragment, and destroy aquatic and terrestrial environments (Drummond and Loveland 2010; Napton et al. 2010; Terando et al. 2014). We used radio-telemetry to elucidate the movements and habitat use of these three species in a forest with diverse aquatic resources in the southern Piedmont ecoregion to identify required habitats and movement corridors.

Materials and Methods

Study area.—The study area consisted of two forested landscapes within the Piedmont ecoregion of northwestern South Carolina, USA (Fig. 1A, B). Northwestern South Carolina is centrally located within the Atlanta, Georgia to Charlotte, North Carolina transportation corridor, an area experiencing an especially rapid rate of land use change (Napton et al. 2010; Campbell, C.E., J. Allen, and K.S. Lu. 2008. Modeling growth and predicting future developed land in the Upstate of South Carolina. Proceedings of the 2008 South Carolina Water Resources Conference, Charleston, South Carolina, USA. Available from http://tigerprints.clemson.edu/cgi/viewcontent.cgi?article=1038&context=scwrc [Accessed 29 October 2016]). In this context, there is an urgent need for ecological studies that identify critical habitats, movement corridors, and functional conservation units for maintaining amphibian diversity. The first study landscape contained a first order stream, two ephemeral wetlands with differing degrees of geographic isolation, a formerly ephemeral wetland that became permanent and connected surficially with the stream due to beaver damming activity, and a cypress swamp with surficial hydrological connections with the stream and lake (Fig. 1C). The second study landscape contained a second order stream, an ephemeral floodplain wetland, and a marsh with surficial hydrological connections with a lake (Fig. 1D).

Field methods.—We installed drift fence/pitfall trap arrays following the protocols described by Corn (1994) and Dodd and Scott (1994) in the two study landscapes to capture anurans. We checked the arrays daily for captured animals. We also opportunistically captured anurans found within the study landscapes. Upon capture, we recorded the date, time, weather conditions, capture location and method, species, and sex for each individual. We weighed each individual to the nearest 0.1 g using an Ohaus pocket scale (± 0.1 g; Ohaus Corporation, Pine Brook, New Jersey, USA).

We radio-tagged 15 Wood Frogs, 11 Southern Leopard Frogs, and six Green Frogs with a BD-2 or PD-2 transmitter (Holohil Systems Ltd., Carp, Ontario, Canada) attached by a custom-fitted belt made of Stretch Magic Bead Cord (Pepperell Braiding Company, Pepperell, Massachussetts, USA; detailed method described in Groff et al. 2015). Total mass of the transmitter and belt was ≤ 9.3% of body mass (mean = 5.8 ± [SD] 1.5%), which is < 10% recommended by Richards et al. (1994). We released radio-tagged

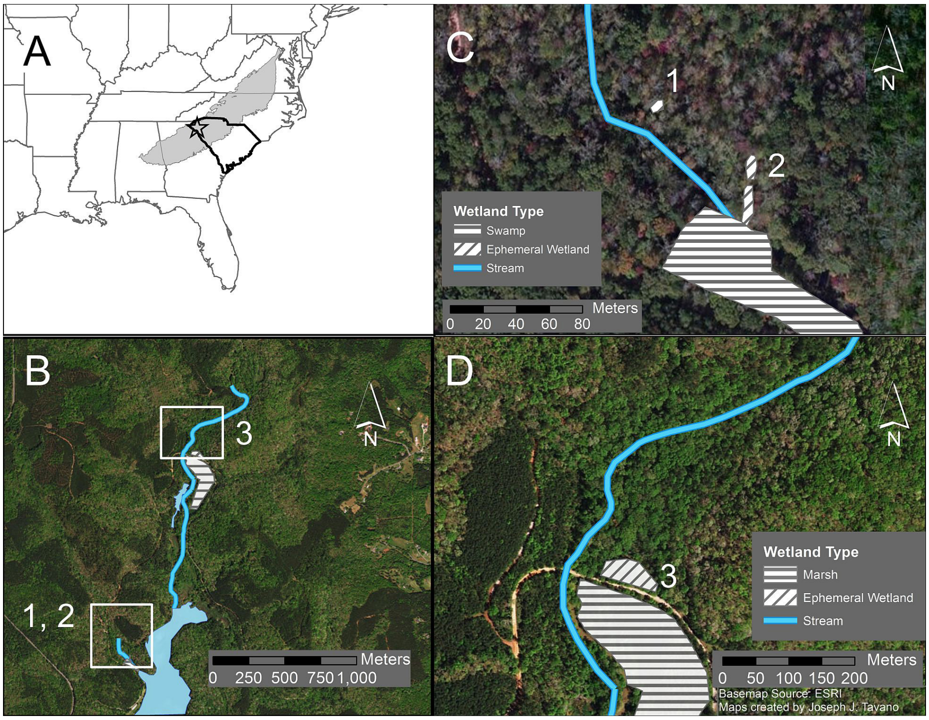

Figure 1. Location of study landscapes within the Piedmont ecoregion of South Carolina, USA. A) Location of the study landscapes (star) within the Piedmont ecoregion (gray shading) of South Carolina (bold outline). B) Location of the two study landscapes (boxes) relative to each other, and stream and lake (blue). C) Close-up view of the first study landscape, showing small isolated ephemeral wetlands (1) and (2), swamp, and stream. D) Close-up view of the second study landscape, showing an ephemeral floodplain wetland (3), marsh, and stream. Basemap source: ESRI, Redlands, California, USA

individuals near their capture site along their movement trajectory, ensuring that individuals would not be immediately recaptured in the pitfall traps. We used a R-1000 receiver (Communications Specialists, Orange, California, USA) and RA-23K VHF rubber ducky "H" type antenna (Telonics, Inc., Mesa, Arizona, USA) to track individuals. We typically located individuals one to two times per week between 0800–1900 with visual confirmation or local triangulation ≤ 1 m of the individual. At each location event, we recorded geographic coordinates using a global positioning system unit, and the date, time, and weather conditions. For locations ≤ 20 m of the previous location, we measured the bearing using a Silva model 515 Ranger compass (Johnson Outdoors Inc., Racine, Wisconsin, USA) and distance from the prior location in centimeters using a measuring tape. For distances > 20 m, we calculated distance using the movement.pathmetrics command in Geospatial Modeling Environment (GME) Version 0.7.7.0 (Available from http://www.spatialecology.com/gme [Accessed 15 October 2016]).

To assess habitat selection, we estimated a suite of biologically relevant habitat variables in a 1-m^2 plot centered on each individual (location plots) and at two plots located 2 m and 20 m from the location plot in a random direction (random plots) each time we located an individual. We selected the distances of random plots to represent available habitat at microhabitat and macrohabitat spatial scales relevant to the daily movement pattern of an anuran (Baldwin et al. 2006). We estimated percentage cover (1–5, 6–25, 26–50, 51–75, > 75%) within each plot of tree trunk/root bole, shrubs, standing water, deciduous leaf litter, bryophyte, herbaceous growth, soil, gravel, rock, trail/forest road, fine and coarse woody debris, and other. For each location and random plot, we used a Field Scout TDR 100 with 12 cm probes (Spectrum Technologies, East Plainfield, Illinois, USA) to measure soil moisture within 10 cm of the location of an individual and in the center of the random plots. We used an Extech Precision Psychrometer (Extech Instruments, Waltham, Massachusetts, USA) to measure microhabitat relative humidity and temperature < 3 cm from each individual and macrohabitat relative humidity and temperature while standing at the center of each plot. We used a 10 BAF cruising prism (GHC Specialty Brands, LLC, Janesville, Wisconsin, USA) to measure the relative abundance of tree species while standing at the center of each plot. We used an Extech Foot Candle/Lux Light Meter (Extech Instruments, Waltham, Massachusetts, USA) to measure forest floor light levels 3 cm immediately above each frog. We measured canopy openness with a Model-A Spherical Densiometer (Forest Densiometers, Bartlesville, Oklahoma, USA).

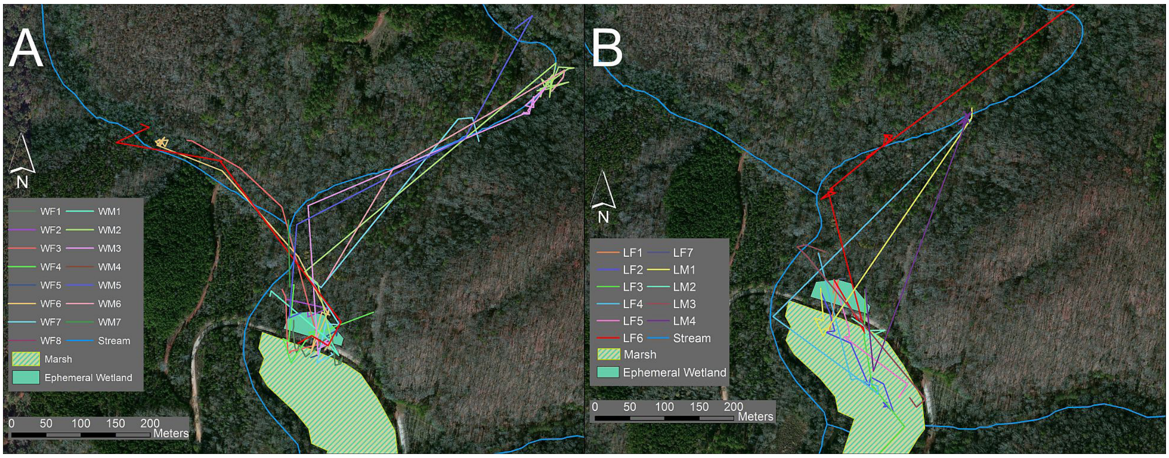

Figure 2. A) Wood Frog (*Lithobates sylvaticus*) and B) Southern Leopard Frog (*Lithobates sphenocephalus*) movement in a study landscape in the Piedmont ecoregion of South Carolina, USA depicted by colored lines connecting observation points. Codes (e.g., WF1) refer to individual frogs. The first letter of the code (i.e., W, L) refers to the species (Wood Frog, Southern Leopard Frog) and the second letter (i.e., F, M) refers to the sex (female, male). Basemap source: ESRI, Redlands, California, USA.

Spatial and statistical analysis.—We mapped all locations in ArcMap 10.2.2 (Esri, Redlands, California, USA). We used GME to calculate straight-line distance traveled between location events and summed straight-line distance traveled for each individual to estimate total path distance traveled. We estimated use of space for each species by both the minimum convex polygon (MCP) method and utilization distribution (UD) via the k-local convex hull (k-LoCoH) method (Getz and Wilmers 2004; Getz et al. 2007). Home range estimation using MCP is the oldest and most widely used method, but because it is simply a boundary around all or some subset of the points in a dataset such that no interior angle is >180°, it tends to overestimate the area used (Getz and Wilmers 2004). However, MCP values are useful for comparison with previous studies. Utilization distribution using LoCoH is created by aggregating convex hulls around each point into isopleths (Getz and Wilmers 2004). The LoCoH method of home range estimation has been shown to be relatively successful at capturing the actual use of space, and has been widely used (Getz et al. 2007). We created 95% MCPs using GME and 95% UDs using the adehabitat package (Calenge 2006) with LoCoH script in R (R Development Core Team 2014). We calculated area of MCPs and UD isopleths in ArcMap 10.2.2. We pooled data by species in the spatial analyses owing to a low number of observations per individual. Thus, values should not be interpreted as individual home range sizes, but rather a proxy for the identification of habitats where activities were concentrated (e.g., critical habitats, migration corridors) for all tracked individuals of each species. However, we also calculated individual MCP home ranges for individuals with > 10 locations.

We evaluated habitat selection for each species using conditional logistic regression for matched-pairs data (paired logistic regression) and *a priori* model selection using Akaike's Information Criterion corrected for small sample size (AICc; Compton et al. 2002). We pooled data by species owing to a low number of observations per individual. We calculated Spearman's rank correlation coefficients to identify highly correlated ($\rho \geq 0.6$) variables. We removed highly correlated variables and variables with limited representation in the data set. From the remaining suite of variables, we developed biologically meaningful *a priori* models for habitat selection for each species based on the natural history of the species and published literature. We standardized all variables to have a mean of zero and a standard deviation of one.

Results

Movement.—We tracked 15 Wood Frogs ($n_{males} = 7$, $n_{females} = 8$), 11 Southern Leopard Frogs ($n_{males} = 4$, $n_{females} = 7$), and six Green Frogs ($n_{males} = 3$, $n_{females} = 3$) between 27 January and 30 June 2012. We captured only Green Frogs (n = 2) at the first study landscape and all three species at the second study landscape. We tracked individual Wood Frogs (n = 15) for a mean of 44 ± (SE) 7.5 d (range, 4–95 d) and a mean total path distance traveled of 421.2 ± 77.9 m (range, 32.0–1048.2 m). We tracked Southern Leopard Frogs (n = 11) for a mean of 52 ± 9.0 d (range, 1–108 d) and a mean total path distance traveled of 391.7 ± 88.2 m (range, 9.9–907.8 m). We tracked Green Frogs (n = 6) for a mean of 51 ± 10.2 d (range, 11–84 d) and a mean total path distance traveled of 213.1 ± 53.1 m (range, 43.5–393.9 m).

Wood Frogs moved primarily among three distinct types of aquatic habitats: ephemeral wetland, marsh, and stream (Fig. 2A). We observed tagged Wood Frogs congregating, calling, and/or breeding in the ephemeral wetland and in shallow water within the edge of the marsh. Wood Frog egg masses were also abundant in

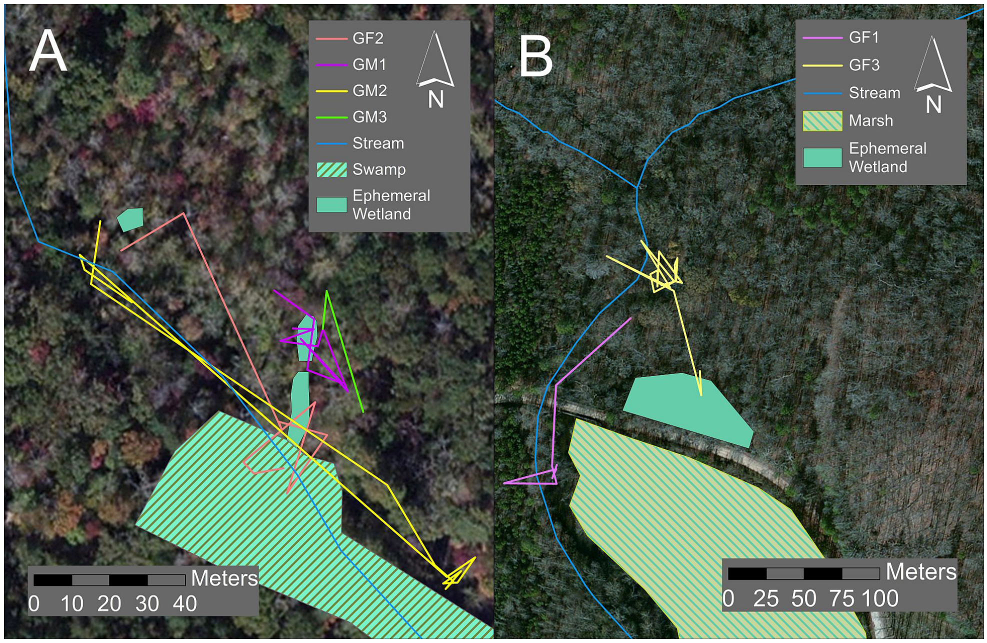

Figure 3. Green Frog (*Lithobates clamitans*) movement in two study landscapes in the Piedmont ecoregion of South Carolina, USA. A) Study landscape 1 contains a stream, ephemeral wetlands, and swamp with surficial hydrological connections to a lake. B) Study landscape 2 contains an ephemeral wetland, stream, and marsh. Symbology and background image source as in Fig. 2.

these areas. Wood Frogs that successfully migrated from their observed breeding habitat (ephemeral wetland, marsh edge) to their summer habitat (tunnels in stream bank) traveled a mean total path distance of 623.2 ± 67.8 m (range, 320.9–1,048.2 m, n = 9). Tunnels were holes apparently created when tree roots had rotted or fallen out, where soil had pulled away from roots creating a gap, or where the stream had undercut the bank. Southern Leopard Frogs also moved primarily among three distinct types of aquatic habitats: ephemeral wetland, marsh, and stream (Fig. 2B). We observed tagged Southern Leopard Frogs congregating, calling, and/or breeding in the ephemeral wetland and marsh. Southern Leopard Frog egg masses were also abundant in these areas. Southern Leopard Frogs that successfully migrated from their observed breeding habitat (ephemeral wetland, marsh) to their summer habitat (tunnels in stream bank) traveled a mean total path distance of 464.0 ± 90.6 m (range, 125.2–907.8 m, n = 9). Green Frogs moved primarily among three distinct types of aquatic habitats: ephemeral wetland, stream, and swamp (Fig. 3). Due to the timing of the tracking period cessation and the Green Frog active season, we were unable to fully evaluate the movements of the Green Frogs between their breeding and summer habitats.

Table 1. Spatial use estimates for Wood Frogs (*Lithobates sylvaticus*), Southern Leopard Frogs (*Lithobates sphenocephalus*), and Green Frogs (*Lithobates clamitans*) at two study landscapes (1 and 2) in the Piedmont ecoregion of South Carolina, USA. Abbreviations are n = number of individuals for which data were pooled to calculate spatial use estimates for each species, k = number of nearest neighbors used in calculation of utilization distribution, 95% UD = 95% utilization distribution area in m^2 using the LoCoH method, and 95% MCP = 95% minimum convex polygon area in m^2.

Species	n	k	95% UD (m^2)	95% MCP (m^2)
Wood Frog	15	15	21,366.1	137,977.2
S. Leopard Frog	11	14	19,794.3	81,130.5
Green Frog 1	2	4	455.2	4,150.9
Green Frog 2	4	6	2,193.5	9,605.0

Spatial use and home range.—Total polygonal area estimates were greatest for Wood Frogs (Fig. 4, Table 1; see Appendix 1 for MCP home ranges for individuals with > 10 locations). Green Frogs had the smallest area estimates, but calculated values are likely underestimates due to the timing of the tracking period relative to the active season of the species (Fig. 4, Table 1; Appendix 1). Utilization distribution polygons revealed concentrated use of ephemeral wetland, stream, and swamp habitats by Green Frogs in study landscape 1 and ephemeral wetland, marsh, and stream habitats by all three species in study landscape 2 (Fig. 4).

Habitat selection.—The model that best described Wood Frog habitat selection at the 2-m scale was the forest with deciduous leaf ground cover model (Table 2). The most important variable in the model was deciduous leaf ground cover, and the odds ratio (OR = 3.04; Table 3) suggests a one categorical unit increase in leaf litter increases the odds of habitat selection by

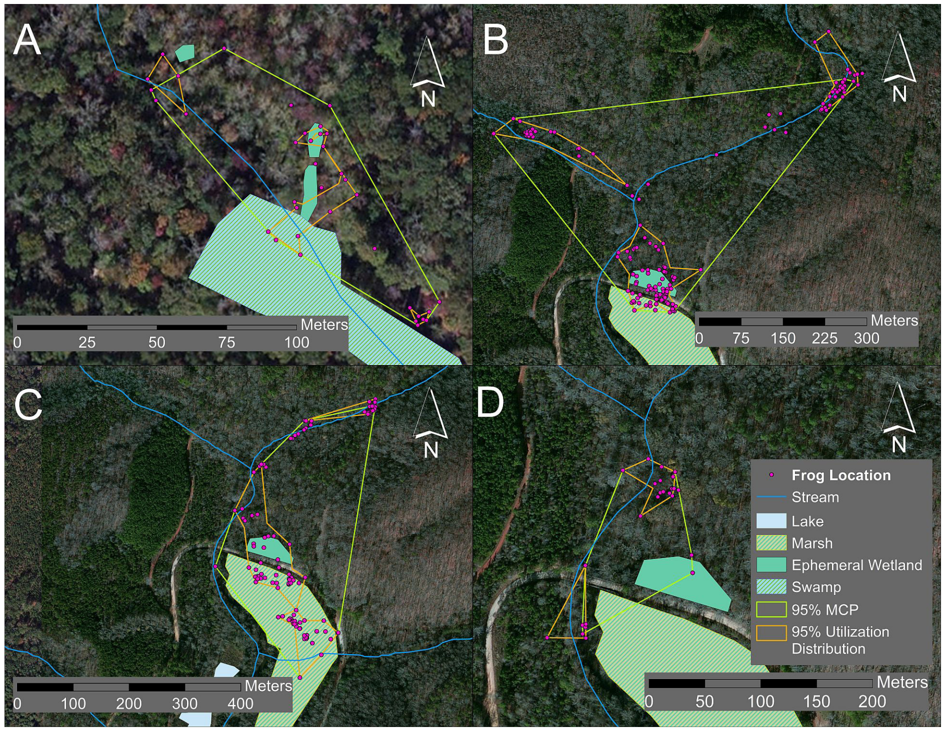

Figure 4. Spatial use estimates for A) two Green Frogs in the first study landscape, and B) 15 Wood Frogs, C) 11 Southern Leopard Frogs, and D) four Green Frogs in the second study landscape. Yellow polygons represent 95% minimum convex polygons (MCP). Orange polygons represent 95% utilization distributions. Background image source as in Fig. 1.

204%. Wood Frogs selected for cooler temperatures, increased canopy openness, deciduous leaf litter, and relative humidity, and slightly less soil moisture (Table 3). The best model for Southern Leopard Frogs at the 2-m scale was the wet meadow 1 model (Table 2). The most important variable in the model was fern cover, and the odds ratio (OR = 1.7; Table 3) suggests a one categorical unit increase in fern cover increases the odds of selection by 70%. Southern Leopard Frogs also selected for increased grass and herbaceous cover, increased relative humidity, and slightly denser understory (Table 3). The model that best described Green Frog habitat selection at the 2-m scale was also the forest with deciduous leaf ground cover model (Table 2). The most important variable in the model was deciduous leaf ground cover, and the odds ratio (OR = 10.08; Table 3) suggests a one categorical unit increase in leaf litter increases the odds of selection by 908%. Additionally, Green Frogs selected for increased soil moisture and fine woody debris, and fewer trees (Table 3).

At the 20-m scale, the best supported model for Wood Frogs was the forest with fine woody debris ground cover (Table 4). The most important variable in the model was relative humidity, and the odds ratio (OR = 1.90; Table 5) suggests a unit increase in relative humidity increases the odds of selection by 90%. Other variables selected for were increased fine woody debris, a slight increase in canopy openness, and lower temperature and soil moisture (Table 5). At the 20-m scale for Southern Leopard Frogs, the best supported model was the forest wetland model (Table 4). The most important variable in the model was water cover, and the odds ratio (OR = 2.25; Table 5) suggests a one categorical unit increase in water cover increases the odds of selection by 125%. Also selected for were increased shrub cover, slight presence of bare soil, and lower light levels (Table 5). For Green Frogs, the best supported model at the 20-m scale was the swamp model (Table 4). The most important variable in the model was water cover, and the odds ratio (OR = 1.68; Table 5) suggests a one categorical unit increase in water cover increases the odds of selection by 68%.

Discussion

Anurans moved among ephemeral wetlands, permanent wetlands (marsh, swamp), and permanent streams. They used different aquatic features at different times and, as much as we could observe, for different purposes. For example, we found tagged Wood Frogs and Southern Leopard Frogs engaged in breeding activities in an ephemeral wetland and marsh, but those that successfully migrated to their summer habitat occupied tunnels created by tree roots in the stream bank post-breeding. Utilization distributions illustrate

Table 2. Paired logistic regression models of habitat selection by Wood Frogs (*Lithobates sylvaticus*), Southern Leopard Frogs (*Lithobates sphenocephalus*), and Green Frogs (*Lithobates clamitans*) at the 2-m scale in two study landscapes within the Piedmont ecoregion of South Carolina, USA.

Species	Model	Variables	AICc value	Rank	Model weight
Wood Frog	Forest with deciduous leaf ground cover	temperature + canopy openness + relative humidity + soil moisture + deciduous leaf litter	157.57	1	0.84
	Global model	all variables	161.01	2	0.15
	Forest with fine woody debris ground cover	temperature + canopy openness + relative humidity + soil moisture + fine woody debris	168.06	3	< 0.01
	Forest with herbaceous ground cover	temperature + canopy openness + relative humidity + soil moisture + herbaceous cover + grass	172.64	4	< 0.01
Southern Leopard Frog	Wet meadow 1	herbaceous cover + grass + fern + understory openness + relative humidity	116.95	1	0.75
	Wet meadow 2	herbaceous cover + grass + reeds	121.16	2	0.09
	Floodplain forest	light + grass + shrub + herbaceous cover	122.64	3	0.04
	Global model	all variables	122.91	4	0.04
	Marsh	water + reeds + relative humidity	123.05	5	0.04
	Forest with deciduous leaf ground cover	light + deciduous leaf litter	124.39	6	0.02
	Forest wetland	light + water + shrub + soil	124.45	7	0.02
Green Frog	Forest with deciduous leaf ground cover	soil moisture + trees + fine woody debris + deciduous leaf litter	64.35	1	0.94
	Marsh grass	water + grass	71.94	2	0.02
	Global model	all variables	72.03	3	0.02
	Swamp	water + tree	72.98	4	0.01
	Forest with herbaceous ground cover	soil moisture + trees + herbaceous cover + shrub	74.61	5	< 0.01
	Shrubby shoreline	water + shrub	77.46	6	< 0.01

the concentrated use of ephemeral wetland, stream, and swamp habitats by Green Frogs in study landscape 1 and ephemeral wetland, marsh, and stream habitats by all three species in study landscape 2. These results corroborate a growing body of evidence that anurans are reliant on and readily use a variety of lotic, lentic, permanent, and temporary aquatic features within the larger landscape, and that habitat connectivity among them is required (Pillsbury and Miller 2008; Richardson 2012). The use of stream systems post-breeding by both Wood Frogs and Southern Leopard Frogs has been observed in other portions of their ranges. For example, Rittenhouse and Semlitsch (2007) observed that Wood Frogs in Missouri moved to stream drainages with abundant leaf litter for their spring and summer habitat after leaving breeding ponds. Similarly, Rudolph and Dickson (1990) found that Southern Leopard Frogs used closed canopy stream riparian zones with abundant leaf litter in eastern Texas. Roloff et al. (2011) suggested that probability of Wood Frog occupancy in sites in southern Michigan may be inversely related to distance from wetland. Having a variety of aquatic features within a landscape could be particularly important for species where periodic drought is common (e.g., southeastern U.S.), especially as climate change is predicted to alter hydroperiods (Wuebbles et al. 2014).

Habitat selection analysis revealed that Wood Frogs were the most terrestrial species, selecting areas with ample deciduous leaf ground cover at the 2-m scale and terrestrial areas with high relative humidity at the 20-m scale. Southern Leopard Frogs selected areas with ample fern ground cover at the 2-m scale, and aquatic areas at the 20-m scale. Green Frogs selected habitats with ample deciduous leaf ground cover at the 2-m scale, but preferred aquatic environments at the 20-m scale. These results are consistent with previously published data that indicate Wood Frogs are highly associated with deciduous leaf litter and other moist habitats (e.g.,

Table 3. Conditional maximum likelihood coefficients and odds ratios (OR) for best fit models for Wood Frogs (*Lithobates sylvaticus*), Southern Leopard Frogs (*Lithobates sphenocephalus*), and Green Frogs (*Lithobates clamitans*) at the 2-m scale in two study landscapes within the Piedmont ecoregion of South Carolina, USA.

Species	Model	Variable	Coefficient	OR
Wood Frog	Forest with deciduous leaf ground cover	Temperature	-0.4018	0.669
		Canopy openness	0.3212	1.379
		Relative humidity	0.4958	1.642
		Soil moisture	-0.1756	0.839
		Deciduous leaf	1.1121	3.041
Southern Leopard Frog	Wet meadow 1	Herb	0.2955	1.344
		Grass	0.0380	1.039
		Fern	0.5305	1.700
		Understory openness	-0.4232	0.655
		Relative humidity	0.2019	1.224
Green Frog	Forest with deciduous leaf ground cover	Soil moisture	0.5199	1.682
		Fine woody debris	0.5330	1.704
		Tree	-0.7971	0.451
		Deciduous leaf	2.3111	10.09

Table 4. Paired logistic regression models of habitat selection by Wood Frogs (*Lithobates sylvaticus*), Southern Leopard Frogs (*Lithobates sphenocephalus*), and Green Frogs (*Lithobates clamitans*) at the 20-m scale in two study landscapes within the Piedmont ecoregion of South Carolina, USA.

Species	Model	Variables	AICc value	Model weight	Rank
Wood Frog	Forest with fine woody debris ground cover	temperature + canopy openness + relative humidity + soil moisture + fine woody debris	139.771	1	0.58
	Forest with deciduous leaf ground cover	temperature + canopy openness + relative humidity + soil moisture + deciduous leaf litter	141.103	2	0.30
	Global model	all variables	143.288	3	0.10
	Forest with herbaceous ground cover	temperature + canopy openness + relative humidity + soil moisture + herbaceous cover + grass	146.261	4	0.02
Southern Leopard Frog	Forest wetland	light + water + shrub + soil	109.53	1	0.63
	Wet meadow 1	herbaceous cover + grass + fern + understory openness + relative humidity	110.88	2	0.32
	Global model	all variables	114.92	3	0.04
	Marsh	water + reeds + relative humidity	118.31	4	< 0.01
	Forest with deciduous leaf ground cover	light + deciduous leaf litter	121.8	5	< 0.01
	Floodplain forest	light + grass + shrub + herbaceous cover	123.44	6	< 0.01
	Wet meadow 2	herbaceous cover + grass + reeds	126.78	7	< 0.01
Green Frog	Swamp	water + tree	66.905	1	0.45
	Marsh grass	water + grass	68.348	2	0.22
	Forest with herbaceous ground cover	soil moisture + trees + herbaceous cover + shrub	68.872	3	0.17
	Shrubby shoreline	water + shrub	69.987	4	0.09
	Forest with deciduous leaf ground cover	soil moisture + trees + fine woody debris + deciduous leaf litter	70.826	5	0.06
	Global model	all variables	74.968	6	< 0.01

Table 5. Conditional maximum likelihood coefficients and odds ratios (OR) for best fit models for Wood Frogs (*Lithobates sylvaticus*), Southern Leopard Frogs (*Lithobates sphenocephalus*), and Green Frogs (*Lithobates clamitans*) at the 20-m scale in two study landscapes within the Piedmont ecoregion of South Carolina, USA.

Species	Model	Variable	Coefficient	OR
Wood Frog	Forest with fine woody debris	Temperature	-0.3267	0.721
		Canopy openness	0.3088	1.362
		Relative humidity	0.6404	1.897
		Soil moisture	-0.8026	0.448
		Fine woody debris	0.5362	1.71
Southern Leopard Frog	Forest wetland	Light	-0.1257	0.882
		Water	0.8096	2.247
		Shrub	0.6521	1.92
		Soil ground cover	0.0389	1.04
Green Frog	Swamp	Water	0.5163	1.676
		Trees	-0.505	0.604

sphagnum) during the non-breeding season (Prather and Briggler 2001; Regosin et al. 2003; Baldwin et al. 2006; Rittenhouse and Semlitsch 2007). While Green Frogs are more commonly associated with aquatic habitats, Southern Leopard Frogs are often found in upland and bottomland habitats with sufficient humidity, but become less active and seek more permanent bodies of water during times of drought (Wygoda 1984; Dodd 2013). The southern Piedmont ecoregion experienced drought during the study period, and this may have been reflected in the observed habitat use of tracked anurans. In terrestrial environments, all species were associated with habitat features that provide cover and maintain high relative humidity (e.g., deciduous leaf and herbaceous ground cover). Anurans, like all amphibians, are susceptible to desiccation, and forest ground cover offers refugia with higher relative humidity levels, thus reducing the potential for desiccation (Seebacher and Alford 2002; Rittenhouse et al. 2008; Dodd 2013).

The results support those of a large number of studies suggesting that intact forested landscapes with a variety of ephemeral and permanent aquatic features are necessary for anuran population persistence (Cushman 2006). The availability and distribution of diverse aquatic features may be particularly important for amphibians in drought-prone regions, especially as climate change progresses (Piha et al. 2007). Large, permanent water bodies are generally offered some level of protection or regulatory oversight through international (e.g., Ramsar Convention) and national policies (e.g., U.S. Clean Water Act, formally known as the Federal Water Pollution Control Act 33 U.S.C. § 1251 et seq. 1972). However, small, ephemeral, and isolated wetlands remain imperiled in part due to their lack of representation in maps and conservation plans, and the generally lacking or ambiguous levels of regulatory protection (Zedler 2003; Pitt et al. 2012; Calhoun et al. 2014). The integrity of the terrestrial habitat surrounding aquatic features must also be maintained for effective biodiversity conservation (Semlitsch 2000; Gibbons 2003). The use of leaf litter for diurnal refugia in terrestrial habitats suggests that forested landscapes with ample ground cover provide important habitats and migratory corridors for anurans moving among seasonal habitats. These results are consistent with previous findings from various regions (Semlitsch et al. 2009; Pitt et al. 2013). Green Frogs, Wood Frogs, and Southern Leopard Frogs are known to use distinct habitats for breeding, foraging, refugia, and overwintering (Dodd 2013). The variation in habitat use by the three anuran species we studied supports the importance of conserving heterogeneous features within a landscape in order to maintain biodiversity. Studies that examine species-specific movement ecology to better identify critical habitats and migratory corridors are key for the development of effective conservation strategies. We encourage such studies be implemented in various regions throughout the geographic distribution of each species to account for regional variation in habitat use and movement ecology. Similarly, we encourage that studies be implemented in multiple years to better elucidate how climatic variation influences habitat use and movement ecology. Species-specific data are generally lacking (Cushman 2006), but technological advances leading to smaller, more affordable transmitters and the recent focus on the importance of movement ecology (e.g., Jeltsch et al. 2013; Driscoll et al. 2014; Barton et al. 2015) may minimize this deficiency.

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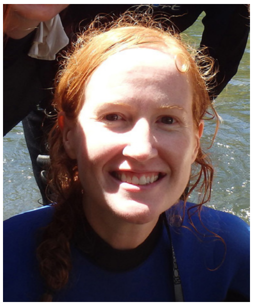
Appendix 1. Spatial use estimates of the 95% minimum convex polygon (MCP) home range for individual Wood Frogs (*Lithobates sylvaticus*), Southern Leopard Frogs (*Lithobates sphenocephalus*), and Green Frogs (*Lithobates clamitans*) with > 10 locations in two study landscapes in the Piedmont ecoregion, South Carolina, USA. Mass is the mass of the individual at time of initial capture.

Frog ID	Species	Sex	Mass (g)	MCP (m^2)
WF1	Wood Frog	Female	18.4	2755.43
WF6	Wood Frog	Female	33.5	19814.38
WM2	Wood Frog	Male	14.5	33845.75
WM3	Wood Frog	Male	18.9	39986.60
LF2	Southern Leopard Frog	Female	47.8	4055.67
LF6	Southern Leopard Frog	Female	37.0	50162.39
LM4	Southern Leopard Frog	Male	26.5	12178.95
GF3	Green Frog	Female	30.1	2440.65
GM2	Green Frog	Male	25.4	1680.33



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