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Author(s): Robert F. Baldwin, Aram J. K. Calhoun, Phillip G. deMaynadier
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Conservation Planning for Amphibian Species with Complex Habitat Requirements: A Case Study Using Movements and Habitat Selection of the Wood Frog *Rana sylvatica*

ROBERT F. BALDWIN,[1,2,3] ARAM J. K. CALHOUN,[1,4] AND PHILLIP G. DEMAYNADIER,[2,5]

[1]*Department of Plant, Soil and Environmental Sciences, University of Maine, Orono, Maine 04469, USA*
[2]*Maine Department of Inland Fisheries and Wildlife, 650 State Street, Bangor, Maine 04401, USA*

ABSTRACT.—**Conservation of fauna breeding in vernal pools is challenging given their complex life histories. Many species, including the widespread North American Wood Frog (*Rana sylvatica*), require both aquatic and terrestrial habitat, yet insufficient information exists about movements between these environments, nor fine-scale selection patterns within them. To inform conservation planning, we conducted a radio-telemetry study of seasonal patterns of Wood Frog movements and habitat selection in southern Maine. Forty-three frogs were tracked an average of 25.6 days each, April to November 2003. In early spring, Wood Frogs generally selected damp leaf litter retreats on the margins of breeding pools. Following breeding, frogs selected forested wetlands (9.3% of the landscape) over forested uplands (90.7% of the landscape) in 75.3% of radio locations ($N = 544$). Postbreeding movements from breeding pools to nearby, closed-canopy, forested wetlands ranged from 102–340 m (median 169m, $N = 8$) and included stopovers in upland forest floors ranging from one to 17 days (median two days, $N = 7$). Summer refugia were characterized by shady, moist (nonaquatic), and sphagnum-dominated microhabitats. In urbanizing areas, we recommend a shift from a core-habitat conservation model to a spatially explicit approach that considers pool-breeding amphibian habitat as a network of migration-connected habitat elements (e.g., breeding pools, upland forest, nearby forested wetlands). In our study, this approach reduced the amount of land potentially requiring protection by $>$ 2/3 from that of core habitat models. With the rapid dissemination of GIS technology, spatially explicit planning for pool-breeding amphibians is increasingly feasible.**

Conserving wide-ranging species that require seasonally distinct and spatially discrete habitats is challenging in human-dominated landscapes. Amphibians that breed in vernal pools have complex life histories requiring access to multiple habitats in both aquatic and terrestrial environments to provide conditions suitable for breeding, foraging, estivating, migrating, and overwintering (Semlitsch, 2000). One of the most widespread pool-breeding species in North America is the Wood Frog (*Rana sylvatica*), with an ecological analogue (*Rana temporaria*) in Europe (Reh and Seitz, 1990). Wood Frogs breed in vernal pools in the early spring and reportedly then migrate to upland forests and neighboring forested wetlands (Heatwole, 1961; Bellis, 1965; Stockwell and Hunter, 1989; Regosin et al., 2003). Two of these key habitat elements—vernal pools and isolated forested wetlands—are among the most threatened of freshwater wetlands globally (Holland et al., 1995; Dahl, 2000; Brinson and Malvarez, 2002; Range, 2003). Similarly, upland forests that buffer and link isolated wetlands used by pool-breeding species are continually degraded and destroyed by human land use (Semlitsch and Bodie, 2003). Wood Frog populations may be adversely affected in landscapes where forest cover has been reduced by 50% or more (Kolozsvary and Swihart, 1999; Homan et al., 2004; Porej et al., 2004) and are reportedly declining in urbanizing areas (Klemens, 1993). Little is known, however, about the seasonal pattern and extent of movements connecting Wood Frog breeding wetlands with postbreeding habitat, or the importance of specific microhabitats therein.

To conserve pool-breeding species dependent upon high-risk habitat elements, conservation planners often seek cost effective strategies that will both ensure population persistence and limit land-use restrictions imposed on property owners. The objective of this paper is to document Wood Frog movements and postbreeding habitat selection as a foundation for developing conservation strategies for wetland fauna with spatially and ecologically complex habitat requirements. We studied movement

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[3] Corresponding Author. Present address: Two Countries, One Forest, c/o Department of Forest Management, 103 South Annex B, University of Maine, Orono, Maine 04469, USA; E-mail: rob_baldwin@umenfa.maine.edu
[4] E-mail: calhoun@maine.edu
[5] E-mail: phillip.demaynadier@maine.gov

patterns and microhabitat selection of Wood Frogs outfitted with radio transmitters. We then used Wood Frog habitat selection patterns to develop an alternative conservation model that focuses on linking locally critical habitat elements. Finally, we compared the economic and ecological efficacy of this spatially explicit approach to a more traditional core habitat approach for pool-breeding amphibians that focuses on conserving land in uniform circular zones around breeding pools.

Materials and Methods

Study Area.—This study took place at four wetland complexes including breeding pools (i.e., vernal pools) and nearby forested wetlands (i.e., wooded swamps) (complexes ≥ 3.7 km apart) in three southern Maine townships. Three complexes occurred in midsuccessional mixed oak and pine forests (red and white oak [*Quercus rubra* and *Quercus alba*], white, red, and pitch pine [*Pinus strobus, Pinus resinosa*, and *Pinus rigida*]). The fourth complex was characterized by mature forest dominated by eastern hemlock (*Tsuga canadensis*), yellow birch (*Betula lutea*), and red oak. Southern Maine is biophysically similar to central and southern New England (Foster, 1992), a region where widespread urbanization is threatening pool-breeding amphibian habitat (Klemens, 1993). Two freshwater wetland types, believed to be important habitat for Wood Frogs, are common throughout the region: vernal pools (defined here as seasonal pools suitable for successful reproduction of animals adapted to temporary waters) and forested wetlands (defined here as wooded swamps that may or may not include depressions that serve as seasonal breeding pools; Golet et al., 1993).

Radiotelemetry.—We tracked 43 Wood Frogs (16 females, 25 males, and two subadults) for varying durations from 16 April through 12 November 2003. Individual frogs were tracked for an average of 25.6 days each (1–83 days). At any one time, 1–12 radios were deployed (Fig. 1F). Wood Frogs were captured for telemetry during visual surveys of breeding pools, neighboring uplands, and forested wetlands at each of the study sites. Searches were conducted during or following rain events when animals were more active and detectable. A light stick was used to tap the substrate while searching to dislodge hidden frogs. Holohil BD-2A transmitters (Carp, Ontario), with expected battery life of 21 days, were externally attached to the waist of subadult and adult frogs using 1-mm Stretch Bead Cord. The transmitter-belt package was ~ 9% of the average frog mass (8.1 ± 3.3 g). Signals were followed with a R-1000 receiver and Yagi 3-element antenna (Communications Specialists, Orange, CA). For each frog, a second channel was programmed to improve discrimination in signal strength at < 1 m (http://www.com-spec.com). We obtained precise visual locations at 87.5% of radio locations; the rest were estimated using local (< 1 m) triangulation.

After 20 days animals still on the air were captured and reoutfitted with new transmitters. When animals were lost to predation, transmitter failure, belt slippage, or unknown causes, we replaced them with animals captured within the same complex of pools and neighboring forested wetlands. Twenty-four tracked frogs were outfitted with transmitters only once, 10 received a second transmitter, five received three transmitters, and four were outfitted four times. Twelve frogs were tracked until they were depredated (by Garter Snakes [*Thamnophis sirtalis*], raptors, or unknown predators), three until they were found dead of unknown causes, 18 until the signal was lost, eight until the belt slipped off, and one until hibernation (Appendix 1). We located animals daily from mid-April to 20 May (leaf out) and subsequently two to three times weekly.

Postbreeding Movements.—We recorded emigration movement distances as a field-measured, straight-line distance from the breeding pool to arrival at the neighboring wetland habitat in which they remained for the summer. Long movements (> 100 m) were measured with hand-held GPS, then plotted and checked for accuracy on scaled maps in a geographic information system. At each sighting, activity state was estimated noting posture as tucked or alert/active (Duellman and Trueb, 1994). We also noted diurnal refugia used by frogs en route to postbreeding habitat. Diurnal refugia were categorized as retreats composed of dry leaf, saturated leaf, or sphagnum moss. To summarize seasonal patterns of movements, we used the total set of 528 radio locations (from 43 frogs) for the study period 16 April to 12 November 2003.

Postreeding Habitat Selection.—To determine the relative use of wetland versus upland, we calculated the total wetland area (all classes; using National Wetland Inventory maps and aerial photography), and the total upland area within a radius from the center of the pool complex to the longest Wood Frog migration observed there. We evaluated the expected versus observed number of locations in wetland and upland habitat relative to available area using a Chi-square test. Macrohabitat use was also summarized graphically across the entire study period in association with data on seasonal climate and activity state (Fig. 1).

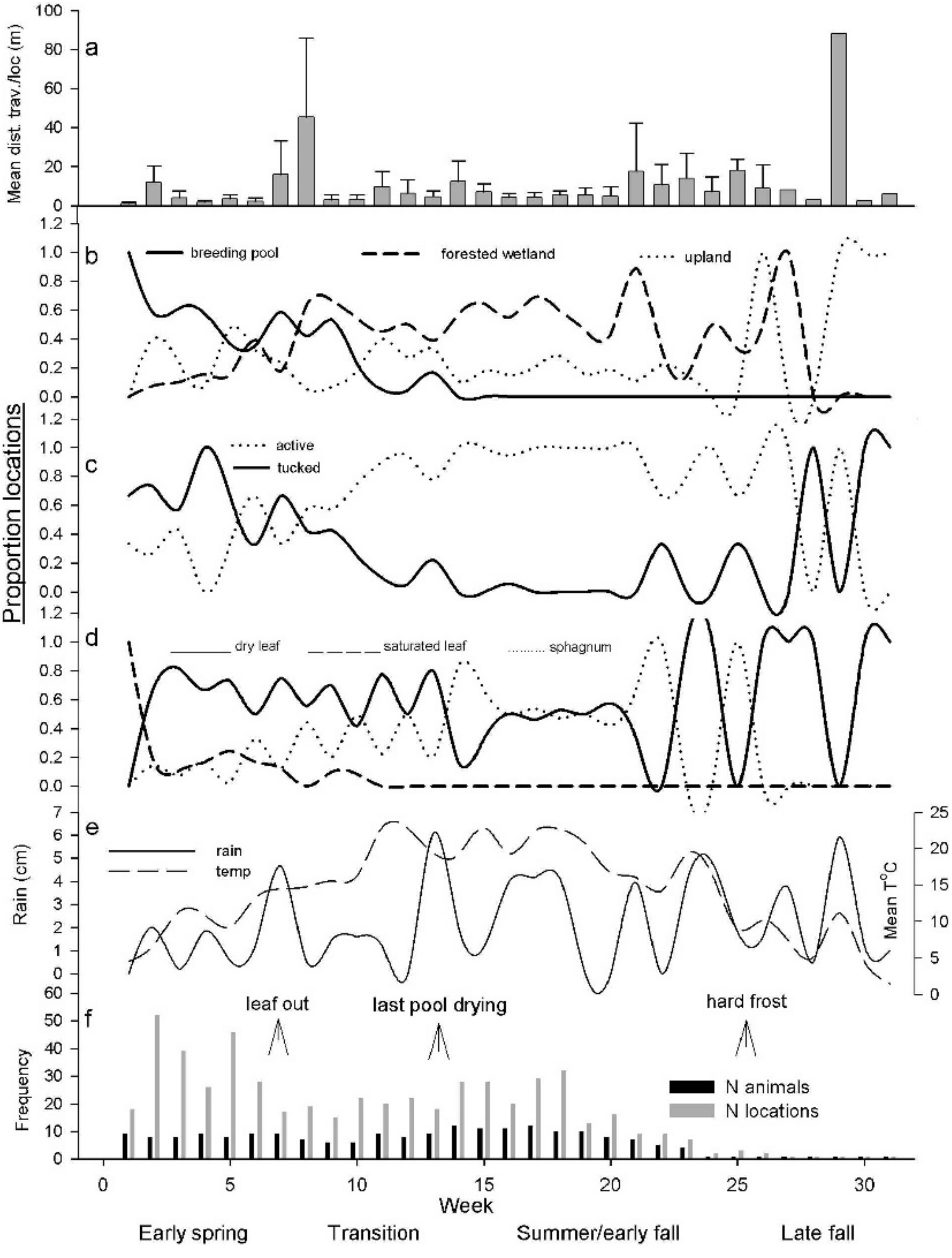

FIG. 1. Seasonality of Wood Frog migration (A), macrohabitat (B), activity state (C), microhabitat (D), local climate (E), and sample size (F), from April to November 2003. Both seasonal periods (''early spring,'' ''transition,'' ''summer/early fall,'' and ''late fall'') and significant phenological events (peak leaf-out, timing of last pool drying, and hard frost) are indicated.

To assess postbreeding microhabitat selection, we collected data from every animal location paired with randomly positioned nonuse locations. Specifically, we sampled 1-m radius habitat plots at the animal location and at four neighboring nonlocation sites 2 m and 20 m from the location site. Nonlocation distances were chosen to represent two potential within-macrohabitat movement scales (Heatwole, 1961; Bellis, 1965), and nonlocation directions were based on the animals' movement trajectory (two plots in direction of last movement and two plots 90° to that trajectory). We recorded location, 2-m and 20-m plot data, during late spring, summer, and fall. For both use and nonuse plots, we collected data on soil moisture, forest structure, and plant species composition. Specifically, we measured soil moisture with a Field Scout TDR 200 with 12-cm probes (Spectrum Technologies, East Plainfield, Il) proximate to the animal's location (within 10 cm) by slowly angling the probes under the resting animal. We recorded relative humidity and air temperature < 3 cm from the animal with an Oakton thermohygrometer 35612 (Vernon Hills, Il) by placing the probe inside the animal's retreat (or nearest estimate if nonvisual location) and in comparable retreat material in nonlocation plots. A 5× prism plot was used to measure relative abundance of tree species at the plot center. We measured forest floor light levels after leaf out with a light meter (Extech Instruments, Waltham, MA) at 3 cm immediately above the frog and percent canopy openness using hemispheric canopy photos from a Nikon Coolpix 885 and fisheye converter. Finally, we estimated percent cover within each plot (1–5, 6–25, 26–50, 51–75, $> 75\%$) of tree/root bole, shrubs (< 30 cm), standing water, saturated leaf litter, bryophyte cover, and graminoids.

We used canonical variates analysis (CVA) to discriminate microhabitat selection patterns by season. To examine habitat use, we constructed four seasonal periods based on phenological events: "early spring" for preleaf out; "transition" for leaf out to the date the last breeding pool dried; "summer/early fall" for pool drying to hard frost; and "late fall" for after hard frost. Although included in graphical analyses of seasonal selection patterns (Fig. 1), "late fall" was omitted from the CVA because of insufficient sample size. To reduce temporal autocorrelation, we only included habitat data from radio locations taken a minimum of two days apart. Individual variables were selected by forward stepwise selection with a Bonferroni-adjusted significance level of 0.0019. Habitat plot groups, defined by the first axis, were compared using a permutation test, and scatter plots (with and without outliers) helped to clarify the discrimination (C. J. F. ter Braak and P. Smilauer, CANOCO Reference Manual and CanoDraw for Windows User's Guide, Microcomputer Power, Ithaca, NY, 2002). Ordination diagnostics were used to define the biological importance of each axis.

To determine whether microhabitat plots differed in light and soil moisture, we conducted univariate analyses of the differences among animal locations, 2-m and 20-m plots. Available light values collected after leaf out, at location ($N = 170$), 2m ($N = 336$), and at 20 m ($N = 339$) plots, were tested using a Kruskal-Wallis one-way ANOVA, followed by Bonferroni-adjusted Mann-Whitney U pairwise comparisons ($\alpha = 0.017$; SYSTAT Software, Inc., Richmond, CA, 2002), and similarly evaluated soil moisture values (location $N = 239$, 2m $N = 233$, 20m $N = 441$). Additionally, we compared percent relative humidity inside and outside upland forms using a paired sample t-test ($N = 83$).

To create a predictive model for percent canopy openness, we used pairs of light and percent canopy openness data available from the subset of the habitat plots for which canopy data were available ($N = 349$). The best-fit equation (SigmaPlot, SPSS Inc., Chicago, 2001) was solved for percent canopy openness at median light values for location, 2-m and 20-m plots. Daily averages for ambient temperature, dewpoint, and total rainfall during the study period were downloaded from the National Oceanic and Atmospheric Administration (NOAA) station at the Sanford, Maine, airport. All statistical analyses were conducted using significance levels of tests set at $\alpha = 0.05$, except when Bonferroni-adjusted as indicated above. Means are given ± 1 SD.

RESULTS

Postbreeding Movements.—Long distance postbreeding emigration movements were recorded for eight adult frogs (median 169 m; Appendix 1). Of the eight observed long-distance movements, all were highly directional toward neighboring moist, forested habitats. Five involved movements to neighboring breeding pools or forested wetlands (median = 120 m) and three involved movements to a sphagnum-bordered forested stream (median = 215 m). Frogs traversed several potential landscape barriers including an esker (long, narrow ridge deposited by glacial meltwater, 10 m high and 35° slope; $N = 1$ frog), silvicultural gaps (30–70 m wide; $N = 3$), a fast, shallow stream (1.5 m wide; $N = 3$), and a slow, deep stream (3 m wide; $N = 1$).

Most emigrations (six of eight) were punctuated by stopovers in which Wood Frogs spent up to 17 nights in a terrestrial retreat before resuming long-distance movement. The longest stopover in a single retreat was for 17 days in a deep leaf litter dam on the slope of an esker, 310 m from its forested wetland destination. Emigration generally occurred in the context of rainfall events (Fig. 1A,E). Emigration movements following rainfall within the previous 24 h were longer (71.2 ± 90.69 m) than movements with no rainfall within the previous 24 h (12.2 ± 14.7 m; $t_{38} = -2.8$, $P = 0.008$). This could only be calculated for the spring period 16 April to 3 June, when daily movement data were available.

Aside from sporadic, rainfall-dependent migration, Wood Frog activity was localized inside forested wetlands during the summer months ($N = 38$ tracked frogs). Summer movements were generally short (median 2.8 m, range 61 m, $N = 217$) but did include some longer, rain-associated movements (maximum 61 m) to nearby wetlands. Long-distance migrations may have resumed in the fall ($N = 2$, 115 m and 50 m), but sample size was too small to conclusively establish a trend.

During the early spring (prior to leaf out), we found Wood Frogs primarily at the margins of potential breeding pools in tucked postures. Weekly average temperature was negatively correlated to the weekly frequency of tucked postures ($r_S = -0.65$, $P < 0.05$, $N = 31$). By the first week of July, activity state shifted from low (tucked postures) at breeding pools in the early spring, to high (active postures) in forested wetlands during the summer (Fig. 1C).

Postbreeding Habitat Selection.—Wood Frogs seemed to prefer forest floor retreats that helped to conserve humidity. During spring, diurnal retreats consisted primarily of leaf litter, their composition reflecting the oak-forest setting of the breeding pools. Prior to adult emigration from breeding pools Wood Frogs typically used saturated leaf retreats where their ventral surfaces were in contact with standing, cold water. Upland diurnal retreats used during travel stopovers consisted of several dry leaves loosely covering the frog. The microclimate inside these upland retreats (74 ± 21.2%) was moister than ambient conditions (63 ± 26.8%; $t_{165.3} = 2.6$, $P < 0.01$). In neighboring forested wetlands, retreats were generally dominated by sphagnum moss (Fig. 1D).

For the 43 tracked Wood Frogs, 75.3% of all postbreeding locations occurred in wetlands, whereas wetlands made up only 9.3% of the landscape ($\chi^2_1 = 2601$, $P < 0.001$). The diversity of wetland types used by Wood Frogs expanded seasonally from breeding pools in the early spring, to other vernal pools, neighboring forested wetlands, and stream edges by late spring and summer (Fig. 1B). The first axis of the canonical variates analysis statistically supports this seasonal shift, constructed using 55.7% of the variance in the plot data and discriminating habitat plot characteristics collected during the early spring when frogs were using vernal pools, from those collected during the late spring and summer when frogs were using sphagnum-rich forested wetlands ($F = 97.6$; $P = 0.005$).

Within the pool and hummock microtopography of our forested wetlands, Wood Frogs tended to occur on sphagnum hummocks and riparian leaf litter margins rather than in open pools. Both location and near-location (2-m) plots tended to be characterized by moist or aquatic conditions compared to far location (20-m) plots. For example, near location (2-m) plots had greater combined values of standing water, saturated leaf litter, and soil moisture, than far location (20-m) plots, and volumetric water content (vwc) was significantly greater at location plots (median = 33%) and 2-m plots (median = 34%) than plots 20m away (median 11% vwc; $H = 197$, $P < 0.0001$).

In addition to moist microhabitats, Wood Frogs were found using more deeply shaded areas. Canopy cover and light level varied among habitat plots (medians: location 1011.5 lux, 2m 1200 lux, 20m 1600 lux; $H = 13.3$, $P = 0.001$) with location plots being significantly more shaded ($U = 34416.5$, $P < 0.0001$) than 20-m plots. Percent canopy openness values for location and nonlocation plots, predicted from light levels by the best fitting curve (modified two-parameter exponent) were 23.9% (location plots), 24.7% (2-m plots), and 26.0% (20-m plots), typical of intact forests of the study area (range 6.8–69%, 24.7 ± 10.3%).

DISCUSSION

Postbreeding Movements and Habitat Selection.—As with other pool-breeding amphibians, Wood Frog movements are seasonal, facilitated by rainfall, and directed to specific, often spatially disjunct habitats (Dodd and Cade, 1998; Madison and Farrand III, 1998; Lamoureux et al., 2002; Faccio, 2003). Specifically, we observed migration movements from spring breeding pools to adjacent upland forest and forested wetlands, in one case as far as 340 m distant. At least seven other anuran species are known to migrate similar or longer distances from their breeding sites (reviewed by Semlitsch and Bodie, 2003). Given the logistical difficulty of documenting rare, long-distance amphibian movement events (Marsh and Trenham, 2001), it is likely that further study will reveal the potential for even greater Wood Frog migration capability. Nonetheless, our Wood Frog movements are the first to be reported using replicated, radio-telemetry observations and contribute to the growing consensus that a landscape approach connecting seasonally discrete habitats is likely warranted for the conservation of many pool-breeding amphibians (Gibbs, 1993; Semlitsch, 2000).

The postbreeding movement and habitat selection patterns observed in this study support the hypothesis that Wood Frogs and potentially other semiterrestrial anurans are dependent on moisture islands in upland landscapes during the driest portion of the year (Thorson, 1955; Bellis, 1962; Prather and Briggler, 2001). We provide information on how a shifting sample of radiotagged Wood Frogs (1–12) from four habitat complexes changed habitat selection patterns seasonally. The pattern that emerges from our four study populations is that Wood Frogs survive dry periods by occupying moisture-retaining forms of forest floor material (mainly deep litter or sphagnum) and by selecting moist macrohabitats (i.e., forested wetlands) in which to spend the summer. Although further study throughout the Wood Frog's geographic range is likely to reveal habitat selection patterns for other moist habitat types (e.g., riparian forests, sinkholes, and caves), we conclude that a habitat mosaic of closed-canopy, moss-dominated forested wetlands connected to seasonal breeding pools by intact, upland forest may be critical for Wood Frogs and potentially other pool-breeding amphibians in northeastern North America. Although we occasionally observed Wood Frogs in silvicultural gaps during migration, and others have reported their movements across large openings such as clearcuts, roads, and fields (Gibbs, 1998; deMaynadier and Hunter, 1998, 2000), most of our postbreeding observations occurred in dark, moist conditions under closed-canopy forests.

Intact riparian forests have long been recognized for their contributions to water quality and aquatic habitat (Gregory et al., 1991). More recently, the value of upland forest has also been recognized as a critical element of the habitat mosaic for pool-breeding amphibians (Semlitsch, 1998, 2000). In our study, intact upland forests surrounding forested wetlands and breeding pools provide migratory stopover habitat, in addition to potential overwintering habitat. To our knowledge, we provide the first quantitative evidence that Wood Frogs spend extended periods in terrestrial, forest floor retreats during postbreeding migrations to disjunct summer habitats. Additionally, although anecdotal evidence exists for Wood Frog hibernation in upland settings (Wright, 1914; Holmes, 1927), Regosin et al. (2003) provided the first systematic observations of Wood Frogs overwintering in upland forest, proximate to their breeding pools (in contrast to other anurans that migrate outside of summer-breeding ranges to hibernate; Lamoureux and Madison, 1999). We hope that further telemetry studies will better define the spatial and microhabitat aspects of overwintering in Wood Frogs. Yet, our results support Regosin et al. (2003) in that we radiotracked an adult female into the late fall period, and she selected a shallow hibernaculum buried beneath leaf litter in the organic horizon of an upland soil type. By hibernating in well-drained upland soils, Wood Frogs and other pool-breeding amphibians (Windmiller, 1996) may avoid becoming covered by thick ice following fall wetland recharge—conditions that could lead to excessive body tissue freezing and delayed arrival at breeding pools.

Conservation Planning.—Wood Frogs, and other aquatic-breeding amphibians, use an interconnected network of wetland and upland habitats to meet their life-history needs (Semlitsch, 2000; Joyal et al., 2001), yet maintaining landscape connectivity is extremely challenging in urbanized portions of human-dominated landscapes (Gibbs, 2000). Landscape-scale linkages have traditionally been considered in relation to large vertebrate conservation (Noss, 1983), but they may be equally important for protecting smaller fauna such as pool-breeding amphibians. The annual round trip migration for a vertebrate is generally estimated as twice the average seasonal migration (Berger, 2004). This equates to an average annual round trip migration of 385m for Wood Frogs in our study. Corrected for body size in grams, this annual movement distance translates to 47 m/g/yr—roughly equal to values reported for barren ground caribou (*Rangifer tarandus*; 41.5 m/g/yr), and 13 times greater than for wildebeest (*Connochaetes taurinus*; 3.7m/g/yr; Eisenberg, 1981). Highly visible land migrations by large animals often garner public attention and support for conservation projects. Recognition of the relatively dramatic migratory patterns of smaller, less visible fauna is similarly critical for their successful conservation.

A dominant paradigm for conservation planning of pool-breeding amphibians creates "core habitats" by centering circular terrestrial habitat zones (based on average migratory distances for groups of species) around breeding pools. For example, recent studies have recommended protection of core areas of specific radial distances for pool-breeding amphibians generally (164 m; Semlitsch, 2002) and for wetland-

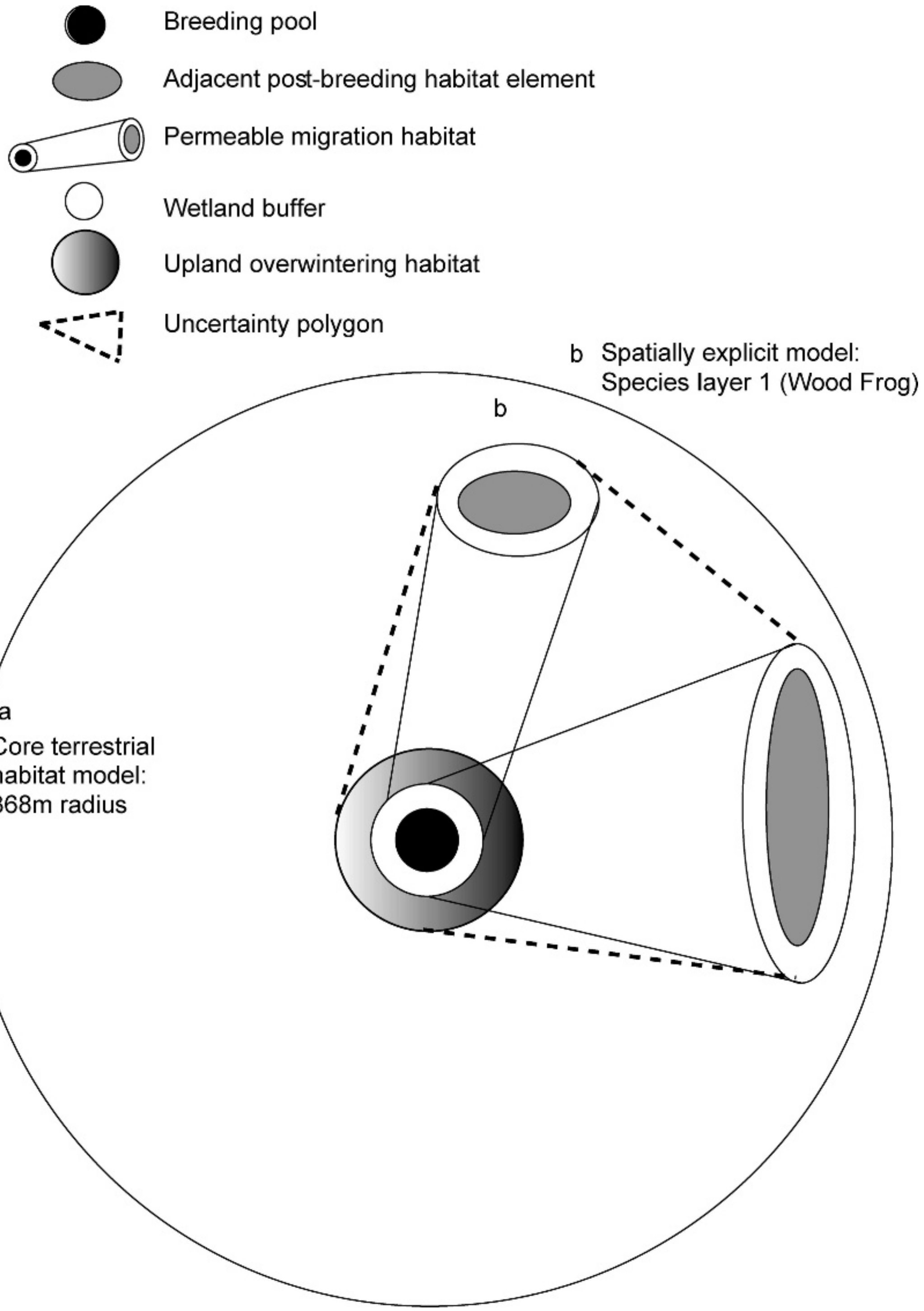

FIG. 2. A spatially explicit model for conserving pool-breeding amphibian habitat where land is prohibitively expensive. A core terrestrial habitat model (a), shown for comparison, includes a breeding pool surrounded by a circular habitat buffer based on average migratory distances for multiple pool-breeding amphibian taxa (Semlitsch, 2002). A habitat connectivity model (b) connects and conserves locally important habitat elements (e.g., vernal pools and forested wetlands) specific to individual taxa (e.g., Wood Frogs; species layer 1), within

TABLE 1. A comparison of land area required for implementing core terrestrial habitat (A) versus spatially explicit (B) approaches to the conservation of habitat for Wood Frogs at three of our study sites. Column (C) represents additional area that should be added to the spatially explicit approach to recognize data limitations and behavioral variability. Areas for (B) and (C) were calculated by applying the general model (Fig. 2) to maps of three of our field study sites (simply connecting outer limits of known neighboring habitats and buffers). Core terrestrial habitats are published models providing a postbreeding habitat buffer zone around breeding pools, at a radius determined by multiple species-specific migratory distances.

Study site	(A) Core area approach (368-m radius)	(B) Spatially explicit approach	(C) Spatially explicit approach plus uncertainty polygon	Relative proportion of land area required for (B)
A	42.5 ha	10.7 ha	24.1 ha	25.20%
B	42.5 ha	14.2 ha	27.5 ha	33.40%
C	42.5 ha	13.4 ha	24.7 ha	31.50%

breeding anurans specifically (368 m; Semlitsch and Bodie, 2003). This approach is readily transferable to policy and is well suited for public lands and large private land holdings where a single fee acquisition or uniform management approach is desirable. However, we suggest that the core habitat approach is potentially limited on private lands in rapidly urbanizing areas by two major constraints: (1) when the core area is too small, critical habitat elements can be omitted (in our study, 50% of postbreeding movements occurred outside of a 164-m radius core area); and (2) when the core area is too large, limited funds are spent conserving nonessential habitat. The incidental conservation of potentially lower value habitat for pool-breeding amphibians is less problematic on larger public conservation lands, but when limited resources are being expended to purchase development rights (or mitigate wetland losses) on private lands, protecting generic core habitat that does not specifically capture important neighboring habitat elements (e.g., forested wetlands) is not efficient. For example, protecting a single core area (368-m radius) in our study area might cost > $1 million (Housing Unit Forecast by Town to 2015, Maine State Planning Office, Augusta, 2003), whereas applying a locally informed habitat element conservation plan (Fig. 2) could reduce the cost by 75–66% (Table 1).

In the context of urbanizing landscapes dominated by private property, we recommend consideration of a spatially explicit habitat connectivity approach in which essential pool-breeding amphibian habitat is viewed as a network of locally specific habitat elements (Fig. 2). Under this approach, conservation planners need to identify, link, buffer, and protect discrete habitat elements (such as isolated breeding pools, upland overwintering forest, and forested wetlands for Wood Frogs) within known *maximum* migratory distances from breeding pools. The use of maximum migration distances recognizes the nature of incomplete sampling inherent to most long distance movement studies (Marsh and Trenham, 2001). Furthermore, because of the inevitable uncertainty and variability associated with the extent and directionality of pool-breeding amphibian migrations, we recommend application of an ''uncertainty buffer'' whose perimeter and area is defined by the location of locally identified important habitat elements and their intervening matrix (Fig 2). With the rapid assimilation of GIS technology by local government and nongovernmental organizations (Theobald et al., 2000), such complex spatial planning for pool-breeding amphibians at a local scale is not out of reach.

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observed maximum migration distances (i.e., 340 m for the Wood Frog). Additional species-specific habitat elements for the Wood Frog include forested wetland buffers to protect (1) breeding and postbreeding wetland moisture conditions within 30–50 m (e.g., Calhoun and deMaynadier, 2004), and (2) adjacent upland overwintering habitat within 50–100 m (Regosin et al., 2003). An ''uncertainty polygon'' serves to connect and buffer all of the locally identified habitat elements. As habitat elements for additional pool-breeding taxa are added (species layers 2, 3, etc.), the habitat connectivity model incorporates more of the surrounding landscape but likely remains skewed in shape and smaller in area than applications of the core terrestrial habitat model.

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APPENDIX 1. Radiotracking data and movement characteristics for 43 Wood Frogs followed April through November 2003. [a]Study sites are Filgate (F), Land Trust (LT), Norris (N), and Worthen (W). [b]Sex = male M, female F, and unknown subadult (U). [c]Seasonal periods are early spring (ES), transition (TR), summer/early fall (SUM/EF) and late fall (LF). [d]Fates of tracked frogs are lost signal (LS), slipped belt (SB), death with no sign of predation (D), predation (PR; raptor-r; snake-s; unknown-u), and transmitter removed at study completion (Rem).

Frog ID	Sex[a]	Site[b]	Dates tracked	Seasonal period (s) tracked within[c]				# locations	# days tracked	Average daily distance (m)	Minimum distance between successive locations (m)	Maximum distance between successive locations (m)	Spring emigration (m)	Fate[d]
				ES	TR	SUM/EF	LF							
1	M	F	4/16–5/6	X				18	21	1.72	0	8		LS
2	M	F	4/16–5/5	X				16	20	1.84	0	15		SB
3	F	LT	4/17–5/9	X				22	23	9.49	0	201	201	SB
4	M	N	4/17–6/19	X				38	56	2.35	0	70	120	PRr
5	M	LT	4/20–5/3	X				10	14	5.89	0	50		PRs
6	M	N	4/18–6/30	X	X			40	70	2.16	0	30		D
7	M	N	4/19–6/18	X	X			34	56	8.07	0	189	320	PRs
8	F	W	4/20–6/23	X	X			38	60	4.41	0	53	105	PRs
9	M	LT	5/8–5/25	X	X			14	18	1.62	0	15		LS
10	F	LT	5/8–5/20	X				12	13	4.30	0	40		SB
11	M	LT	5/8–6/8	X	X			18	30	14.59	0	308	340	SB
12	F	LT	5/19–5/27	X	X			5	9	2.33	0.5	13		PRu
13	M	LT	5/28–7/5		X	X		16	37	4.30	0	68	102	LS
14	M	LT	5/27–6/7		X			4	12	19.25	0	213	215	PRr
15	F	W	6/10–6/26		X			10	17	4.25	0	18		SB
16	F	N	6/19–8/6		X	X		24	50	2.64	0	39		LS
17	U	N	6/24–6/25		X			1	1	1	0	1		D
18	F	W	6/23–9/15		X	X		32	83	3.17	0	113	137	PRu
19	M	W	6/25–7/8		X	X		6	14	1.94	3.2	15		SB
20	U	N	6/30–7/4		X	X		6	5	4.94	1.2	12.5		LS
21	F	N	7/2–7/29			X		13	27	4.19	1.1	29		SB
22	M	N	7/9–8/19			X		15	42	2.86	0.18	61		D
23	F	N	7/9–8/19			X		19	42	0.70	0	5		SB
24	F	W	7/9–7/17			X		6	9	0.87	0	6.5		LS
25	M	W	7/9–7/14			X		3	6	2.5	0	15		PRr
26	M	N	7/15–7-16			X		2	1	10	0	10		PRu
27	M	N	7/17–8/19			X		13	34	1.02	0	8.5		LS
28	M	N	7/17–8/19			X		11	34	0.94	0	9		LS
29	F	N	7/17–7/23			X		3	7	2.07	2.5	12		LS
30	M	N	7/22–8/6			X		7	16	1.51	0.9	8		LS
31	M	N	7/23–8/5			X		6	14	3.63	0	32		PRu
32	M	N	7/29–8/13			X		3	16	0.53	2.5	6		LS
33	F	N	7/30–9/2			X		11	35	0.76	0	6		LS

Appendix 1. Continued.

Frog ID	Sex[a]	Site[b]	Dates tracked	Seasonal period (s) tracked within[c]				# locations	# days tracked	Average daily distance (m)	Minimum distance between successive locations (m)	Maximum distance between successive locations (m)	Spring emigration (m)	Fate[d]
				ES	TR	SUM/EF	LF							
34	F	N	8/5–9/2			X		9	29	1.08	0.02	18.5		LS
35	M	N	8/6–9/15			X		14	41	0.79	0	10		LS
36	M	N	8/12–9/2			X		8	22	7.41	0	115		LS
37	M	N	8/12–8/26			X		7	15	2.36	0	42		LS
38	M	N	8/19–8/26			X		3	8	1.47	3	19		PRu
39	M	N	8/26–9/2			X		3	8	0.56	0	3.25		LS
40	M	W	9/2–9/15			X		4	14	5.5	0	43		LS
41	F	W	9/7–9/11			X		3	5	9	0	33		SB
42	F	N	9/8–9/14			X		3	7	5.07	0	34		PRu
43	F	W	9/16–11/12			X	X	14	58	4.07	0	88		Rem
Mean								12.70	25.6	3.93	0.35	48.49	192.50	
SD								10.48	20.0	3.86	0.85	65.88	94.70	
Median								10	18	2.5	0	19	169	