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Cover Photograph: An adult Wood Frog (*Lithobates sylvaticus*) being radio-tracked through a residential area in Bangor, Maine, USA as part of a habitat selection study. Photo taken by Thomas Hastings.

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Hibernacula Selection by Wood Frogs (*Lithobates sylvaticus*) in a Developing Landscape

Thomas Hastings[1,*], Kristine Hoffmann[1,2], Laura Kleist[2], Aram Calhoun[1], and Malcolm Hunter, Jr.[1]

Abstract: Landscape development alters natural environments and has the potential to extirpate local wildlife populations. This threat can be particularly significant for animals with complex life cycles with strong ties to both aquatic and terrestrial habitats, such as pool-breeding amphibians. Data on how landscape development is affecting hibernal habitat characteristics of pool-breeding amphibians that overwinter terrestrially is sparse. We radio-tracked eight Wood Frogs to their hibernacula and established random locations within the forest and residential area. At each location we measured weekly snow depths and monitored the microclimate using thermochrons. None of the frogs spent the winter within the residential yards. Five of the seven frogs that hibernated in the dry edge of the forest between lawns and the forested wetland were observed in the spring; one escaped, and one died in its hibernaculum. The eighth frog hibernated within the forested wetland and did not survive the winter. The soil temperatures at hibernacula were significantly warmer than those at random points in the residential area and forest. This suggests the frogs were selecting to spend the winter in the less variable and warmer forest hibernacula than in and around lawns. Snow depth was generally greater at random forest and neighborhood locations than at hibernacula and was less variable at hibernacula than at random neighborhood locations in March when soil temperatures were lowest. Therefore, snow cover alone may not be sufficient to insulate hibernacula conditions. We suggest that developers and urban planners can help conserve Wood Frogs by leaving some upland forest and summer refugia habitats (e.g., forested wetlands or other moist refugia) connected and intact, in addition to not disturbing the breeding vernal pool.

Introduction

Land cover change is one of the greatest ongoing threats to natural environments and biodiversity (Seto et al. 2011). According to the National Land Cover Database, between 2001 and 2016, developed land cover in the United States expanded by 7.2% and continues to increase (Homer et al. 2020). Furthermore, models predict that under intermediate levels of economic and population growth, global urban land cover is expected to triple by 2030 over the 2001 baseline (Seto et al. 2011). Such developed land varies in impervious surface coverage and ranges from highly developed urban centers to single family properties within forested landscapes (Homer et al. 2020). Residential development must be considered when studying land cover change. In the United States, residential development has expanded at rates faster than population growth since the 1940s (Mockrin et al. 2013). Furthermore, residential development along the edge of natural environments and undisturbed vegetation can have negative ecological impacts on fragmented forest patches (e.g., increased wind and air temperature and decreased humidity) at various spatial scales (Magnago et al. 2015, Radeloff et al. 2005). In 2000, nearly 10% of total land area in the United States was residential area bordering undeveloped land and vegetation (Radeloff et al. 2005).

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Regardless of development intensity, land cover change contributes to habitat loss and altered microhabitat conditions (Carlson and Arthur 2000, Nowak and Greenfield 2018, Seto et al. 2011). More specifically, landscape development that decreases vegetation cover and increases impervious surface cover has the potential to decrease evapotranspiration and surface moisture availability and increase surface runoff, surface temperatures and air temperatures (Arthur-Hartranft et al. 2003, Carlson and Arthur 2000, Chapman et al. 2017, Ziter et al. 2019). Natural landscapes surrounding the altered environments are also impacted through processes such as invasive species introductions and altered environmental conditions (e.g., increased light exposure) (Bar-Massada et al. 2014, Carlson and Arthur 2000). Furthermore, the overall detrimental effects on native species from residential housing may be greater for low density development than for high density development if low density developments are spread across a commensurately larger area for the same number of housing units (Mockrin et al. 2013, Radeloff et al. 2005).

Developing landscapes could be particularly impactful for animals that require different habitat types to meet breeding, foraging, and overwintering requirements. For example, many pond breeding amphibians, such as our study species *Lithobates sylvaticus* LeConte 1825 (Wood Frog), have a complex life cycle consisting of an aquatic larval stage and a terrestrial juvenile and adult stage. Pond breeding amphibians benefit not only from different habitat types, but also from connectivity between the various habitat types when making seasonal migratory movements (Baldwin et al. 2006, Groff et al. 2017). Freshwater wetlands, some of which provide important ephemeral breeding locations for amphibians, are a highly threatened habitat type and are at risk due to residential development (Eakin et al. 2019, Hu et al. 2017, Urban and Roehm 2018). Amphibians that use freshwater wetlands, like vernal pools, are threatened by habitat loss, degradation, and fragmentation following development because of resultant reductions in breeding potential and survival (Eakin et al. 2019, Semlitsch 2000). In New Hampshire vernal pools for example, amphibian egg mass abundance decreased as road densities increased within 1000 m of breeding locations (Veysey et al. 2011). The breeding habitat in our study will be hereafter be referred to as a vernal pool.

After breeding and following metamorphosis, adult and juvenile Wood Frogs move from vernal pools to various types of terrestrial forest habitat, respectively. In our region, forested wetland habitat composed of mineral to organic hydric soils, patches of shallow, standing water, sphagnum mosses, and poorly decomposed leaf litter substrate, is common summer refugia. Forest habitats, including but not limited to forested wetlands, provide terrestrial microhabitats during active periods for Wood Frogs to forage, to avoid predators, and to maintain physiological requirements (e.g., body temperature and water balance) (Baldwin et al. 2006, Peterman and Semlitsch 2014, Seebacher and Alford 2002). These forest patches may be referred to as foraging activity centers used by amphibians for an extended, non-migratory period (Groff et al. 2017). In the fall, some terrestrial amphibians including the Wood Frog, migrate for hibernal habitat selection (Groff et al. 2016, 2017). Wood Frogs use small depressions in the ground, typically located in upland forests, as hibernacula (Larson et al. 2014). Hibernacula are critical in buffering Wood Frogs from extreme and fluctuating temperatures during the winter and the quality of hibernacula vary with environmental factors such as snow cover (Groff et al. 2016, O'Connor and Rittenhouse 2016).

Similar to the breeding habitat and forested wetland activity centers used by amphibians, terrestrial hibernal habitat is also at risk. Loss of upland forest habitat could reduce the number of hibernacula locations available to Wood Frogs that remain within migratory distance of breeding locations or post-breeding terrestrial habitat (Groff et al. 2016). Increasing winter temperatures may also be detrimental for hibernating Wood Frogs if coupled with reduced insulating snow cover that leaves frogs susceptible to fluctuating and cooler temperatures, and more freeze thaw-cycles (Groff et al. 2016, O'Connor and Rittenhouse 2016, Sinclair et al. 2013). While there is research that demonstrates that land use change impacts amphibians (Semlitsch 2000, Urban and Roehm 2018), there is a lack of information available about how developing landscapes alter the characteristics of habitat used by amphibians during their hibernal period.

The paucity of information on how residential development impacts amphibians during the winter holds great importance given the proportion of time that Wood Frogs spend in hibernacula (e.g., >54% of the year in Maine) relative to other habitat types during their life cycle (Groff et al. 2017). To address this gap in amphibian landscape ecology, we radio-tracked eight adult Wood Frogs to their hibernacula locations at a residential environment. We monitored the microclimate of Wood Frog hibernacula as well as random forest and neighborhood locations with the use of thermochrons and made weekly snow depth measurements. We hypothesized that microclimates and environmental conditions impact Wood Frog hibernacula selection because site differences may affect overwinter survival or mortality. Given this hypothesis, we predicted that Wood Frog hibernacula soil temperatures would be warmer and less variable than soil temperatures at random forest hibernacula locations and cooler and less variable than soil temperatures at random neighborhood locations, indicating active site selection. Furthermore, we predicted that snow depth at Wood Frog hibernacula would be greater than at random forest hibernacula because selection of more open canopy cover promotes earlier and increased snow cover (Groff et al. 2016). However, we also expected snow depth at Wood Frog hibernacula to be lower than at random neighborhood locations that lack forest canopy cover. This research will help identify hibernal habitat characteristics that can support Wood Frogs in developing landscapes during a life history period that may be overlooked.

Field-site description

We examined the microclimate of Wood Frog hibernacula in a neighborhood along Mount Hope Ave in Bangor, Maine, USA (44.81°N, 68.75°W, elevation = 109 m). We identified a vernal pool located adjacent to the road and surrounded by anthropogenic disturbance as a breeding site of a population of Wood Frogs (Fig. 1). The pool was isolated on the border of a small forest patch (approx. 2,300 m^2) with single family homes surrounding it on three sides and hayfields across the road to the southeast. No Wood Frogs remained in this small forest patch following the breeding season. The neighborhood spread to the north and west in the late 1900s with 1,000–2,000 m^2 parcels. Houses were surrounded by lawns with some mature trees and shrubs as landscaping and demarcating property boundaries. Approximately 165 m to the northeast of the pool, beyond the houses, was a forested wetland patch containing shallow, standing water, sphagnum mosses, poorly decomposed leaf litter substrate, and deciduous tree cover. *Acer rubrum* L. (Red Maple) and *Pinus strobus* L. (Eastern White Pine) were the dominant tree species in this area. Along the edge of the forested wetland patch adjacent to the neighborhood was a narrow area of bordering upland forest with better drained soil. All breeding Wood Frogs migrated through the neighborhood to reach this forested wetland and bordering upland forest patch used for summer and winter habitat. All references to forest habitat at our site, unless otherwise specified, is considered forested wetland habitat.

Materials and Methods

As part of a broader study on Wood Frog habitat selection in developing landscapes, we followed radio-tagged frogs to their hibernacula and then monitored the microclimate at these hibernacula and at random locations. Frogs were captured in minnow traps during breeding in April or by hand in the forested wetland from 27 June–16 November 2016. We attached a 0.65 g, model R1615 transmitter (Advanced Telemetry Systems, Insanti, Minnesota, USA) to each adult Wood Frog using stretch bead cord (Stretch Magic, Pepperell Braiding Company, Pepperell, Massachusetts, USA) belts, such that the belt and transmitter combined did not exceed 10% of the mass of the frog (Groff et al. 2015, Heyer et al. 1994). We located each frog at least once every 3 days using a model R-1000 telemetry receiver (Communications Specialist Inc., Orange, California, USA) and a model RA-23K VHF antenna (Telonics, Mesa, Arizona, USA).

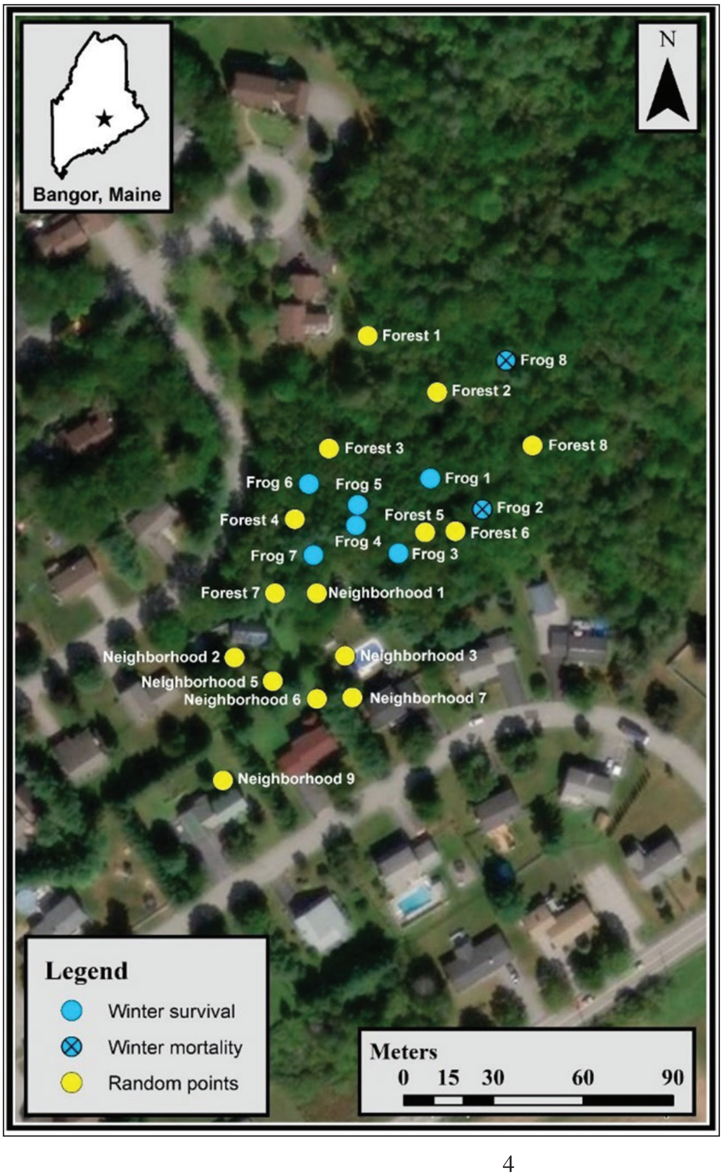

Figure 1. Green dots indicate Wood Frog hibernacula (n = 8) during the winter of 2017 and yellow dots indicate random points within the forest and neighborhood. Saratoga Ave, Glencove Ave, and Mount Hope Ave, Bangor, Maine, are shown, with the breeding, vernal pool near the bottom of the image outlined in blue. The insert map indicates the location of the site within Maine, USA.

When the frogs buried themselves in the leaf litter or substrate and had not moved for two weeks, we considered them to be settled for hibernation. We constructed enclosures of reinforcing bar (i.e., rebar), polyvinyl chloride (PVC) pipe, and seine netting around each hibernating frog (n = 8), random points in the neighborhood (n = 7), and random points in the forest (n = 8) according to Groff et al. (2016). The enclosures were secured to the forest floor with galvanized nails staked through the netting about every 2 cm (Fig. 2). Starting on 7 April 2017 we checked the enclosures daily for emerging frogs. We removed their spent transmitter and released them within a meter of the enclosure. Due to a lack of snow cover at all hibernacula locations and soils warming to above freezing on 14 April 2017, we assumed all remaining frogs were deceased or had escaped, opened the remaining enclosures, and dug by hand to search for the remaining frogs.

During the hibernation period we used thermochrons (model DS-1922L-F5#, Maxim Integrated, San Jose, CA, USA) to record hourly soil and air temperature at each hibernacula enclosure. We waterproofed the thermochrons by coating them in Plasti Dip (Plasti Dip International, Blaine, MN, USA) and allowed them to dry for 24 hours. At hibernacula, we buried one thermochron in an artificial burrow at the same depth as the frog (Table 1) and within 7 cm horizontally from the frog (Groff et al. 2016), and hung a second thermochron from a tree branch 2 m above the ground. At the random forest and neighborhood locations, we buried one thermochron in the center of each enclosure at a randomly generated depth between 3– 5 cm. No thermochrons were deployed to measure air temperature at random locations. We also visited each frog and random enclosure weekly to measure snow

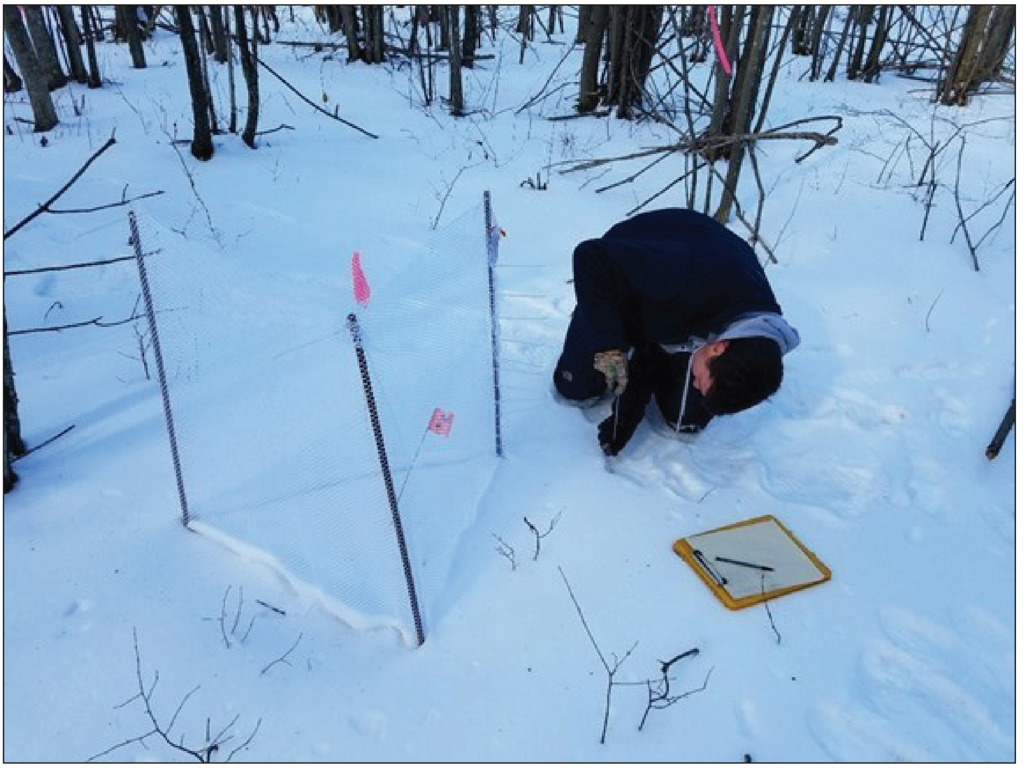

Figure 2. TH measures snow depth near an enclosure surrounding a hibernating Wood Frog in Bangor, Maine, USA. Picture taken by Kristine Hoffmann, used with permission.

and ice depth. We dug through the snow and chipped away at the ice until we reached the leaf litter or grass below, then measured from the ground to the surface of the ice and snow. The total snow and ice depth was measured outside of enclosures to ensure that hibernacula conditions were not impacted.

Statistical analyses

We compared temperatures across strata (i.e., air, soil) and treatments (i.e., hibernaculum, random neighborhood, and random forest). We reduced the hourly temperature data set to daily minimum, maximum, range (i.e., daily maximum minus daily minimum), and coefficient of variation, and calculated medians and interquartile ranges for each stratum and treatment. We compared the cumulative distributions of the strata and treatments with nonparametric two-sample Kolmogorov-Smirnov tests and compared the snow depth among treatments with a separate nonparametric two-sample Kolmogorov-Smirnov tests. All statistical analyses were conducted with R (R Core Development Team 2018). For all statistical tests, $\alpha < 0.05$.

We intended our results to be applied directly to the conservation of habitat needed for survival and persistence of Wood Frog populations in developing areas so that managers can choose how to better conserve anurans. We did not have enough mortality events to determine if hibernacula where frogs survived differed in temperatures or snow cover from those where frogs did not survive, so we removed hibernacula where frogs did not survive the winter (mortalities in Fig. 1) from the dataset. We are wary of using animals who may have selected ecological traps or otherwise unsuitable habitat as we make recommendations for species management. However, we added the dead frogs' hibernacula back into the dataset for a separate *post hoc* analysis. While we did not consider the results of these comparisons in our conclusions, including the hibernacula of frogs who did not survive could be more informative for readers interested in unbiased behavior of Wood Frogs.

Table 1. Hibernaculum and leaf litter depth and date of last movement by radio tracked Wood Frogs (*Lithobates sylvaticus*) in a forest fragment in a neighborhood in Bangor, Maine, USA.

Enclosure	Frog ID	Sex	Burrow depth (cm*)	Leaf Litter depth (cm)	Date caught	Date of Last Movement	Weight(g) at Emergence	Date Emerged	Min Ground Temp (°C)
Hib 1	801	M	3.0	3.0	6/27/16	10/29/16	7.8	4/11/17	-4.52
Hib 2	861	?	3.0	3.0	8/30/16	11/4/16	NA	Dead	-3.63
Hib 3	901	F	5.0	3.0	8/31/16	11/16/16	11.4	4/13/17	-4.34
Hib 4	881	?	3.5	-	10/21/16	11/22/16	10.6	4/13/17	-3.39
Hib 5	961	M	2.0	2.0	8/6/16	11/4/16	6.6	4/11/17	-3.62
Hib 6	821	F	3.9	3.0	10/21/16	11/6/16	18.8	4/10/17	-3.90
Hib 7	841	?	4.5	3.0	11/16/16	11/20/16	NA	Missing	-1.24
Hib 8	981	?	2.8	1.0	10/21/16	10/24/16	NA	Dead	-5.11

*rounded to nearest half cm
We are unsure if frogs at hibernacula 3 and 4 emerged on 12 or 13 April and therefore we use 13 April to be more conservative.

Results

The eight Wood Frogs burrowed 2.8– 5.0 cm into the soil beneath 1.0–3.0 cm of leaf litter between 24 October to 22 Nov 2016 and remained there until 10 April to 13 April 2017 (Table 1). No frogs chose to hibernate within the neighborhood (Fig. 1). Seven frogs selected hibernacula in the forest, where the ground surface was slightly higher (>2m) in elevation than the wetland and did not flood. One of these seven frogs was not found in spring and presumably escaped its enclosure (hibernaculum 7), while another frog was found dead when excavated on April 4th (hibernaculum 2). Its hibernaculum was similar to those of surviving frogs and its' cause of death is unknown. The eighth frog hibernated within the forested wetland (hibernaculum 8) and died there. This area was later flooded and then covered with over 10 cm of solid ice and reached the coldest minimum ground temperature of all hibernacula (Table 1).

We measured temperature at the eight Wood Frog hibernacula, eight random locations in the forest, and seven random locations in a neighborhood, from 24 December 2016 to 13 April 2017 when heavy rain occurred in the early morning, triggering migration to the vernal pool. All hibernacula soil temperature metrics (i.e., daily minimum, maximum, range, and cv) were significantly different than those of the hibernaculum air strata (Table 2). Although daily minimum air temperature reached -21.8°C, the coldest hibernaculum temperature recorded for a surviving frog was -4.5 °C (Table 1, Fig. 3). Daily minimum soil temperatures of hibernacula were generally higher and had less variation than daily minimum air temperatures at hibernacula (Fig. 3). Hibernaculum soil daily minimum and maximum temperatures differed significantly from random neighborhood locations and from random forest locations (Table 2). The coefficient of variation differed significantly between hibernacula and random points in the forest but not random points in the neighborhood. Soil at neighborhood random locations reached the lowest soil temperatures (min = -8.78 °C), followed by soil at forest random locations (min = -5.87) and then soil at hibernacula (min = -4.52 °C; Fig. 4).

We recorded weekly snow depth, including underlaying ice, from 29 December 2016–14 April 2017 at hibernacula and all random points. Six of the hibernacula were under snow at the start of this period. The following week all hibernacula were covered with snow excluding hibernaculum 8, which was positioned in the wetland and resulted in mortality. Snow depth peaked (mean = 49.9 cm, sd = 8.1) on 17 Feb at the hibernacula. All random points were under snow at the start of recording. Snow depth at hibernacula was significantly lower

Table 2. Results of two-sample Kolmogorov-Smirnov tests used to compare the temperature (temp.) of the Wood Frog hibernaculum (HIB, n=6) soil stratum, and snow depth at the hibernaculum, to that of the hibernaculum air strata, and random location (RND, n = 8) soil stratum and snow depth in forest and neighborhood locations. P-values and D-statistics (parentheses) provided; nonsignificant results in bold. The hibernacula of the two frogs that did not survive the winter were excluded from this analysis.

	HIB air	RND forest	RND neighborhood
Min. temp.	<0.001 (0.692)	<0.001 (0.133)	<0.001 (0.106)
Max. temp.	<0.001 (0.656)	<0.001 (0.156)	<0.001 (0.117)
Temp. range	<0.001 (0.970)	0.124 (0.060)	0.054 (0.071)
Temp. cv	<0.001 (0.300)	0.001 (0.098)	0.275 (0.053)
Snow Depth	-	<0.001 (0.155)	<0.001 (0.092)

than snow depth at random locations in both the forest and neighborhood (Table 2). Random points within the neighborhood varied considerably in March and April compared to other areas (Fig. 5).

When we included the hibernacula with mortalities in our *post-hoc* analysis, all comparisons between the ground temperature and other temperatures were significantly different. Snow depths at the hibernacula were significantly different from both the neighborhood random points and the forest random points. This differs from our *ad-hoc* results for comparisons of the range of temperatures at hibernacula and random points and comparison of the coefficient of variation in temperature between hibernacula and random points in the neighborhood.

Discussion

Our results support the hypotheses that snow depth at Wood Frog hibernacula differ from snow depth at random locations, and that soil temperature at Wood Frog hibernacula differ from random neighborhood and forest location soil temperatures. We found the microclimate of hibernacula to be warmer and less variable than the surrounding microclimate, and the snow depth at hibernacula locations to be lower than at random forest and neighborhood locations. We suggest that these conditions help Wood Frogs reduce the likelihood of freezing during the winter. The results also reflect the ability of Wood Frogs to find hibernacula in bordering upland forest habitat with better drained soil and suitable microclimate conditions in a housing development landscape.

The buffered microclimate conditions of hibernacula observed in our study is consistent with previous research and is likely a key aspect to overwintering survival of Wood Frogs. While Wood Frogs in our residential study area did not make long-distance migration move-

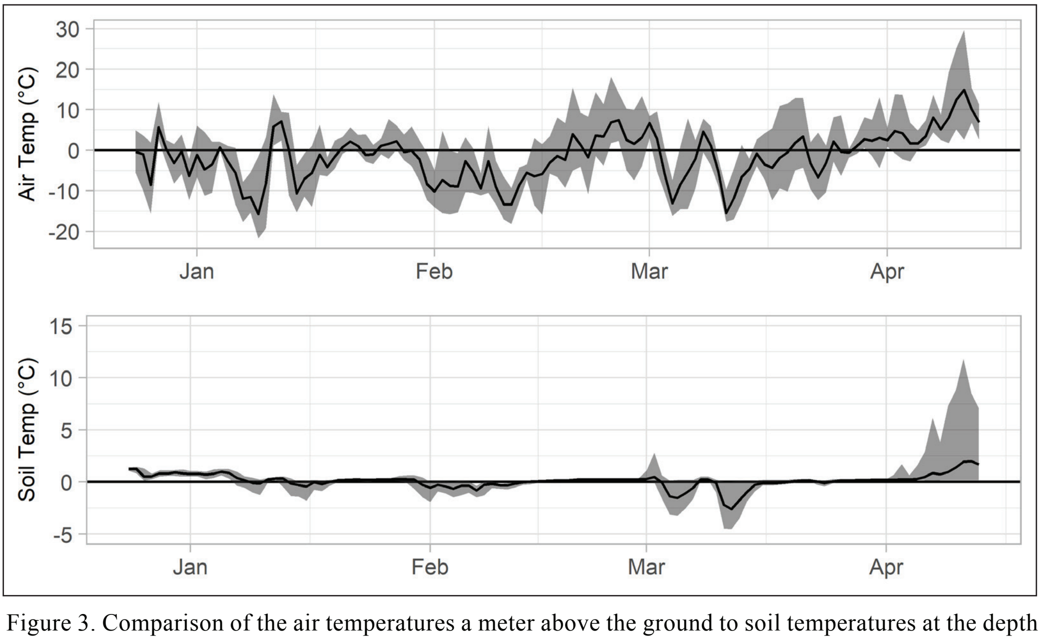

Figure 3. Comparison of the air temperatures a meter above the ground to soil temperatures at the depth of each frog at hibernacula (n = 6) in a forest along the edge of a neighborhood in Bangor Maine. Frogs that did not survive the winter are excluded from these plots. Lines show the mean temperature per day, with shaded areas indicating the maximum and minimum temperature of hibernacula.

ments from their summer foraging activity center to their winter hibernacula locations, the differences in microclimate conditions between hibernacula and the surrounding environment do follow patterns similar to previous findings. In north-central Maine Wood Frogs moved 193 m on average from their foraging activity center to hibernal habitat in upland forests (Groff et al. 2016). Wood Frogs in southern Maine and Connecticut were also observed making long-distance movements (e.g., 50-314 m) in the fall prior to hibernation (Baldwin et al. 2006; O'Connor and Rittenhouse 2016). Fall migration movements from foraging activity centers

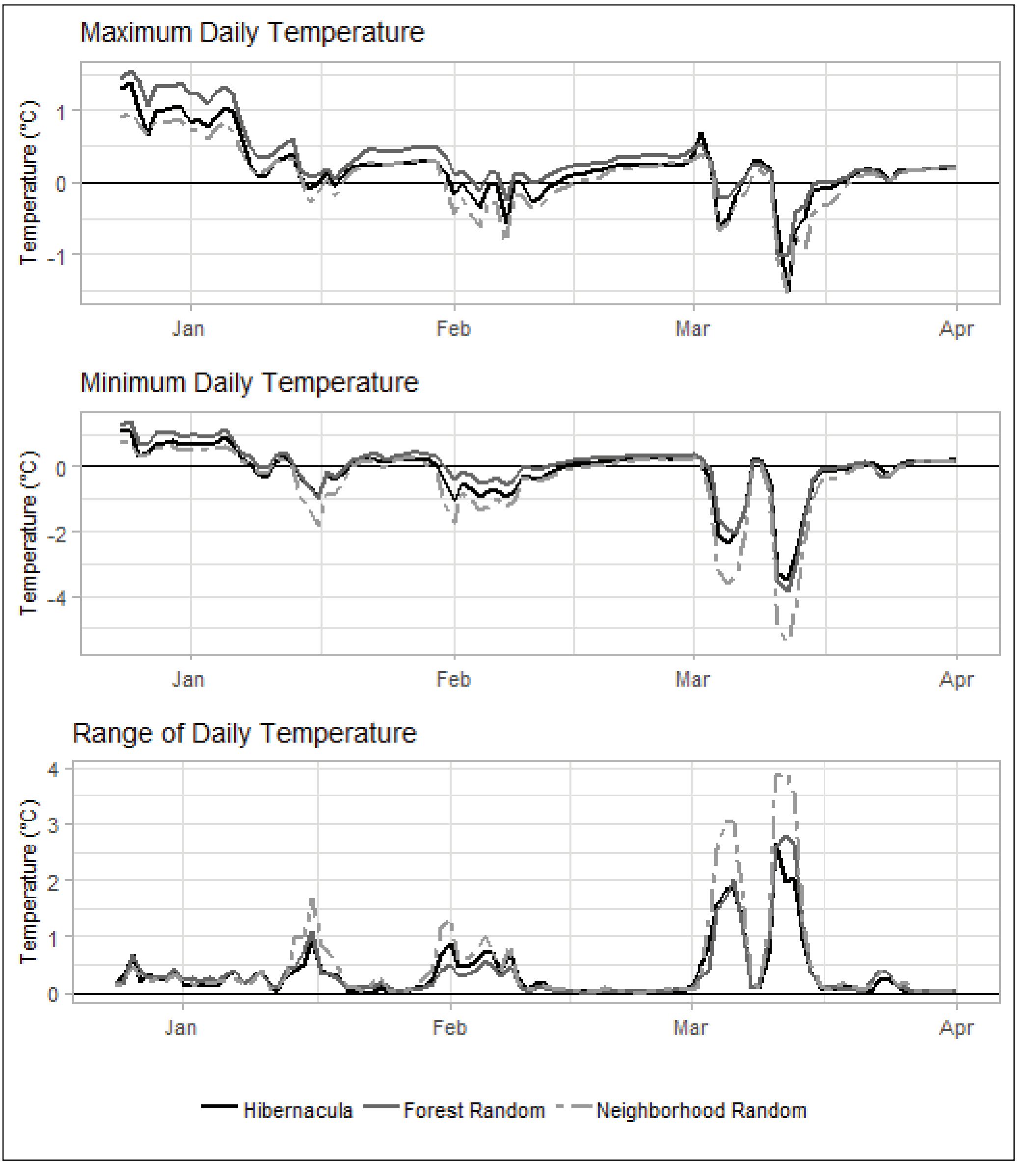

Figure 4. Comparison of soil temperatures of three treatments in a developing landscape in Bangor, Maine: the hibernacula of Wood Frogs (n = 6); random points within a forest (n = 8); and random points within lawns of a neighborhood (n = 7). Hibernacula of frogs that did not survive the winter are excluded from these plots (n = 2).

to upland forests allow frogs to select hibernal habitats with characteristics such as more open canopies and increased snow cover that promotes winter survival by avoiding more pronounced freeze events (Groff et al. 2016, O'Connor and Rittenhouse 2016). Although the frogs in our study only moved short distances to a bordering upland forest patch, Wood Frogs located in north-central Maine and interior Alaska similarly selected hibernacula that provided warmer soil temperatures (-6.1 and -18.1 °C minimum) than the surrounding air that reached a minimum of -26.78 and -36.8 °C, respectively (Groff et al. 2016, Larson et al. 2014). The daily range of hibernacula temperatures in north-central Maine were less variable than air temperatures (Groff et al. 2016), consistent with our findings. Wood Frogs also select hibernacula that buffers frogs from extreme temperature minima and that reduce variation in soil temperature (Larson et al. 2014). Temperature control in hibernacula is important for minimizing physiological stress, increases in metabolism, and energy consumption during freeze-thaw cycles that might otherwise be more frequent, and thus may have contributed to the survival of most of our frogs (Fitzpatrick et al. 2020, Groff et al. 2016, Larson et al. 2014, O'Connor and Rittenhouse 2016). Our study demonstrates that Wood Frogs can find more well drained hibernacula and survive harsh winter conditions without fall migration movements to separate forest patches.

With increasing threats to terrestrially hibernating amphibians during the winter, it is important to maintain forest habitat surrounding breeding wetlands to ensure that habitat is available during all life periods of amphibians such as the Wood Frog. Although the Wood Frogs in this study did not have a suitable forest habitat surrounding the vernal pool, the frog's movement through a neighborhood environment to reach a forest patch reinforces the need for forest cover to be near breeding habitat. Research has shown that Wood Frogs require up to 340 and 317 m of buffered forest habitat around a vernal pool to find terres-

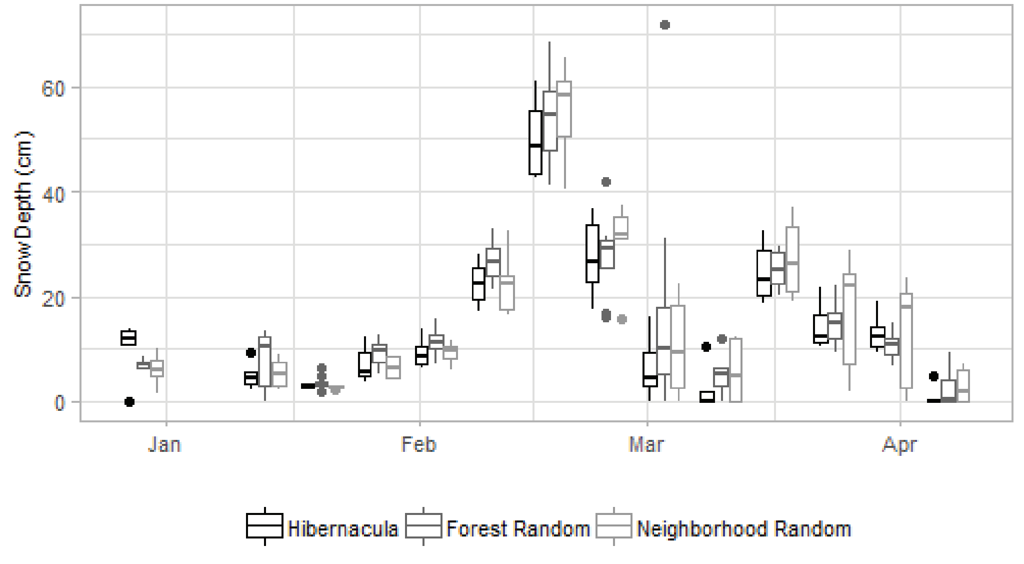

Figure 5. Comparison of the variation in snow depth of three treatments in a developing landscape in Bangor, Maine: the hibernacula of Wood Frogs (n = 6); random points within a forest (n = 8); and random points within lawns of a neighborhood (n = 7). Snow depth is the total depth of both snow and accumulated ice above the leaf litter. Hibernacula of frogs that did not survive the winter are excluded from these plots (n = 2).

trial habitat during their summer activity and hibernation periods, respectively (Baldwin et al. 2006, Groff et al. 2016). Forested habitat around breeding habitat is important not just because they provide important microhabitats, but because connected forest habitat reduces risk during migration movements to reach microhabitats in forested wetlands and upland forests (Baldwin et al. 2006, Rittenhouse and Semlitsch 2007). Therefore, when possible, adjacent forest around breeding pools should be maintained to help increase connectivity among forested wetland and upland forest macrohabitats.

Upland forests, or similar macrohabitats, must also be protected to include all habitat requirements of amphibians with complex life cycles. We recommend that in addition to protection of wetlands as breeding habitat and forested wetlands as important foraging activity centers (Baldwin et al. 2006; Groff et al. 2017), that developers and managers should also conserve forested locations with unsaturated soils or greater elevational changes that increase drainage. While most of the frogs in this study successfully hibernated in the same forest patch used during the summer foraging period, the frogs moved more upslope into a bordering upland forest area to avoid flooded locations. Such behaviors were likely to avoid saturated soils that would support significant ice formation within the hibernacula (Baldwin et al. 2006). Therefore, managers and developers must consider conserving locations within forest patches that will be able to remain unsaturated throughout winters to support suitable hibernacula conditions. Protection of forested patches that contain both wetland and upland habitat may be ideal to reduce the need of long-distance movements between summer and winter habitat for animals with complex annual life cycles. This may be especially important for frogs in fragmented landscapes such as a residential environment (Regosin et al. 2003).

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