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Calling Phenology in *Rana sylvatica* (Wood Frog) at High-elevation Ponds in the White Mountains, New Hampshire

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Abstract - Permanent, fishless, alpine and subalpine ponds are extremely rare in New England, and amphibians occupying these ponds are unique bioindicators of environmental change because they are subject to different ecological pressures compared with lowland populations. Further, alpine and montane ecosystems are expected to undergo rapid change in the coming decades. Therefore, uncoupling the interacting effects of temperature, precipitation, and ice-out on breeding efforts may identify specific ecological mechanisms driving reproduction of amphibians. The reproductive phenology of amphibians in climatically extreme alpine environments in the eastern United States is historically under-reported and remains poorly understood. To evaluate the reproductive phenology of amphibians near the upper extreme of their vertical distribution in the White Mountains, NH, we digitally recorded amphibian calls between 2010 and 2020 at 3 permanent, fishless ponds: Hermit Lake (1180 m), Eagle Lake (1278 m), and Lakes of the Clouds (1546 m). Our study revealed dynamic changes in species assemblages and provides the first report of *Hyla versicolor* (Gray Tree Frog) in a subalpine context (at Hermit Lake). We analyzed the calling phenology of the earliest breeding North American anuran, *Rana sylvatica* (Wood Frog), and found differences in calling phenology among the 3 ponds and temporary changes in calling phenology correlated with interpolated daily weather parameters. We stress the need for further research to understand both short- and long-term, weather-driven reproductive dynamics in amphibian phenology in high mountains and their corresponding demographic effects.

Introduction

Climate change is a central contemporary issue affecting life on Earth, and its effects are expected to be more pronounced in mountain ecosystems compared to lowland regions (Auer et al. 2007, Gobiet et al. 2014). In the northeastern US, alpine and subalpine ecosystems have already undergone complex shifts in forest-cover types (Beckage et al. 2008, Foster and D'Amato 2015) with demonstrable effects on vertebrate species distribution (Cordier et al. 2020, DeLuca and King 2017). Growing evidence suggests that shifts in climate can trigger a cascade of changes in abiotic environments (Brook 2004) and biological diversity (Beebee 1995, Blaustein et al. 2010, Cannone et al. 2007, Grabherr et al. 2010, Keller et al.

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2005), with phenology of amphibian activity being one of the key elements subject to change (Beebee 1995, Gibbs and Breisch 2001). However, there is considerable variability in changes of weather patterns regionally (Hayhoe et al. 2007), along elevation gradients (Seidel et al. 2009), and in response to changing weather patterns in different species of amphibians (Beebee 2002, Blaustein et al. 2010). In addition, interactions among different climate components and their cumulative effect on species of amphibians are often complex, and mechanisms of their actions are difficult to untangle (Blaustein et al. 2010, Shearin et al. 2012).

In temperate lowlands and mid-elevations, seasonal ponds typically have short hydroperiods, which exclude inhabitation by fish and constrain diversity and density of aquatic predators and are essential for many pond-breeding amphibians (Hopey and Petranka 1994, Wiggins et al. 1980). To maximize fitness, amphibians using such ponds for reproduction must complete metamorphosis before their pond dries (Brooks 2004, Wiggins et al. 1980). In alpine and tundra environments, such ponds experience lower temperatures and evapotranspiration rates, higher precipitation, delayed thawing, earlier freezing, lower water temperatures, extended hydroperiods up to permanence during the active season of amphibians, and extreme cold-season interruptions of hydroperiod due to freezing solid (Svenson 2002). Permanent, fishless, alpine and subalpine ponds are extremely rare in New England, and amphibians occupying these ponds are subject to different adaptive ecological pressures compared with those occupying lowland seasonal pools. Adaptations of amphibians from permanent ponds in the alpine zone of New England is poorly understood and should be researched in more detail and over time.

Amphibians inhabiting arctic–alpine environments have been primarily studied in Europe (Merila et al. 2004, 2008; Sztatecsny et al. 2013) and western North America (e.g., Sierra Nevada [Knapp et al. 2007, Matthews et al. 2001]; Denali National Park [Hokit and Brown 2006]; Colorado [Whiteman and Wissinger 2005]; Churchill, MB, Canada [Berven and Gill 1983, Davenport et al. 2016). Despite the value of amphibians as indicators of ecosystem and environmental change, quantitative studies of amphibian communities from alpine or subalpine ecosystems in New England have been limited (Groff et al. 2016, Jones and Smyers 2010, Trombulak and Andrews 1995). Most available information prior to the 1990s is found either in unpublished reports (e.g., Andrews 2017) or anecdotal observations (e.g., Thoreau 1858). In the statewide treatments of amphibian distributions in New England, the states with the largest extent of alpine tundra in the northeastern United States (Jones and Willey 2018) do not specifically mention the occurrence, ecology, or status of amphibians associated with alpine or subalpine ponds (Maine [Hunter et al. 1999], New Hampshire [Taylor 1993], and New York [Gibbs and Breisch 2001]). But note that Trombulak and Andrews (1995) reported 7 species of amphibians from a site at 1200 m on Mount Mansfield, VT. Brief ecological descriptions of amphibians were provided in a field guide to the northeastern alpine summits (Slack and Bell 1995). Jones (2005) and Jones and Smyers (2010) reported species assemblages and habitat descriptions at 5 specific ponds within the high elevation zones in the White Mountains of New Hampshire and noted the presence of the following amphibians: *Rana sylvatica* Le Conte (Wood Frog), *Lithobates clamitans* (Latreille) (Green Frog), *Pseudacris crucifer* (Wied-Neuwied) (Spring Peeper), *Anaxyrus americanus* (Holbrook) (American Toad), *Ambystoma maculatum* (Shaw) (Spotted Salamander), and *Notophthalmus viridescens* (Rafinesque) (Eastern Newt). Amphibian taxonomy herein follows www.amphibiaweb.org.

Of the 4 anuran species reported in alpine and subalpine habitats by Jones and Smyers (2010), Wood Frogs occured at every alpine or subalpine pond surveyed. Wood Frogs can survive subfreezing temperatures for limited periods during their active season (Larson et al. 2014, Layne and Lee 1995), overwinter buried in the surface layer of the soil just below non-decomposed organic material such as leaf litter (Regosin et al. 2003), thaw quickly as the ground thaws (Kessel 1965), and are the first species to begin calling even when ponds are partly covered in ice and patchy snow remains in the surrounding uplands (Gibbs and Breisch 2001). Due to plasticity in their larval period (68–130 days) and ability and tendency to colonize ponds with short hydroperiods (Berven and Gill 1983, Dodd 2013), Wood Frogs have a broad geographic range from Alaska to Labrador and south to Colorado and Georgia (Davenport and Hossack 2016, Martof and Humphries 1959).

Male Wood Frogs arrive at the pond after snowmelt, and they begin calling to attract females. In robust populations, calls can vary from sparse to continuous and overlapping depending on the time of the year and weather conditions (Cook et al. 2011, Gibbs and Breisch 2001, Wright 1914). Courtship and breeding occur within a soundscape of calling frogs, and the intensity of calling can be used as a proxy for reproductive effort (Cook et al. 2011, Crouch and Paton 2002). Calling 500–600 times per hour (Wells and Bevier 1997) is energetically expensive (Taigen and Wells 1985, Taigen et al. 1985). Short duration of calling and breeding activity (Cook et al. 2011) is a presumed adaptation to the short hydroperiod of seasonal pools. However, the consequences of longer hydroperiods and lower temperatures in alpine lakes on duration of breeding activity of Wood Frogs remain poorly understood. In the present study, we examined calling phenology of Wood Frogs in alpine tundra settings by comparing 3 high-elevation ponds—Hermit Lake, Eagle Lake, and Upper Lake at Lakes of the Clouds—using call records (Blumstein et al. 2011, Peterson and Dorcas 1994), exploring temporary changes in calling phenology using the call records collected across the 3 ponds between 2010–2020 and examining the possible relationships between calling patterns and weather variables.

Field-site Description

Our study area encompassed 3 alpine ponds or "pond complexes" situated at different elevations above 1100 m in the White Mountain National Forest of Grafton and Coos counties, NH (Fig. 1). All ponds are permanent but are void of fish, have been studied previously (Jones and Smyers 2010), contain communities of anurans, and are accessible by public hiking trails.

Eagle Lake is an oval-shaped pond ~0.42 ha in area, situated at 1278 m, near the treeline on the western shoulder of Mount Lafayette, Grafton County, NH (44°9'37.98"N, 71°39'32.688"W). Eagle Lake occurs within the Kinsman

Granodiorite lithology, a Devonian-age exposure of the New Hampshire Plutonic Suite (Lyons et al. 1997). The Eagle Lake basin is composed primarily of large boulders and thick organic sediments and is surrounded by krummholz coniferous and subalpine ericaceous vegetation composed primarily of *Picea mariana* (Mill.) Britton, Sterns, and Poggenb. (Black Spruce) and *Abies balsamea* (L.) Mill.

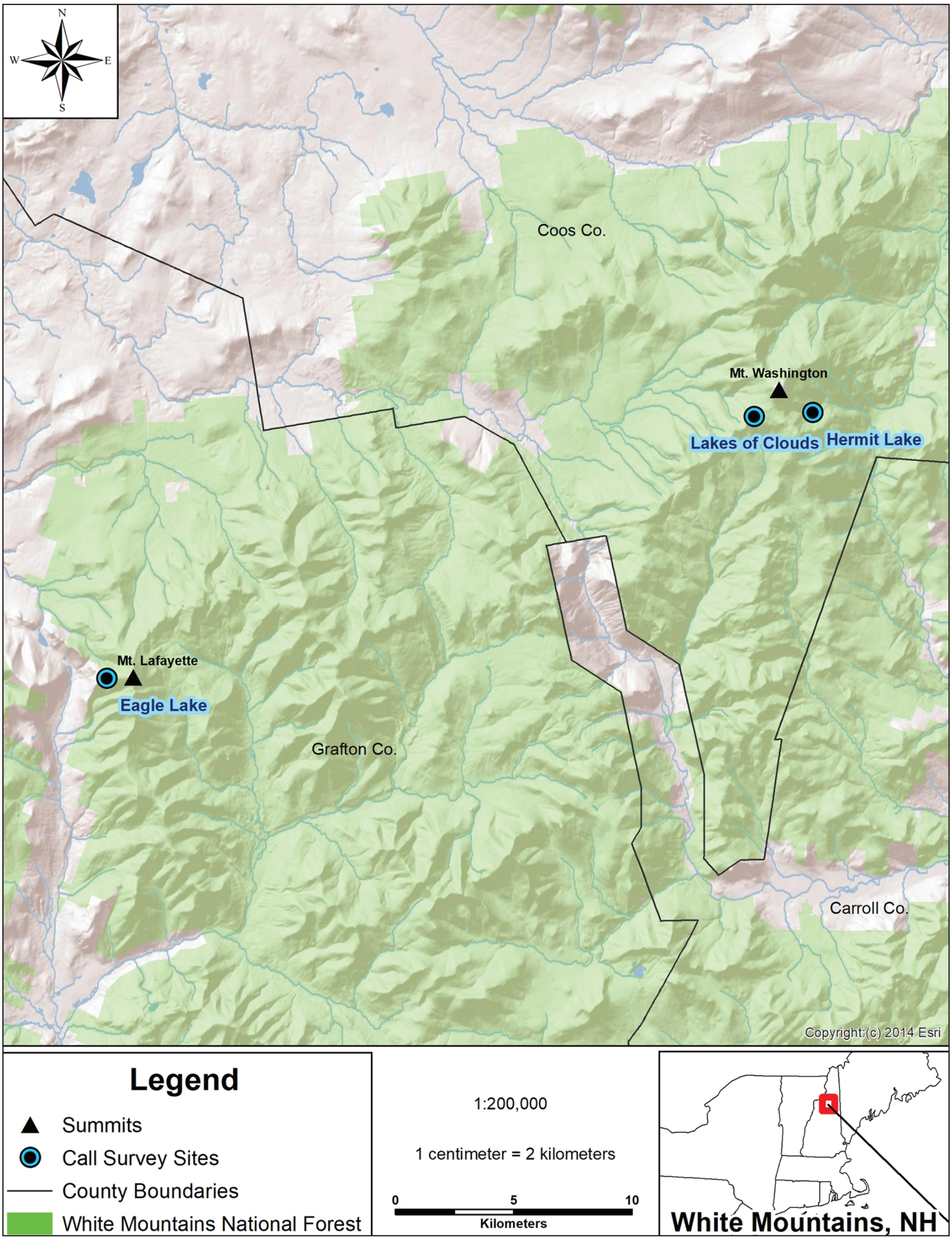

Figure 1. Locations of song meters in this study.

(Balsam Fir). A perennial outlet flows south from Eagle Lake. Although not part of this study, a smaller pond ~0.08 ha in surface area is located to the northwest of Eagle Lake with a well-developed *Sphagnum* mat surrounding a deep (>1 m) pool of open water with unconsolidated organic sediment. Wood Frogs have been found in this smaller pond (Jones and Smyers 2010).

Hermit Lake is an oval-shaped tarn (0.16 ha) situated at 1180 m on the floor of Tuckerman Ravine, a pronounced glacial cirque on the southeast shoulder of Mount Washington, Coos County, NH (44°15'38.844"N, 71°17'8.952"W). Hermit Lake has an estimated average depth of 1–2 m with thick, organic substrate and partially submerged boulders representing metamorphic Littleton formation, a Lower Devonian complex of metasedimentary and metaigneous rock (Lyons et al. 1997), and is surrounded by Balsam Fir forest with patches of *Sphagnum*-dominated communities along the shoreline.

Upper Lake of the Clouds is the smaller of 2 glacial tarns (Lakes of the Clouds) located ~50 m apart above the treeline at the head of the Ammonoosuc Ravine on the southern shoulder of Mount Washington, Coos County, NH. The Lakes of the Clouds are situated within the Littleton Formation (Lyons et al. 1997). The pond is oval-shaped and ~0.16 ha, situated at 1546 m (44°15'33.4074"N, 71°19'0.66"W). Exposed bedrock and boulders surround the pond, and the dominant upland vegetation includes low ericaceous shrubs such as *Vaccinium uliginosum* L. (Alpine Blueberry), *Rhododendron groenlandicum* (Oeder) Kron and Judd (Labrador Tea), *Vaccinium vitis-idaea* L. (Mountain Cranberry), and *Kalmia polifolia* Wangenh. (Bog Laurel) as well as krummholz stands of Black Spruce and Balsam Fir, *Sphagnum*-dominated communities, and other forbs and graminoids typical of the Acadian–Appalachian alpine tundra (Harris 1977, Jones and Willey 2018).

Methods

Between 2010 and 2020, we installed 1 acoustic recorder per site (various Song Meter models including SM1, SM2, SM3, or SM4; Wildlife Acoustics, Inc., Maynard, MA) at approximately the same location each year within 2 m of the shore (western shore of Eagle Lake, northern shore of Hermit Lake, and northern shore of Upper Lake of Lakes of the Clouds). We attached SMs to trunks of trees at a height of approximately 0.5–1.5 m using screws or strapping and hidden from view. Due to the depth of snow when SMs were installed, in some years we re-positioned the SM after the snow had melted to decrease its conspicuousness. We programmed the SMs to record for 10 minutes (Crouch and Paton 2002) 4 times per day: midnight, sunrise, noon, and 1 hour after sunset. For the present study, we only analyzed the noon, sunset, and midnight periods, because those were associated with higher probability of detecting Wood Frog calls. We programmed the units to adjust for variation in photoperiod, such that the time of the sunset recording changed throughout the season.

We examined recordings using SongScope or Kaleidoscope (Wildlife Acoustics, Inc.) and searched for visual signatures to identify each species and the maximum call intensity per day according to the index values (0–3) based on a modified version of the North American Amphibian Monitoring Program (Weir and Mossman 2005), as follows: call index 0 = no calls; call index 1 = individual calls, with single or multiple, non-overlapping distinct calls; call index 2 = overlapping calls, with 2 individuals' calls overlapping during any portion of the recording, and there may be occasional overlapping by 3 individuals; call index 3 = chorus, with overlapping and continuous calls sustained for at least 30 seconds such that it is difficult to determine the number of calling individuals. In the data analyses, we used the maximum call-intensity value recorded on a given date. For some batches of recordings, we trained volunteers to examine recordings then cross-checked their scores by experts (S.D. Smyers or M.T. Jones) to minimize observer bias. However, for most years, the recordings were divided between all authors with cross-checking where species or intensity was in question until we agreed on the species and score. Biologically, a chorus (call index 3) is indicative of mating (Dodd 2013). Therefore, we used call index 3 as an indicator of reproductive activity. We also used call data to generate species lists for each site per year.

Although not the primary focus of this study, we conducted visual surveys for egg masses during some years to quantify the duration of the chorus and oviposition. We also used these data to estimate the time between the beginning and the end of chorus and the beginning and the end of oviposition (Arietta et al. 2020, Crump and Scott 1994). We surveyed for egg masses early in the season in 2015, 2017, and 2020 and later in the season in 2020. We considered the presence of fresh, unswollen egg masses as an indicator of recent oviposition (Arietta et al 2020). To examine the relationship between duration of the chorus and duration of oviposition, we juxtaposed the egg-survey data with frog-call data per year.

We used 6 variables to characterize differences in daily weather during the calling period among the study sites and to broadly test the association between weather and Wood Frog calling activity: precipitation (PRCP, mm/day), shortwave radiation (SRAD, W/m^2), snow water equivalent (SWE, kg/m^2), maximum air temperature (Tmax,°C), minimum air temperature (Tmin, °C), and vapor pressure (VP, Pa) (ORNL 2020; Thornton et al. 1997, 2000, 2020). We sourced these variables from Daymet, which represents interpolated and extrapolated daily values from near-surface meteorological observations saved in the form of 1 km x 1 km gridded surfaces (M.M Thornton et al. 2020; P.E. Thornton et al. 1997, 2000), and lacks the site-specific microhabitat detail required to model specific pond activity. We selected these variables to make our results comparable to a similar study on Wood Frogs (Arietta et al. 2020) and used them to assess broad patterns only.

Data analysis

We defined the dates of the first and the last calls, irrespective of their intensity (call index 1–3) as the beginning and the end of calling activity, and the dates of the first and the last chorus based on call index 3. To analyze date ranges, we converted dates into year-days (yday 1–365) and constrained the temporal extent of all analyses to the period between 20 April (yday 111) and 7 July (yday 186). We selected this period because it covered the entire duration of Wood Frog calls, across all 3 study sites. We calculated the following 8 annual calling-activity attributes for each pond in each year: (1) start of calling activity (first yday of any call index 1–3), (2) start of chorus (first yday with call index 3), (3) median day of chorus (median yday with call index 3), (4) end of chorus (last yday with call index 3), (5) end of calling activity (last yday of any call index 1–3), (6) duration of calling activity (end of calling activity–start of calling activity), (7) active calling days (number of days with any frog calls), and (8) chorus days (number of days with chorus).

To compare yday of the 8 annual calling-activity attributes between sites and between years, we computed and used descriptive statistics (mean ± SD and min–max) of each attribute. We statistically evaluated differences between sites for the 8 annual calling attributes using one-way ANOVA with post-hoc pairwise comparisons using Tukey's test. We further explored the interaction between site and yday in describing whether frogs would call on a given day using logistic regression via the glm function in R (Bates t al. 2015, R Core Team 2020) and compared quadratic models with and without interaction terms using a likelihood ratio test. We used a Hosmer–Lemeshow goodness of fit test via the ResourceSelection package (Lele et al. 2019) in R to assess fit.

We used Mann–Whitney U tests to compare the differences in daily weather variables on days with and without calling activity of Wood Frogs. Given the large number of tests conducted for mean comparisons, we set the probability of rejecting the null hypothesis (alpha) to 0.01. To assess whether the relationships between calling and weather were unimodal, we built simple logistic regression models, pooled across sites and years, with each weather variable as a predictor and whether or not frogs were calling on that day as the response. We assessed all models with and without a quadratic term, comparing them with Akaike information criterion (AIC).

To view temporary changes in frog-call patterns, we generated and examined scatter plots of calling-activity attributes 1–5, with moving-average trendlines. To estimate temporal change in the initiation of calling activity (start yday), we calculated the difference between the last and first year of the time series. To explore significance of temporal changes of median yday of chorus and weather variables, we calculated and plotted weather variable averages for the calling activity period (yday 111–186). We tested the significance of temporal changes using a non-parametric Mann–Kendall test performed using the 'trend' package (Pohlert 2020). Mann–Kendall tests require continuous data to be used. Because we did not always have call data available for every consecutive year, we applied Mann–Kendall test only to continuous segments of data. We also explored correlations among median yday for each site in each year and average weather variables during the calling season (yday 111–186) in time series using Pearson's correlation coefficients (r). Because of the small sample size in our time series, we set alpha to 0.05 for tests performed on time-series data to prevent type II error due to small sample size.

Computations were performed in the R statistical computing environment (R Version 3.5.5; R Core Team 2020).

Results

Our call surveys revealed the presence of 5 anuran species. Wood Frogs, Spring Peepers, and American Toads were recorded in every study pond. Green Frogs were detected only in Hermit Lake. We recorded a single *Hyla versicolor* Le Conte (Gray Treefrog) at Hermit Lake in 2018. The first species to call each spring was the Wood Frog, followed by Spring Peeper, American Toad, and finally Green Frog. American Toads were confirmed at Hermit Lake and Lakes of the Clouds throughout our study period, but only recorded in Eagle Lake in 2016. Calling intensity of Green Frogs decreased at Hermit Lake between 2010 and 2016. Green Frog calls were recorded at call category 2 on 6–7 July 2010 and 11–12 July 2011, and tadpoles were abundant in the spring and summer of 2012. However, in 2012, 2014, and 2015, Green Frogs did not call as intensely (never attaining level 2). In 2016, there were no calls of Green Frogs, but they were recorded at level 1 in 2018 and 2020. In 2020, we observed 2 males and 1 female in Hermit Lake. In 2013, 2017, and 2019, the recording device malfunctioned during the Green Frog breeding period.

The beginning of Wood Frog calling varied by 22 days at Hermit Lake, 26 days at Eagle Lake, and 20 days at Lakes of the Clouds (Table 1). Differences in the average yday of the start of calling activity, start of chorus, median chorus, and end of chorus between Eagle and Hermit Lakes were not statistically significant (Tables 1, 2). The average number of days with chorus at Hermit Lake was significantly higher compared to both Eagle Lake and Lakes of the Clouds (Tables 1, 2). The start of the calling period, start of chorus, and median chorus at Lakes of Clouds were significantly later compared with both Eagle and Hermit Lakes (Tables 1, 2). End of chorus at Lakes of the Clouds was significantly later compared to Eagle Lake (Tables 1, 2). Duration of calling activity did not differ significantly among our study sites (Tables 1, 2). The median day of chorus is correlated with start date ($r = 0.91$, $P \leq 0.001$). Comparison of logistic regression models with and without an interaction suggested there was a significant interaction between site and yday when assessing whether a frog was calling on a given day ($P < 0.001$; Fig. 2).

Visual-encounter surveys revealed egg masses present as summarized in Table 3. Juxtaposition of these limited visual-survey results with call intensity demonstrates that the first egg masses were present at 7, 5, and 12 days after the first chorus at the Eagle Lake, Hermit Lake, and Upper Lakes of the Clouds, respectively.

Within the period of calling activity of Wood Frogs in early spring, the daily weather variables on days with and without calling varied considerably (Table 4). Across all sites, the calling activity began an average of 16.14 (SD = 8.59, min–max = 1–31) consecutive days with Tmax above 0 °C, and an average of 2.7 (SD = 2.93, min–max = 0–10) consecutive days with Tmin above 0 °C. Using logistic regression pooled across sites and years, 6 variables showed significant quadratic relationships with probability of calling on a given day (Fig. 3, Table 5), with yday having the strongest relationship and solar radiation lacking a significant relationship at the 0.01 level.

Between 2010 and 2020 (Fig. 4), there was a statistically significant delay in beginning of calling activity at Eagle Lake (26 days [2011–2016]; Mann-Kendall

Table 1. Comparison of mean activity parameters (ydays) in *Rana sylvatica* (Wood Frog) among Eagle Lake, Hermit Lake, and Lakes of the Clouds (LOTC), using one-way ANOVA. * indicate variables with P-values ≤ 0.05, showing statistical significance.

	Eagle Lake			Hermit Lake			LOTC			
Variables	*n*	Mean ± SD	Min–max	*n*	Mean ± SD	Min–max	*n*	Mean ± SD	Min–max	*P*-value
Start of calling activity*	7	127.9 ± 9.0	112.0–138.0	10	133.9 ± 6.8	124.0–146.0	8	143.4 ± 6.8	131.0–151.0	<0.001
Start of chorus*	7	131.7 ± 9.5	113.0–140.0	10	137.4 ± 8.2	124.0–154.0	8	149.0 ± 7.5	135.0–159.0	<0.001
Median chorus*	7	139.4 ± 7.9	126.5–147.5	10	145.5 ± 6.8	133.5–155.5	8	155.0 ± 8.9	139.0–168.5	<0.001
End of chorus*	7	149 .0± 6.9	137.0–160.0	10	153.5 ± 7.2	141.0–164.0	8	160.7 ± 9.0	144.0–173.0	<0.05
End of calling activity	7	159.4 ± 10.0	145.0–172.0	10	165.4 ± 6.6	158.0–178.0	8	170.3 ± 9.3	152.0–181.0	> 0.05
Duration of calling activity	7	31.6 ± 3.5	27.0–37.0	10	31.5 ± 5.3	24.0–43.0	8	26.9 ± 4.9	20.0–32.0	> 0.05
Active days*	7	22.9 ± 4.6	15.0–30.0	10	26.8 ± 3.9	21.0–33.0	8	20.7 ± 3.4	18.0–26.0	<0.05
Chorus days*	7	10.0 ± 2.8	8–.016.0	10	14.8 ± 5.6	3.0–23.0	8	8.8 ± 2.2	6.0–12.0	<0.001

test: $P < 0.05$, $n = 7$; Fig. 5), but not at Hermit Lake (22 days; Mann–Kendall test: $P > 0.05$, $n = 10$) or at Lakes of the Clouds (20 days: Mann–Kendall test: $P > 0.05$, $n = 8$). Therefore, we focused on weather peculiarities of Eagle Lake only (Fig. 5). At Eagle Lake, Tmin and mean daily VP, which are highly correlated (Table 6), both declined between 2011 and 2020. However, the median yday of chorus did not significantly correlate with average seasonal Tmin and VP (Table 6). The change in median yday of chorus correlated with SRAD and SWE (Table 6), both of which significantly increased throughout the study period (Fig. 5).

Table 2. Post-hoc pairwise comparisons of the calling-activity variables (ydays in Table 1) among Eagle Lake (EAGLE), Hermit Lake (HERMIT) and Lakes of the Clouds (LOTC) summarized in Table 1, using Tukey's test. * indicate *P*-values ≤0 .05, showing statistical significance.

Variables	EAGLE–HERMIT	LOTC–EAGLE	LOTC–HERMIT
Start of calling activity	>0.05	<0.001*	<0.01*
Start of chorus	>0.05	<0.001*	<0.01*
Median chorus	>0.05	<0.001*	<0.05*
End of chorus	>0.05	<0.05*	>0.05
End of calling activity	>0.05	>0.05	>0.05
Active duration	>0.05	>0.05	>0.05
Active days	>0.05	>0.05	<0.05*
Chorus days	<0.01*	>0.05	<0.001*

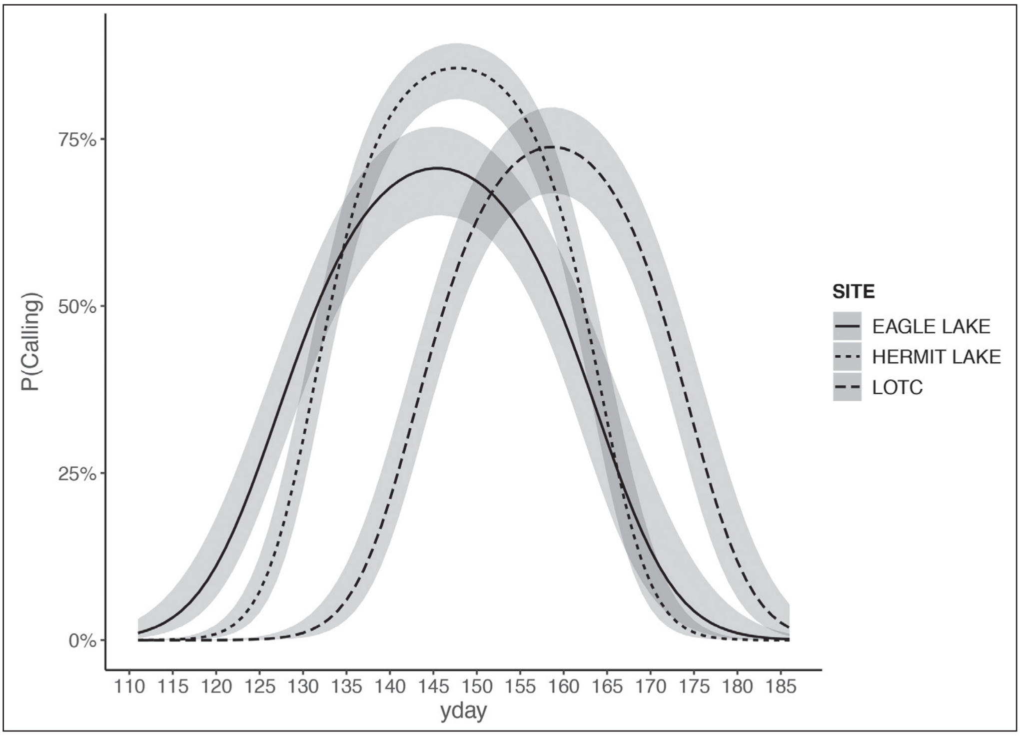

Figure 2. Results of logistic regression model depicting the interaction between yday and site in predicting the probability of a frog calling on a given day.

Discussion

Despite great interest in the exploration of the White Mountains (specifically on Mount Washington) by professional and amateur naturalists dating back to the mid-1800s (e.g., Scudder 1863, Slosson 1893), early reports contained conflicting data on amphibian assemblages in alpine and subalpine ecosystems. For example, Antevs (1932) reported that amphibians were absent from the Lakes of the Clouds on Mount Washington, while Arenberg (1939) described “toads” at the summit feeding on insects attracted to a light. Thoreau (1858) reported unidentified “pollywogs”

Table 3. Summary of early season visual egg mass surveys (2015–2020). Numbers under the study site names indicate interval from the first chorus (in days). yday = days since start of year. LOTC = Lakes of the Clouds.

Dates	yday	Eagle Lake	Hermit Lake	LOTC
10 June 2015	161	-	-	16
24 May 2017	144	-	7	-
8 June 2017	159	-	-	12
26 May 2020	147	7	-	-
31 May 2020	152	-	5	-
19 June 2020	171	-	-	12

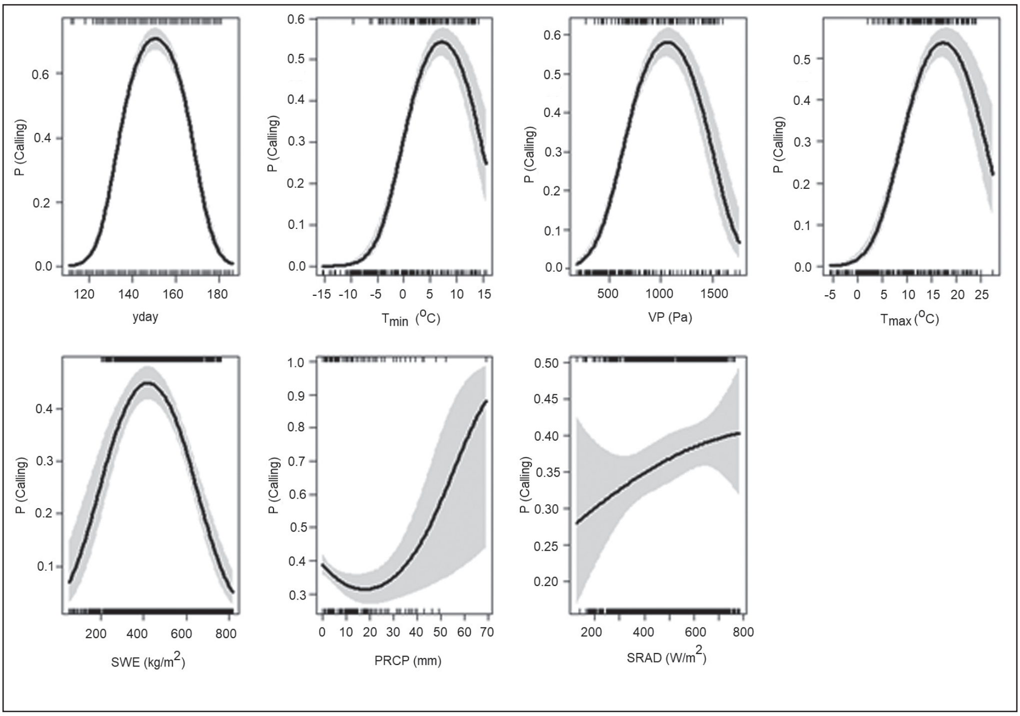

Figure 3 . Relationship between probability of calling at high-elevation ponds and Daymet variables modeled using logistic regression. All variables were fit as a quadratic relationship except solar radiation.

Table 4. Pairwise comparisons (Mann–Whitney U test) of weather variables (see text for abbreviations) between days with and without calling activity, within the activity season (days 111 – 186), years (2011, 2012, 2013, 2015, 2016, 2020) across all sites. * indicate variables with *P*-values ≤ 0.01 showing statistical significance.

	No calling activity			Calling activity			
Weather variables	*n*	Mean ± SD	Min–max	*n*	Mean ± SD	Min–max	*P*-values
PRCP (mm/day)	235	5.23 ± 7.67	0.00–39.00	168	4.12 ± 6.92	0.00–42.00	>0.05
SRAD (W/m^2)*	235	497.84 ± 149.76	140.80–776.10	168	539.54 ± 143.06	162.79–758.40	<0.01
SWE (kg/m^2)*	235	379.34 ± 100.58	144.00–532.00	168	366.23 ± 63.12	204.00–496.00	<0.01
Tmax (°C)*	235	9.57 ± 6.19	-5.00–24.04	168	14.20 ± 4.328	2.00–24.00	<0.001
Tmin (°C)*	235	0.41 ± 5.98	-14.04–15.16	168	4.28 ± 4.45	-9.50–13.50	<0.001
VP (Pa)*	235	682.10 ± 295.72	206.38–1721.80	168	862.50 ± 259.15	280.00–1560.00	<0.001

from Eagle Lake on 15 July 1858 and heard a "bullfrog" at Hermit Lake on 5 July 1858, while also reporting toads in nearby uplands at each Lake. Published lists of aquatic odonates from Hermit Lake and aquatic beetles and mayflies from Lakes of the Clouds (Alexander 1940) demonstrate that naturalists were making careful observations of aquatic wildlife in some of the same ponds we studied, yet there have been no published inventories or any studies focusing on amphibians. The first detailed reports of amphibian diversity in alpine and subalpine ponds from the White Mountains included 4 anuran and 2 caudate amphibian species (Jones 2005, Jones and Smyers 2010). Our results confirm persistence of 4 anuran species in Eagle Lake, Hermit Lake, and Lakes of the Clouds and present the first report of the Gray Treefrog at our study sites. Wood Frog, Green Frog, American Toad, and Spring Peeper are common throughout New England and have been reported from 3 types of lower-elevation forests in Kilkenny Wildlife Management Unit of White Mountains National Forest (Degraaf and Rudis 1990) and from other alpine sites in the region including Mount Mansfield, VT (Trombulak and Andrews 1995) and Chimney Pond, Baxter State Park, ME (Jones and Willey 2018). Green Frog and Eastern Newt are the 2 species that occur the least frequently and both require ponds that do not freeze solid to overwinter (Hunter et al. 1999). Wood Frog, Spring

Table 5. Results of logistic regression models assessing the probability of calling on a given day as a function of Daymet variables, pooled across sites and years. Each variable (see text for abbreviations) was fit as both a simple and quadratic model and compared using AIC. Parameter estimates, standard errors, and *P*-values are provided for the best fitting model for each variable. Quadratic models fit better for all variables except Solar Radiation.

			Parameter estimates for best fitting model				
Variables	Simple model AIC	Quadratic model AIC	Simple term estimate	SE	Quadratic term estimate	SE	*P*-value
yday	2072.7	1557.9	1.39E+00	8.44E-02	-4.61E-03	2.83E-04	<0.001
Tmin	1956.8	1880.5	2.70E-01	2.32E-02	-1.87E-02	2.37E-03	<0.001
VP	2002.2	1891.5	1.32E-02	1.18E-03	-6.19E-06	6.45E-07	<0.001
Tmax	1956.4	1895.5	4.82E-01	5.31E-02	-1.38E-02	1.94E-03	<0.001
SWE	2129.8	2075.3	1.47E-02	2.43E-03	-1.75E-05	2.60E-06	<0.001
PRCP	2144.0	2137.3	-3.73E-02	1.30E-02	1.06E-03	3.89E-04	<0.01
SRAD	2140.2	2142.0	-3.73E-02	3.63E-04			0.033

Table 6. Correlation matrix among median yday of chorus and Daymet weather variables(see text for abbreviations) based on seasonal (yday 111–186) averages at Eagle Lake.

Variable	Median yday of chorus	PRCP	SRAD	SWE	Tmax	Tmin	VP
Median yday of chorus		-0.73	0.81	0.84	-0.82	-0.57	-0.54
PRCP	-0.73		-0.71	-0.41	0.71	0.53	0.49
SRAD	0.81	-0.71		0.87	-0.66	-0.85	-0.79
SWE	0.84	-0.41	0.87		-0.58	-0.65	-0.62
Tmax	-0.82	0.71	-0.66	-0.58		0.69	0.72
Tmin	-0.57	0.53	-0.85	-0.65	0.69		0.94
VP	-0.54	0.49	-0.79	-0.62	0.72	0.94	

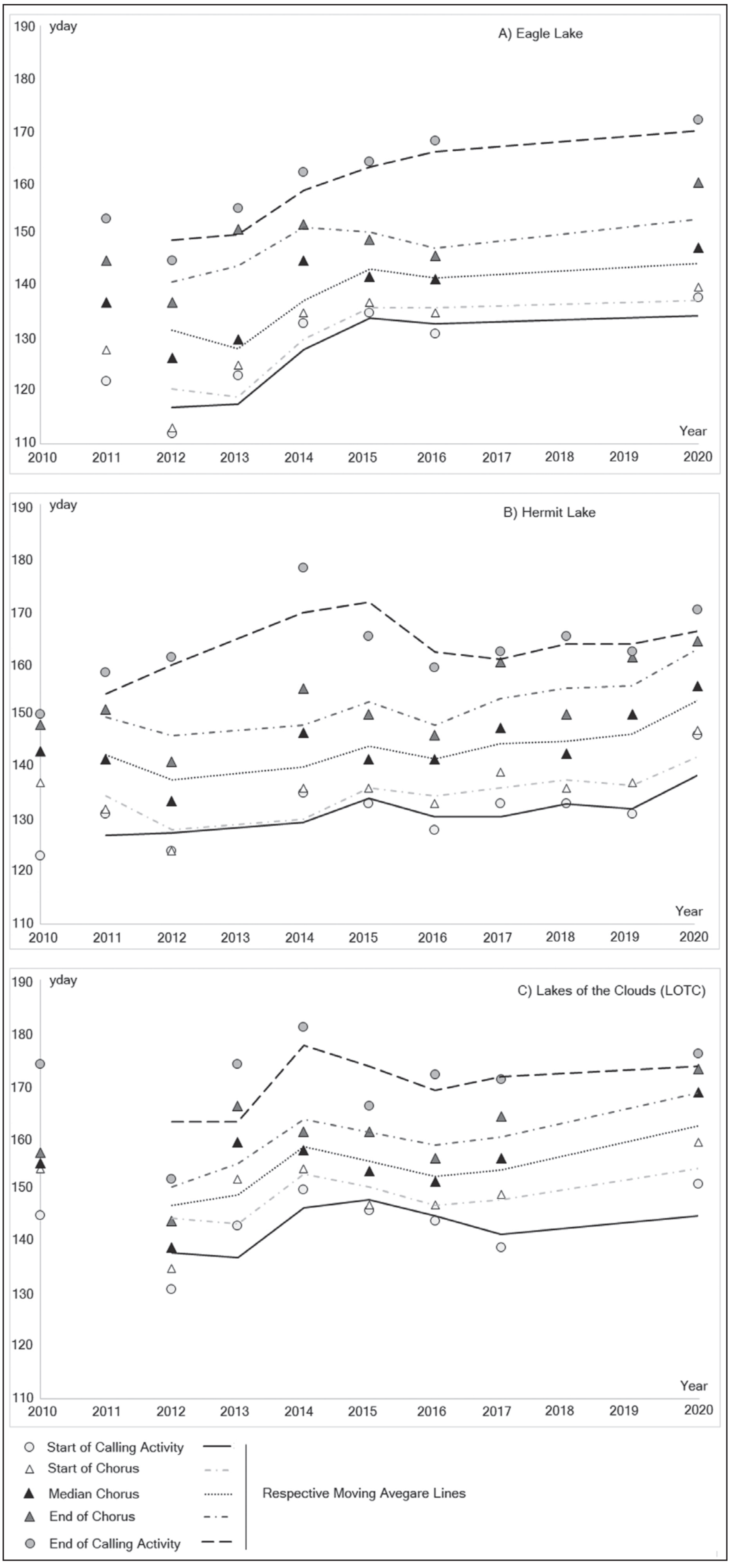

Figure 4. Temporary changes in the call activity of Wood Frogs at 3 study sites between 2010 and 2020.

Peeper, Gray Treefrog, and American Toad—which overwinter terrestrially (Dodd 2013)—are likely better adapted to the alpine and subalpine habitat where many wetlands and ponds regularly or occasionally freeze solid.

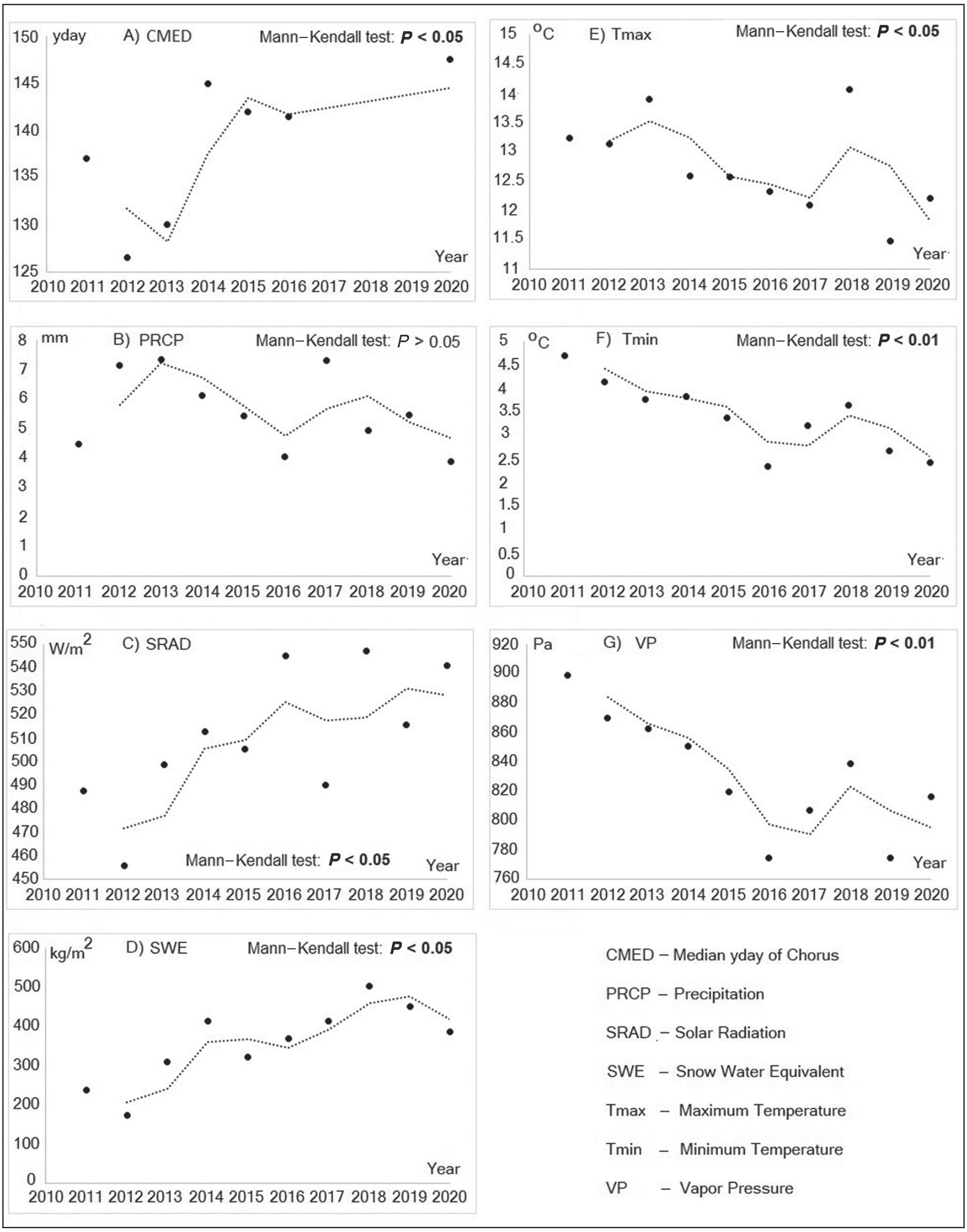

Figure 5. Temporary changes in the median yday of chorus of Wood Frogs (2011–2020) and average daily weather variables on ydays 111–186 (2011–2020) at Eagle Lake. Note that due to missing call recordings in 2017–2019, Mann-Kendall test for median yday of chorus of Wood Frogs was run for 2011–2016 data only.

Our recordings revealed changes in species assemblages over the study period including the apparent decline of Green Frog at Hermit Lake between 2010 and 2016 followed by an apparent rebound through 2020 and only 1 year of calling American Toad at Eagle Lake (2016). Natural population fluctuations can contribute to detectability, seasonally, while species-specific attributes such as explosive breeding (Wood Frog) may also result in low detectability (Cook et al. 2011, Shearin et al. 2012, Werner et al. 2009). Other explanations include abiotic perturbations associated with weather and timing of vocalization recording (Shearin et al. 2012), pollution (Daszak et al. 2003, Blaustein et al. 2010), disease (Hayes et al. 2010, Blaustein et al. 2010), predators (Alford 1989, Blaustein et al. 2010), and recent colonization (Blaustein et al. 2010), which were not studied across our sites. Therefore, it is important to continue monitoring these populations closely to document trends and compare life-history variation over time.

Mainly due to its freeze tolerance (Layne and Lee 1995, Storey and Storey 1984), the Wood Frog is the earliest breeding amphibian species established farther north than any other terrestrial ectothermic vertebrate in North America (Kessel 1965) and occurs at the highest ponds in the Appalachian Mountains of the northeastern United States (Jones and Smyers 2010, Jones and Willey 2018). Latitude- and elevation-driven climate gradients result in varying timing of calling activity, breeding, oviposition, foraging, growth, and development (Berven 1995, Berven 1983, Dodd 2013, Guttman et al. 1991). These influences might be greater for species that breed early in the year (Crouch and Paton 2002). Significant differences in average dates of the beginning of calling activity, beginning of chorus, and the median date of chorus among our study sites (Tables 1, 2), generally reflect elevation-driven differences in weather among Lakes of the Clouds, Eagle Lake, and Hermit Lake.

Furthermore, at our sites, beginning of chorus dates, which are expected to be closely associated with the reproduction, were also closer to those at College, AK (64°52' latitude, 142 m a.s.l., yday 115–139; Kessel 1965), and substantially later compared with reproduction dates (yday 74–113) reported at Yale Myers Forest in northwestern Connecticut (41°57'N latitude, 190–296 m a.s.l.; Arietta et al 2020) and beginning of chorus in Washington County, southern Rhode Island (41°N latitude, ~41–71 m a.s.l., yday 61–66; Crouch and Paton 2002). Based on our literature review, we did not find references with relevant data from New Hampshire to compare with our results.

Wood Frogs call and mate under cold conditions when food is scarce (McCauley et al. 2000), thus they rely on energy reserves accumulated during the prior season (Dodd 2013). Acoustic advertisement is among the most energetically expensive activities regularly undertaken by anurans (Pough et al 1992, Taigen and Wells 1985). Waldman (1981) conducted direct observations of breeding behavior over 4 seasons, and oviposition occurred within 2–6 days (Tompkins County, NY) while Cook et al. (2010) used frog-call surveys (including recordings) over 6 years and reported 1–9 days (mean = 3.3) in the calling season (Barnstable County, MA). The duration of calling activity at the alpine ponds we studied was much longer than what was reported in those studies and did not differ between our study sites, unlike the beginning of calling activity (Table 1). The number of chorus days, on the other hand, differed among our study sites (Table 1) but was close to the values reported in literature (Cook et al. 2011, Dodd 2013). Herreid and Kinney (1967) reported eggs appearing 4–6 days after the first frog encounters. Our egg-mass surveys (Table 3) revealed fresh eggs present at the lakes 5–17 days after the beginning of chorus. Thus, our phenological observations suggest that Wood Frogs at alpine and subalpine lakes, and in particular at Hermit Lake, exhibit a less-compressed breeding season compared to lowland populations. Explosive breeding has been associated with selective advantages resulting from early oviposition in females (Waldman 1982), and maximizing post-breeding feeding and energy-recovery opportunities in both sexes (Dodd 2013, McCauley et al. 2000). If females are available for mating for an extended breeding season at alpine and subalpine ponds, individual male Wood Frogs may keep calling until either the last female spawns, those males exhaust their energy reserves, food becomes widely available, or any combination of these factors. More research is needed to better understand advantages and shortcomings of explosive breeding in an environment with unpredictable weather variations that influences reproduction, foraging, and seasonal food availability.

Life history and reproductive behavior in most temperate amphibians is regulated primarily by temperature (Reading 1998, Weir et al. 2005), but also by rainfall (Green 2017, Tryjanowski et al. 2003), photoperiod (Canavero and Arim 2009, Green 2017), and time after sunset, moonlight, and wind (Johnson and Batie 2001, Weir et al. 2005). Shearin et al. (2012) studied the vocalization of amphibians across 2 biophysical regions of Maine and concluded that the probability of calling activity in Wood Frogs was strongly predicted by date, but also by decreased precipitation, moonlight, cloud cover, and wind. We did not have consistent weather data collected at our sampling sites. Therefore, we explored calling activity patterns in the context of daily weather variables obtained from DayMet (Version 4; ORNL 2020, Thornton et al. 2020). DayMet data consists of interpolated and extrapolated values based on the nationwide weather station data at 1-km^2 resolution (Thornton et al. 1997). Due to its generality, such data cannot directly account for microhabitat selection or localized patterns of activity. Navas et al. (2013) found that the temperature data obtained from Bioclim, which also uses extrapolated or interpolated weather station data, severely underestimated body temperatures of frogs at temperatures <15 °C, and overestimated body temperatures at high temperatures >20 °C. Due to this generality, patterns derived with use of Daymet weather data are intended for general exploration, and should be cautiously interpreted if applied to understanding Wood Frog's physiological responses to in situ climate variables. In general, our findings (Table 4) suggest that Wood Frogs call on days that are significantly warmer, have higher VP, and lower SWE than on days they do not call, but that each of these has a unimodal relationship with probability of calling (Table 5, Fig. 3), and Wood Frogs were less likely to call at the highest values of each of these variables. Across our study sites, yday, Tmin, and VP had higher predictive scores on probability of calling of Wood Frogs as compared with SWE and PRCP (Fig. 3).

The delayed start of calling activity at Lakes of the Clouds may be due to lower temperatures at higher elevation or may be associated with effects of sudden frozen precipitation or frosts extending into the activity season of the Wood Frog, which forces frogs to begin calling later in the season when the days are warm enough. Precipitation was ranked low in our calling-probability model compared to temperature and other variables (Table 6, Fig. 3), which could be due to broadscale nature of the weather data, or a characteristic of these sites. Future monitoring with pond-specific weather data would help to elucidate these relationships.

Many amphibians advance the timing of reproduction in response to warming weather (Caroll et al. 2009, Gibbs and Breisch 2001, Hughes 2000, Tryjanowski et al. 2003). Based on long-term observations of breeding phenology in amphibians in the UK, Beebee (2002) concluded that the European ecological equivalent of Wood Frog—the explosive-breeding *Rana temporaria* L. (Common Frog) — as well as *Bufo bufo* (L.) (Common Toad) have shown little sign of change in timing of reproduction in response to changing climate, as compared with later, non-explosive breeding species. Our time series indicated a statistically significant delay in the onset of calling at 1 of 3 sites (Eagle Lake), likely due in large part to the timing of onset in 2012–2013 (Fig. 4). DayMet data at this site suggest a concurrent decrease in average Tmin, Tmax, and Vp on ydays 111–186, along with the increase in SRAD and SWE during our study period (Fig. 5). The phenology of the Wood Frog may be associated with the cumulative effect of interacting weather variables. Decreasing Tmin slows down the rate of thawing, and if cold enough, additional frozen precipitation can replenish the snowpack (SWE). Increasing SRAD, on the other hand, may prevent Tmax from following the pattern of Tmin. In this context, the delay of the beginning of calling activity in Wood Frogs at Eagle Lake appears to be associated with the effects of decreasing Tmin and delayed thawing of snow. This pattern likely results in the extension of winter weather into the time-frame of the calling activity of Wood Frog, and may constitute a counterintuitive example of how longer-term warming trends in a region can include earlier dates of winter–spring snowmelt throughout the region (Arietta et al. 2020, Hodgkins and Dudley 2006, Seidel et al. 2009) but also extended winter conditions within the same region's alpine and subalpine ecosystems. Long-term studies of amphibians can reveal trends in phenology and population dynamics (Arietta et al. 2020, Gibbs and Breisch 2001, Whiteman and Wissinger 2005) and make possible exploration of climatic covariates (Arietta et al. 2020, Green 2017). However, the variability in observations, outliers, and gaps in phenological observations may substantially affect conclusions about the magnitude of such temporary trends (Green 2017). For instance, in Wood Frogs from Alaska, the first date of calling varied by as much as 3 weeks between years and was influenced by annual variations in temperature and snowmelt (Kessel 1965). Because of limited duration (10 years), missing years, and occasional incomplete coverage in our call-phenology data, the phenological delay of calling at Eagle Lake should be interpreted with caution. We consider the observed delay to be a hypothesis warranting further research with consistent data-collection via monitoring of calling phenology in anurans across our study sites and possibly other alpine ponds in the White Mountains.

As weather patterns continue to change, alpine environments may be some of the most susceptible (Gobiet et al. 2014, Grabherr et al. 2010) or may change more slowly (Seidel et al. 2009), offering refuge to lower-elevation species. This study serves as a baseline to assess how these alpine ponds and their amphibians may change over time. Our data may be important for comparison to other populations throughout the species' extensive range and may inspire and justify future research on local biodiversity of alpine and subalpine ponds in the northeastern United States. Our phenological analysis juxtaposed with weather data provides a deeper insight and better understanding of the biology of Wood Frogs at the extreme of their elevational distribution in the northern Appalachian Mountains.

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