Herpetological Conservation and Biology 19(3):466–474.
Submitted: 2 November 2023; Accepted: 8 November 2024; Published: 16 December 2024.

Onset of Early Spring Activity by Amphibians in Ithaca, New York, USA

Patrick J. Baker[1,4], *Rachel Hughes*[2], *and James Hughes*[1,3]

[1]*Department of Geography and Environmental Engineering, United States Military Academy, 646 Swift Road, West Point, New York 10996, USA*
[2]*Environmental Sciences Graduate Program, Oregon State University, 2900 Southwest Jefferson Way, Corvallis, Oregon 97331, USA*
[3]*Department of Physics and Meteorology, United States Airforce Academy, 2354 Fairchild Drive, Colorado Springs, Colorado 80840, USA*
[4]*Corresponding author, e-mail: patrick.baker@westpoint.edu*

Abstract.—**In the northeastern U.S., average temperature and precipitation have increased since the early 20th Century and extreme precipitation events have become more frequent. In response, the timing of life-history transitions has changed in some populations of early spring-breeding amphibians. Migration from their upland hibernacula is stimulated by environmental cues that may forecast favorable conditions at breeding sites; however, in what is called a false spring, the earliest amphibians may be exposed to lethal low temperatures after breaking dormancy. Spotted Salamanders (*Ambystoma maculatum*), Spring Peepers (*Pseudacris crucifer*), and Wood Frogs (*Lithobates sylvaticus*) frequently co-occur in vernal pond communities and breed at the earliest opportunity each spring. To better understand how changes in climate have influenced the timing and risk of early activity in this group we compared their first appearance and attendant environmental conditions between published accounts from the early 1900s and recent observations (2016–2024) from iNaturalist. We found that Spotted Salamanders, Spring Peepers, and Wood Frogs advanced activity by 13.4, 17.5, and 11.8 d, respectively. Onset of activity in 2016–2024 was associated with greater precipitation (Spring Peepers) and higher maximum daily temperatures (Spotted Salamanders) relative to the early 1900s. Species-specific values for snow depth, days from snow melt, mean 3-day temperature, and thermal accumulation above 3° C, however, were similar between periods for all three species. The earlier onset of activity observed in 2016–2024 was associated with greater freezing risk to all three species which is consistent with the False Spring hypothesis.**

Key Words.—climate change; emergence; frog; migration; phenology; salamander

Introduction

Global climate change interacts with the geographic characteristics of specific regions to produce a climate change signal unique to that region (Hayhoe et al. 2008). In the northeastern U.S., average temperature and precipitation have increased since the early 20th Century and the region has experienced the most rapid increase in the number and frequency of extreme precipitation events (Jessica Whitehead et al. 2023. Northeast. *In* Fifth National Climate Assessment. Crimmins, A.R., C.W. Avery, D.R. Easterling, K.E. Kunkel, B.C. Stewart, and T.K. Maycock (Eds.). U.S. Global Change Research Program, Washington, D.C., USA. Available from https://doi.org/10.7930/NCA5.2023.CH21. [Accessed 1 May 2024]). In response to these changes in regional climate, many organisms in the northeast are experiencing changes to their phenology (e.g., Butler 2003; Fuccillo Battle et al. 2022).

As a group, amphibians exhibit a general trend towards earlier breeding in response to global climate change (While and Uller 2014); however, populations in the northeastern U.S. and Canada exhibit both advancement (Gibbs and Breisch 2001; Walpole et al. 2012; Green 2017) and delay (Arietta et al. 2020; Moldowan et al. 2022). By identifying the abiotic cues that drive these behaviors, we can gain insight into how climate change may impact phenological variation among different groups, which, in turn, can provide valuable information on how populations and ecological communities may be affected (Chmura et al. 2019; Benard and Greenwald 2023).

Although average annual air temperature and annual precipitation have both increased in the region, high interannual variability in the timing of environmental cues (e.g., snowmelt date, minimum temperature thresholds) may require long-term datasets to detect shifts in phenology related to climate change (Lovett 2013; Green 2017). Studies that incorporate a combination of historical observations and modern observations have been successful in documenting phenological change (e.g., Gibbs and Breisch 2001; Fuccillo Battle et al. 2022; Iwanycki Ahlstrand et al. 2022). Citizen science programs that generate reliable observations (e.g., New York State Amphibian and Reptile Atlas Project, iNaturalist) expand our ability to document natural history phenomena beyond the constraints of time and space that limit any single investigator or study site (Gibbs and Breisch 2001; Forti et al. 2022).

Although warmer winters may stimulate earlier breeding, earlier onset of spring activity under the influence of a changing climate may be harmful to amphibian populations (Benard 2015; Bison et al. 2021; Moldowan et al. 2022). For example, the false spring hypothesis suggests that earlier onset of activity may result in lowered reproductive success (Buss et al. 2021; Yermokhin and Tabachishin 2022). For early spring-breeding amphibians, a frost that occurs after the onset of activity increases risk of freezing for adults, eggs, and larvae (Hinckley 1882; Wright 1914; Harris 1980; Frisbie et al. 2000).

We examined the timing of first appearance in a group of widely distributed and well-studied North American amphibian species that frequently co-occur in woodland pond communities (Husting 1965; Paton et al. 2000; Kirk et al. 2019). Spotted Salamanders (*Ambystoma maculatum*), Spring Peepers (*Pseudacris crucifer*), and Wood Frogs (*Lithobates sylvaticus*) hibernate terrestrially and initiate migration to breeding ponds at the earliest opportunity each spring (Wright 1908). Onset of activity is relatively synchronous for these three species (Wright 1908); however, the proximate cues that trigger the onset of activity in individual species are complex and likely vary in time and space (e.g., Blanchard 1930; Baldauf 1952; Sexton et al. 1990; Benard and Greenwald 2023). It is generally agreed that onset of activity for these species occurs after snowmelt in late winter/early spring on relatively warm, humid evenings (Sexton et al. 1990).

Given the earlier onset of what is called first voice in Spring Peepers and Wood Frogs in Ithaca, New York, USA (Gibbs and Breisch 2001), we hypothesized that first appearance has changed in recent years compared to early 1900s. We predicted that first appearance of Spring Peepers and Wood Frogs should occur earlier. We also predicted that Spotted Salamanders would also appear earlier based on the historic similarity to Spring Peepers and Wood Frogs in their reaction norms to temperature and precipitation cues. Further, we hypothesized that first appearance of early spring-breeding amphibians is forecasted by the same favorable environmental conditions that occur earlier in recent years than they did at the beginning of the last century. We predicted first appearance would occur when the maximum daily temperature and the daily precipitation total were similar to the corresponding values reported for first appearance in the 1900s. Finally, we tested the False Spring hypothesis by determining if the freezing risk after the onset of activity has increased for these early spring-breeding amphibians since the 1900s.

Materials and Methods

We extracted dates of first appearance (DFA) for early spring-breeding amphibians in the vicinity of Ithaca, New York, USA, for the period 1900–1911 from historic accounts by Albert Hazen Wright (Wright 1908, 1914; Wright and Allen 1909). Wright compiled his personal observations and those by members of the Department of Zoology at Cornell University with a focal area at the southern end of Cayuga Lake (Reed and Wright 1909). Most of his observations were recorded within a radius of 5 km from the Cornell University campus (Wright 1914).

For recent observations, we examined all verifiable, research grade observations with photographs of amphibians (Category = Amphibia) in Ithaca, New York, for the period 1 February to 30 April for the years 2016–2024 from iNaturalist (www.inaturalist.org). To approximate the spatial extent of Wright (1914), we established a circular boundary for observations with a 5-km radius centered on the Cornell University campus (42.45° N, 76.48° W; Fig. 1). These data were exported to Zenodo (https://doi.org/10.5281/zenodo.13997066). The date of the first observation of each species in each year was designated as the DFA. We converted all dates to ordinal day (y-day) to account for leap years and facilitate statistical analysis.

We obtained meteorological data for Ithaca from 1900–1911 and 2016–2024 (https://www.nrcc.cornell.edu/wxstation/ithaca/ithaca.html). The weather station is located on the Cornell University campus near the center of the area established for iNaturalist observations. Available data from this station include daily values for maximum, minimum, and average temperatures (°F), precipitation (inches), snowfall (inches), and snow depth (inches). All values were converted to standard scientific units prior to analysis.

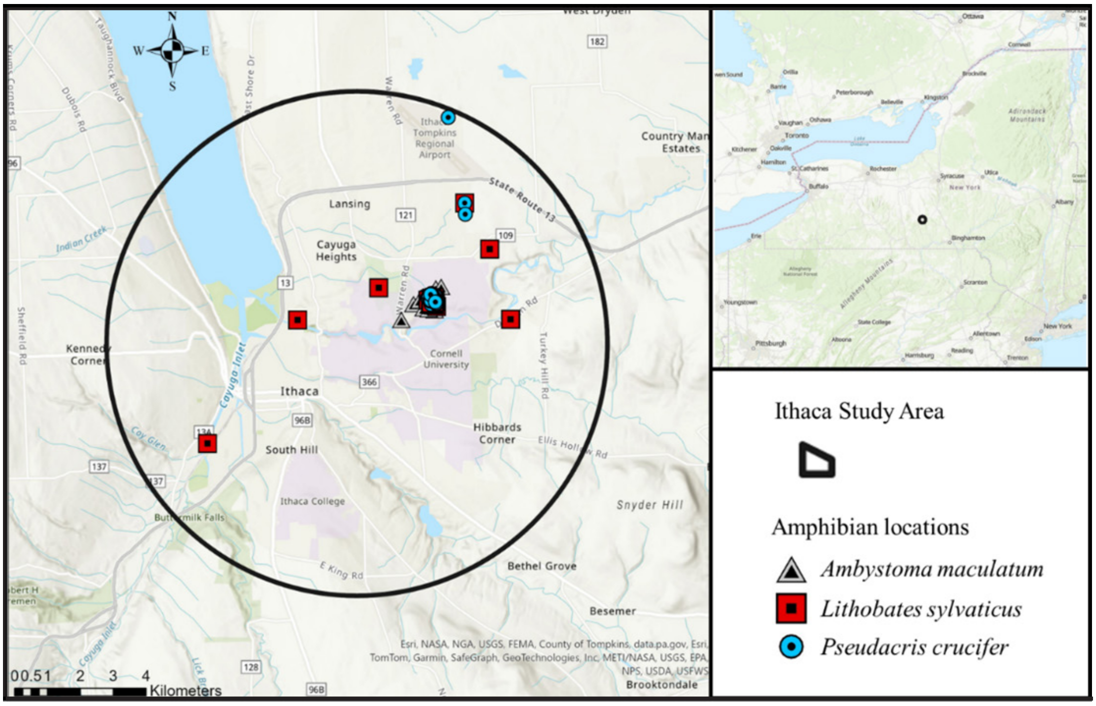

Figure 1. Area of observations for onset of early spring breeding amphibians (2016–2024) in the vicinity of Ithaca, New York, USA. The black circle delineates an area with a radius of 5 km centered on the Cornell University campus (42.45°N, 76.48°W). Filled symbols indicate all locations on the day of first appearances of Spotted Salamanders (*Ambystoma maculatum*, gray triangles), Spring Peepers (*Pseudacris crucifer*, blue circles), and Wood Frogs *(Lithobates sylvaticus*, red squares) in each year of study.

Precipitation is an important variable in the phenology of early spring breeding amphibians because rainfall may stimulate activity, and the presence of snow will generally preclude the onset of activity (Blanchard 1930; Sexton et al. 1990; Arietta et al. 2020; Bison et al. 2021). An accumulation of snow on the landscape insulates the shallow subterranean habitats of terrestrially hibernating amphibians from the influence of variable air temperatures (Bison et al. 2021). Onset of amphibian activity usually occurs several days after the snow has melted because of the additional energy required to thaw frozen soil and melt ice-covered ponds (Blanchard 1930; Baldauf 1952; Bison et al 2021). We recorded snow depth on the DFA for each species and, when snow was absent, calculated the number of days between DFA and the last day with measurable snow. Daily precipitation values in the meteorological record from Ithaca follow a 24 h clock beginning/ending at 0700. We recorded the precipitation total for the 24 h period that includes the DFA.

To better understand the cumulative influence of air temperature on activity, we computed two metrics that have been associated with the onset of amphibian activity. Following Sexton et al. (1990), we calculated a running average of mean temperature for the DFA and the two days prior (mean 3 d). We also calculated thermal accumulation with a basal temperature of 3° C from 1 February to the DFA for each species in each year of the study. Although a range of basal temperatures can be used in degree day approaches, we selected the 3° C degree day (T3DD) because this metric was the best predictor of date of first calling for Spring Peepers in southern New York (Lovett 2013). T3DD was calculated as the difference between average daily temperature (°C) and 3° C. By this method, a day with an average temperature ≤ 3° C yields 0 T3DD and a day where the average temperature = 10° C yields seven T3DD. We summed daily T3DD values for the period of observation (February-April) beginning on 1 February (y-day = 32) and recorded species-specific values for accumulated T3DD on the DFA.

To test the False Spring hypothesis, we quantified days of freezing risk (DFR) associated with the onset of amphibian activity. For each species in each year, we computed the cumulative freezing risk after the DFA. Following the methods of Bison et al. (2021), we calculated DFR as the number of days when the minimum daily temperature was < -2° C. DFR was summed for each species from the DFA to 30 April.

Table 1. Number of iNaturalist observations (1 February to 30 April) for three species of early spring-breeding amphibians: Spring Peepers (*Pseudacris crucifer*), Wood Frogs (*Lithobates sylvaticus*), and Spotted Salamanders (*Ambystoma maculatum*). Observations were in the vicinity of Ithaca, New York, USA, over 9 y (2016–2024).

Species	2016	2017	2018	2019	2020	2021	2022	2023	2024	Total
Spring Peepers	2	4	14	9	10	21	28	39	10	137
Spotted Salamanders	7	20	41	28	24	55	193	108	70	546
Wood Frogs	1	1	2	6	3	4	10	26	10	65

We analyzed our data in R Statistical Software (v4.2.2; R Core Team 2022). We compared DFA, metrics of precipitation (snow depth, days from snow melt, and daily precipitation), metrics of temperature (maximum daily, mean 3 d, and T3DD), and DFR for each species between 1900–1911 and 2016–2024 with a Wilcoxon Rank Sum Test with continuity correction. We accepted significance when $P \leq 0.05$. We mapped locations of amphibians on DFA in Ithaca using ArcGIS Pro 3.1.0 (Esri, Redlands, California, USA). We created boxplots of DFA and DFR using ggplot2 (v3.4.4; Wickham et al 2016).

Results

Based on our review of several papers published by Albert Hazen Wright, we identified records of the first appearance of adults for nine Spotted Salamanders (1900–1908), 12 Spring Peepers (1900–1911), and six Wood Frogs (1904–1908, 1911). Wright (1908) reported observations of Wood Frogs for each year in the period 1900–1911, but the 1900–1903 and 1909–1910 observations were based on egg masses suggesting activity began days earlier. We followed Wright (1914) and excluded first appearance dates for Wood Frogs when the DFA was based on the observation of egg masses without adults present. The iNaturalist query for observations of amphibians in the vicinity of Ithaca yielded 1,256 research grade observations of amphibians of which 748 were of the three focal species (Table 1). Spotted Salamanders had the greatest number of observations in each of the 9 y and the most observations overall (546).

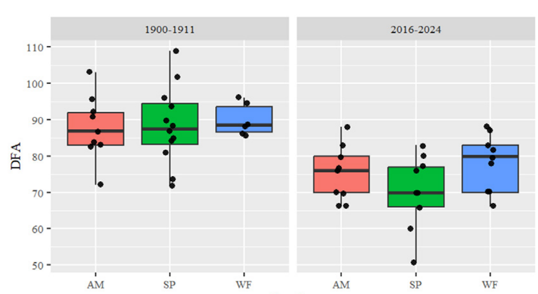

Figure 2. Box plot of days of first appearance (DFA) for Spotted Salamanders (*Ambystoma maculatum*; AM), Spring Peeper (*Pseudacris crucifer*; SP), and Wood Frog (*Lithobates sylvaticus*; WF) for (left) the early 1900s, and for (right) 2016–2024 in the vicinity of Ithaca, New York, USA. The horizontal lines through each box are the median values, the bottom and the top of the boxes are the 1st and 3rd quartiles, and black dots are the DFA value for each year of the study.

We found DFA significantly advanced in recent years relative to the early 1900s for Spotted Salamanders ($W = 10.0$, $P = 0.008$), Spring Peepers ($W = 9.0$, $P = 0.002$), and Wood Frogs ($W = 4.5$, $P = 0.009$; Fig. 2). When comparing recent observations of DFA to the phenophase of first appearance given by Wright, we found a 13.4, 17.5, and 11.8 d advance in DFA for Spotted Salamanders, Spring Peepers, and Wood Frogs, respectively, since the early 1900s. We found little difference in the environmental cues associated with DFA between periods of observation. No measurable snow was present on DFA for any species in 1900–1911. In recent years, measurable snow was recorded on DFA in 2023 when 7.6 cm of snow was present for Spotted Salamanders and Spring Peepers. Although the daily measurement of snow depth is determined at 0700, photographs accompanying several iNaturalist observations confirm the presence of snow that evening. No measurable snow was recorded the following morning. Days from snow melt were also similar for both time periods. In 1900–1911, the average for each species ranged from 11.2–13.2 d and in 2016–2024 the average for each species ranged from 8.4–9.9 d. Precipitation associated with DFA was significantly greater in 2016–2024 for Spring Peepers ($W = 85.5$, $P = 0.022$), but not for Spotted Salamanders ($W = 56.0$, $P = 0.173$) or Wood Frogs ($W = 18.0$, $P = 0.307$; Table 2). Maximum daily temperature associated with DFA was significantly greater in 2016–2024 for Spotted Salamanders ($W = 67.0$, $P = 0.021$), but not for Spring Peepers ($W = 72.0$, $P = 0.212$) or Wood Frogs ($W = 38.0$, $P = 0.215$; Table 3). Species-specific values for mean 3-d temperature, and thermal accumulation (T3DD) on the DFA were similar between time periods for each species ($P > 0.05$). Freezing risk for Spotted Salamanders ($W = 76.0$, $P = 0.002$), Spring Peepers ($W = 97.0$, $P = 0.002$), and Wood Frogs ($W = 95.5$, $P = 0.004$) was significantly greater in recent

Table 2. Precipitation cues on day of first appearance for three early spring-breeding amphibians (Spring Peepers, *Pseudacris crucifer*, Wood Frogs, *Lithobates sylvaticus*, and Spotted Salamanders, *Ambystoma maculatum*) in the vicinity of Ithaca, New York, USA. Early observations of Spotted Salamanders are from 1900–1908. Values are mean ± standard error. Sample sizes were nine for all entries except Spring Peepers (n =12) and Wood Frogs (n = 6) for 1900–1911. Bolding indicates a significant difference between time periods based on a Wilcoxon Rank-Sum Test.

	1900–1911	2016–2024	*P*-value
Spring Peepers			
Snow depth (cm)	0.0 ± 0.0	0.1 ± 0.1	0.834
Days after snowmelt	13.2 ± 2.1	8.4 ± 2.3	0.182
Precipitation (mm)	1.1 ± 0.9	2.1 ± 0.6	**0.022**
Wood Frogs			
Snow depth (cm)	0.0 ± 0.0	0.0 ± 0.0	--
Days after snowmelt	12.5 ± 3.0	9.9 ± 1.8	0.478
Precipitation (mm)	2.7 ± 1.4	0.5 ± 0.4	0.307
Spotted Salamanders			
Snow depth (cm)	0.0 ± 0.1	0.1 ± 0.1	1.000
Days after snowmelt	11.2 ± 1.4	9.0 ± 2.2	0.594
Precipitation (mm)	0.8 ± 0.7	1.4 ± 0.6	0.173

Table 3. Temperature cues on day of first appearance for three early spring-breeding amphibians (Spring Peepers, *Pseudacris crucifer*, Wood Frogs, *Lithobates sylvaticus*, and Spotted Salamanders, *Ambystoma maculatum*) in the vicinity of Ithaca, New York, USA. Early observations of Spotted Salamanders are from 1900–1908. Values are mean ± standard error. Sample sizes were nine for all entries except Spring Peepers (n =12) and Wood Frogs (n = 6) for 1900–1911. Bolding indicates a significant difference between time periods based on a Wilcoxon Rank-Sum Test.

	1900–1911	2016–2024	*P*-value
Spring Peepers			
Maximum Daily Temperature (°C)	11.0 ± 2.2	15.4 ± 2.0	0.189
Mean 3d Temperature (°C)	6.1 ± 1.2	2.8 ± 2.3	0.203
Thermal Accumulation	35.5 ± 5.7	31.7 ± 5.7	0.792
Wood Frogs			
Maximum Daily Temperature (°C)	12.2 ± 2.4	16.2 ± 1.8	0.215
Mean 3d Temperature (°C)	7.2 ± 2.2	6.2 ± 1.4	0.607
Thermal Accumulation	33.6 ± 6.3	40.4 ± 5.2	0.529
Spotted Salamanders			
Maximum Daily Temperature (°C)	9.4 ± 1.4	15.5 ± 1.7	**0.021**
Mean 3d Temperature (°C)	4.9 ± 0.7	5.2 ± 1.5	1.000
Thermal Accumulation	33.7 ± 6.4	36.4 ± 4.4	0.387

years than in the early 1900s (Fig. 3). On average, DFR has almost tripled for Spotted Salamanders (2.7 × DFR1900s), Spring Peepers (2.9 × DFR1900s), and Wood Frogs (2.8 × DFR1900s), with species-specific increases of 11.2, 13.0, and 9.9 DFR, respectively.

Discussion

Our study leverages publicly available citizen science data from iNaturalist to demonstrate an advance in the onset of activity in Spotted Salamanders, Spring Peepers, and Wood Frogs relative to data collected by faculty and students at Cornell University in the early 1900s. We recognize that unstructured citizen science datasets (e.g., iNaturalist) have the potential to introduce spatial or temporal bias in observations of phenological events (Gibbs and Breisch 2001; Callaghan et al. 2019; Geurts et al. 2023). By restricting the area of interest to approximate the area studied by Wright and colleagues at Cornell University, we reduced, but did not eliminate spatial bias in the 2016–2024 dataset. For example, the specific locations were not available for each of the observations by Wright; however, several first appearances were reported from areas adjacent to Cayuga Lake (e.g., base of West Hill and Renwick Marsh; elevation 117 m). In the 1900s, these low-lying areas had a slightly warmer microclimate than higher elevation locations (Reed and Wright 1909). We found no DFA observations in the 2016–2024 dataset from the remnants of Renwick Marsh at the south end of Cayuga Lake. Many observations, especially those of Spotted Salamanders and Spring Peepers, were from natural areas at higher elevations (about 300 m) and immediately adjacent to the Cornell University campus. All else being equal, favorable conditions for amphibians should occur later at this higher elevation location.

A second potential bias in unstructured citizen science datasets is the variability in observer sampling effort (Callaghan et al. 2019; Geurts et al 2023). Wright was motivated to accurately describe the life cycle of amphibians by detecting the earliest and latest observations of several life-history events (e.g., first appearance, first voice-record, first eggs, last appearance) in each year and is presumed to have made daily observations (Gibbs and Breisch 2001). We do not know the motivation of the iNaturalist observers in this study; however, observations of

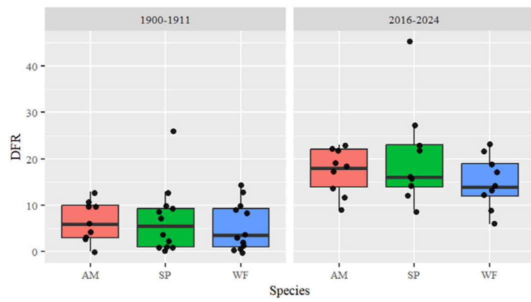

Figure 3. Box plot of days of freezing risk (DFR) after the first appearance for Spotted Salamanders (*Ambystoma maculatum*; AM), Spring Peeper (*Pseudacris crucifer*; SP), and Wood Frog (*Lithobates sylvaticus*; WF) for (left) the early 1900s, and for (right) 2016–2024 in the vicinity of Ithaca, New York, USA. The horizontal lines through each box are the median value, the bottom and the top of the boxes are the 1st and 3rd quartiles, and black dots are the DFR value for each year of the study.

DFA for migrating amphibians were typically made at night, during the work week, and in public spaces on the Cornell University campus suggesting some observers actively sought the time and place to record sightings of these relatively cryptic species. We cannot rule out the influence of convenience in the selection of locations for these observations (Callaghan et al. 2019). Given the potential differences in location of observations and sampling effort, we should expect the citizen-science data to underestimate the DFA; however, the extent of the underestimate is partially offset by the greater number of observers active in a similar geographic area. Recognizing that no dataset is without bias (Geurts et al. 2023), these observations contribute important ecological data that allowed us to address three basic variables about a key phenological event for early spring-breeding amphibians.

Timing of early spring-breeding amphibians.—Based on the differences between contemporary and historic observations of the onset of activity, we conclude that Spotted Salamanders, Spring Peepers, and Wood Frogs appear above ground earlier in recent years than they did in the early 1900s. This study is the first, that we know of, to document an advance in the onset of spring activity in Spotted Salamanders. Our data complement the finding of advancing activity by Spring Peepers and Wood Frogs in Ithaca and elsewhere (Gibbs and Breisch 2001; Walpole et al. 2012).

The first appearance of Spotted Salamanders, Spring Peepers, and Wood Frogs in the vicinity of Ithaca, New York has advanced 1.05–1.56 d/decade since the early 1900s. Gibbs and Breisch (2001) found the phenophase first voice advanced by 1.36 and 1.30 d/decade for Spring Peepers and Wood Frogs, respectively between 1900 and 2000. The rate of change observed for DFA in Ithaca is low relative to the rate of advancement observed in other studies of amphibians (Parmesan et al. 2007; While and Uller 2014). The low rate of change may reflect the high interannual variation in the timing of environmental cues that drive the breeding phenology in these species.

Changes in environmental cues.—Among U.S. climate regions, the Northeast has had the greatest increase for intensity and frequency of heavy precipitation events since 1901 (Jessica Whitehead et al. 2023, *op. cit.*). Accordingly, we found that the earlier onset of spring activity in Spring Peepers was associated with greater precipitation now than in the early 1900s. Most of first appearance records by Wright for Spring Peepers (eight of 12 y) and Spotted Salamanders (seven of 9 y) occurred on nights with little (0.1 mm) to no (0.0 mm) precipitation. In recent years, the DFA for these species was always associated with at least 0.5 mm precipitation. The consistency of precipitation as a cue for Wood Frogs aligns with observations by Benard et al. (2023) who found that ambystomatid salamanders responded to thermal accumulation (more warmer days in a row) than Wood Frogs, whereas Wood Frogs required longer precipitation lags (more rainy days in a row) than ambystomatid salamanders.

Based on his observations in Ithaca, Wright (1908) considered a temperature of 50° F (10° C) to stimulate activity in Spotted Salamanders. The average maximum temperature (15.5° C) on the DFA for Spotted Salamanders in recent years was significantly higher. Temperatures that exceeded 16° C were occasionally observed prior to the actual commencement of spring activity, but other environmental factors (e.g., snow depth, pond ice, soil temperature) likely inhibited the onset of activity.

We found that the onset of spring activity in Spotted Salamanders, Spring Peepers, and Wood Frogs, was associated with a thermal accumulation using a base temperature of 3° C (Lovett 2013). Given that this thermal cue did not differ significantly between time periods, we pooled values to calculate an average (± standard error) for thermal accumulation on the DFA for 18 Spotted Salamanders (35.0 ± 3.8 T3DD), 21 Spring Peepers (34.8 ± 3.9 T3DD), and 15 Wood Frogs (37.7 ± 4.0 T3DD). The T3DD values observed in our study are similar to the average value (44.3 T3DD; n = 15 y) accumulated on what Lovett

(2013) called the day of first call for Spring Peepers in southern New York.

Observations of early spring-breeding amphibians in Ithaca before 20 T3DD have accumulated are rare. Wright (1914) notes that the earliest of his first appearance of Spring Peepers, 13 March 1911 (y-day = 72; T3DD = 4.4), occurred in a marsh completely covered with ice. Wright recorded the date of first voice for this species on 5 April 1911 (y-day = 95; T3DD = 25.6) and noted the 23-d lag from the date of first appearance, which he called extreme for this species. In recent years, the earliest DFA of a Spring Peeper in Ithaca occurred on 20 February 2018 (y-day = 51; Maximum Daily Temperature = 8.3° C; T3DD = 10.2). After a brief warm period in February, the maximum daily temperatures decreased, and snow cover persisted from 2 to 24 March. Spotted Salamanders and Wood Frogs were first observed on 29 March (y-day = 88; Maximum Daily Temperature = 7.8° C; T3DD = 37.3). Of 54 first appearances of the focal species in this study, 48 occurred after 18.7 T3DD had accumulated and before 55.7 T3DD was reached.

Increased risk of freezing,—We found that earlier onset of activity observed in Ithaca in recent years is associated with an elevated risk of freezing relative to the early 1900s. Earlier environmental cues that stimulate activity are frequently followed by subfreezing conditions that may injure or kill amphibians. Adult Spotted Salamanders are not freeze tolerant (Storey and Storey 1986; Jon Costanzo, pers comm.) and may be killed or damaged by frost exposure in all life stages (Walters 1975; Harris 1980; Brodman 1995). In Durham, North Carolina, USA, adult female Spotted Salamanders and their eggs were killed after migrating to a vernal pond during a warm period in January (Harris 1980). Favorable conditions were followed by 11 d with an average temperature < -2° C. In addition to 38 dead adult females, this early cohort had significantly lower embryonic survival (23%) relative to later breeding waves in the same pond (Harris 1980).

Adult Spring Peepers and Wood Frogs are freeze tolerant during hibernation; however, their ability to survive freezing decreases in spring (Storey and Storey 1987). Adult frogs that encounter subfreezing temperatures during the breeding season may die or experience neurobehavioral impairment that reduces reproductive success (Costanzo et al. 1997). Frisbie et al. (2000) found that embryos of Wood Frogs from Kentucky, USA, were tolerant of freezing when exposed to subfreezing temperatures, but not to the extent of adult Wood Frogs. Brief (3.5 h) exposure to -2° C is lethal to embryos of Wood Frogs (Frisbee et al. 2000). In addition to direct mortality of eggs and larvae by freezing, frost damage to the outer jelly of amphibian egg masses can facilitate predation (Walters 1975).

Conclusions.—Spotted Salamanders, Spring Peepers, and Wood Frogs have advanced the timing of their first appearance in Ithaca, New York, relative to the early 1900s. Onset of activity remains relatively synchronous as these species appear to respond to similar environmental cues. Taking the earliest opportunity to breed may confer competitive advantages to species and individuals that arrive first in ephemeral ponds, but early activity also increases the risk of death or injury by freezing.

Acknowledgments.—We wish to thank John Iverson and Jon Costanzo for discussions of amphibian phenology and physiology. We also wish to thank Ian Davies (iandavies), Joe Barron (joey_swamps), and the many contributors to iNaturalist who share their observations publicly and make analyses like this possible.

Literature Cited

Arietta, A.A., L.K. Freidenburg, M.C. Urban, S.B. Rodrigues, A. Rubinstein, and D.K. Skelly. 2020. Phenological delay despite warming in Wood Frog *Rana sylvatica* reproductive timing: a 20-year study. Ecography 43:1791–1800.

Baldauf, R.J. 1952. Climatic factors influencing the breeding migration of the Spotted Salamander, *Ambystoma maculatum* (Shaw). Copeia 1952:178–181.

Benard, M.F. 2015. Warmer winters reduce frog fecundity and shift breeding phenology, which consequently alters larval development and metamorphic timing. Global Change Biology 21: 1058–1065.

Benard, M.F., and K.R. Greenwald. 2023. Environmental drivers of amphibian breeding phenology across multiple sites. Diversity 253. https://doi.org/10.3390/d15020253.

Bison, M., N.G. Yoccoz, B.Z. Carlson, G. Klein, I. Laigle, C. Van Reeth, and A. Delestrade. 2021. Earlier snowmelt advances breeding phenology of the Common Frog (*Rana temporaria*) but increases the risk of frost exposure and wetland drying.

Frontiers in Ecology and Evolution 9: https://doi.org/10.3389/fevo.2021.645585.

Blanchard, F.N. 1930. The stimulus to the breeding migration of the Spotted Salamander, *Ambystoma maculatum* (Shaw). American Naturalist 64:154–167.

Brodman, R. 1995. Annual variation in breeding success of two syntopic species of *Ambystoma* salamanders. Journal of Herpetology 29:111–113.

Buss, N., L. Swierk, and J. Hua. 2021. Amphibian breeding phenology influences offspring size and response to a common wetland contaminant. Frontiers in Zoology 18(1):31. https://doi.org/10.1186/s12983-021-00413-0.

Butler, C.J. 2003. The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. Ibis 145:484–495.

Callaghan, C.T., J.J. Rowley, W.K. Cornwell, A.G. Poore, and R.E. Major. 2019. Improving big citizen science data: moving beyond haphazard sampling. PLoS Biology 17:1–11. https://doi.org/10.1371/journal.pbio.3000357.

Chmura, H.E., H.M. Kharouba, J. Ashander, S.M. Ehlman, E.B. Rivest, and L.H. Yang. 2019. The mechanisms of phenology: the patterns and processes of phenological shifts. Ecological Monographs 89:1–22.

Costanzo, J.P., J.T. Irwin, and R.E. Lee, Jr. 1997. Freezing impairment of male reproductive behaviors of the freeze-tolerant Wood Frog, *Rana sylvatica*. Physiological Zoology 70:158–166.

Forti L.R., F. Hepp, J.M. de Souza, A. Protazio, and J.K. Szabo. 2022. Climate drives anuran breeding phenology in a continental perspective as revealed by citizen-collected data. Diversity and Distributions 28:2094–2109.

Frisbie, M.P., J.P. Costanzo, and R.E. Lee, Jr. 2000. Physiological and ecological aspects of low-temperature tolerance in embryos of the Wood Frog, *Rana sylvatica*. Canadian Journal of Zoology 78:1032–1041.

Fuccillo Battle, K., A. Duhon, C.R. Vispo, T.M. Crimmins, T.N. Rosenstiel, L.L. Armstrong-Davies, and C.E. de Rivera. 2022. Citizen science across two centuries reveals phenological change among plant species and functional groups in the Northeastern US. Journal of Ecology 110:1757–1774.

Gibbs, J.P., and A.R. Breisch. 2001. Climate warming and calling phenology of frogs near Ithaca, New York, 1900–1999. Conservation Biology 15:1175–1178.

Geurts, E.M., J.D. Reynolds, and B.M. Starzomski. 2023. Turning observations into biodiversity data: broadscale spatial biases in community science. Ecosphere 14:p.e4582. https://doi.org/10.1002/ecs2.4582.

Green, D.M. 2017. Amphibian breeding phenology trends under climate change: predicting the past to forecast the future. Global Change Biology 23:646–656.

Hayhoe, K., C. Wake, B. Anderson, X.Z. Liang, E. Maurer, J. Zhu, J. Bradbury, A. DeGaetano, A.M. Stoner, and D. Wuebbles. 2008. Regional climate change projections for the Northeast U.S. Mitigation and Adaptation Strategies for Global Change 13:425–436.

Harris, R.N. 1980. The consequences of within-year timing of breeding in *Ambystoma maculatum*. Copeia 1980:719–722.

Hinckley, M.H. 1882. Notes on the development of *Rana sylvatica* LeConte. Proceedings of the Boston Society of Natural History 22:86–87.

Husting, E.L. 1965. Survival and breeding structure in a population of *Ambystoma maculatum*. Copeia 1965:352–362.

Iwanycki Ahlstrand, N., R.B. Primack, and A.P. Tøttrup. 2022. A comparison of herbarium and citizen science phenology datasets for detecting response of flowering time to climate change in Denmark. International Journal of Biometeorology 66:849–862.

Kirk, M.A., M.L. Galatowitsch, and S.A. Wissinger. 2019. Seasonal differences in climate change explain a lack of multi-decadal shifts in population characteristics of a pond breeding salamander. PloS ONE 14: e0222097. https://doi.org/10.1371/journal.pone.0222097.

Lovett, G.M. 2013. When do peepers peep? Climate and the date of first calling in the Spring Peeper (*Pseudacris crucifer*) in southeastern New York State. Northeastern Naturalist 20:333–340.

Moldowan, P.D., G.J. Tattersall, and N. Rollinson. 2022. Climate-associated decline of body condition in a fossorial salamander. Global Change Biology 28:1725–1739.

Paton, P., S. Stevens, and L. Longo. 2000. Seasonal phenology of amphibian breeding and recruitment at a pond in Rhode Island. Northeastern Naturalist 7:255–269.

R Core Team. 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://

www.R-project.org/.
Reed, H.D., and A.H. Wright. 1909. The Vertebrates of the Cayuga Lake Basin, N.Y. Comstock University Press, Ithaca, New York, USA.
Sexton, O.J., C. Phillips, and J.E. Bramble. 1990. The effects of temperature and precipitation on the breeding migration of the Spotted Salamander (*Ambystoma maculatum*). Copeia 1990:781–787.
Storey, K.B., and J.M. Storey. 1986. Freeze tolerance and intolerance as strategies of winter survival in terrestrially-hibernating amphibians. Comparative Biochemistry and Physiology A 83:613–617.
Storey, K.B., and J.M. Storey. 1987. Persistence of freeze tolerance in terrestrially hibernating frogs after spring emergence. Copeia 1987:720–726.
Walpole, A.A., J. Bowman, D.C. Tozer, and D.S. Badzinski. 2012. Community-level response to climate change: shifts in anuran calling phenology. Herpetological Conservation and Biology 7:249–257.
Walters, B. 1975. Studies of interspecific predation within an amphibian community. Journal of Herpetology 28:267–279.
While, G.M., and T. Uller. 2014. Quo vadis amphibia? Global warming and breeding phenology in frogs, toads and salamanders. Ecography 37:921–929.
Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York, New York, USA
Wright, A.H. 1908. Notes on the breeding habits of *Amblystoma punctatum*. Biological Bulletin 14:284–289.
Wright, A.H. 1914. North American Anura: Life-histories of the Anura of Ithaca, New York. Carnegie Institution of Washington, Washington D.C., USA.
Wright, A.H., and A.A. Allen. 1909. The early breeding habits of *Amblystoma punctatum*. American Naturalist 43:687–692.
Yermokhin, M.V., and V.G. Tabachishin. 2022. False spring in the Southeastern European Russia and anomalies of the phenology of spawning migrations of the Pallas' Spadefoot Toad *Pelobates vespertinus* (Pelobatidae, Amphibia). Russian Journal of Herpetology 29:206–214.

Patrick Baker is an Associate Professor in the Department of Geography and Environmental Engineering at the U.S. Military Academy (West Point, New York, USA). He earned a B.A. in Natural Sciences and Mathematics from Bard College in Annandale-on-Hudson, New York, USA, and M.S. and Ph.D. in Zoology from Miami University in Oxford, Ohio, USA. His research interests include the winter biology, acoustic ecology, and breeding phenology of amphibians. (Photographed by Patrick Baker).

Rachel Hughes is a graduate student studying Data Analytics at Oregon State University, Corvallis, Oregon, USA. She has a B.S. in Physics and Mathematics from Houghton College (Houghton, New York, USA), an M.S. in Meteorology from the Naval Postgraduate School (Monterey, California, USA), and a P.S.M. in Environmental Science from Oregon State University (Corvallis, Oregon, USA). Her continuing research interests include amphibian and insect bioacoustics (Photographed by Rachel Hughes).

James Hughes is a Lieutenant Colonel and the Director of Meteorology in the Department of Physics and Meteorology at the U.S. Air Force Academy, Colorado Springs, Colorado, USA. He entered the Air Force in 2003 with a B.S. in Atmospheric and Oceanic Sciences from the University of Wisconsin-Madison, USA, later earning a M.S. in Meteorology from the Naval Postgraduate School (Monterey, California, USA). His previous roles include Flight Commander in Germany, Detachment Commander in Australia, Squadron Operations Officer in Florida, and Instructor at the United States Military Academy (West Point, New York, USA). (Photographed by Jon Malinowski).