

Amphibian breeding phenology trends under climate change: predicting the past to forecast the future

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Abstract

Global climate warming is predicted to hasten the onset of spring breeding by anuran amphibians in seasonal environments. Previous data had indicated that the breeding phenology of a population of Fowler's Toads (*Anaxyrus fowleri*) at their northern range limit had been progressively later in spring, contrary to generally observed trends in other species. Although these animals are known to respond to environmental temperature and the lunar cycle to commence breeding, the timing of breeding should also be influenced by the onset of overwintering animals' prior upward movement through the soil column from beneath the frost line as winter becomes spring. I used recorded weather data to identify four factors of temperature, rainfall and snowfall in late winter and early spring that correlated with the toads' eventual date of emergence aboveground. Estimated dates of spring emergence of the toads calculated using a predictive model based on these factors, as well as the illumination of the moon, were highly correlated with observed dates of emergence over 24 consecutive years. Using the model to estimate of past dates of spring breeding (i.e. retrodiction) indicated that even three decades of data were insufficient to discern any appreciable phenological trend in these toads. However, by employing weather data dating back to 1876, I detected a significant trend over 140 years towards earlier spring emergence by the toads by less than half a day/decade, while, over the same period of time, average annual air temperature and annual precipitation had both increased. Changes in the springtime breeding phenology for late-breeding species, such as Fowler's Toads, therefore may conform to expectations of earlier breeding under global warming. Improved understanding of the environmental cues that bring organisms out of winter dormancy will enable better interpretation of long-term phenological trends.

Keywords: *Anaxyrus fowleri*, climate change, Fowler's Toad, global warming, long-term study, spring emergence

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Introduction

Global climate warming is predicted to affect many aspects of the behaviour and ecology of organisms (Karl & Trenberth, 2003; Le Roux & McGeoch, 2008; Melles *et al.*, 2011). Effects of a warming climate should particularly be expressed in the phenology of reproduction, migration and winter dormancy among species with behaviours tied to the cycle of the seasons (Root *et al.*, 2003; Kovach *et al.*, 2013), especially at higher latitudes (Parmesan, 2007; While & Uller, 2014). The complexities of species' interactions with climatic factors make predicting precisely how they will respond to climate change both crucial and difficult (Buckley & Kingsolver, 2012; Diez *et al.*, 2014).

Pond-breeding, temperate zone amphibians may be important bellwethers of the effects of climate warming (Li *et al.*, 2013; Gerick *et al.*, 2014). An earlier onset of spring breeding behaviour correlated with a warming climate has been observed among various pond-breeding

frogs and toads in Europe (Beebee, 1995; Tryjanowski *et al.*, 2003; Scott *et al.*, 2008), Asia (Kusano & Inoue, 2008; Primack *et al.*, 2009) and North America (Gibbs & Breisch, 2001; Walpole *et al.*, 2012), yet other species may exhibit either a trend towards later commencement of spring breeding or no trend at all (Todd *et al.*, 2011; Klaus & Loughheed, 2013). For example, Fowler's Toads, *Anaxyrus fowleri*, at Long Point in southern Ontario appeared to be breeding some 5.3 days later per decade, based on my own observations of 13 dates of first breeding recorded over 19 years (Blaustein *et al.*, 2001). Root *et al.* (2003) noted how anomalous this particular result was compared to observations of other organisms and Parmesan (2007) proposed to explain it by reference to climate trends at a site in northern Ontario, in a different climatic zone. These toads do not differ significantly, however, from other temperate zone amphibians in terms of the proximal environmental cues for emergence from hibernation (Green *et al.*, 2016).

Spring breeding phenology in relation to climate change must be considered in the context of the environmental conditions that trigger the behaviour (Broatch

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et al., 2006; Matthysen *et al.*, 2011; Williams *et al.*, 2015). These triggers are becoming better understood for some terrestrially hibernating amphibians (Reading, 2003; Arnfeld *et al.*, 2012; Green *et al.*, 2016). Amphibians will not be active below particular temperatures (Oldham, 1969; Reading, 1998), but other environmental factors are also associated with the timing of their emergence from winter dormancy and subsequent breeding activity. In various species of toads, the timing of breeding may be correlated with both air temperature and certain phases of the lunar cycle (Reading, 1998, 2003; Grant *et al.*, 2009; Green *et al.*, 2016). Spring breeding activity in toads is in part triggered by rainfall in some species (Oseen & Wassersug, 2002; Corn, 2003; Richter-Boix *et al.*, 2006; Todd *et al.*, 2011) but not in others (Gittins, 1983; Reading, 1998; Arnfeld *et al.*, 2012).

Most animals that overwinter terrestrially seek refuges where they can survive away from harsh weather conditions aboveground. Freeze intolerant toads (Storey & Storey, 1986) burrow below the frost line to where temperatures remain just above freezing (Breckenridge & Tester, 1961; Van Gelder *et al.*, 1986), where they can maintain a minimal rate of metabolism (Tattersall & Ultsch, 2008). European Common Toads, *Bufo bufo*, in the Netherlands may descend 80 cm into the earth during winter (Van Gelder *et al.*, 1986), whereas Canadian Toads, *Anaxyrus hemiophrys*, in North Dakota may dig to depths of a metre or more (Breckenridge & Tester, 1961). At such depths, soil temperature and humidity are largely invariable from day to day (Baldwin & Maun, 1983). Thus, the spring emergence of toads, or other animals that hibernate deep underground, cannot occur until the animals have moved upwards through the ground to near the surface, where atmospheric conditions can directly affect them.

An overwintering animal's ascent from deep in the ground to the surface can begin only when the ground temperature profile has reversed in early spring as air temperatures rise, snow melts, rain falls and heat once again penetrates the ground from above (Campbell & Norman, 1998; Maun, 2009; Kurylyk *et al.*, 2013). If the timing of surface events influences the thermal profile of the ground and the start of the animals' vertical movement, there may be climatic conditions at certain times during late winter and early spring that correlate with the timing of the animals' subsequent spring emergence. If that is true, then it should also prove possible to formulate a predictive model that can be applied to recorded environmental data to determine the likely timing of same event in other years, under the reasonable assumption that the behavioural responses of animals to their environment do not change. Using such a model to predict past events (a.k.a. 'retrodiction'; Berlin, 1960), unlike simply

projecting a regression line backwards (i.e. 'backcasting'), may provide an improved basis for determining the presence of long-term phenological trends.

The Fowler's Toads at Long Point overwinter in sand dunes that run parallel to the shore of Lake Erie. There, ground frost can penetrate a metre or more during winter, forcing the toads to descend deep into the sand. During May, these toads resume surface activity and commence breeding in response to increased daytime air temperatures and the presence of a gibbous moon (Green *et al.*, 2016). Using an unbroken 24-year phenological record, I address the influence of early spring climatic conditions on the timing of springtime emergence from winter dormancy in this population, assess the predictability of the animals' springtime emergence, reconsider the evidence for a phenological trend towards later breeding as reported by Blaustein *et al.* (2001) and test for any long-term trend in phenology using associated environmental data dating back well over a century.

Materials and methods

I used recorded capture dates of adult male Fowler's Toads during annual spring surveys for 24 seasons, from 1989 through 2012, within a study area along 8.5 km of the Lake Erie north shore (42°35'N, 80°22' – 28'W) at the western base of Long Point, Ontario (Green *et al.*, 2016). For analysis, I standardized the calendar to account for leap years and the precession of the equinoxes by converting all dates to days relative to the timing of the vernal equinox, which I considered to occur on Day 0. Because the animals are nocturnal, I considered their 'day' to begin at sundown. Thus, if the vernal equinox occurred any time from sunset until midnight on a given calendar date, I set the following date to be Day 0. Because dates of 'first appearances' or 'first arrivals' are sensitive to abundance, behaviour, detectability and observer effort (Tryjanowski *et al.*, 2003; Van Strien *et al.*, 2008), I followed Green *et al.* (2016) in considering the 'day of emergence' (DayE) in any particular year to be the day when 10% or more of the males estimated to be present in the population that year were known to be active aboveground. Male toads tend to emerge relatively synchronously to form breeding choruses and are readily identifiable by their secondary sexual characteristics.

I obtained long-term temperature and precipitation records from weather recording stations located around eastern Lake Erie (Fig. 1). All of these weather stations fall within the historical range of Fowler's Toads in the region and, except for the station at the Long Point Tip, have near identical climate and weather patterns as my study area at the base of Long Point. I used contemporary weather data primarily from the Port Colborne, Ontario, weather station (42°53'N, 79°15'W; Climate ID: 6136606) located 100 km ENE of the Long Point study site. This station has been operating since 1964. Where data were missing from the Port Colborne weather record, I filled in the gaps with data from the Fort Erie weather station (42°53'N, 78°58'W; Climate ID: 6132470), located 23 km E of

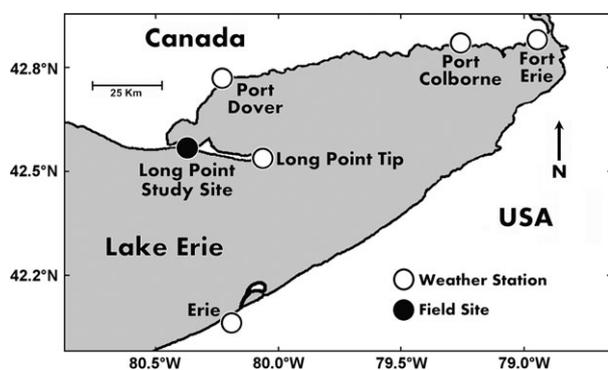


Fig. 1 Map of eastern Lake Erie showing the location of the field study site at Long Point, Ontario, Canada, and nearby weather stations.

Port Colborne. To test the generality of weather patterns in the eastern Lake Erie Basin, I also referred to weather data recorded at the Erie International Airport (Menne *et al.*, 2012), which is located on the south shore of Lake Erie in Pennsylvania (42°5'N; 80°11'W; GHCND: USW00014860), 48 km SSE of the Long Point study site. Unlike the Canadian weather stations, the Erie weather station records precipitation (= rain and/or snow) but does not separately record rainfall. My source for historical weather data was the weather station at Port Dover, Ontario (42°47'N, 80°13'W; Climate ID: 6136643), located 25 Km N of my study site. The Port Dover weather station operated from 1873 to 1983, affording a 19-year overlap with records from Port Colborne. This allowed me to compare between results based on the two stations' recorded data and identify any discrepancies between them. Taken together, the two data sets provided a near continuous record of springtime weather conditions dating from 1876 to the present day. I did not refer to the data record from the Long Point station (42°33'N, 80°03'W; Climate ID: 6134F10) located at the tip of Long Point. This station ceased functioning in 1986 and was replaced by an automated recorder in 1995, but there is an additional 2-year gap in its data record from mid-2003 through mid-2005. Furthermore, the climate at the tip of the point is affected by the lake to a much greater degree than that of other coastal locations. Springtime weather at the tip is routinely colder and windier than it is at mainland sites.

To identify and assess environmental correlates associated with the animals' presumed early spring ascent although the soil from deep underground, I performed what may best be described as a 'correlation hunt'. For both the Port Colborne data set and the Erie data set, I computed 7–18-day running averages of maximum daily temperature, daily rainfall (Port Colborne only), daily snowfall and daily precipitation over the 61 days (Day –20 to Day 40, or about March 1st through April 30th) preceding the earliest recorded springtime detection date of any active Fowler's Toads at Long Point. For each of the 732 sets of running averages generated for each weather parameter, I computed Pearson's correlation coefficient (R) against the observed day of emergence (DayE_{obs}). This allowed me to identify significant correlations (i.e., $|R| > 0.4044$ for $n = 24$ years and $\alpha = 0.05$) on graphs of R vs.

Day pre- or postequinox. I retained those data generating the greatest values of $|R|$ for further analysis. This procedure was performed in Excel 2013 (Microsoft Corp., Redmond, WA, USA) using separate spreadsheets for each weather variable. I regressed any potentially significant weather variables I identified in this way against DayE_{obs} to determine levels of significance. I then compared all possible multiple regression models employing significant weather variables derived from the Port Colborne data set, which has separate records for rainfall and snowfall, to identify the most informative model, or models, using Akaike's information criterion adjusted for small sample size (AICc). For each model, I calculated AICc, ΔAICc and Akaike weight. I selected the model with the lowest AICc score (Burnham & Anderson, 2003), as well as any other model with $\Delta\text{AICc} < 2.00$. If two or more most informative models differed by $\Delta\text{AICc} < 5.00$, I also computed an averaged model.

To identify the most predictive model possible, I also used data on the illumination of the moon, which is known to correlate with the toads' resumption of surface activity in spring (Green *et al.*, 2016). Because the 29.5-day lunar cycle is highly predictable, I used data averaged over the 13-day time period, from Day –2 to Day 10, centred precisely two lunar cycles prior to the average date of emergence of the toads. I obtained day-by-day values for percent illumination of the moon from World Clock (www.timeanddate.com/worldclock/astronomy) using Erie, Pennsylvania, as the geographic reference point.

I used the coefficient of determination, R^2 , as the criterion for goodness of fit of a model's output, that is the expected day of emergence (DayE_{exp}), with DayE_{obs} . I used the model that returned the highest value of R^2 to derive a parameterized prediction formula for DayE in the form of a linear equation incorporating terms for maximum daily air temperature (T_{max}), rainfall (RAIN), snowfall (SNOW) and/or moon illumination (MOON). I tested the predictive ability of the chosen model by applying it to weather data from 2013, 2014 and 2015 vs. determinations of DayE made during those years using the same procedure as in Green *et al.* (2016). I performed all model selection and regression analyses with JMP 11 statistical software (SPSS Corp., Cary, NC, USA). Averaged values are reported as means ± 1 SE.

I used the resulting predictive model to retrodict dates of emergence of the toads over the same time period (1980–1998) reported on by Blaustein *et al.* (2001), filling in the 6-year gap, 1982–1987, in their data. I converted the Julian dates reported by Blaustein *et al.* (2001) into days postequinox and evaluated the goodness of fit of this data set vs. the estimated dates of emergence using R^2 . I then used the retrodicted estimates of DayE to supply the missing years, 1982–1987, in the data reported by Blaustein *et al.* (2001) and recalculated any temporal trend in these data, and its statistical significance, using linear regression.

I then applied the predictive model to the historical record of weather data from the Port Dover weather station to retrodict DayE_{exp} for every year for which weather data were available back to 1876. To do this, I evaluated the comparability of the Port Colborne and Port Dover data sets by calculating DayE_{exp} for each of the 19 years (1965–1983, incl.) for which

weather data from both stations were available and comparing the results using R^2 as the measure of goodness of fit. If the two sets of results proved to be highly correlated (i.e. $R^2 > 0.800$, $P \ll 0.001$), I derived retrodictions of DayE_{exp} from 1876 to 1964 using Port Dover data, from 1965 to 1983 using the averaged results of using Port Dover weather data and Port Colborne weather data, and from 1984 to the present using Port Colborne weather data. This produced a sequence of values for DayE_{exp} for this population of toads spanning 140 years (1876–2015). Finally, I examined the weather records over the same time period for evidence of comparable trends in annual mean air temperature and total annual precipitation in the vicinity of the study site.

Results

As reported by Green *et al.* (2016), there was considerable variance the timing of the day of emergence, DayE , of 10% of the estimated number of male Fowler's Toads at my study site in Long Point, Ontario, over the 24 years from 1989 through 2012 (Table 1). The earliest date of DayE was 03 May 2012 (Day 44) and the latest was 26 May of both 1997 and 2005 (Day 67), with an average date of 14 May (Day 55 ± 1.4 days). The date of DayE exhibited no significant trend ($R^2 = 0.005$, $F_{1,22} = 0.116$, $P = 0.736$, slope = 0.072) over the 24 years.

Weather variables recorded at Port Colborne (daily maximum temperature, rainfall and snowfall averaged over 24 years) exhibited the trends expected for late winter and early spring during the 61-day period prior to the earliest recorded day of emergence of toads (Fig. 2). Daily maximum temperature rose significantly ($R^2 = 0.961$, $F_{1,59} = 1453.205$, $P < 0.001$) from Day -20 to Day 40 by 0.228 °C per day and exhibited a variance (S^2) of 17.12 around a mean of 8.22 ± 0.53 °C. Rainfall also rose significantly ($R^2 = 0.189$, $F_{1,59} = 13.762$, $P < 0.001$) by 0.03 mm per day ($S^2 = 1.343$, mean = 2.08 ± 0.15 mm), whereas snowfall decreased ($R^2 = 0.412$, $F_{1,59} = 41.282$, $P < 0.001$) by 0.020 cm per day ($S^2 = 0.309$, mean = 0.40 ± 0.07 cm). Total precipitation, though, showed no significant trend ($R^2 = 0.016$, $F_{1,59} = 0.956$, $P = 0.332$), rising by only 0.008 mm per day ($S^2 = 1.357$, mean = 2.49 ± 0.15 mm), showing that the trends in rainfall and snowfall were reciprocal.

I identified specific critical time periods, ranging in length from 7 to 16 days, when weather data recorded at Port Colborne or at Erie significantly correlated with the eventual DayE of the toads (Fig. 3; Table 2). For maximum daily temperature, a 12-day (Port Colborne) or 16-day (Erie) period, centred just after the equinox, was negatively correlated with eventual DayE for both data sets, although the relationship was only borderline significant ($P = 0.050$) in the case of the Erie data. An 8-day period of rainfall immediately prior to the equinox in the Port Colborne data was positively correlated

Table 1 Date of vernal equinox, estimated abundance of toads, observed timing of spring emergence of 10% of the estimated number of male toads and associated environmental variables each year at Long Point, Ontario, over 24 years, 1989–2012

| Year | Date of vernal equinox* | Estimated abundance of toads (N)† | Observed emergence of 10% of toads | |
|------|-------------------------|-----------------------------------|------------------------------------|-----------------|
| | | | Date | Day postequinox |
| 1989 | March 20 | 41 | May 17 | 58 |
| 1990 | March 21 | 156 | May 9 | 49 |
| 1991 | March 21 | 430 | May 10 | 50 |
| 1992 | March 20 | 307 | May 11 | 52 |
| 1993 | March 20 | 394 | May 9 | 50 |
| 1994 | March 21 | 93 | May 21 | 61 |
| 1995 | March 21 | 43 | May 16 | 56 |
| 1996 | March 20 | 39 | May 17 | 58 |
| 1997 | March 20 | 31 | May 26 | 67 |
| 1998 | March 21 | 191 | May 6 | 46 |
| 1999 | March 21 | 74 | May 5 | 45 |
| 2000 | March 20 | 63 | May 12 | 53 |
| 2001 | March 20 | 69 | May 11 | 52 |
| 2002 | March 21 | 240 | May 24 | 64 |
| 2003 | March 21 | 134 | May 18 | 58 |
| 2004 | March 20 | 174 | May 10 | 51 |
| 2005 | March 20 | 89 | May 26 | 67 |
| 2006 | March 21 | 48 | May 10 | 50 |
| 2007 | March 21 | 42 | May 9 | 49 |
| 2008 | March 20 | 42 | May 25 | 66 |
| 2009 | March 20 | 37 | May 13 | 54 |
| 2010 | March 20 | 20 | May 23 | 64 |
| 2011 | March 21 | 15 | May 13 | 53 |
| 2012 | March 20 | 21 | May 3 | 44 |

*Relative to sundown.

†From Greenberg & Green (2013).

with DayE . I also found that a 9-day period of rainfall recorded in the Port Colborne data and a 7-day (Port Colborne) or 8-day (Erie) period of precipitation, all centred about 4 weeks after the equinox, were negatively correlated with DayE . The concurrence of these particular relationships indicated that the Erie precipitation data were mainly rainfall. A 9-day (Port Colborne) or 15-day (Erie) period of snowfall beginning 5–6 days after the equinox was positively correlated with DayE for both data sets, as was a largely coincident 14-day period of precipitation in the Port Colborne data, indicating snowfall rather than rainfall. I also found a negative correlation with DayE for an 8-day period of precipitation spanning the equinox in the Erie data, although whether this was due to snowfall, rainfall, or a mixture of the two could not be determined. Based on these results, I identified four unambiguous weather variables from the Port Colborne data set for

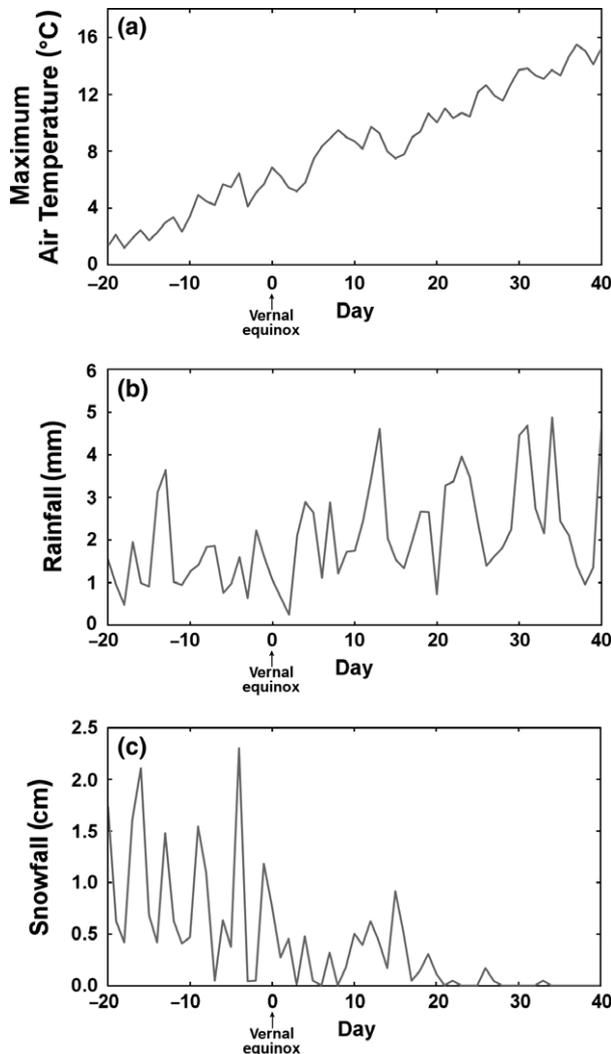


Fig. 2 Weather data recorded at Port Colborne, Ontario, during the 60-day period from approximately March 1–May 1 spanning the date of the vernal equinox (= Day 0), averaged over 24 years (1989–2012). (a) Maximum daily air temperature, (b) daily rainfall, (c) daily snowfall.

use in further analysis: maximum daily temperature from Day 0 to Day 11 (i.e. T_{\max}), early rainfall from Day -8 to Day 1 (i.e. RA_{INE}), late rainfall from Day 24 to Day 32 (i.e. RA_{INL}) and snowfall from Day 5 to Day 19 (i.e. $SNOW$). In addition, percent lunar illumination averaged over Day -2 to Day 10 (i.e. $MOON$) was also significantly correlated with the DayE ($R^2 = 0.447$, $F_{1,23} = 17.745$, $P < 0.001$).

The most informative multiple regression model explaining variation in DayE in terms of climatic variables (i.e. Model 1, Table 3) was composed of the three variables, T_{\max} , RA_{INL} and $SNOW$ ($AIC_c = 144.3$, $R^2 = 0.710$, $F_{3,20} = 16.410$, $P < 0.001$); all three

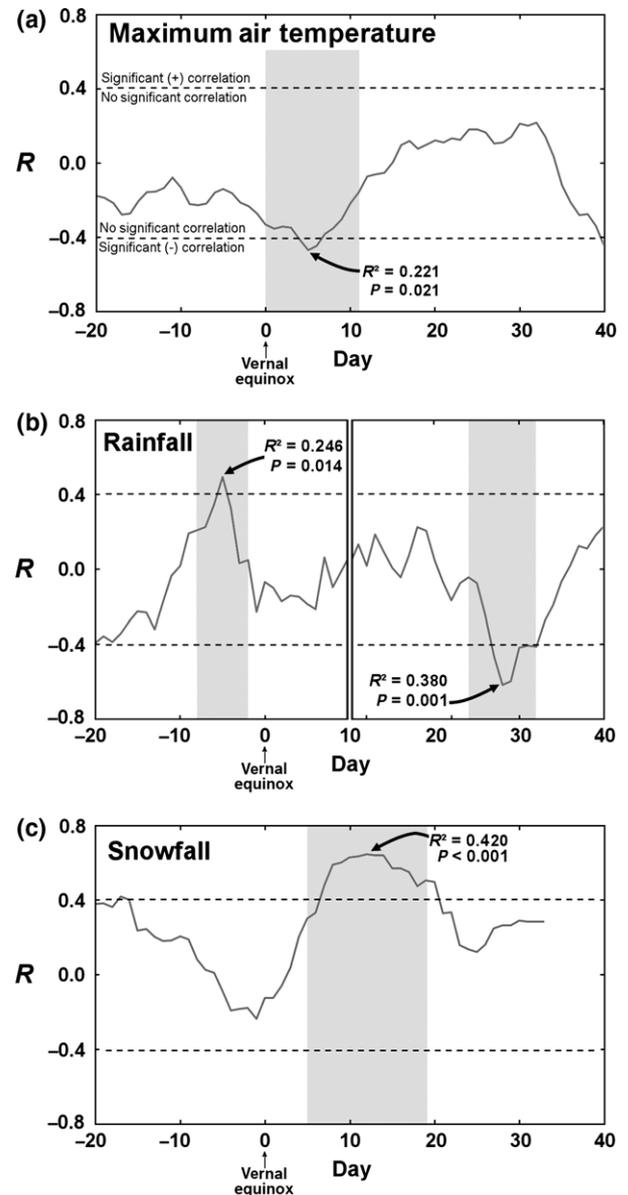


Fig. 3 Correlation hunt: Pearson's correlation coefficient, R , for correlations of successive running averages of varying periodicity of weather variables vs. the day of emergence of Fowler's Toads at Long Point, Ontario, during the 60-day period from approximately March 1–May 1, spanning the date of the vernal equinox (= Day 0), over 24 years, 1989–2012. Graphs depict those running averages that returned the most significant correlations for each parameter (i.e. $|R| > 0.040$, $\alpha = 0.05$, as indicated by dashed lines). The most significant correlations (arrows) and their periods (grey bars) are indicated. Values of R are for the average of the range of days in the grey bar, centred on the day in the middle. (a) 12-day running average of maximum daily air temperature. (b) 8-day (left) and 9-day (right) running averages of daily rainfall. (c) 15-day running average of daily snowfall.

Table 2 Significant correlations between late winter and early spring weather variables and the day of spring emergence of 10% or more of the male Fowler's Toads known to be present each year at the study site at Long Point, Ontario, 1989–2012, incl

| Parameter | Data set | Span of days* (<i>n</i>) | <i>R</i> | <i>R</i> ² | <i>F</i> _{1,22} | <i>P</i> |
|---------------------------|---------------|----------------------------|----------|-----------------------|--------------------------|----------|
| Maximum daily temperature | Port Colborne | Day 0 to Day 11 (12) | −0.470 | 0.221 | 6.227 | 0.021 |
| | Erie | Day −4 to Day 11 (16) | −0.404 | 0.163 | 4.282 | 0.050 |
| Rain | Port Colborne | Day −8 to Day 1 (8) | 0.497 | 0.246 | 7.120 | 0.014 |
| | Port Colborne | Day 24 to Day 32 (9) | −0.617 | 0.381 | 13.542 | 0.001 |
| Precipitation | Port Colborne | Day 4 to Day 17 (14) | 0.455 | 0.207 | 5.788 | 0.025 |
| | Port Colborne | Day 25 to Day 32 (8) | −0.637 | 0.406 | 15.016 | 0.001 |
| | Erie | Day −2 to Day 5 (8) | 0.558 | 0.311 | 9.450 | 0.005 |
| Snow | Erie | Day 26 to Day 32 (7) | −0.489 | 0.239 | 6.611 | 0.015 |
| | Port Colborne | Day 5 to Day 19 (15) | 0.648 | 0.420 | 15.919 | <0.001 |
| | Erie | Day 6 to Day 14 (9) | 0.430 | 0.185 | 4.984 | 0.036 |

*Counted relative to the date of the vernal equinox (= Day 0).

variables in this model were significant (T_{\max} : $P = 0.002$, RAINI: $P = 0.004$, SNOW: $P = 0.023$). The second most informative model (Model 2) was composed of all four climatic variables (AICc = 145.01, $R^2 = 0.732$, $F_{3,20} = 13.040$, $P < 0.001$), only three of which were significant (T_{\max} : $P = 0.004$, RAINE: $P = 0.227$, RAINI: $P = 0.010$, SNOW: $P = 0.036$). The difference in AICc between these two models was small ($\Delta\text{AICc} = 0.89$). Comparing these models, and the averaged model, Model 2 returned the best goodness of fit when regressed against observed DayE (Model 1: $R^2 = 0.710$, Model 2: $R^2 = 0.741$, averaged model: $R^2 = 0.729$).

Of all the possible models, as well the averaged model, the one with the best goodness of fit when regressed against observed DayE was composed of all four climatic variables plus MOON ($R^2 = 0.802$, $F_{5,23} = 14.569$, $P < 0.001$). This model (Table 4) yielded the following prediction formula:

$$\text{DayE}_{\text{exp}} = 59.62 - 0.879 * T_{\max} + 0.355 * \text{RAINE} - 1.458 * \text{RAINI} + 2.542 * \text{SNOW} + 8.763 * \text{MOON}.$$

Using this formula, my estimations of the timing of DayE, based on Port Colborne weather data and moon illumination (Table 5), were 89.5% correlated (i.e.

Table 3 Model selection for identified late winter and early spring climate parameters in relation to the day of spring emergence of 10% of the known number of male Fowler's Toads present each year

| Model* | | <i>K</i> | <i>R</i> ² | AICc | ΔAICc | <i>w</i> |
|--------|--|----------|-----------------------|--------|---------------------|----------|
| 1. | $T_{\max} + \text{RAINI} + \text{SNOW}$ | 3 | 0.710 | 144.13 | 0.00 | 0.44 |
| 2. | $T_{\max} + \text{RAINE} + \text{RAINI} + \text{SNOW}$ | 4 | 0.741 | 145.01 | 0.89 | 0.28 |
| 3. | $T_{\max} + \text{RAINE} + \text{RAINI}$ | 3 | 0.676 | 146.78 | 2.65 | 0.12 |
| 4. | $T_{\max} + \text{RAINI}$ | 2 | 0.625 | 147.07 | 2.94 | 0.10 |
| 5. | $T_{\max} + \text{RAINE} + \text{SNOW}$ | 3 | 0.627 | 150.17 | 6.04 | 0.02 |
| 6. | $T_{\max} + \text{SNOW}$ | 2 | 0.552 | 151.32 | 7.19 | 0.01 |
| 7. | $\text{RAINI} + \text{SNOW}$ | 2 | 0.535 | 152.20 | 8.08 | 0.01 |
| 8. | $\text{RAINE} + \text{RAINI} + \text{SNOW}$ | 3 | 0.579 | 153.05 | 8.92 | 0.01 |
| 9. | $\text{RAINE} + \text{SNOW}$ | 2 | 0.503 | 153.82 | 9.69 | 0.00 |
| 10. | SNOW | 1 | 0.420 | 154.61 | 10.48 | 0.00 |
| 11. | $\text{RAINE} + \text{RAINI}$ | 2 | 0.461 | 155.74 | 11.61 | 0.00 |
| 12. | RAINI | 1 | 0.381 | 156.19 | 12.06 | 0.00 |
| 13. | $T_{\max} + \text{RAINE}$ | 2 | 0.425 | 157.32 | 13.19 | 0.00 |
| 14. | RAINE | 1 | 0.247 | 160.89 | 16.76 | 0.00 |
| 15. | T_{\max} | 1 | 0.219 | 161.74 | 17.61 | 0.00 |
| | Null | | | 165.05 | 20.93 | 0.00 |

K is the number of parameters in the model (not including the residual error term), R^2 is the coefficient of determination, AICc is Akaike's information criterion corrected for small sample size, ΔAICc is the difference between a given model and the model with the lowest value of AICc, *w* is the relative AICc weight of a given model.

*Parameters: T_{\max} = maximum daily temperature averaged over days 0 to 11 relative to the vernal equinox; RAINE = early rainfall, averaged over days −8 to 1; RAINI = late rainfall, averaged over days 24 to 32; SNOW = snowfall averaged over days 5 to 19. See Table 2.

$R = 0.895$) with observed DayE of the toads (Fig. 4) and differed from them each year by no more than 7 days in either direction (average = 0.0 ± 0.7 days). Average

Table 4 Parameter estimates of the most predictive model resulting from multiple regression of all four climate variables and the illumination of the moon against the day of spring emergence of 10% of the known number of male Fowler's Toads present each year

| Parameter* | Estimate | <i>t</i> Ratio | <i>P</i> |
|------------|--------------------|----------------|----------|
| T_{\max} | -0.879 ± 0.255 | -3.450 | 0.003† |
| RAINE | 0.355 ± 0.667 | 0.530 | 0.601 |
| RAINL | -1.458 ± 0.426 | -3.420 | 0.003† |
| SNOW | 2.542 ± 2.371 | 1.070 | 0.298 |
| MOON | 8.763 ± 3.727 | 2.350 | 0.030† |
| Intercept | 59.624 ± 3.263 | 18.270 | <0.001† |

*Parameters: T_{\max} = maximum daily temperature, RAINE = early rainfall; RAINL = late rainfall, SNOW = snowfall (see Table 3). MOON = moon illumination.

†Statistically significant at $\alpha = 0.05$.

estimated DayE was 54.8 ± 1.4 days postequinox, whereas average observed DayE was 54.9 ± 1.4 days postequinox. The formula predicted that DayE of the toads in 2013, 2014 and 2015 should have been, respectively, days 55, 55 and 56. Observed DayE during those years were days 57, 55 and 47.

The observed dates of first calling for the years 1980, 1981 and 1988–1998 presented by Blaustein *et al.* (2001) and the model's estimated dates of DayE (Fig. 5) were highly correlated ($R^2 = 0.731$, $F_{1,12} = 29.888$, $P < 0.001$). The estimated dates of DayE over all years (1980–1998) demonstrated a nonsignificant trend towards later spring emergence by the toads of just 0.26 days per decade ($R^2 = 0.001$, $F_{1,18} = 0.012$, $P = 0.912$) compared to the trend in the Blaustein *et al.* (2001) data of 5.53 days later per decade ($R^2 = 0.249$, $F_{1,12} = 3.644$, $P = 0.083$). For the Blaustein *et al.* (2001) data with the missing years, 1982–1987, filled in with retrodicted estimates of DayE, the trend was 2.62 days/decade and not significant ($R^2 = 0.065$, $F_{1,18} = 1.186$, $P = 0.291$).

Table 5 Temperature, rainfall, snowfall and moon illumination during identified critical periods in late winter and early spring prior to the eventual emergence of 10% of the known number of male Fowler's Toads each year at Long Point, Ontario, including predicted dates and their equivalents in terms of days postequinox derived from these data

| Year | Pre-emergence critical period data (averages)* | | | | | Estimated emergence of 10% of toads | |
|------|--|------------|------------|-----------|----------|-------------------------------------|-----------------|
| | T_{\max} (°C) | RAINE (mm) | RAINL (mm) | SNOW (cm) | MOON (%) | Date | Day postequinox |
| 1989 | 8.8 | 3.4 | 1.9 | 0.4 | 93.4 | May 20 | 61 |
| 1990 | 4.9 | 1.9 | 2.5 | 0.1 | 7.3 | May 13 | 53 |
| 1991 | 8.4 | 2.3 | 5.4 | 0.0 | 76.7 | May 13 | 52 |
| 1992 | 4.0 | 0.0 | 5.2 | 0.4 | 65.3 | May 13 | 55 |
| 1993 | 6.6 | 0.0 | 3.0 | 0.1 | 5.8 | May 10 | 50 |
| 1994 | 6.6 | 3.7 | 0.5 | 1.4 | 92.4 | May 21 | 66 |
| 1995 | 6.8 | 2.0 | 1.6 | 0.3 | 33.6 | May 16 | 56 |
| 1996 | 4.3 | 0.0 | 4.4 | 0.3 | 31.2 | May 11 | 52 |
| 1997 | 7.0 | 4.7 | 0.4 | 0.6 | 97.2 | May 24 | 65 |
| 1998 | 11.2 | 2.5 | 4.6 | 0.0 | 13.6 | May 8 | 45 |
| 1999 | 8.0 | 0.0 | 4.3 | 0.0 | 65.4 | May 12 | 52 |
| 2000 | 11.5 | 0.8 | 3.6 | 0.0 | 79.9 | May 13 | 52 |
| 2001 | 5.2 | 0.8 | 1.4 | 0.0 | 4.3 | May 13 | 54 |
| 2002 | 4.7 | 2.0 | 0.3 | 0.4 | 84.9 | May 23 | 64 |
| 2003 | 8.5 | 2.1 | 0.8 | 0.8 | 46.5 | May 19 | 58 |
| 2004 | 8.2 | 0.3 | 4.6 | 0.0 | 17.3 | May 7 | 47 |
| 2005 | 6.8 | 0.5 | 0.6 | 1.6 | 96.0 | May 24 | 65 |
| 2006 | 8.1 | 0.0 | 3.2 | 0.0 | 23.5 | May 11 | 50 |
| 2007 | 10.9 | 0.3 | 2.7 | 0.0 | 51.7 | May 12 | 51 |
| 2008 | 2.8 | 1.7 | 0.0 | 0.4 | 90.5 | May 24 | 66 |
| 2009 | 8.6 | 0.1 | 3.8 | 0.3 | 8.3 | May 8 | 48 |
| 2010 | 7.1 | 2.5 | 0.7 | 0.0 | 66.1 | May 18 | 59 |
| 2011 | 2.4 | 1.8 | 8.4 | 0.0 | 60.8 | May 10 | 51 |
| 2012 | 15.7 | 0.3 | 2.0 | 0.0 | 7.9 | May 7 | 44 |

*Parameters: T_{\max} = maximum daily temperature, RAINE = early rainfall, RAINL = late rainfall, SNOW = snowfall (see Table 3). MOON = moon illumination.

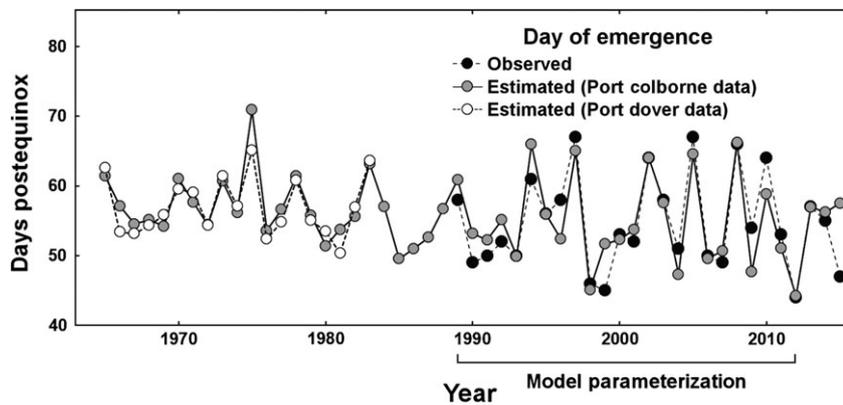


Fig. 4 Observed days of emergence of Fowler's Toads at Long Point, Ontario, each year in relation to estimated days of emergence based on Port Colborne weather data and estimated days of emergence based on Port Dover weather data, back to 1965. Days are numbered relative to the timing of the vernal equinox (= Day 0). Observations from 1989 to 2012 were used to parameterize the predictive model (see text).

The retrodicted estimations of DayE based on Port Colborne data vs. Port Dover data over the 19 years, 1965–1983, incl. (Fig. 4), were highly correlated ($R^2 = 0.798$, $F_{1,18} = 67.239$, $P \ll 0.001$), justifying the use of the Port Dover weather data to retrodict DayE back to 1876. There were insufficient data to estimate DayE for only seven of the 140 years, 1876–2015. The resulting estimates of DayE (Fig. 6) indicated that the Fowler's Toads at Long Point have been emerging from their winter dormancy in spring slightly, but significantly, earlier ($R^2 = 0.091$, $F_{1,129} = 12.773$, $P < 0.001$), on average by 0.39 days/decade. Over the same time period, annual mean air temperature in the vicinity of the study site (Port Dover and Port Colborne) increased by $0.13\text{ }^\circ\text{C}/\text{decade}$ and total annual precipitation increased by $9.63\text{ mm}/\text{decade}$ (Fig. 6).

Discussion

It is apparent from my results that air temperature and precipitation do affect the behaviour of Fowler's Toads overwintering underground, most probably in initiating subterranean vertical movements by the toads prior to their eventual emergence in spring. Taking into account the importance for amphibians of environmental conditions during winter (Benard, 2014; Gerick *et al.*, 2014), the animals should respond positively to the direction of the soil temperature gradient (Smits & Crawford, 1984; Van Gelder *et al.*, 1986) and begin to move upwards towards the surface once the soil above them thaws and the temperature profile in the ground reverses (Maun, 2009) as winter becomes spring. The timing of the springtime turnover in the soil temperature gradient should depend on how much heat reaches the ground from above and on the thermal conductivity of the soil (Campbell & Norman, 1998; Kurylyk *et al.*, 2013).

At Long Point, Fowler's Toads overwinter in sand dunes. The thermal conductivity of sand is a complex property dependent upon grain size, porosity and saturation with water (Chen, 2008; Smits *et al.*, 2010). Although dry sand is a poor conductor of heat, damp sand has high thermal conductance (Baldwin & Maun, 1983). Thus rain, at the right time, can increase the flow of heat through the ground. Snow cover, on the other hand, is an insulator (Goodrich, 1982) that impedes the penetration of both ground frost in winter and of warmth in spring. This means that rainfall late in spring, after the snow cover has disappeared, is likely to increase the flow of heat from the surface downward and accelerate the ground thaw. Conversely, snowfall late in spring does not just indicate cold weather but results in an insulating layer of snow that further delays the thaw. However, rainfall that occurs too early

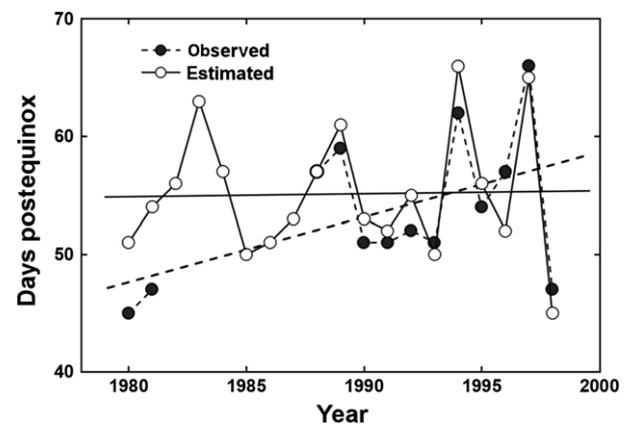


Fig. 5 Estimated dates of emergence of Fowler's Toads at Long Point, Ontario, based on Port Colborne weather data (1980–1998, incl.), vs. dates of first calling by the toads as reported by Blaustein *et al.* (2001) at the same locality, adjusted relative to the date of the vernal equinox.

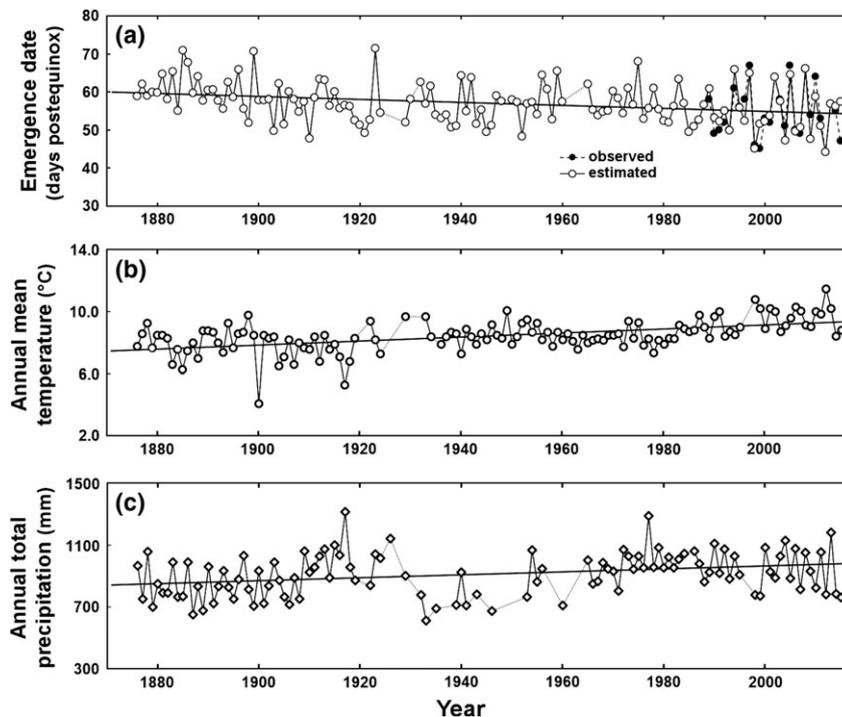


Fig. 6 Observed and estimated dates of spring emergence of Fowler's Toads at Long Point, Ontario, relative to date of the vernal equinox, over 140 years (1876–2015) based on historical weather data in comparison with temperature and precipitation. (a) Estimated and observed days of emergence each year. (b) Average annual air temperature. (c) Total annual precipitation.

in spring, insofar as it reduces snow cover, saturates the ground and then freezes, should tend to keep the ground colder for longer and also inhibit the thaw. There is much more to be learned about these processes but my results indicate that air temperature alone, averaged over some period of time in late winter or early spring (Reading, 2003; Arnfeld *et al.*, 2012), has only limited influence on the timing of spring breeding activity. This is not to say that the animals are not influenced by proximal environmental cues to emerge in spring. At Long Point, the Fowler's Toads preferentially emerge for the first time in spring on warm, dry, calm, moonlit nights (Green *et al.*, 2016).

Considering the underground effects of surface conditions more in terms of heat flux and conductance through the soil should be broadly applicable to other organisms that lay dormant below ground during winter, including even the root systems of plants. Not all overwintering amphibians hibernate so deep underground as do the Fowler's Toads at Long Point, nor in so uniform a substrate. In localities where winter temperatures less frequently get below freezing, as in the southern UK (Reading, 2007; Scott *et al.*, 2008; Carroll *et al.*, 2009), overwintering frogs and toads may not need to go so deep within the ground to escape the frost and thus may respond relatively quickly to changes in air temperature. Freeze tolerant species,

such as spring peepers, *Pseudacris crucifer*, and wood frogs, *Lithobates sylvaticus*, are also able to overwinter close to the ground surface where winter conditions can be more severe (Storey, 1990). Resolving how many of these animals respond to underground soil temperature changes during winter and spring will require better understanding of precisely how deep they go and what conditions they are subject to as they overwinter.

I have shown that a model based on environmental conditions many weeks in advance of the day of emergence can predict the temporal window during which animals are poised to emerge onto the surface. Adding in the predictable pattern of lunar illumination should increase the accuracy of such a model if the species is attuned to the lunar cycle, whereas the unpredictability of the weather should account for much of the remaining variance. Thus, springtime breeding phenology, at least of Fowler's Toads at their northern range limit, can be predicted with considerable accuracy. This predictability, in turn, shows that historical weather records can be used to interpret observation records and fill in gaps. The assertion that the Fowler's Toads at Long Point, Ontario, were breeding later by more than 5 days/decade (Blaustein *et al.*, 2001) now appears to be incorrect, and perhaps largely the artefact of the 6-year gap in observations of the toads' dates of first breeding. Furthermore, Blaustein *et al.* (2001) relied on

observations of first calling by breeding males, which does not necessarily represent when a significant part of the population has emerged (Tryjanowski *et al.*, 2003; Van Strien *et al.*, 2008) and may account for the particularly early dates recorded in 1980 and 1981. The result produced by filling in the 6-year gap via retrodiction contradicts neither the trends towards earlier spring phenologies observed in most other species (Root *et al.*, 2003; Parmesan, 2007), nor the inability to discern any significant trend in my later, unbroken, 1989–2012 record of observations.

Although 24 consecutive years of data may not be sufficient to detect a temporal trend in the breeding phenology of Fowler's Toads at Long Point, an extended data set retrodicted back to 1876 does indicate a slight, but significant, trend towards breeding earlier by about less than half a day per decade. This trend is much slower than the trends seen in some other anuran species (Terhivuo, 1988; Reading, 2003; Scott *et al.*, 2008; Carroll *et al.*, 2009; Todd *et al.*, 2011) but is in accordance with past (Zhang *et al.*, 2000; Fritzsche, 2011a,b) and projected (Gronewald *et al.*, 2013; Thi-beault & Seth, 2014; Wang *et al.*, 2014) climatic trends for the Great Lakes and St. Lawrence climatic region. It may be that the magnitude of climate warming in the Great Lakes Region, which is relatively slight, owes much to the moderating influence of the Great Lakes (Notaro *et al.*, 2013; Bartolai *et al.*, 2015).

In other parts of north-eastern North America, patterns of earlier calling can be discerned mainly among early spring breeding frogs and toads, such as wood frogs, *L. sylvaticus*, Northern Leopard Frogs, *Lithobates pipiens*, or spring peepers, *P. crucifer*, but not for later spring breeders, such as bullfrogs, *Lithobates catesbeianus*, and green frogs, *Lithobates clamitans* (Gibbs & Breisch, 2001; Walpole *et al.*, 2012; Klaus & Loughheed, 2013). Observations like these in a variety of organisms have prompted the idea that phenologies of late-breeding species may be relatively unaffected by climate warming (Pau *et al.*, 2011). My results indicate, though, that it may not be possible to detect trends in late-spring breeding species without very long, unbroken strings of methodologically consistent observations. Gibbs & Breisch (2001) based their results on data from two time periods, 1900–1912 and 1990–1999, separated by a gap of 78 years. Walpole *et al.* (2012) had only 14 years of data available. Klaus & Loughheed (2013) used citizen science records of dates of first calling or first observation, which can be problematic (Tryjanowski *et al.*, 2005; Van Strien *et al.*, 2008), for no more than 29 years within a span of four decades. In fairness, very long, reliable data sets are extremely difficult to come by when data are accrued at the rate of one point per year. For want of direct observations,

retrodiction can be a valuable approach. With a good quantitative model, data can be estimated based on particular, relevant, historical weather data. Predicting the past in this way can be valuable for forecasting the future.

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