

## COMMUNITY-LEVEL RESPONSE TO CLIMATE CHANGE: SHIFTS IN ANURAN CALLING PHENOLOGY

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**Abstract.**—We explored how climate change affects reproductive phenology in a community of amphibians. We examined temporal trends in spring and summer temperatures in the Lake Simcoe watershed, Ontario, Canada. As we were interested in quantifying how temperature was related to amphibian reproductive behavior, we explored relationships between spring and summer temperatures and peak calling date for seven common amphibian species in the watershed. Spring temperatures increased over the course of the 14 year study. We detected interspecific variation in peak calling trends during the period 1995 to 2008 in response to spring temperatures, demonstrating a link between increasing temperatures and advancing phenology of spring breeding amphibians. Early spring-breeding anurans such as Wood Frog (*Lithobates sylvaticus*), Spring Peeper (*Pseudacris crucifer*), and Northern Leopard Frog (*L. pipiens*) called earlier in the season over time, as temperature increased, whereas later breeding anurans such as Green Frog (*L. clamitans*) showed no change in peak calling date. We combined our empirical results with a Coupled Global Climate Model, which showed that under assumptions of the A2 scenario we could see an advance in peak calling of nearly 11 days by the year 2100 and a 30% increase in the breadth of the breeding season in this community of anurans. Our results illustrate the asymmetric impacts of climate change among species and suggest how these impacts may affect reproductive processes within a community.

**Key Words.**—anuran; amphibian; calling; climate change; climate change scenario; community; phenology; temperature

### INTRODUCTION

Climate is a major driver of biological processes. Indeed, studies link a number of processes with variation in climate, including reproduction (Langvatn et al. 1996), plant pollination (Wall et al. 2003; Memmott et al. 2007), predation (Both et al. 2009), hybridization (Garroway et al. 2010), and extinction (Thomas et al. 1996; Pounds et al. 1999). The impacts of changing climate manifest themselves in numerous and diverse ways, including altered sex ratios of reptile offspring (Janzen 1994), shifts in the emergence dates of insects (Dingemanse and Kalkman 2008), earlier annual leaf out and flowering in plants (Cleland et al. 2007; Miller-Rushing and Primack 2008), range expansions of numerous taxa (Parmesan et al. 1999; Bowman et al. 2005; Myers et al. 2009; Melles et al. 2010), and changes in reproductive phenology (Beebee 1995; Dunn and Winkler 1999).

Interspecific variation in phenology due to climate change is concerning because it may affect species interactions through reduced synchrony within communities and ecosystems (Parmesan 2006; Primack et al. 2009). For example, in the Netherlands, the spring bud burst of oak has advanced with increasing annual temperatures as have caterpillar hatch dates (Both et al. 2009). Further up the same food chain, however, passerines and Sparrow Hawks (*Accipiter nisus*) failed to

track these climate-induced changes, and as a result their reproductive timing is no longer correlated with peak food availability (Both et al. 2009). The Netherlands study illustrates the variation in responses of species to climate change within communities that ultimately can lead to altered or disrupted ecological processes (Tylianakis et al. 2008; Both et al. 2009).

Amphibians appear particularly vulnerable to environmental change; variations in temperature and moisture regimes have been linked to changes in breeding (Beebee 1995; Todd et al. 2010) and abundance (Pounds et al. 1999) of many species. Indeed, several studies have documented phenological responses of frogs and toads to changes in temperature resulting from climate change that had implications for reproduction, survival, and development (Donnelly and Crump 1998). For example, earlier breeding in anurans has been correlated with increasing spring temperatures (Beebee 1995; Blaustein et al. 2001; Gibbs and Breisch 2001). Similarly, the reproductive periods of fall-breeding amphibians have extended later in concert with warming fall temperatures (Todd et al. 2010). Positive relationships between temperature and reproduction seem somewhat intuitive. However, while some species within a community have responded to increasing temperatures by breeding earlier, other species within the same community have either not responded (Beebee 1995; Gibbs and Breisch 2001) or have bred later in the

season (e.g., *Anaxyrus fowleri* in Ontario; Blaustein et al. 2001). These findings illustrate the potential for asynchronies in amphibian community dynamics as a result of changing climatic conditions. Asynchronous responses by amphibians to climate change could alter the type and strength of species interactions and simplify ecological communities by favoring species with wide physiological and ecological requirements (Yang and Rudolf 2010).

We sought to explore how climate change affects reproductive phenology within a community of spring and summer breeding amphibians. In particular, we examined the hypothesis that climate change is causing amphibians to reproduce earlier in the year. To test this hypothesis, we examined phenological responses by seven anuran species to changing climate within a watershed in Ontario, Canada. We examined: (1) temporal trends in spring and summer temperatures between 1995 and 2008; (2) relationships between within-year survey date, year, and temperature between 1995 and 2008; and (3) relationships between calling phenology and temperature. We predicted that the annual timing of reproductive calling by amphibians would be correlated with spring temperatures, and thus, we also predicted that peak calling dates for each species would advance over time as spring temperatures warmed. We combined our empirical results with a climate scenario model to explore potential impacts of future climate change on the anuran community.

#### MATERIALS AND METHODS

We first set out to investigate trends in spring and summer temperature over time in the Lake Simcoe watershed of Ontario, Canada (44°24.76'N, 79°21.46'W). We used Pearson correlations to compare year (1995–2008) with mean monthly ambient temperature for April to July, inclusive (based on Environment Canada data for Orillia, Ontario). Temperature data for some years were missing in Orillia (2007 and 2008). However, temperatures in Orillia were strongly positively correlated with temperatures in nearby Peterborough (all  $r > 0.94$ ,  $n = 12$ ,  $P < 0.001$ ) and these data were used as representative of Orillia temperatures for some analyses during this study.

We then examined relationships between peak calling date by anurans and survey year. We used 14 years of data from Bird Studies Canada's Great Lakes Marsh Monitoring Program (MMP: <http://www.bsc-eoc.org/volunteer/glmmp/index.jsp?lang=EN&targetpg=index> [Accessed 18 October 2010]) for the Lake Simcoe watershed to perform these analyses. The MMP monitored amphibian populations each year using standardized call surveys conducted once early, once mid-way, and once late in the anuran breeding season at

fixed stations located in emergent wetlands. We chose the timing of visits to capture the greatest diversity of species throughout the season. The first visit occurred when temperature at night reached 5 °C, the second visit at 10 °C, and the third visit at 17 °C. In our study area, the first visit occurred from about 15 April to 30 April, the second visit from 15 May to 31 May, and the third visit from 15 June to 15 July. The survey stations were located along roadsides and were visited by volunteer marsh monitors between dusk and midnight. The marsh monitors recorded the relative abundance of individuals calling during each survey visit for a 3-min listening period. Marsh monitors estimated the relative abundance of amphibians with a calling code index that ranged from one to three. They assigned a calling code of one to surveys in which the calls of individuals did not overlap and the number of calling amphibians could be easily counted. They assigned a calling code of two when individual calls overlapped but the number of individuals could still be estimated. They assigned a calling code of three to surveys when amphibian calls overlapped to produce a continuous full chorus and an estimate of the number of individuals was impossible (for details see Marsh Monitoring Program 2008). A collection of stations within close proximity of a target wetland constituted a survey route. Our analysis used an average of 21 routes per year (range 12–31), where variation across years was due to volunteer surveyor effort. The number of sites surveyed did not vary with spring temperature (e.g., for April temperature,  $r_s = 0.149$ ,  $n = 14$ ,  $P = 0.605$ ).

To estimate peak calling date of different anuran species, we averaged calling data for each species across the stations for each route. Twelve anuran species were detected along the routes in the study area between 1995 and 2008. Seven species were detected in every year of the monitoring program and we restricted our analysis to these species (Table 1). For each of the seven species, we estimated the peak calling date per year based on the average date across survey routes when the most individuals were calling (highest calling code). Thus, peak calling date represented an average calling date weighted by the calling code. We examined trends in calling behavior over time by regressing peak calling date against year. We assessed significance of regression relationships using permutation tests. Probabilities were estimated as the proportion of randomized parameter estimates derived from 10,000 randomized permutations that exceeded (one-tailed test) the observed at a significance level of 0.95. Permutation tests are not constrained by assumed data distributions and allow for robust examinations of statistical significance that are immune to the confounding influences of temporal autocorrelation inherent in time series analysis (Crowley 1992).

**TABLE 1.** Linear regression results comparing changes in peak calling dates of anurans in the Lake Simcoe watershed, Ontario, Canada, to year between 1995 and 2008. Peak calling date is expressed as day of year, and thus, negative coefficients indicate a phenological advance. *P*-values were computed from randomized permutations tests with 10,000 iterations with Standard error (SE) and confidence intervals (CI) around the coefficients. Species are listed in order of coefficient size.

Species	Scientific name	Intercept <sup>1</sup>	Coefficient	SE	<i>P</i> -value	-95% CI	+95% CI
Wood Frog	<i>Lithobates sylvaticus</i>	3086.374	-1.470	0.344	< 0.001	-2.079	-0.861
Northern Leopard Frog	<i>Lithobates pipiens</i>	2296.855	-1.065	0.448	0.017	-1.858	-0.272
Spring Peeper	<i>Pseudacris crucifer</i>	1501.012	-0.669	0.332	0.032	-1.257	-0.081
Gray Tree Frog	<i>Hyla versicolor</i>	712.864	-0.260	0.297	0.206	-0.786	0.266
American Toad	<i>Anaxyrus americanus</i>	477.571	-0.151	0.303	0.317	-0.688	0.386
Green Frog	<i>Lithobates clamitans</i>	188.067	0.005	0.374	0.509	-0.657	0.667
American Bullfrog	<i>Lithobates catesbeianus</i>	-591.560	0.397	1.117	0.614	-1.581	-0.861

<sup>1</sup>The unit of the intercept is the day of year of peak calling when the coefficient is zero.

To visualize the variation in magnitude of response by species in relation to their breeding period, we estimated a Spearman correlation between the slope estimates of the temporal trend for each species (magnitude of change in calling date) and the intercept estimate for each species. We also sought to investigate relationships between peak calling of anurans, variation in survey date, and temperature. We expected that changes in peak calling date over time were due to changes in spring temperature. We were also concerned, however, that the variation in annual survey dates might influence our measures of anuran calling phenology, especially for early breeding species. Thus, for species that demonstrated significant or near significant trends in peak calling date over time, we conducted multiple linear regressions of peak calling date against single and additive combinations of first survey date and mean April temperature. We used Akaike’s Information Criteria corrected for small sample size (AIC<sub>c</sub>) and Akaike’s weights to rank the models and evaluate model parsimony. We averaged top ranking candidate models with AIC<sub>c</sub> < 2 units from the top model to create a composite model of peak calling date (Burnham and Anderson 2002). We assessed statistical significance of the variables in the multiple regression models of peak calling using permutation tests following methods described above (Crowley 1992).

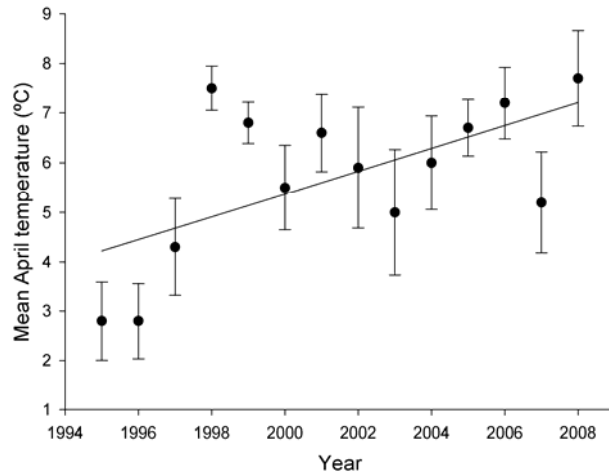
Finally, for species with peak calling dates influenced by temperature, we explored possible trends in peak calling under a future climate change scenario. We used the Coupled Global Climate Model version 3.1 (CGCM 3.1; Flato et al. 2000; Flato and Boer 2001) under the International Panel on Climate Change (IPCC) A2 emissions scenario (Nakicenovic et al. 2000) to assess changes in spring temperatures and thus peak anuran calling dates in the Lake Simcoe watershed between contemporary conditions (1970–2011) and 2100. We averaged maximum and minimum temperature scenarios from the CGCM 3.1-A2 model to estimate mean

monthly temperatures in April for time periods 2011–2040, 2041–2071, and 2071–2100 and applied these future temperature scenarios to the observed phenological relationships. We then examined the scenarios of future calling dates to make inferences about the impacts of future climate change on anuran communities.

## RESULTS

Mean monthly temperature between 1995 and 2008 strongly increased in April ( $r = 0.61$ ,  $n = 14$ ,  $P = 0.021$ , Fig. 1) but did not change in May, June, or July (all  $|r| < 0.20$ ,  $n = 14$ ,  $P > 0.05$ ). We found that the average first survey date per year (generally between 20 April and 4 May) was not related to April ( $r = -0.42$ ,  $n = 14$ ,  $P = 0.13$ ) or May ( $r = -0.07$ ,  $n = 14$ ,  $P = 0.80$ ) mean temperature but did advance over time (1995–2008;  $r = -0.57$ ,  $n = 14$ ,  $P = 0.03$ ). We detected no relationship between year and date of second and third surveys (all  $|r_s| < 0.40$ ,  $N = 14$ ,  $P > 0.2$ ).

During 1995 to 2008, there was a declining trend in peak calling date of Wood Frog (*Lithobates sylvaticus*), Northern Leopard Frog (*L. pipiens*), and Spring Peeper (*Pseudacris crucifer*). We also observed non-significant and yet declining trends in peak calling date by Gray Tree Frog (*Hyla versicolor*) and American Toad (*Anaxyrus americanus*; Fig. 2, Table 1). Peak calling dates of Green Frog (*L. clamitans*) and American Bullfrog (*L. catesbeianus*) exhibited positive, but non-significant trends between 1995 and 2008 (Fig. 2, Table 1). To compare the breadth of responses across the anuran community, we rank transformed the slopes and intercepts of the regression relationships between peak calling date and year for each species. We interpreted the ranked slope as the magnitude of change in peak calling date by a species, and this was strongly correlated to the regression intercept for each species ( $r_s = -0.93$ ,  $n = 7$ ,  $P = 0.003$ ; Fig. 3).



**FIGURE 1.** Trend in mean monthly temperature in April between 1995 and 2008 in the Lake Simcoe watershed, Ontario, Canada (Environment Canada data). The line represents a linear regression trend line and the error bars represent one standard error of the mean.

Exploratory analysis revealed that peak calling date for some species was strongly correlated with mean monthly temperature in April (Wood Frog:  $r = -0.64$ ,  $n = 14$ ,  $P = 0.015$ ), and May (American Toad:  $r = -0.55$ ,  $n = 14$ ,  $P = -0.042$ ), indicating that peak calling date was linked with spring temperature. For all other species-month combinations (April to July) there were non-significant correlations (all  $|r| < 0.6$ ,  $n = 14$ ,  $P > 0.05$ ) between peak calling date and mean monthly temperature, although some species demonstrated nearly-significant correlations with April temperatures (Spring Peeper:  $r = -0.50$ ,  $n = 14$ ,  $P = 0.072$ ; American Toad:  $r = -0.52$ ,  $n = 14$ ,  $P = 0.057$ ).

We conducted multiple regressions on peak calling date of Wood Frog, Northern Leopard Frog, and Spring Peeper against spring temperature and mean date of first survey visit each year to assess effects of temperature while considering potential effects of survey methodology. We selected these three species for modelling because they were early spring breeders and as such, they exhibited declines in peak calling date over time (Fig. 2). We selected mean April temperatures as indicative of spring temperature. We detected no correlation among the explanatory variables ( $r = -0.42$ ,  $n = 14$ ,  $P = 0.123$ ) indicating an absence of multicollinearity. We estimated a variance inflation factor ( $\hat{c}$ ) for the global models and found that  $\hat{c} = 1.218$  and  $\hat{c}$  was the same for all species, which indicates an absence of overdispersion (Lebreton et al. 1992). Permutation tests demonstrated significant relationships between spring temperature and calling behavior in both Spring Peeper and Wood Frog (Table 2). All other relationships were non-significant ( $P > 0.05$ ). Model selection results indicated that temperature was the most important factor affecting calling behavior in both

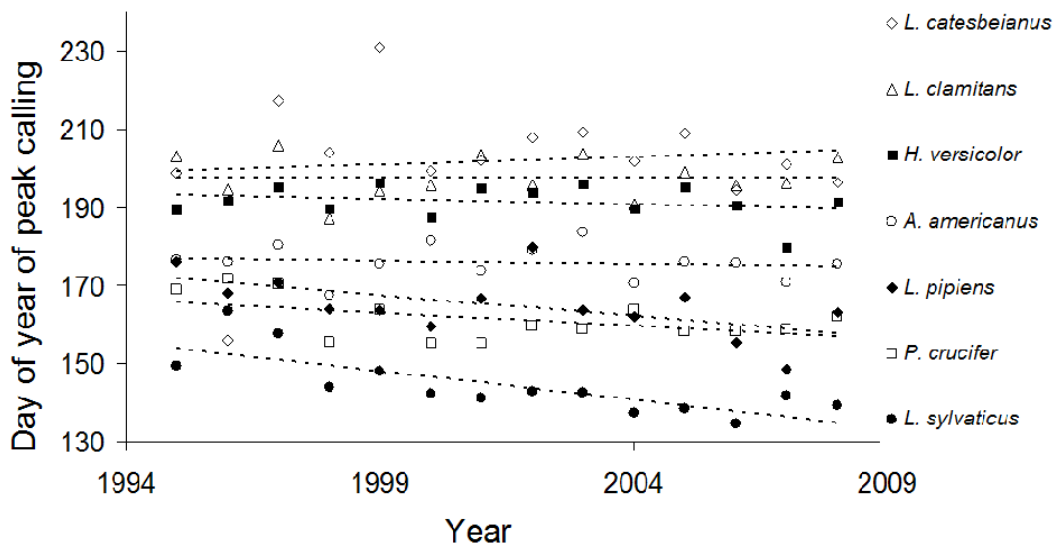
**TABLE 2.** Model selection results for peak calling date of Northern Leopard Frog, Spring Peeper, and Wood Frog where K is the number of model parameters, n is the sample size, RSS is the residual sum of square, AICc is Akaike's Information Criteria corrected for small sample size, and  $\Delta_i$  is the AICc unit difference from the top model. The temperature variable represents the mean monthly temperature in April (°C) and First visit is the day of year of the first survey visit. Regression model significance was determined with  $P$ -values computed from randomized permutations tests of variable coefficients with 10,000 iterations.  $P$ -values for variables in additive models are separated by a comma with the first  $P$ -value referring to the first variable in the additive model.

Model	K	n	RSS	AICc	$\Delta_i$	$P$
<u>Northern Leopard Frog</u>						
First visit	3	14	595.409	100.633	0.000	0.975
Temperature	3	14	713.170	103.160	2.527	0.124
First visit + temperature	4	14	580.290	104.317	3.684	0.538, 0.163
<u>Spring Peeper</u>						
Temperature	3	14	207.560	85.880	0.000	0.002
First visit + temperature	4	14	193.160	88.917	3.037	0.621, 0.720
First visit	3	14	315.620	91.747	5.867	0.933
<u>Wood Frog</u>						
First visit + temperature	4	14	245.680	92.284	0.000	0.092, 0.243
Temperature	3	14	374.710	94.150	1.866	0.003
First visit	3	14	447.440	96.633	4.349	0.995

Spring Peeper and Wood Frog (Table 2). Coefficients for temperature were negative for both species (Table 3).

Survey visit date, however, was also an important predictor of calling behavior, especially in Northern Leopard Frog and to a lesser degree in Wood Frog (Table 2). This variable had a positive relationship with peak calling date for these two species and the confidence intervals for this variable did not overlap zero in Wood Frog (Table 3). The model coefficients for temperature and survey visit date in Wood Frog had importance values of 0.925 and 0.664, respectively, suggesting that mean April temperature was the strongest predictor of peak calling for this species (Table 3). We did not perform model averaging for Northern Leopard Frog or Spring Peeper as first visit date and temperature were the single best ranking models for these species, respectively.

The CGCM3.1-A2 climate scenario suggested that average spring (April) temperatures will increase 4.06 °C in the watershed by the 2070–2100 period. The earliest breeding species in our study were Wood Frog, Spring Peeper, and Northern Leopard Frog, all of whose peak calling date advanced over time and with increasing spring temperatures. When applied to projected



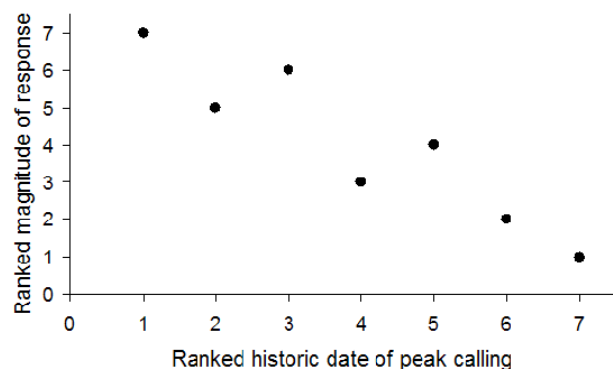
**FIGURE 2.** Trends in the day of year of peak calling by seven anuran species detected through calling surveys at stations located throughout the Lake Simcoe watershed, Ontario, Canada, from 1995 to 2008. The dashed lines represent linear regression trend lines fitted to the average peak calling dates for each species across the years studied and occur in the same order (top to bottom) as the species listed in the legend. The seven species include: *Anaxyrus americanus*, *Hyla versicolor*, *Lithobates catesbeianus*, *Lithobates clamitans*, *Lithobates pipiens*, *Lithobates sylvaticus*, *Pseudacris crucifer*.

spring temperatures in the 2070–2100 period, the top ranking regression model for Spring Peeper presented scenarios in which peak calling date would advance up to 11 days (based on temperature differences between the contemporary and the 2070–2100 climate model). The regression model for Wood Frog was complicated by including the additive effects of both spring temperature and the first visit date. Nonetheless, the influence of temperature was greater on Wood Frog calling date than it was on Spring Peeper, suggesting that Wood Frog calling date would advance by an even greater number than the 11 days estimated for Spring Peeper. Peak calling date by Northern Leopard frog was best predicted by the timing of the first survey. Thus, although peak calling in Northern Leopard frogs may be linked to temperature, we could not predict changes in calling phenology for this species with our models. The peak calling dates of later breeding species, namely American Toad, Gray Tree Frog, Green Frog, and American Bullfrog, were also not related to temperature (all  $|r_s| < 0.6$ ,  $n = 12-14$ ,  $P > 0.05$ ). Thus, if we assume no change in the peak calling date of later breeding amphibians, the CGCM scenarios suggests the potential for a 30% increase in the breadth of the breeding season by the next century (time between earliest and latest calling date) for the anuran community in the Lake Simcoe watershed (from 38.7 days to 50.3 days).

## DISCUSSION

Most anurans call as a precursor to reproduction to attract mates and affirm territories (Gerhardt 1994). For many species, the timing of their calling period is linked to climate (Gibbs and Breisch 2001). Our study illustrates a relationship between calling of spring-breeding amphibians and temperature. We found that early spring-breeding anurans have begun calling earlier in the year since 1995. This effect appears to be a result of observed increases in mean monthly spring temperatures. At the same time, phenology of later breeding anurans has not similarly advanced. Thus, our study shows how asymmetric effects of increasing spring temperatures have led to an increase in the breadth of the breeding period for the community of anurans we studied. The asymmetric response by different anuran species may affect the type and strength of interspecific relationships as previously suggested by Donnelly and Crump (1998). Ultimately, varying responses by species to changes in temperature could alter the species composition of these communities and their constituent ecological processes (Yang and Rudolf 2010).

Our analysis revealed some relationships between amphibian calling behavior and spring temperature that were unbiased by the timing of the surveys. Calling in the earliest breeding species, including Wood Frog and Spring Peeper, was most strongly influenced by spring temperature. However, we also observed a trend of



**FIGURE 3.** Relationship between ranked historic date of peak calling (pre-1995) and ranked magnitude of response ( $r_s = -0.893$ ,  $N = 7$ ,  $P > 0.05$ ). Magnitude of response was estimated by rank transforming the slope of the trend in peak calling from 1995–2008 and the historic date of peak calling is the rank transformed intercept of the same trend (Table 1). A greater magnitude of response represents a steeper negative slope of the trend in calling dates and higher ranked date of peak calling indicates later dates.

advancing survey initiation date (1995–2008). Thus, we were concerned about the potential influence of the surveys on our models of peak calling. We were able to account for this influence, however, in our regression models.

The timing of the first survey visit was the best predictor of peak calling date in Northern Leopard Frog and was also associated with calling behavior in Wood Frog. The timing of the first survey visit had no influence on the calling behavior of Spring Peeper. Further, we detected no relationship between the number of sites surveyed and spring temperature, which suggests that the patterns that we identified were not due to collinearity between surveyor effort and mean April temperature. Thus, while survey methodology was somewhat associated with peak calling in some early breeding species (Wood Frog and Northern Leopard Frog), our findings ultimately suggest that the trends in peak calling were not predetermined by the timing of the surveys but instead associated with rising spring temperatures.

Our finding that early spring-breeding amphibians respond more strongly to climate change than late breeding species is largely consistent with findings from other studies of amphibians (Gibbs and Breisch 2001; Todd et al. 2010). Clearly the impacts of climate change, though manifested differently across space, ultimately depend on a species' life-history requirements (Both et al. 2009; Primack et al. 2009). Our results add support to this conclusion and highlight a pattern of reproductive shifts in response to climate change that could potentially lead to disrupted interactions between species in a community.

In the case of Ontario's pond breeding amphibians, reproducing early likely minimizes the risks of

reproductive failure when vernal ponds dry out later in the season. Vernal ponds offer a nursery environment with relatively few predators (Skelly 1996) but the ephemeral nature of these systems demands rapid growth to metamorphosis (Werner et al. 2009). The earliest breeding amphibians in our study, Wood Frog and Spring Peeper, use vernal ponds for reproduction (Heatwole 1961; Skelly 1996), whereas the mid- to late-breeding amphibians in our study are more facultative in their use of wetlands (Gilbert et al. 1994; Petranka et al. 1994). This is an important characteristic because the rate that ponds or wetlands dry up can affect the probability of reproductive success or failure in a given year (Paton and Crouch 2002). Importantly, climate change is expected to not only advance wetland hydroperiods but also cause intermittent inundation of these ephemeral water bodies due to more infrequent and higher intensity precipitation (Brooks 2004, 2009). Our study suggests that some species are shifting their phenologies and reproducing earlier in the year. The implication of these shifts in relation to changing hydroperiods remains unclear.

According to the climate model CGCM3.1-A2, mean air temperatures in the spring are expected to rise 4 °C by the year 2100 in the Lake Simcoe watershed. Our results suggest that there will be varying responses to climate change by anurans. Peak calling date by Spring Peepers could occur up to 11 days earlier by the year 2100 and may occur earlier for Wood Frogs. Conversely, the reproductive phenologies of later breeding anurans, such as Green Frogs and American Bullfrogs, were not correlated with temperature and thus, would not be expected to change predictably with climate, at least given current known relationships. If

**TABLE 3.** Regression model coefficients for the peak calling date of Northern Leopard Frog, Spring Peeper, and Wood Frog where SE represents standard error of coefficient, and  $W_i$  represents Akaike's importance weights. The temperature variable represents the mean monthly temperature in April (°C) and first visit is the day of year of the first survey visit.

Parameter	Coefficient	SE	Upper	Lower	$W_i$
<u>Northern Leopard Frog</u>					
Intercept	62.521	49.688	173.225	-48.183	–
Visit	0.691	0.335	1.437	-0.055	–
<u>Spring Peeper</u>					
Intercept	175.551	4.333	185.206	165.897	–
Temperature	-2.464	0.733	-0.831	-4.097	–
<u>Wood Frog</u>					
Intercept	139.207	46.611	243.056	35.357	–
Temperature	-3.026	1.119	-0.533	-5.519	0.925
Visit	0.596	0.244	1.140	0.051	0.664

projections from climate models prove accurate, then we can expect an advance in the reproductive timing of spring breeding anurans to a greater degree than late breeding species. These changes would have the potential to influence levels of niche overlap between species (Todd et al. 2010), affect competitive interactions (Yang and Rudolf 2010), and produce asynchronies in predator-prey systems (Winder and Schindler 2004; Both et al. 2009; Thackeray et al. 2010).

Finally, we detected strong trends toward early breeding over a relatively short (14 year) timeframe. Gibbs and Breisch (2001) noticed similar shifts in first calling date by amphibians between 1900 and 1999, Todd et al. (2010) detected an advancing trend in the pond arrival dates of salamanders and toads over a 30-year period, and Beebee (1995) demonstrated an acceleration in spawning dates by amphibians over a 17 year period. These studies emphasize the short temporal scale over which the effects of climate change can be observed and suggest that shifts in amphibian communities may occur rapidly over a relatively short time period. However, the full implications of these rapid community shifts remain unclear.

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