Comments

Amphibian Breeding and Climate Change: Importance of Snow in the Mountains

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The breeding phenologies of ectotherms are inextricably linked to weather, and amphibians in some temperate locations may have been breeding earlier in recent years in response to warmer spring temperatures (Beebee 1995; Forchhammer et al. 1998; Gibbs & Breisch 2001). Directional change in the timing of breeding resulting from climate change may have consequences for the fitness of individuals and may affect the persistence of amphibian populations (Ovaska 1997; Donnelly & Crump 1998). Blaustein et al. (2001) contribute valuable information to the small, but growing, data set of long-term observations of amphibian breeding phenology. As in other studies, Blaustein et al. found a significant relationship between air temperature and phenology, with earlier breeding associated with warmer air temperatures for boreal toads (*Bufo boreas*) and Cascades frogs (*Rana cascadae*) in Oregon and for spring peepers (*Pseudacris crucifer*) in Michigan. Contrary to other studies, however, there was no trend toward earlier breeding relative to year for any of these species or for Fowler's toads (*B. fowleri*) in Ontario. These results are important in demonstrating that changes in breeding phenology due to climate change are not universal among amphibians.

The analysis by Blaustein et al. differs from other investigations of amphibian breeding phenology because they used data from species in mountain habitats (*B. boreas* and *R. cascadae* in Oregon). The behavior of montane organisms is driven more by the timing of snowmelt than by temperature, and winter snow accumulation can be a better predictor of breeding phenology than temperature for these species (Inouye et al. 2000; Corn & Muths 2002). Blaustein et al. also compared breeding activity at four sites to temperature data from a single weather station (located up to 32 km away and 1070 m lower in elevation). In mountain habitats, weather can vary over a small spatial scale, and weather stations far from a breeding site may not represent local conditions experienced by the animals using a particular breeding site. I re-analyzed the data set of Blaustein et al for the timing of breeding by *B. boreas*. I used temperature and snow data from automated (SNOTEL) and manual snow survey stations (www.wcc.nrcs.usda.gov [accessed 31 January 2002]) much closer to their study sites. I found significant relationships between dates of breeding and both snow accumulation and air temperature that have important implications for the effects of climate change on amphibians in the Pacific Northwest.

Blaustein et al. reported on *B. boreas* breeding at three locations in the Cascade Mountains in Oregon: Lost Lake (lat. 44°25.8′N, long. 121°54.7′W, 1215 m elevation), Little Three Creeks Lake (lat. 44°6.1′N, long. 121°38.6′W 2040 m elevation), and Todd Lake (lat. 44°1.8′N, long. 121°44.1′W, 1870 m elevation). I interpreted the dates of first breeding by *B. boreas* at these sites from field notes supplied by D. Olson (U.S. Forest Service, Corvallis, Oregon), which were the same source for the data used by Blaustein et al. except for 3 years at Lost Lake (1986, 1998, 1999), 2 years at Todd Lake (1988, 1990), and 1 year at Little Three Creeks Lake (1988). For those years not in Olson's notes, I extracted dates of first breeding from Fig. 1 of Blaustein et al. (2001) by capturing a digital image of the figure and drawing lines perpendicular from the y-axis to each data point. During any century, however, the vernal equinox occurs earlier in the year at the end of the century than at the beginning (Sagarin 2001). This bias is slight, but to eliminate it I converted the calendar dates of first breeding to the number of days between the vernal equinox (dates obtained from http://aom.giss.nasa.gov/srvernal.html [accessed 11 February 2002]) and first breeding (hereafter days). I compared days each year of *B. boreas* at Lost Lake to snow and air temperature data from the Santiam Junction SNOTEL station (lat. 44°25.8′N, long. 121°55.8′W, 1143 m elevation), which is 2.5 km west of Lost Lake and 72 m lower in elevation. I calculated a single mean days each year for Todd Lake and Little Three Creeks Lake because timing of breeding at

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these two sites was highly correlated ($r = 0.94$) and these sites were being compared with a single weather station. This single mean-days value was compared with the snow and air temperature data from the Three Creeks Meadow SNOTEL station (lat. 44°9′N, long. 121°37.8′W, 1722 m elevation), 5 km north and 13 km northeast and 318 m and 148 m lower than Little Three Creeks Lake and Todd Lake, respectively. I used snow water equivalent (SWE, the water depth that would result if the snow were melted instantaneously) as a measure of snow accumulation. SNOTEL records SWE remotely and automatically, and manual snow survey data indicate that SWE and snow depth are highly correlated (Three Creeks Meadow, data for the end of March, 1929–1989, $r = 0.96$). The SWE on either 1 April (Santiam Junction) or 1 May (Three Creeks Meadow) was converted to the percentage of the long-term average of the maximum SWE for each winter.

The average maximum SWE from 1979 to 2001 was 46.4 cm at Santiam Junction and the 1 April SWE varied between 0% (1996) and 196% (1999) of this value. The 1 May SWE at Three Creeks Meadow varied between 0% (1992) and 195% (1999) of the 1981–2001 average maximum SWE of 52.2 cm. There were strong relationships between percent SWE and days at both locations (Fig. 1), with breeding taking place closer to the vernal equinox in years with low snow accumulation.

Blaustein et al. (their Table 1) found significant negative relationships between dates of first breeding at Todd Lake and Three Creeks Lake and the mean maximum air temperature at Sisters, Oregon, for the 90 days prior to breeding. They found no relationship between air temperature and breeding by *B. boreas* at Lost Lake. In addition to the problem of a distant weather station, however, the independent variable (mean maximum air temperature for the 90 days prior to breeding) used by Blaustein et al. (see also Reading 1998) is not the most appropriate for assessing relationships between temperature and breeding activity because it is confounded with the dependent variable, date of breeding. I used the mean air temperature for March and April (61 days) and found significant negative regressions, with earlier breeding associated with warmer temperatures at both locations (Fig. 1).

Blaustein et al. did not find any significant relationships between date of first breeding and year. This is somewhat surprising, given the trends in the western United States toward warmer spring temperatures and earlier snowmelt in the last 20 years (Cayan et al. 2001). Although there has been a nonsignificant trend toward *B. boreas* breeding earlier in recent years at one site (Lost Lake), breeding at Lost Lake was actually 16 days later in 1999 than in 1982.

The opposing trends in the observed versus the predicted data illustrate the variability of amphibian breeding phenology. Long-term data are needed to determine whether there is directional change in the timing of

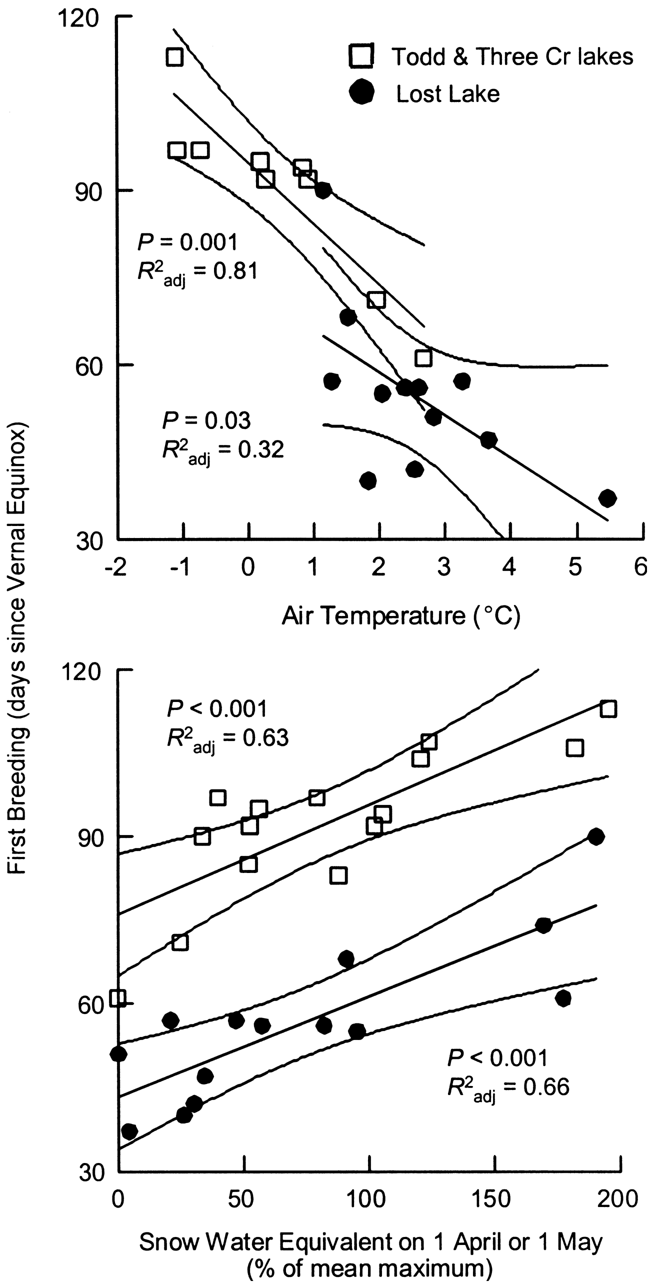

Figure 1. Timing of breeding by Bufo boreas *in Oregon relative to air temperature and snow accumulation. Dates of first breeding were taken from Blaustein et al. (2001) and the date of the vernal equinox each year was subtracted from them. Dates for Todd Lake and Three Creeks Lake were averaged. Air temperature is the mean from 1 March to 30 April. Snow accumulation is the snow-water equivalent (SWE) on 1 April (Lost Lake) or 1 May (Three Creek and Todd lakes), expressed as the percentage of the mean maximum SWE. Regressions include 95% confidence bands.*

breeding by amphibians, but most data sets currently available (e.g., Beebee 1995; Reading 1998; Blaustein et al. 2001) cover approximately 20 years and are too short to reveal significant trends when there is large interannual variation. Longer time series (37 and 26 years) of plant phenology data (purple lilac [*Syringa vulgaris f. purpurea*], and honeysuckle [*Lonicera* spp] first-bloom dates, which are comparable in variability to amphibian data) show trends toward earlier blooming in response to warmer springs since the late 1970s in the western United States (Cayan et al. 2001).

The relationship between breeding and snow accumulation and the existence of snow survey data over several decades allow longer predictions of when breeding by montane amphibians may have occurred in the past. Manual snow surveys (snow courses) were conducted approximately monthly during winters from 1941 to 1983 at Santiam Junction and from 1929 to 1989 at Three Creeks Meadow. Manual surveys were discontinued when SNOTEL sites became operational. I regressed days at Lost Lake and at the mean of Three Creeks and Todd lakes on SWE on 1 April at Santiam Junction and Three Creeks Meadow, respectively, and used the resulting equations to predict days for years before amphibian observations are available. The SWE has slightly lower predictive ability than percent SWE, but maximum SWE is not available from manual snow surveys.

The relationship between predicted days and year differed between the two sites (Fig. 2). I used distance-weighted least squares (Cleveland 1979) to plot trend lines. Predicted breeding now occurs about 15 days earlier in the year at Lost Lake than in 1950, but there is no trend apparent at Three Creeks. This may be causing phenology to diverge according to elevation. Predicted breeding by *B. boreas* in 1950 occurred about 22 days earlier at Lost Lake than at Three Creeks, which is at least 650 m higher than Lost Lake. By 2001 the gap in predicted breeding had grown to 35 days (actual breeding at Lost Lake from 1995 to 1999 averaged 42 days earlier than the average at Todd and Three Creek lakes). However, there is enormous annual variation in days. Although the linear regression of predicted days on SWE was significant at Lost Lake ($p = 0.002$), the predictive power of this relationship was low (adjusted $R^2 = 0.14$).

One of the key predictions of future climate change in North America is that snow cover will be reduced in extent and duration (MacCracken et al. 2001). In the mountains, this will tend to increase the differences in phenology related to elevation because high elevation sites will retain snow longer than will lower-elevation sites. Despite the variability in predicted breeding (Fig. 2), it is at least a reasonable hypothesis that climate change is already affecting the breeding behavior of toads in the Oregon Cascades.

Major shifts in breeding phenology may have consequences for the persistence of populations (Donnelly

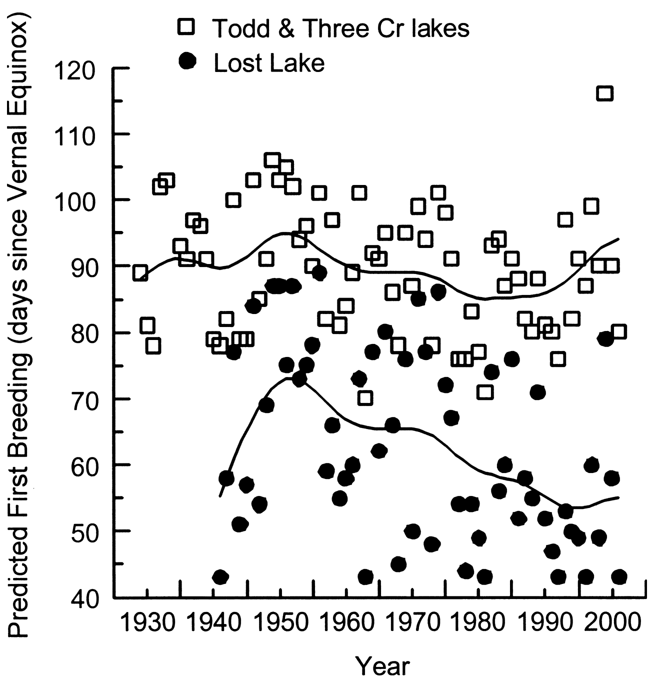

Figure 2. Predicted number of days between the vernal equinox and date of first breeding by Bufo boreas *at two locations in the Cascade Mountains in Oregon.*

and Crump 1998). At the locations studied by Blaustein et al. (2001), earlier breeding resulted from reduced precipitation. Reduced winter precipitation in the Cascades is associated with El Niño/Southern Oscillation (ENSO) events, and increased mortality of *B. boreas* and *R. cascadae* eggs at these study sites occurs in years with reduced precipitation (Kiesecker et al. 2001). If predicted increases in the frequency of ENSO events caused by global warming occur (Timmermann et al. 1999), then populations of *B. boreas* and *R. cascadae* may be at risk in the Cascades. I predict that, if this occurs, populations at lower elevations will be affected first. Long-term observations of natural history, such as those reported by Blaustein et al. (2001), are invaluable for interpreting and predicting the effects of our changing environment on animal and plant populations. In mountain habitats, however, air temperature alone is insufficient to explain the timing of breeding, and dates of breeding by montane amphibians also need to be compared to snow accumulation.

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