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THE MATHEMATICS OF SPRING PEEPERS

Image from Diane Gerereux

My grandmother was very fond of spring peepers. She would lower her car windows in the sunny-but-still-cold days of early spring, seeking out roads lined with wetlands, in hopes of hearing the mating calls of male peepers, which are also known as chorus frogs. When eventually my grandmother did hear the frogs, she would mention them to everyone she knew, sometimes attempting to give her own rendition of their choruses — an ambitious undertaking for one human, as the spring-peeper choristers calling together in a given pool typically number in the hundreds.

I never learned of the exact origin of my grandmother's great enjoyment of spring peepers, but I did inherit it. To my delight, the peepers' genus — currently, *Pseudacris* — is widely distributed through the United States. I've been very fortunate to hear the calls of *Pseudacris* species starting in January in Atlanta, February near Seattle, and March in Westfield, where, as in much of the Northeast, the local species is *P. crucifer*, which are so named in reference to the tiny cross-shaped coloration on their backs. (The photo at left features a peeper I saw at Wolf Pit Meadows in Westfield in April of 2015.)

Even my limited observations in various parts of the US would suggest that the timing of the frogs' first spring calls is related to the conditions they use as cues for emergence. But which factors are most important? Chorus frogs overwinter in a state of near-dormancy amid leaf litter and under the bark of trees. My grandmother's searches were inspired by sunshine and climbing temperatures, both of which would seem to predict conditions appropriate for the move from the comparative isolation of the winter forest to the frenzy of the wetlands. But is temperature alone sufficient to explain the timing of peepers' move to wetlands, and the beginning of their calls? Or could other factors be more important?

It was this question that motivated Gary Lovett, an ecologist at the Cary Institute of Ecosystems in Upstate New York, to undertake a systematic study of potential associations of chorus-frog emergence with temperature, day length, sunshine, and rainfall. In a 2013 EcoFocus column for the *Poughkeepsie Journal*[1], summarizing data that he had previously published elsewhere[2], Lovett noted that, for years, ecologists had offered only speculative explanations — for example, that frogs routinely emerge "after the first spring rain". This and other claims may be generally reliable, but they fail to explain how frogs distinguish the cold first rain of spring from the cold last rain of winter.

Lovett's findings revealed that peepers' mathematics are substantially more intricate than a threshold value for rainfall or single-day temperature. In Lovett's analysis of longitudinal climate data, thermal sum emerged as the strongest quantitative predictor of chorus-frog's emergence time in Upstate New York. In essence, thermal sum measures the extent to which days within a defined interval exceed a defined base temperature. Frogs seem to hold out for a stretch of days in which temperatures climbed above 37°F. Calculating thermal sum therefore requires storing temperature data over multiple days.

Lovett suggested peepers' impressive freeze tolerance as a possible mechanism for recording longitudinal temperature data. Like the winter moths highlighted in a 2015 Naturalist's Corner piece and in an April 2015 talk by University of Massachusetts biologist Jeff Boettner, *Pseudacris* spp. can survive winter temperatures fatal for many other ectotherms. For peepers, it is glucose that serves as an antifreeze molecule, ensuring a close interaction between freeze tolerance and metabolic processes.

As temperatures drop in the fall, frogs' livers increase the rate of gluconeogenesis, liberating stored glucose into the blood stream through a process similar to the one that goes awry in humans with Type II diabetes. Elevated high blood glucose can harm blood vessels and organs in humans; in frogs, it provides crucial protection. As glucose accrues in the extracellular space, water moves by osmosis out of frogs' organs, reducing the risk of organ damage and cell rupture upon freezing. Also, just as salt ensures that brackish rivers freeze much later than fresh ones, glucose reduces the freezing point of frogs' blood, keeping it fluid for a while after the onset of winter cold. Glucose thus enables the heart to pump glucose-rich blood around for a little while longer, ensuring that accumulating glucose can be distributed through the body. Experimental findings have confirmed the value of these physiological responses in fostering freeze tolerance, revealing that food-limited frogs, which have reduced glucose stores, are more vulnerable to rapid temperatures declines, and that direct injection of extra glucose can permit frogs to survive temperature drops even more precipitous that those typical in nature.

When the weather warms in the spring, freeze-tolerant frogs literally thaw out, their blood becoming less viscous, and their hearts eventually beating quickly enough to support the move from upland to aquatic areas. It is at least plausible that frogs track the rate of these "thawing" processes in their own calculations of the thermal sum, resulting in an exquisite tuning of emergence time to the conditions of a given year. Indeed, Lovett's analysis [2,3] revealed that the timing of the first peeper calls currently averages 11 days earlier than it was in 1949, suggesting that peepers' first calls have largely kept pace with shifting temperatures.

Peepers' ability to tune their timing to the temperatures of a given year would seem to bode well for their capacity to adjust to climate change. Perhaps confidence is especially warranted in light of Lovett's finding that, following the warm winter of 2002, which included several runs of days with temperatures greater than 37°F, frogs didn't start calling until after a strong rainstorm, suggesting that they are not fooled by the occasional warm winter.

But there are worries still, owing in part to peepers' reliance on the timing of the other organisms. For instance, *Pseudacris* tadpoles dine on diatoms and tree pollen, and are preyed upon by large aquatic insects. Adult peepers hunt spiders, beetles and ants, and are prey for skunks, snakes, and even some large frogs. If this diverse set of organisms were to respond in parallel to climate change, peepers might persist essentially unscathed. But what if these other organisms cue into alternate signals, such as day length, winter snowfall, etc.? In an animal for whom glucose functions as antifreeze, anything increasing the risk of turning in for winter on a less-than-full stomach, for example, could jeopardize prospects for surviving to spring. Any such perturbation could be especially harmful in the context of the chemical[3] and noise [4] pollution already well established as threats to amphibian populations worldwide. One such threat — rapid habitat loss — has already inspired a conservation project focused on Illinois's chorus frog, *P. streckeri illinoensis* [5].

On a warm afternoon in mid-March of this year, just the sort of day on which my grandmother would have rolled down her car windows and sought out wetlands, I walked through the Broad Meadow Brook Audubon Sanctuary in Worcester (see p. 4 for information on a planned trip to this site). Once I had walked by three or four suitable-looking pools, encountering no calls, it occurred to me that I might be listening for peepers too early in the season. Compared to *P. crucifer*, I am poorly attuned to thermal sum. Surely, the frogs had thawed already; but perhaps not enough days had reached 37ºF?

Just when I'd begun to consider turning back, I walked around a bend in the trail and was greeted by a wonderfully strong and optimistic-sounding chorus. To me, the pool was indistinguishable from those I'd encountered earlier. It was of similar size, and, like the others, surrounded by low vegetation that could provide refuge from would-be predators. Somehow, though, these frogs had chosen this particular spot. Was this a random event — the result of a few frogs crawling out from under tree bark and hopping their way here, just by chance? Had latecomers simply following the early frogs' lead? Was there something special about conditions in this pool? Perhaps the other pools would soon be visited by frogs whose overwinter microhabitats took just a few more days to achieve the critical thermal sum? I stood there for a while, enjoying the sounds, and realizing that there's much more to learn before we can fully understand how well peepers' intricate calculations will accommodate the uncertainties of climate change.

~Diane Genereux

References

1. Lovett, 10 March 2013, *Poughkeepsie Jrnl.*, p1.;**2.** Lovett, 2013, *Northeastern Naturalist*, 20(2):333-340**;** **3.** Tracie, 201*Acta zoológica lilloana* 54 (1–2): 3–10, 2010 **;4.** Layne and Lee, 1995. *Climate Res.* **5:** 53-59.;**5**. *http://www.dnr.illinois.gov/conservation*