Hi Will,

Ok, here's the rundown. For the past few years, I've been studying the relative temperature tolerances of two rare species of salamanders (Peaks of Otter salamanders and Big Levels salamanders) in comparison to their extremely widespread competitor the Northern Red-Backed salamander. Both of rare species are mountaintop endemics with a tiny range restricted to a single ridgetop. The two species are both abundant within their range, but their ranges are very tiny, among the smallest for any known mainland vertebrate species. At the range margins, there's typically a narrow band of overlap with red-backed salamanders, which are super common along in Eastern US from the NC mountains up north into Quebec. Go a little along the ridge or further downslope from the range of either of these species and it's all redbacks.

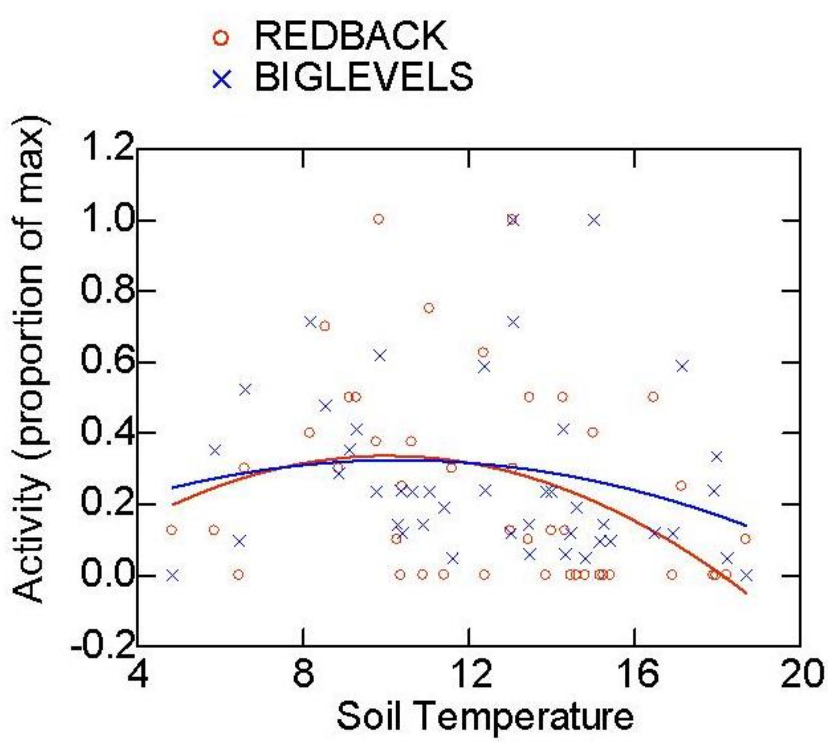
An obvious conservation concern for poorly dispersing mountaintop endemics is climate change. One would expect mountaintop species to be cold-adapted, so that warmer temps should favor their lower elevation competitors. With these salamanders, if warming favored redbacks, they would be predicted to gradually move upslope into the range of the mountaintop endemics, squeezing them even further at the top of the mountain. There is good evidence of some other mountaintop species (e.g. Pika, butterflies) losing populations as a result of climate change.

However, there are some interesting complications with these salamanders. Red-back salamanders (the common competitor species) in southern Virginia are actually near the southern end of their range limit – they go north to Quebec – they seem to be just fine with colder temperatures but not so good with warmer temps. They also tend to reach peak abundance in high elevation areas (rather than low elevation areas) suggesting that they're not the typical warm-adapted species that would be expected to thrive under climate change. In addition, Big Levels salamanders (though not Peaks of Otter salamanders) are actually an isolated offshoot of the Southern Red-Backed salamander, and phylogenetic research has shown that salamanders in this family tend to maintain their thermal niches over substantial periods of evolutionary time. So, in a sense you have a southern lineage at the top of the mountain surrounded by a northern lineage lower down on the mountain. I always liked this project for my classes to work on because there's a fairly straightforward question (which species is more tolerant of higher temperatures?) but the answer isn't at all obvious from the natural history or other prior information. Sounds like a job for data!

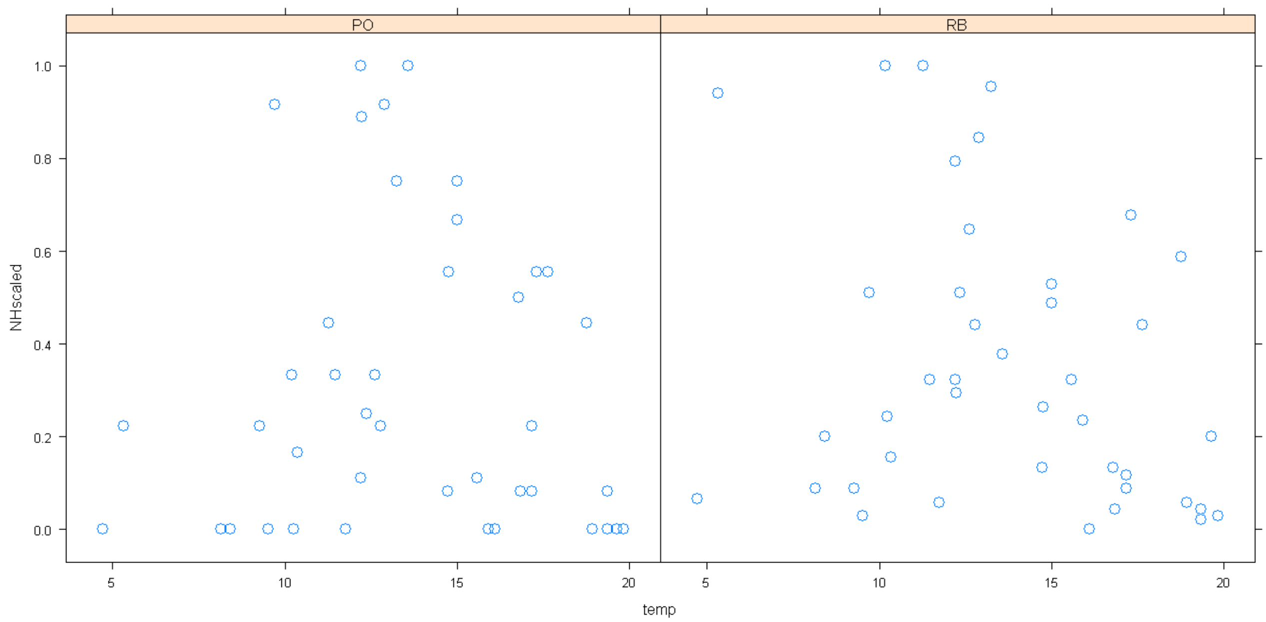
To study temperature tolerance, we set up a grid (or two grids) of cover objects (rocks and logs) in one high elevation and one low elevation contact zone for each species pair. Essentially, these are two completely separate studies – we did this for Big Levels versus Redbacks in 2012-13 and for Peaks of Otter versus redbacks in 2013-14. In each of these years/studies, we surveyed salamanders weekly throughout the year so that we could relate surface activity to soil temperature at the time of the survey. There's an assumption here that surface activity reflects temperature tolerance but I don't think any salamander people would argue with it – there's good evidence from both field and lab studies that that salamanders go underground when it's too hot or too cold.

On each survey date we get counts of salamanders of the two species from either the high elevation or the low elevation plot (not enough time to do both on the same day), along with soil temperature and soil moisture (a linear covariate for both species) on the plot. We have about 40 survey dates in each study. In case you're wondering, we did actually mark salamanders, but recapture rates are too low to be helpful, which is actually what I would have expected (there are lots of salamanders out there, only some of which are on the surface at any given time). Anyway, at the simplest level, the goal is to determine the extent to which the curve relating temperature to salamander count differs between the two species (mountaintop endemic versus red-back).

Animal counts are typically modeled with a negative binomial distribution (activity is temporally clustered and therefore usually overdispersed from a Poisson). I think the simplest function relating count to temperature would be a quadratic – salamanders disappear when it's too hot or too cold and probably have some temperature in the middle that yields peak activity. I don't think this is exactly correct biologically – ectotherms probably have some range of temperatures which are pretty acceptable and then a more rapid decline in activity above or below this range. But I also don't think there's really the data to support a more complex model than a quadratic. Also, there's inherently lots of noise in count data. I've been doing this for 20 years now and sometimes there are lots of salamanders out on days when I wouldn't have expected it and other days when few are out even though it seems like a good day. They're responding to something but I have no idea what it is. Here's a scatterplot that shows the data for Big Levels versus Red-Backed salamanders – the Y axis here is count indexed to be relative to the maximum observed for that species in that plot to allow a more direct visual comparison.



And here's a scatterplot I just drew up for Peaks of Otter salamanders versus redbacks:



Anyway, for a single species, a very simple model would be something like:

SALCOUNT (neg.bin) ~ temp + temp ^2

With soil moisture as a covariate it would be:

SALCOUNT (neg.bin) ~ temp + temp^2 + soilMS

For Big Levels salamanders (but not so much Peaks of Otter salamanders), counts differed between the high and low elevation plots as well, so elevation would also go into the model.

One potential option is to compare models between the two species (i.e. parameter estimates and credibility intervals. I think maybe the vertex of the parabola and the x-intercepts are more relevant parameters than the regression coefficients since they represent the optimal temperature for each specie as well as the high and low activity points. I recall some issues with standard errors of derived parameters but that issue would probably work out differently in a Bayesian context since one is simulating anyway? Alternatively, maybe one could potentially try to estimate an interaction between species and temp coefficients that explicitly represents the difference between the two species. Not sure if one of these options make more sense.

Just so you know what I did previously for conference presentations on this study, I created a hypothesis test by combining the data for both species at a site, including species as a factor and then testing for a significant species*temp (or species*temp^2) interaction. Since I then had two species counts from each day/plot search, I included day as a random effect on the intercept in the model, so it looked like this:

SALCOUNT (neg.bin) ~ SPECIES + temp + temp^2 + SPECIES*temp + SPECIES*temp^2 +soilMS + (~1|date)

I saw some recommendations for only using an interaction term with the linear term in a polynomial regression, but I never saw a convincing argument for this.

For both studies, one sees graphically and in the analyses that the results appear to be consistent with similar temperature tolerances for the two sets of species or with moderately higher temperature tolerances in the mountaintop species (maybe more so for Big Levels salamanders than for Peaks of Otter salamanders). What's interesting is that the results do not seem particularly consistent with the "conventional" view that mountaintop endemics should prefer cooler temperatures as compared to their lower elevation competitors. Either way, I feel like in this example, the focus should really be on the relevant parameter estimates for the two species rather than on any specific hypothesis test.

That should give you enough to get the general picture. I'm still very open on modeling strategy – I don't love the quadratic given the noise (the days with maximum counts are very important biologically but their influence is tempered statistically by days with few or no salamanders out). But as I said, I'm not sure one could really support a much more complex model given the size of the data set. I've used quantile regression models with linear data (which allows you to focus on the maximum values at any level of the predictor variable) but I don't know if that kind of approach would be usable here.

Oh, and I've also attached the Peaks of Otter data so you can see what the data look like. The main count variables are ponh and rbnh – these are peaks of otter counts and red-back counts with no hatchlings – hatchlings do not seem to ever go below ground so their counts are independent of temperature.

Let me know when you've been able to look at this and I'm happy to set up a time to talk.

David M.