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commentary

Hot research on roasted lizards: warming, evolution and extinction in climate change studies

In volume 328 of *Science*, a team headed by Barry Sinervo published a study forecasting the effect of increased temperature in lizards. They demonstrate that climate change has already caused extinctions of lizard populations worldwide. They also forecast that if climate change scenarios come true, 40% of all lizard populations and 20% of all species could be committed to extinction by 2080. Predictions are supported by a model that represents how much activity time will be restricted (i.e., hours of restriction; hr) because operative temperatures are too high.

The study uses a multidisciplinary approach incorporating ecophysiology, evolutionary biology, biogeography and phylogenetics. A special strength of the study is that it uses models that are validated with data from recent population extinctions, which is an extremely rare feature in studies assessing climate change effects on biodiversity (but see Araújo et al. 2005). Sinervo et al.'s study links temperature increases to the organismal biology of the lizards making it possible to predict local extinctions. Unfortunately, such a link leads to a worrisome message: "Climate-forced reptile extinctions are happening now" (Huey et al. 2010).

Forecasts of species extinctions due to climate change are typically based on assessments of changes in climatic suitability for species (e.g. Thomas et al. 2004; Thuiller et al. 2005). Sinervo and colleagues go beyond this climate envelope approach and incorporate aspects of the ecology and behavior that are thought to mediate the re-

sponses of species to climate change. The incorporation of ecological and behavioral mechanisms into models attempting to provide insight of the likely responses of species to climate change is welcomed (Brook et al. 2009), but when such attempts involve large numbers of species and biogeographical scales compromises between precision and generality are inevitable.

One of such compromises is related to the use of estimated operative temperatures (the equilibrium temperature of a lizard with its thermal environment) in the study. Operative temperatures can vary greatly due to micro-environmental heterogeneity (Bauwens et al., 1996). Lizards may select locations with cooler micro-climates instead of moving higher in altitude or latitude. Open habitat species for example, may encroach into forests (Huey et al. 2009). This study would have benefited from integrating small scale thermal heterogeneity into large scale studies, although precisely how this can be accomplished remains a key challenge for mechanistically motivated models of climate change.

Investigators such as Kearney et al. (2008) and Mitchell et al. (2008) have created biophysical models of the thermal environment of reptiles to make predictions on the effect of global warming on individual species. These models use heat and energy balance equations to relate environmental conditions with ecophysiological traits measured in the laboratory. These relationships can be mapped geographically to evaluate climate suitability for the species of interest. Sinervo et al.

uses a simpler approach: modeling hr as a linear function of maximum temperature. While this approach does not include as much mechanistic detail as a full physical model, like Kearney et al.'s, it is noteworthy for integrating an environmental niche model, ecophysiological traits, and extinction probabilities. This simplification allowed generalizing the model to include a large number of species in their forecast — a feature that would have been unfeasible if more complex mechanistic models were used.

Another breakthrough is their explicit modeling of potential evolutionary change, an aspect that is rarely considered when attempting to forecast the species responses to climate change. The authors relate extinctions with strong selective pressure and argue that a heritability of 0.17 for field active body temperature (Tb) measured for *Sceloporus occidentalis* constrains adaptation. However, heritability is species-, population-, and environment-specific, and when measured in the lab, it might not represent the actual heritability in the field. Methods exist to estimate heritability in the field (Weigensberg and Roff 1996), but they have seldom been used.

Sinervo et al. used a phylogenetic OLS linear regression between Tb and critical thermal maximum (CTmax) to provide evidence that CTmax may not evolve as fast as Tb, and they suggest that increasing Tb would bring the animal dangerously close to CTmax. OLS linear regression assumes that the X variable has no measurement error. In this particular case both traits have measurement error, so RMA (Reduced Major Axis) regression might have been more appropriate (Warton et al. 2006) since it does not assume absence of error in X axis. The slope of RMA regression is always steeper than that of OLS. With a slope of 0.51 for OLS, the RMA slope for the phylogenetic regression might actually be close to 1, inviting the interpretation that, contrary to the conclusions derived from OLS regression, CTmax may evolve as fast as Tb.

In temperate regions, extinctions probabilities correlated better with hr in the spring than in other seasons. Sinervo et al. propose that temperature increases are more evident during the

spring and that the spring is more critical than the summer for lizard survival due to either reproductive costs or to a higher need for resources after diapause. However, there are other possible, although non-exclusive reasons that require further scrutiny. Pregnant females, for instance, often have lower Tb resulting in longer hr in springtime (Carretero et al. 2005), and temperature increase may alter egg development (Mitchell et al. 2008). Methods inevitably reflect the need to compromise precision with generality. Like other biogeographic studies with strong implications for policy, the sensitivity of the conclusions to the assumptions and methods requires systematic scrutiny (Whittaker et al. 2005). Nevertheless, this study is a “tour-de-force” that exemplifies research opportunities for biogeographers and provides evidence that reptiles might be more sensitive to climate warming than previously reported (e.g. Araújo et al. 2006). Firstly, the study illustrates the value of interdisciplinary collaborations. Biogeographers interested in climate change should consider collaborating with evolutionary biologists, geneticists, systematists, and ecophysiologicalists. Secondly, the ecophysiological basis for the study helps create a compelling link between climate change and the organismal biology of the lizards. Thirdly, evolutionary changes are modeled in the context of phylogenetic constraints and genetics. All in all, Sinervo et al. has contributed to launching a new pathway for investigation of climate change impacts on biodiversity. Biogeography has always been an interdisciplinary field, but this study suggests that even broader interdisciplinary collaborations are necessary to help understand the effects of climate change on organisms.

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