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# Response to Comment on “Erosion of Lizard Diversity by Climate Change and Altered Thermal Niches”

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We derived physiological models that accurately predicted extinctions of Mexican and other lizards. Clusella-Trullas and Chown argue that global forecasts are unreliable without incorporating variance in microenvironmental temperatures,  $T_e$ . Here, we show that  $T_e$  variance is small relative to  $T_e$  increases from climate warming. Thus, extinction forecasts are reliable ( $\bar{R}^2 = 0.72$ ) even without  $T_e$  variance data.

We predicted extinctions of Mexican *Sceloporus* lizards by deriving physiological models based on field ( $T_b$ ) and preferred body temperatures ( $T_p$ ), maximum daily air temperatures ( $T_{max}$ ), and activity-time restrictions during reproduction,  $h_r$  = cumulative hours/day when  $\bar{T}_e > T_p$  (1). Clusella-Trullas and Chown (2) assert that our failure to include spatial heterogeneity in microenvironmental temperatures ( $T_e$ )—and thus assess thermal opportunities at local population scales—overestimates  $h_r$ , thereby inflating extinction forecasts. Contrary to their assertions, we did not simply apply  $h_r$ ,  $T_{max}$ , and  $T_b$  relations [equation S2 in (1)] to lizard families. We computed family-specific  $h_r$  values using  $T_b$  and  $T_{max}$ -based distributional limits, adjusting  $h_r$  [thereby scaling equation S2 in (1)] to each family. We also cross-validated  $h_r$  estimates with available behavioral data [e.g.,  $h_r = 1.83$ , *Liolaemus lutzae*, table S7A in (1)]. Finally, we validated predicted extinctions derived from family-specific  $h_r$  calibrations with observed extinctions across four other continents, including 192 species spanning seven families, not the single species implied by Clusella-Trullas and Chown (2).

If local  $T_e$  variation is biologically relevant, as Clusella-Trullas and Chown argue, then our model should poorly predict observed extinctions. In fact, the model derived for México accurately predicted other extinctions on four continents and across seven lizard families, explaining 72% of the variation (Table 1). Including additional moments of ectotherm temperature distributions ( $T_e$ ,  $T_p$ , and  $T_b$ ), as suggested by Clusella-Trullas and Chown (2), could refine predictions, but note

that relatively little variation (28%) remains unexplained. More informative refinements would involve adding other climate data—such as duration, frequency, and intensity of warm spells, cloud cover (3, 4) (Fig. 1), and precipitation—and linking these to demography. To illustrate this point, we highlight data on *S. mucronatus* (5), which ceased reproduction at Zoquiapan in 1998, the year when four nearby weather stations recorded the highest  $T_{max}$  during April through June [table S2 in (1)]. Based on historical reconstructions of  $T_e$  and  $T_{max}$  (Fig. 1), this 3-month warm spell greatly elevated  $T_e$  at adjacent sites and caused reproductive arrest of *S. mucronatus* (5); *S. mucronatus* went extinct at two adjacent sites shortly thereafter [table S1 in (1)].

To what extent does local  $T_e$  variation affect extinction forecasts relative to historical  $T_e$  excursions? Even when  $T_e$  distributions exhibit skew or variance, the fraction of thermally permissible habitat will necessarily drop off rapidly as mean  $T_e$  rises above acceptable levels (6). Thus, foraging (and other behaviors) will be severely constrained, even if  $T_e$  remains acceptable at a few sites within a population. We argue (1) that  $T_e$  excursions from climate warming are so large that minor  $T_e$  refuges (e.g.  $T_e$  variation among microsites) at best protect only a fraction of the population, but not enough to avoid demographic collapse.

How large have historical  $T_e$  excursions been compared to microsite  $T_e$  variation? Here, we present new  $T_e$  data for Yucatán *S. serrifer* populations next to extinct sites and for *S. mucronatus* populations adjacent to Zoquiapan and other recorded *S. mucronatus* extinctions (1). These three populations span upland, montane, and tropical habitats. Rising  $T_{max}$  from climate warming at the sites ( $\Delta \bar{T}_{max} = 3.2^\circ\text{C}$ ) (Fig. 1, C and D) has generated historical  $T_e$  increases ( $\Delta T_e$ ) twice as large ( $\Delta \bar{T}_e = 15.1^\circ\text{C}$ ) as SD in  $T_e$  across microsites within populations ( $\sigma_{T_e}^2 = 7.1^\circ\text{C}$ , controlling time of day).  $\Delta T_e$  excursions are also many times as large as  $T_b$  excursions observed during behavioral thermoregulation, which index behavioral plasticity ( $T_{upper} - T_{lower} = 2.4^\circ\text{C}$ ;  $T_p - T_b = 3.6^\circ\text{C}$ ) (Fig. 1). Therefore, for extinction-prone species, historical  $T_e$  increases from climate warming, and those forecast for coming decades (1) overwhelm local  $T_e$  microclimatic variation and available  $T_b$  plasticity. Whether this is true for other modeled families will require additional  $T_e$  studies, but our model remains accurate for contemporary climate-forced extinctions in 7 of 38 families.

Our model uses spatial and temporal variation in  $T_b$  and  $h_r$ , thereby capturing salient  $T_e$  excursions due to climate warming, even though it ignores, as we acknowledge [p. 4, SOM for (1)], factors such as habitat. Ideally, one would like to have complete demographic histories and  $T_e$ ,  $T_b$ , and  $T_p$  distributions across many habitats spanning decades of measurement to match the spatial and temporal scales of global climate data (7). However, few other  $T_e$  data currently exist at scales required to validate climate-forced extinction, besides those in our original  $T_e$  validation for extinct versus persistent Yucatán sites [figure S4 in (1)] or new  $T_e$  data at extinction-prone sites (Fig. 1).

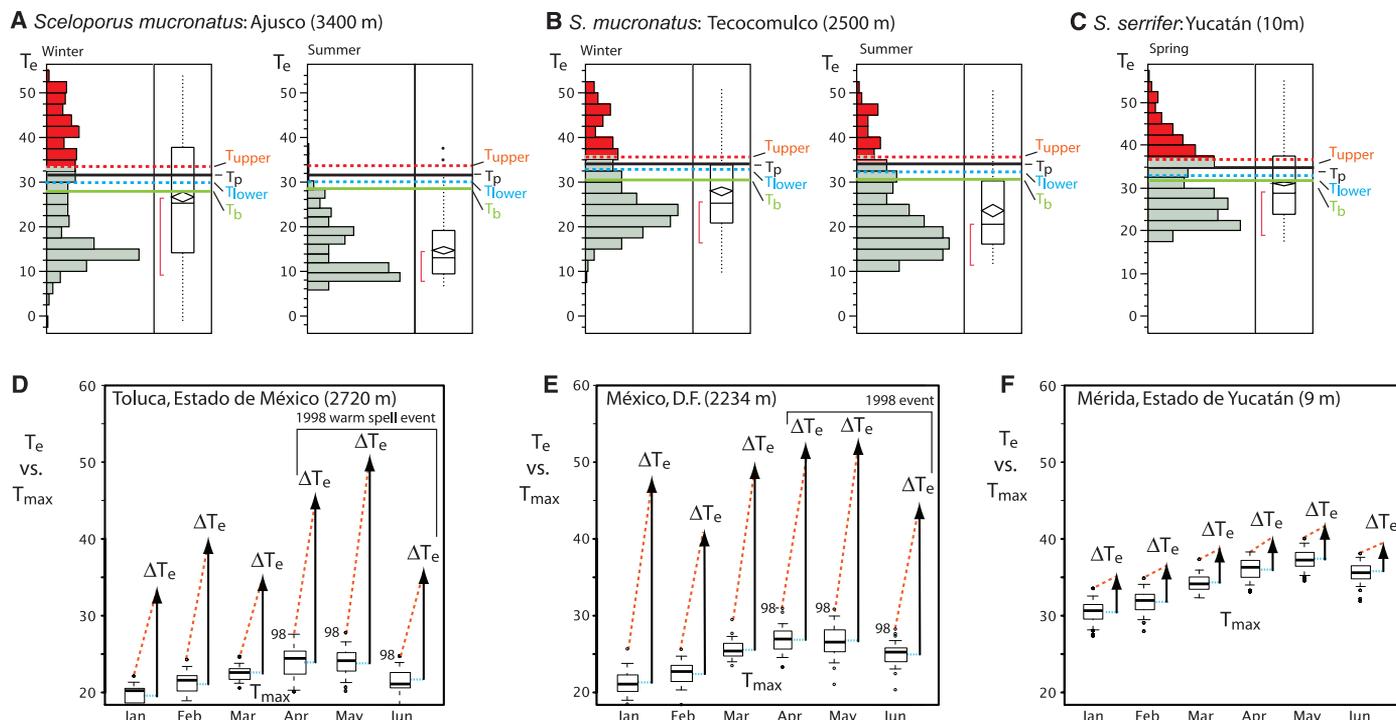
Clusella-Trullas and Chown conflate local short-term microclimatic  $T_e$  variation with historical  $T_e$  increases due to climate warming that are of much greater magnitude. These recent historical  $T_e$  excursions have begun resetting species' distributional limits at the global scale of a warming planet, the scale of our extinction ground-truth for lizards (1).

**Table 1.**  $R$ -squared for the proportion of variation explained by regression of observed extinction incidence and predicted extinctions for a given region/taxon [data from table S7 in (1)], based on the extinction model developed for Mexican *Sceloporus* lizards (family Phrynosomatidae). The extinction validation spans four continents, including heliothermic and thermoconforming lizard families. Weighted  $R$ -squared computed across all geographic regions of the world is 0.72.

| Region/taxon                                                                                                       | $R$ -squared | $N$ sites |
|--------------------------------------------------------------------------------------------------------------------|--------------|-----------|
| Africa (167 sites) and Madagascar (2 sites): Gerrhosauridae, Cordylidae, Chamaeleonidae, Scincidae, and Gekkonidae | 0.98         | 169       |
| Europe: Lacertidae ( <i>Lacerta vivipara</i> )                                                                     | 0.53         | 46        |
| South America: Liolaemidae ( <i>Liolaemus</i> and <i>Phymaturus</i> spp.)                                          | 0.53         | 128       |
| Australia: Scincidae ( <i>Liopholis</i> spp.)                                                                      | 1.00         | 23        |
| Australia: Scincidae ( <i>Liopholis kintorei</i> )                                                                 | 0.19         | 29        |

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**Fig. 1.** Daily  $T_e$  distributions for *Sceloporus* lizards across (A) an upland site (*S. mucronatus*, 2500 m), (B) a montane site (*S. mucronatus*, 3400 m), and (C) a lowland tropical forest site (*S. serrifer*, 10 m), and indices of behavioral thermoregulation (8, 9, 10), including upper and lower thermoregulatory set points ( $T_{upper}$ , red dashed line;  $T_{lower}$ , blue dashed line), preferred body temperature,  $T_p$  (black line), and field body temperature,  $T_b$  (green line). (D to F) Distribution of monthly  $T_{max}$  averages (box plots) at nearby weather stations (1975–2008) along with computed effects of  $T_{max}$  excursions due to climate warming on historical  $\Delta T_e$  excursions (1975–2008).  $\Delta T_e$  reflects change in  $T_e$  from historical values before climate warming. The tips of the arrows do not

indicate the actual  $T_e$ , but the lengths of the arrows indicate the reconstructed increases in  $T_e$  during extreme warm spell events over those observed during average conditions (as reconstructed from  $T_{max}$  excursions among years). Low summer  $T_e$  (and low June  $T_{max}$ ) of *S. mucronatus* at Ajusco (relative to winter  $T_e$ ) is due to summer cloud cover, but such protection that reduces  $T_e$ , reduces  $h_r$ , and thus ameliorates extinction risk is dissipating in México and elsewhere in the world (3, 4). The  $\Delta T_e$  values observed during the 1998 event when *S. mucronatus* ceased reproduction at Zoquiapan are highlighted. Such extreme  $T_e$  events, which have become quite common in the past decade, promote local extinction.

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