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

B. Sinervo,^{1*} D. B. Miles,² N. Martínez-Méndez,³ R. Lara-Resendiz,⁴ F. R. Méndez-De la Cruz⁴

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 (ΔT_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). ΔT_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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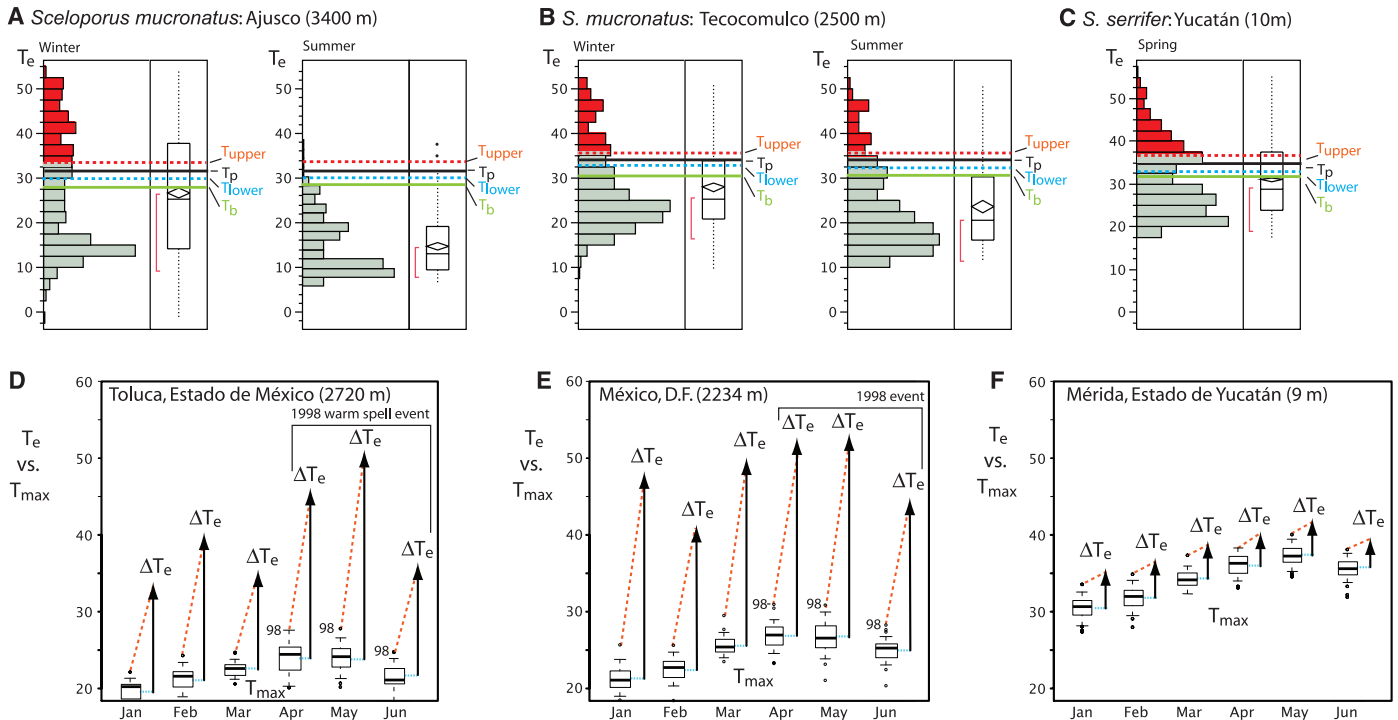


Fig. 1. Daily T_e distributions for *Sceloporus* lizards across (A) an upland site (*S. mucronatus*, 2500 m), (B) a montane site (*S. mucronatus*, 3400 m), and (C) a lowland tropical forest site (*S. serrifer*, 10 m), and indices of behavioral thermoregulation (8, 9, 10), including upper and lower thermoregulatory 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 ΔT_e excursions (1975–2008). ΔT_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 ΔT_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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