# Erosion of Lizard Diversity by Climate Change and Altered Thermal Niches

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could occur in *C. maculatus* through sexual selection on males (*18*, *26*–*28*). If sexual selection is responsible for the greater strength of the $r_{ID\text{-}BV}$ coefficients in males, it raises the possibility of positive feedback, where sexual selection increases the contribution of deleterious mutations to trait expression, in turn increasing both good genes benefits from sexual selection and the benefit of sex itself.

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### Supporting Online Material

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Materials and Methods
SOM Text
Figs. S1 to S6
Tables S1 to S10
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# Erosion of Lizard Diversity by Climate Change and Altered Thermal Niches

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It is predicted that climate change will cause species extinctions and distributional shifts in coming decades, but data to validate these predictions are relatively scarce. Here, we compare recent and historical surveys for 48 Mexican lizard species at 200 sites. Since 1975, 12% of local populations have gone extinct. We verified physiological models of extinction risk with observed local extinctions and extended projections worldwide. Since 1975, we estimate that 4% of local populations have gone extinct worldwide, but by 2080 local extinctions are projected to reach 39% worldwide, and species extinctions may reach 20%. Global extinction projections were validated with local extinctions observed from 1975 to 2009 for regional biotas on four other continents, suggesting that lizards have already crossed a threshold for extinctions caused by climate change.

Global climate change affects organisms in all biomes and ecosystems. Two natural compensatory responses are possible. Given enough time and dispersal, species may shift to more favorable thermal environments, or they may adjust to new environments by behavioral plasticity, physiological plasticity, or adaptation. Alternatively, failure to adjust or adapt culminates in demographic collapse and extinction. Despite accumulating evidence of contemporary climate change affecting species ranges and phenologies (*1*–*3*), evidence of extinctions at either local or global scales is lacking (*4*–*6*). Moreover, current forecasting models (*7*, *8*) are not calibrated with actual extinctions, but are premised on hypothesized effects of thermal physiology on demography and extinction. Alternatively, models are based on range shifts or species-area relations in mobile species (*1*), but not extinctions (*9*). Hence, there is still much uncertainty regarding the expected magnitude of extinctions resulting from climate change (*10*).

Empirical validation of global extinction forecasts requires three forms of evidence. First, actual extinctions should be linked to macroclimate and validated to biophysical thermal causes arising from microclimate (*11*). Second, the pace of climate change should compromise thermal adaptation (*10*), such that evolutionary rates lag behind global warming owing to constraints on thermal physiology (*12*, *13*). Third, extinctions due to climate should be global in extent.

From 2006 to 2008, we resurveyed 48 *Sceloporus* lizard species at 200 sites in Mexico that were first sampled in 1975 to 1995, and 12% of sites were locally extinct by 2009 (table S1).

Although *Sceloporus* lizards are heliotherms that bask and require solar radiation to attain physiologically active body temperatures ($T_b$) (*14*, *15*), activity in hot weather may result in $T_b$ exceeding $CT_{max}$, the critical thermal maximum, leading to death. Lizards retreat to cool refuges rather than risk death by overheating. However, hours of restriction ($h_r$) in thermal refuges limit foraging, constraining costly metabolic functions like growth, maintenance, and reproduction, thereby undermining population growth rates and raising extinction risk. Lizards could evolve higher $T_b$, but this brings them closer to $CT_{max}$, which increases risk of overheating. Extinction risk may increase because of other thermal adaptations. For example, viviparity, which is posited to be a thermal adaptation to cold climates (*16*), may elevate extinction risk because high $T_b$ can compromise embryonic development in utero (*17*).

We analyzed rate of change in maximum air temperature $T_{max}$ at 99 Mexican weather stations and constructed climate surfaces (tables S2 and S3, 1973 to 2008; fig. S1). Rate of change in $T_{max}$ was greatest for winter-spring (January to May; fig. S1 and table S3A) and increased faster in northern and central México and at high elevation, as evidenced by significant coefficients for fitted climate surfaces. We found a correlation between rate of change in $T_{max}$ during winter-spring breeding periods and local extinctions of *Sceloporus* species (table S3).

Many viviparous species in México are confined to high-elevation "islands," where climate change has been most rapid. Logistic regression and multiple regression with phylogenetic independent contrasts (*18*, *19*) revealed that extinction risk was significantly related to low latitudinal and altitudinal range limits (Fig. 1, A and B), where thermal physiology and/or ecological interactions limit species (*20*, *21*). Phylogenetic correlation analysis (*18*) showed that extinction

risk of viviparous lizards (18%) was twice that of oviparous lizards (9%, $n$ =10000 bootstrap replications $P < 0.001$). Moreover, multiple regression based on phylogenetic independent contrasts (PICs; Fig. 1C and table S4) showed that extinction risk of viviparous taxa was significantly related to low $\overline{T}_b$ ($\overline{T}_{b,viviparous} = 31.8°C \pm 0.31$ [SE], $\overline{T}_{b,oviparous} = 34.8°C \pm 0.40$, $t = 5.92$, $P < 0.0001$) and cool montane habitats ($\overline{T}_{air,viviparous} = 22.4°C \pm 1.79$, $\overline{T}_{air,oviparous} = 28.39°C \pm 1.38$, $t = 2.89$, $P < 0.006$), where climate has changed most rapidly in México.

To validate patterns of extinction risk and $T_b$, we deployed thermal models (*22*) that record operative temperatures ($T_e$) at two extinct and two persistent Yucatán sites of *S. serrifer*. Hours of restriction in activity ($h_r$) during reproduction was significantly higher at extinct versus persistent sites ($t = 9.26$, $P < 0.0001$). By April 2009, $h_r$ at extinct Yucatán sites had become so severe that if *S. serrifer* were still present, it would have to retreat shortly after emergence (fig. S4A). Daily $T_{max}$ was positively correlated with $h_r$ assessed by $T_e$ ($P < 0.001$, fig. S4B). The relation between $h_r$ as a function of $T_{max}$ relative to *S. serrifer*'s $T_b$ [$h_r = 6.12 + 0.74 \times (T_{max} - T_b)$, eq. S2 (*23*)] is a general formula for predicting extinctions.

We modeled extinct/persistence status based on values for $h_r$ at *Sceloporus* sites derived from eq. S2 (*23*). The Yucatán ground truth for *S. serrifer* suggests that extinction occurs when $h_r$ exceeds 4. We calibrated this value with extinct/persistent *Sceloporus* sites. Goodness-of-fit tests of the model indicate that the best fit for observed and predicted extinctions at *Sceloporus* sites is $h_r > 3.85$. If a species with a given $T_b$ at a given geo-referenced site, subjected to $T_{max,i}$, experienced $h_r > 3.85$ during the 2-month reproductive period (March to April), we assumed that it would go extinct by 2009. Association of predicted and observed extinctions from this physiological model was significant for oviparous ($\chi^2 = 49.0$, $P < 0.001$) and viviparous taxa ($\chi^2 = 4.2$, $P < 0.04$).

As demography of high-elevation taxa becomes compromised due to climate change, species at low elevation that were previously limited by physiology and competition should expand into historically cooler habitat that is now warmer (*20*, *24*), perhaps accelerating extinction of high-elevation forms. For viviparous taxa, six erroneously assigned extinct sites involved six of the eight cases of range expansion by low-elevation taxa, which all invaded from low to high altitudes or latitudes (table S1; significant by sign test, $P < 0.001$). Adding range shifts of competitors as a factor improved fit significantly between observed and predicted extinctions ($\Delta$log likelihood = 45.37, 1 df, $P < 0.0001$, logistic regression). Therefore, competitive exclusion by invading low-elevation taxa appears to exacerbate climate-change extinctions of high-elevation taxa.

Lizards cannot evolve rapidly enough to track current climate change because of constraints arising from the genetic architecture of thermal preference (*12*, *13*). A phylogenetic correlation between $T_b$ and $CT_{max}$ constrains adaptation. PIC regression of $CT_{max}$ on $T_b$ among Phrynosomatidae suggests that a shift in $T_b$ by 1°C yields only a 0.5°C correlated response in $CT_{max}$ (table S5 and fig. S7). Thus, $CT_{max}$ may not evolve fast enough to keep up with evolved change in $T_b$. Furthermore, adaptive increase in $T_b$ due to climate change is constrained by genetic correlations in which high $T_b$ necessarily requires prolonged activity out of retreat sites (*25*), further increasing risk of overheating. Genetic trade-offs with energetically costly traits such as growth (*25*) also constrain adaptation.

The evolutionary response ($R = h^2 s$; $s$ is the selection differential) necessary to keep pace with climate change is further constrained by low heritability for $T_b$, which we previously estimated at $h^2 = 0.17$ for *Sceloporus occidentalis* in the laboratory (*25*). We used the physiological model to compute the sustained selection differential at each site j, such that $T_{b,j} + \Delta_t T_{b,j}$ evolves to match $T_{max,j} + \Delta_t T_{max,j}$, yielding $\Delta h_{r,j} = 0$ and thereby rescuing population j from extinction [$\Delta_t$ computed over 1975 to 2009 (historical), 2009 to 2050, and 2050 to 2080]. We assumed $s_j = R_j/h^2 = \Delta_t T_{b,j}/h^2$, and generation times of 1 year versus 2 years (i.e., lowland versus montane *Sceloporus*, table S1). We expressed these critical levels of adaptive response as surfaces for $s_{sustained}$, the sustained selection differential (Fig. 2B).

We compared the magnitude of selection allowing a species to adapt to climate change with maximum rates sustained under artificial or natural selection (*26*). Such comparisons are facilitated by dividing each sustained selection differential by the standard deviation ($\sigma_{Tb} = 1.23$ for $T_b$ of Mexican lizards) to obtain $i$, the standardized intensity of selection (*26*). Whereas $i > 0.4$ can be sustained in laboratory artificial selection for nine generations (*27*), studies in nature (*26*) indicate that $i > 0.4$ computed on an annual basis are rare (<5%). We also reference $i$ to other anthropogenic causes of selection. Overfishing of Atlantic cod yielded $i = 0.55$, among the highest measured, but this selection regime caused demographic collapse of the fishery (*28*). In México, extinct sites sustained significantly higher $i$ than persistent sites ($i_{extinct} = 0.34 \pm 0.05$ versus $i_{persistent} = 0.13 \pm 0.02$, $t = 4.17$, $P < 0.001$). The relation between intensity of selection and demographic collapse is simple. If sustained for decades, the mortality fraction necessary for selective shifts to new optima compromises population growth rate precipitating local extinction.

If climate change $T_{max}$ continues unabated in México, 56% of viviparous sites will be extinct by 2050 and 66% by 2080 (Fig. 2B). For oviparous sites, 46% will be extinct by 2050 and 61% by 2080. Based on local extinction of all populations surveyed for species, we project 58% species extinction of Mexican *Sceloporus* by 2080. Species extinction (58% by 2080) mirrors local population extinction (61 to 66%) because high-elevation endemics will go completely extinct as widespread lowland taxa expand to high elevations.

We used the model to derive global extinction projections (Fig. 3) for 34 lizard families (Table 1) with 1216 geo-referenced $T_b$ records (table S6). Our data include heliotherms that bask and thermoconformers that do not bask, but track ambient air and surface temperature. $T_{max}$ was obtained from the WorldClim database (*29*) at 10–arc min resolution (1975, 2020, 2050, and 2080). We used distributional limits of heliothermic lizards of the world in 1975 to calibrate $h_r$ by family, which if exceeded at a given site would precipitate extinction. The extinction model is easily adapted to thermoconformers that maintain $T_b$ close to $T_{air}$ or retreat when $T_{air} > T_{preferred}$. Assuming a sine wave for $T_{air}$ between $T_{min}$ and $T_{max}$ (24-hour period), if the cumulative hours that $T_{air} > T_b$ for a thermoconformer at a given geo-referenced site (table S6) exceeded the $h_r$ of a given lizard family, we assumed it would go extinct. Given $T_{max} - T_b$ at each geo-referenced site, we computed the $h_r$ each species sustained in 1975, and for each family we used

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the upper 95% confidence level of $h_r$ (Table 1) as the extinction threshold (iteratively estimated, given global climate surfaces). Calibration with these 1975 distributional limits for *Sceloporus* yields $h_r = 3.9$, which was cross-validated by $h_r = 3.85$ computed from observed extinctions in México (1975 to 2009), and $h_r = 4$, which was estimated directly from $T_e$ at persistent *S. serrifer* sites on the verge of extinction.

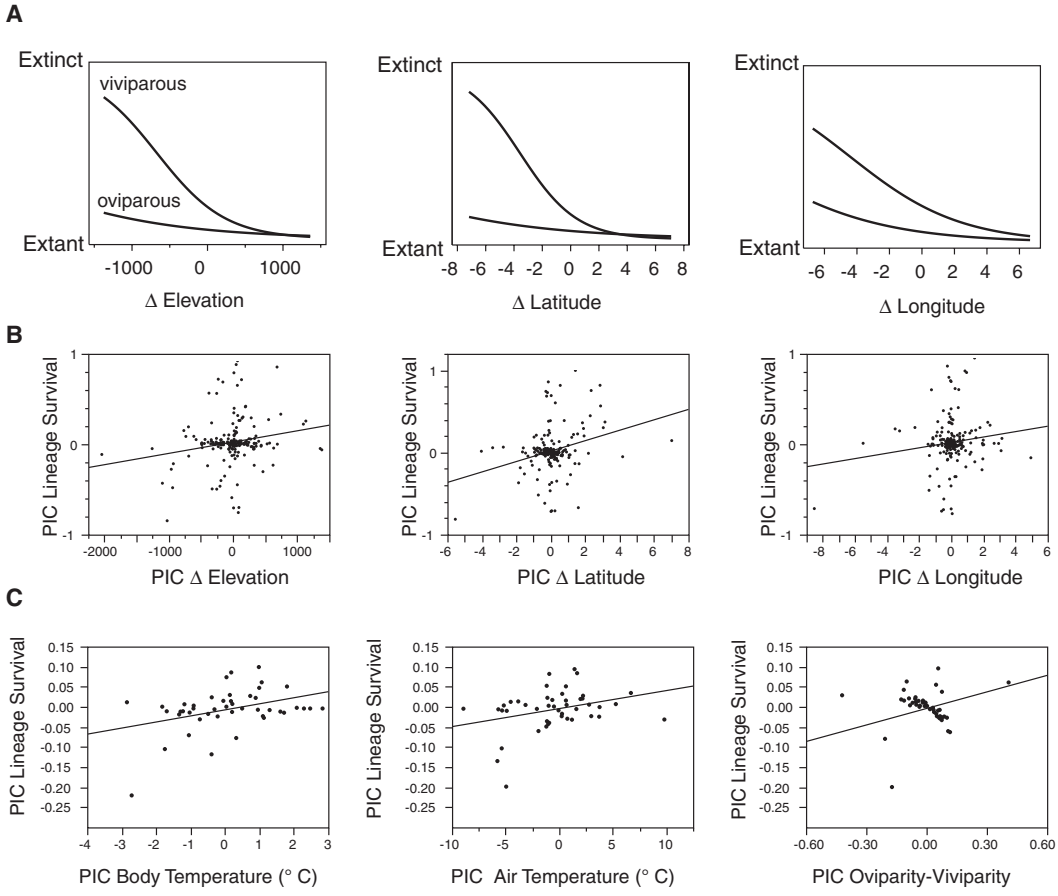


**Fig. 1.** (**A**) Logistic regression of extinction probability (0 = extant, 1 = extinct) of *Sceloporus* lizards and reproductive mode: $\chi^2 = 7.41$, $P = 0.025$, Δelevation ($\chi^2 = 8.53$, $P = 0.014$), Δlatitude ($\chi^2 = 7.14$, $P = 0.004$), and Δlongitude (not significant), where Δ refers to deviations from species range midpoints. (**B**) Phylogenetic independent contrasts (PICs) of lineage survival (survival probability of local populations) and Δelevation ($t = 2.15$, $P = 0.03$), Δlatitude ($t = 3.94$, $P = 0.0001$), and Δlongitude (t = 2.66, $P = 0.009$). (**C**) PICs of lineage survival, $T_b$ ($t = 2.32$, $P = 0.02$), $T_{air}$ ($t = 2.31$, $P = 0.02$), and reproductive mode ($t = -2.92$, $P = 0.005$).

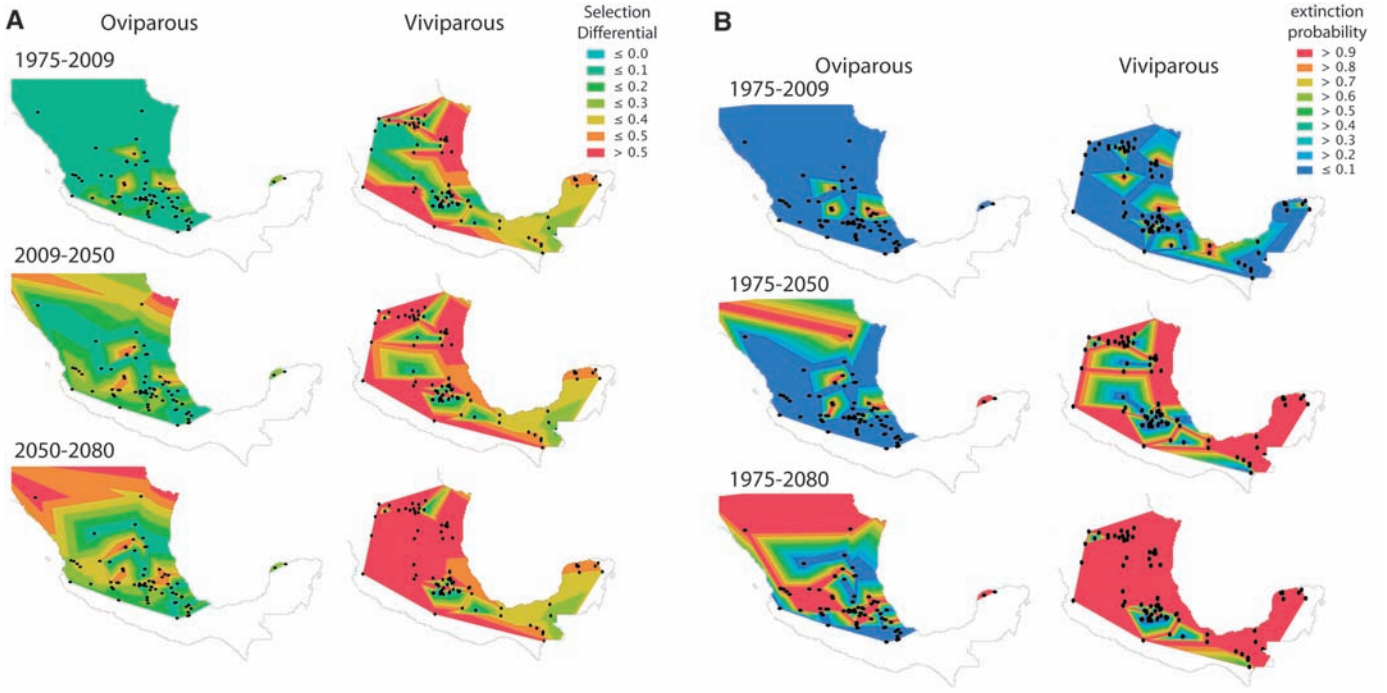


**Fig. 2.** (**A**) Sustained selection differentials per year required for $T_b$ to keep pace with global warming. (**B**) Extinctions of Mexican *Sceloporus* lizards (1975 to 2009, 2009 to 2050, 2050 to 2080).

As in the validation of Mexican *Sceloporus* extinction, we computed $h_r$ for temperate lizards over 2 critical reproductive months, but were conservative in modeling critical months required for $h_r$ to be exceeded in the equatorial zone (±12° latitude) where lizards potentially breed year-round ($h_r$ exceeded over 12 months), and in the wet-dry tropical zone (±12° to 24° latitude: $h_r$ exceeded for 5 to 6 months).

Geo-referenced $T_b$ samples indicate that current (2009) local extinctions average 4% worldwide (Table 1). Global averages will increase fourfold to 16% by 2050 and nearly eightfold to 30% by 2080, while equatorial extinctions will reach 23% by 2050 and 40% by 2080. Assuming reproduction shifts 1 month earlier in temperate zones [$h^2$ = 1.0 lay date (*30*)] and proportionately less to the trade zones (i.e., no shift), 2080 global extinctions jump to 38% because spring seasons are warming faster across the globe. Our model is robust to plasticity in $T_b$ (table S7) and initial assump-

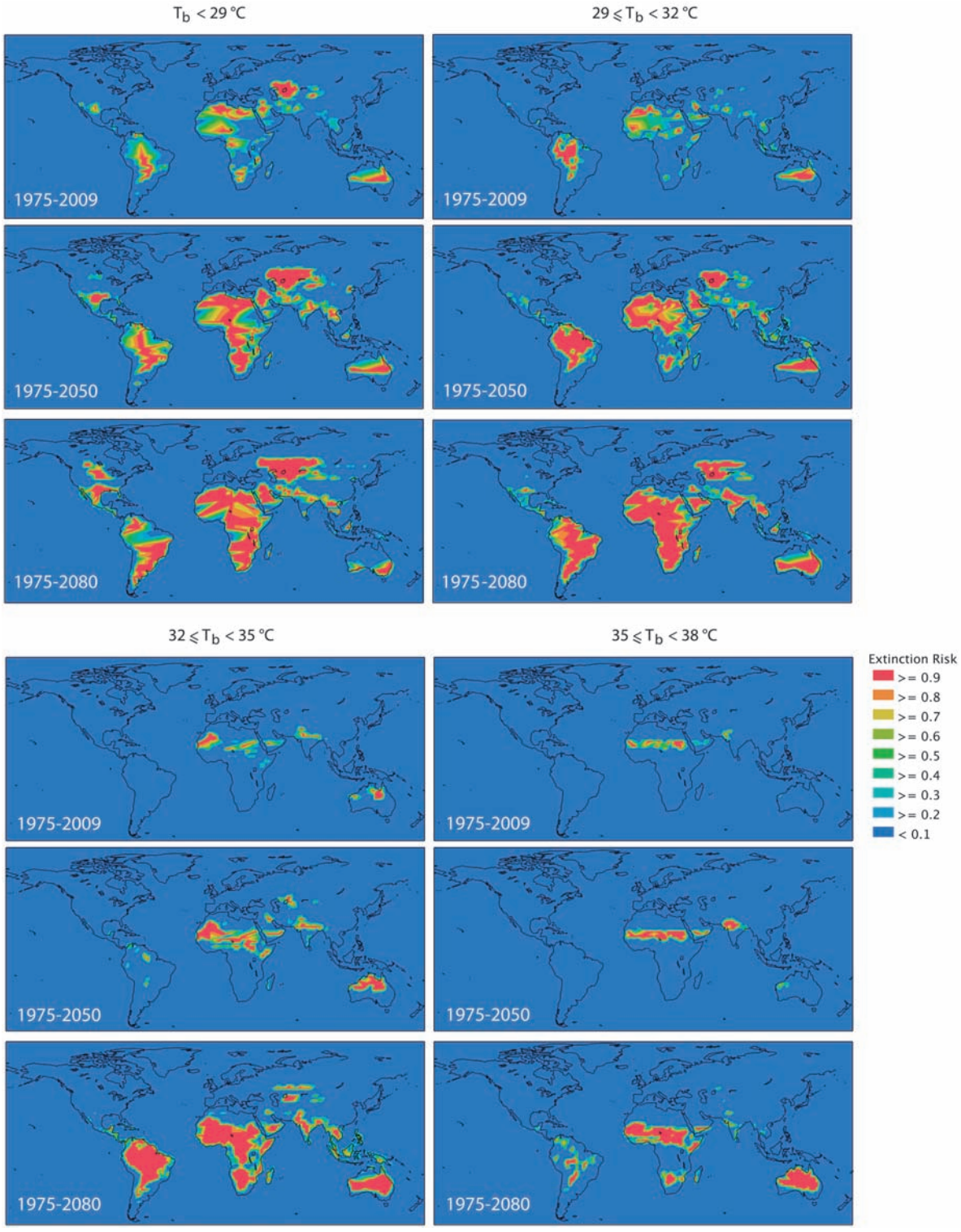


**Fig. 3.** Contour plots of global levels of local extinction for heliothermic lizards (1975 to 2009, 1975 to 2050, 1975 to 2080), assuming $\bar{h}_r$ = 4.55 (*23*) and various $T_b$ values.

**Table 1.** Sample size, $T_b$ range, $\overline{T}_b$ ±SE, $\overline{T}_{max}$, $h_r$, and $n_{species}$ for 34 lizard families. Local extinction rates are based on geo-referenced $T_b$ data and a physiological model of extinction. We also validated model predictions of local extinction risk in 2080 for six families: 57% (±3, $n$ = 200) for Mexican Phrynosomatidae, 13% (±2, $n$ = 3155) for South American Liolaemidae, 56% (±5, $n$ = 117) for European Lacertidae (*L. vivipara*), 13% (±2, $n$ = 1438) for African Cordylidae + Gerrhosauridae, 57% (±4, $n$ = 125) on Madagascar, and 10% (±1, $n$ = 2841) for Australian Egernia Group lizards species. Estimates of species extinctions in each family are derived from the relationships for extinction of all local populations for these six families (table S8).

| Family | $n$ | $T_b$ range | $\overline{T}_b$ ±SE | $\overline{T}_{max}$ | $h_r$ | Mode of thermoregulation | Local extinction levels | | | Species extinction | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | $n_{spp}$ | 2009 | 2050 | 2080 | 2050 | 2080 |
| Agamidae | 74 | 19.0–43.8 | 35.6±0.34 | 29.8 | 7.0 | Heliothermic | 381 | 0.000 | 0.169 | 0.292 | 0.059 | 0.266 |
| Amphisbaenidae | 2 | 21.1–21.2 | 21.2±0.05 | 28.8 | 16.2 | Fossorial thermoconformer | 160 | 0.000 | 0.000 | 0.250 | 0.000 | 0.228 |
| Anguidae | 10 | 21.4–32.3 | 26.7±0.94 | 20.9 | 5.6 | Heliothermic, a few fossorial | 112 | 0.111 | 0.111 | 0.111 | 0.039 | 0.101 |
| Annielliidae | 2 | 21.0–23.6 | 22.3±2.09 | 20.5 | 11.5 | Fossorial thermoconformer | 2 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Chamaeleonidae | 18 | 22.2–33.5 | 30.0±0.70 | 26.8 | 12.0 | Forest thermoconformer | 161 | 0.063 | 0.063 | 0.063 | 0.022 | 0.057 |
| Cordylidae | 11 | 27.8–33.8 | 31.5±0.82 | 23.6 | 6.8 | Heliothermic | 54 | 0.000 | 0.000 | 0.200 | 0.000 | 0.182 |
| Corytophanidae | 4 | 26.0–35.0 | 31.9±1.48 | 29.4 | 13.4 | Forest thermoconformer | 9 | 0.250 | 0.250 | 0.250 | 0.088 | 0.228 |
| Crotaphytidae | 23 | 35.5–38.9 | 37.3±0.62 | 23.3 | 1.2 | Heliothermic | 12 | 0.111 | 0.167 | 0.222 | 0.059 | 0.202 |
| Carphodactylidae | 11 | 15.1–35.5 | 24.5±1.59 | 34.7 | 10.9 | Thermoconformer | 30 | 0.350 | 0.820 | 0.820 | 0.289 | 0.748 |
| Diplodactylidae | 42 | 16.9–35.9 | 27.3±0.59 | 31.2 | 10.9 | Thermoconformer | 141 | 0.070 | 0.190 | 0.190 | 0.067 | 0.173 |
| Eublepharidae | 18 | 26.6–33.0 | 28.5±0.44 | 32.9 | 10.9 | Thermoconformer | 28 | 0.060 | 0.240 | 0.240 | 0.084 | 0.219 |
| Gekkonidae | 40 | 26.0–35.3 | 30.1±0.58 | 32.6 | 10.9 | Thermoconformer | 700 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Phyllodactylidae | 13 | 16.6–38.9 | 30.6±1.42 | 30.4 | 10.9 | Thermoconformer | 100 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Pygopodidae | 21 | 24.9–35.1 | 25.4±0.46 | 17.9 | 11.5 | Fossorial thermoconformer | 38 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Sphaerodactylidae | 19 | 25.3–38.6 | 30.2±0.75 | 33.0 | 10.9 | Thermoconformer | 200 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Gerrhosauridae | 4 | 31.8–33.3 | 32.6±2.09 | 28.3 | 6.8 | Heliothermic | 16 | 0.333 | 0.333 | 0.333 | 0.117 | 0.304 |
| Gymnophthalmidae | 20 | 21.5–29.9 | 26.4±0.66 | 30.3 | 13.8 | Leaf litter thermoconformer | 193 | 0.095 | 0.333 | 0.667 | 0.117 | 0.608 |
| Helodermatidae | 2 | 29.4–30.2 | 29.8±2.09 | 24.8 | 2.7 | Heliothermic/thermal inertia | 2 | 0.000 | 0.000 | 1.000 | 0.000 | 0.912 |
| Iguanidae | 20 | 32.9–42.1 | 37.3±0.79 | 28.1 | 3.7 | Heliothermic | 36 | 0.143 | 0.143 | 0.286 | 0.050 | 0.261 |
| Lacertidae | 89 | 26.7–40.2 | 35.4±0.31 | 25.6 | 3.1 | Heliothermic | 279 | 0.034 | 0.241 | 0.460 | 0.085 | 0.420 |
| Lanthanotidae | 1 | – | 28.0 | 30.5 | 9.4 | Forest thermoconformer | 1 | 1.000 | 1.000 | 1.000 | 0.352 | 0.912 |
| Leiocephalidae | 1 | – | 36.3 | 31.7 | 2.8 | Heliothermic | 29 | 0.000 | 1.000 | 1.000 | 0.352 | 0.912 |
| Liolaemidae | 125 | 24.4–40.8 | 33.7±0.27 | 17.8 | 1.4 | Heliothermic | 219 | 0.027 | 0.071 | 0.107 | 0.025 | 0.098 |
| Opluridae | 3 | 36.2–39.8 | 37.7±1.71 | 31.8 | 4.0 | Heliothermic | 7 | 0.333 | 0.667 | 0.667 | 0.235 | 0.608 |
| Phrynosomatidae | 215 | 26.8–41.5 | 35.2±0.20 | 24.9 | 3.9 | Heliothermic | 125 | 0.037 | 0.087 | 0.149 | 0.031 | 0.136 |
| Polychrotidae | 121 | 19.6–35.0 | 29.6±0.27 | 29.6 | 14.4 | Forest thermoconformer | 393 | 0.018 | 0.043 | 0.068 | 0.015 | 0.062 |
| Scincidae | 210 | 20.3–38.0 | 32.9±0.20 | 26.5 | 6.2 | Heliothermic, a few fossorial | 1305 | 0.015 | 0.092 | 0.308 | 0.032 | 0.281 |
| Sphenodontidae | 1 | 14.5–21.0 | 14.5±2.09 | 18.0 | 10.7 | Nocturnal thermoconformer | 1 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Teiidae | 91 | 26.8–41.3 | 37.9±0.31 | 29.0 | 4.2 | Heliothermic | 121 | 0.012 | 0.136 | 0.210 | 0.048 | 0.192 |
| Trogonophidae | 2 | 22.0–22.5 | 22.3±0.25 | 28.8 | 16.2 | Fossorial thermoconformer | 8 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Tropiduridae | 72 | 26.2–38.0 | 33.7±0.35 | 28.3 | 7.7 | Heliothermic | 111 | 0.043 | 0.058 | 0.087 | 0.020 | 0.079 |
| Varanidae | 46 | 28.8–38.9 | 35.8±0.44 | 29.7 | 4.6 | Heliothermic/thermal inertia | 68 | 0.001 | 0.023 | 0.178 | 0.008 | 0.162 |
| Xantusidae | 8 | 18.7–33.0 | 25.4±1.32 | 20.7 | 0.0 | Thigmothermic thermoconformer | 29 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Xenosauridae | 5 | 20.3–25.6 | 23.2±1.48 | 26.4 | 11.4 | Thigmothermic thermoconformer | 6 | 0.200 | 0.200 | 0.600 | 0.070 | 0.547 |

tions made for reproductive periods in the tropics. If $h_r$ for equatorial taxa is computed over the 9 hottest months of reproduction, rather than the conservative assumption of 12 months, global extinctions increase to 39% by 2080.

The global generality of our model is verified by concordant distributions of current observed and predicted local extinctions of lizard biotas from four other continents (table S7). Our model pinpoints exact locations of two Liolaemid species going extinct in South America (*Liolaemus lutzae*, *Phymaturus tenebrosus*: $\chi^2 = 32.1$, $P < 0.0001$). In addition, the model predicts recent (2009) extinctions among 24 resurveyed populations of *L. lutzae* ($\chi^2 = 8.8$, $P = 0.003$). In Europe, our

resurvey of *Lacerta vivipara* revealed 14 extinct sites out of 46 (30%), which are predicted quite precisely by the model ($\chi^2 = 24.4$, $P < 0.001$). In Australia, the model pinpoints 2009 extinctions of *Liopholis slateri* ($\chi^2 = 17.8$, $P < 0.00001$) and 2009 extinctions of *Liopholis kintorei* ($\chi^2 = 3.93$, $P = 0.047$). In Africa, analysis of Gerrhosauridae and Cordylidae at 165 sites predicts <1% extinctions, and yet the model pinpoints the single extinction reported by 2009 (exact $P$-value = 0.006). We temper this value with extinction projections of 23% for 2009 at Malagasy Gerrhosauridae sites, which is validated by the observed 21% levels of local extinction across several lizard families in Madagascar nature reserves (*23*).

Thermoconforming lizards have been posited (*31*) to be more vulnerable to climate change relative to heliotherms. Even though $\overline{T}_b$ of thermoconformers (27.5°C ± 1.8°) is significantly less than $\overline{T}_b$ of heliotherms (33.5°C ± 1.3, $t = 2.66$, $P < 0.02$, $n = 34$ families; Table 1), PICs show that extinction risk was unrelated to thermoregulatory mode (fig. S8), but was significantly increased by low $\overline{T}_b$, low $h_r$, and high $\overline{T}_{max}$. The similar level of local extinctions in 2009 for Malagasy thermoconformers (21%, $n = 63$) and heliotherms [21%, $n = 34$; (*23*)] supports this view. Evolved changes in thermoregulatory mode, $T_b$, $h_r$, lay date, and habitat preference set risk as $T_{max}$ rises, but owing to trade-offs, $T_b$ and $h_r$ cannot be simultaneously maximized, hence extinction risk is independent of mode (fig. S8). Moreover, extinction risk is not higher for conformers because heliotherms inhabit equatorial regions (i.e., sub-Saharan Africa) that are unavailable to thermoconformers [a factor not considered by (*31*) or other models (*10*)], and these areas are warming rapidly (Fig. 3).

Our model, based on $T_b$, $h_r$ in activity during reproduction, and timing of breeding, assesses salient adaptations that affect thermal extinctions. Concordant verification of 2009 levels of local lizard extinction in North and South America, Europe, Africa, and Australia confirm that extinctions span tropical, temperate, rainforest, and desert habitats. Estimates of evolutionary rates required to keep pace with global change indicate that sustained and intense selection compromises population growth rates, precipitating extinctions. Probability of local extinction is projected to result in species extinction probabilities of 6% by 2050 and 20% by 2080 (table S8). Range shifts only trivially offset losses, because widespread species with high $T_b$ shift to ranges of endemics, thereby accelerating their demise. Although global efforts to reduce $CO_2$ may avert 2080 scenarios, 2050 projections are unlikely to be avoided; deceleration in $\dot{T}_{max}$ lags atmospheric $CO_2$ storage by decades (*4*). Therefore, our findings indicate that lizards have already crossed a threshold for extinctions.

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**Supporting Online Material**

www.sciencemag.org/cgi/content/full/328/5980/894/DC1
Materials and Methods
Figs. S1 to S9
Tables S1 to S8
References

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# Carbon Dioxide Enrichment Inhibits Nitrate Assimilation in Wheat and *Arabidopsis*

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**The concentration of carbon dioxide in Earth's atmosphere may double by the end of the 21st century. The response of higher plants to a carbon dioxide doubling often includes a decline in their nitrogen status, but the reasons for this decline have been uncertain. We used five independent methods with wheat and *Arabidopsis* to show that atmospheric carbon dioxide enrichment inhibited the assimilation of nitrate into organic nitrogen compounds. This inhibition may be largely responsible for carbon dioxide acclimation, the decrease in photosynthesis and growth of plants conducting $C_3$ carbon fixation after long exposures (days to years) to carbon dioxide enrichment. These results suggest that the relative availability of soil ammonium and nitrate to most plants will become increasingly important in determining their productivity as well as their quality as food.**

The concentration of $CO_2$ in Earth's atmosphere has increased from about 280 to 390 μmol $CO_2$ per mol of atmosphere (μmol $mol^{-1}$) since 1800, and predictions are that it will reach between 530 and 970 μmol $mol^{-1}$ by the end of the 21st century (*1*). Plants could mitigate these changes through photosynthetic conversion of atmospheric $CO_2$ into carbohydrates and other organic compounds, yet the potential for this mitigation remains uncertain. Photorespiration is the biochemical pathway in which the chloroplast enzyme Rubisco catalyzes the oxidation of the high-energy substrate RuBP rather than catalyzes the carboxylation of RuBP through the $C_3$ carbon-fixation pathway (*2*). Elevated $CO_2$ (or

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