

Thermoregulatory behaviour limits local adaptation of thermal niches and confers sensitivity to climate change

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Summary

1. Thermoregulation buffers environmental variation, which enables a species to persist during climate change but ultimately hinders adaptation of thermal tolerance by weakening selective pressure.
2. We used a model of optimal thermal physiology to demonstrate how thermoregulatory behaviour limits local adaptation of thermal physiology in a widespread group of lizards, the *Sceloporus undulatus* complex.
3. Empirical data for seven populations demonstrates conservatism of thermal tolerance, consistent with the model's prediction in the case of effective thermoregulation. In an eighth population, from a region where thermoregulation should be less effective, we observed greater heat tolerance and poorer cold tolerance, as predicted by our model.
4. Biophysical modelling indicates that lizards can avoid heat stress through thermoregulation in the coming decades but will ultimately experience an abrupt decline in the effectiveness of thermoregulation. In this scenario, thermoregulators will suffer a greater loss of performance in future climates than thermoconformers will, unless heat tolerance can evolve in a few generations.
5. Our analyses raises a concern that behavioural plasticity, while beneficial in the short term, will ultimately limit the physiological adaptation required to endure a warming climate.

Key-words: body temperature, climate change, critical thermal limits, niche conservatism, *Sceloporus*, thermoregulation

Introduction

Two questions remain central to forecasting ecological and evolutionary responses to climate change. First, to what extent does environmental tolerance vary geographically within species (Violle *et al.* 2012)? And second, how will the presence (or absence) of geographic variation mediate the biological impacts of climate change? Comparisons among species have revealed geographic variation in thermal tolerance (Sunday, Bates & Dulvy 2010), but comparisons within species have yielded conflicting results (Angilletta 2009). Although most efforts to predict the impacts of climate change have ignored local adaptation, phenotypic variation within species can substantially alter geographic distributions in present and future climates

(Buckley 2008; Kolbe, Kearney & Shine 2010). Additionally, migration among locally adapted populations can either hinder or enhance evolutionary adaptation to climate change (Atkins & Travis 2010; Hoffmann & Sgrò 2011).

Although some species rely on physiological mechanisms to tolerate extreme body temperatures, many will behaviourally regulate their body temperatures during climate change (Kearney, Shine & Porter 2009). As suitable microclimates become rare, thermoregulatory behaviours become less effective and more costly (Huey & Slatkin 1976; Angilletta 2009; Kearney, Shine & Porter 2009; Sinervo *et al.* 2010; Huey *et al.* 2012). Animals must devote energy to thermoregulation, while reducing time available for foraging and exposing themselves to predators when seeking sun or shade. The potential to behaviourally compensate for climate warming may decline rapidly, forcing organisms to rely on physiological adapta

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tion (see conceptual model in fig. 7 of Huey *et al.* 2012). However, rates of adaption may be too slow for the organisms to respond to climate warming once thermoregulation becomes ineffective.

Although thermoregulatory behaviour is generally viewed as a way for organisms to buffer climate change, the ability of thermoregulatory behaviour to weaken selection on thermal tolerance might eventually enhance the risk of extinction (Huey & Kingsolver 1993; Huey, Hertz & Sinervo 2003). Behavioural thermoregulation also slows the divergence of thermal tolerances among populations throughout a geographic range. The process of behaviour buffering selection and ultimately reducing local adaptation across geography is known as the Bogert effect (Bogert 1949; Huey, Hertz & Sinervo 2003). This outcome remains largely hypothetical since support for the Bogert effect comes from comparing thermoregulatory behaviours along geographic clines (Huey, Hertz & Sinervo 2003; Huey & Pascual 2009). Additional research, claiming mixed support for the Bogert effect, focused on thermal physiologies across life stages rather than thermal physiologies throughout geographic ranges (Marais & Chown 2008; Mitchell, Sinclair & Terblanche 2013). Few studies have assessed the conservation of thermal tolerance within species (Crowley 1985; Vandamme, Bauwens & Verheyen 1990), but comparisons among species suggest that this phenomenon has general significance among lizards (Vandamme, Bauwens & Verheyen 1990; Cruz *et al.* 2009; Sunday, Bates & Dulvy 2010).

The *Sceloporus undulatus* complex has been a model system for understanding thermal physiology and its consequences for population dynamics and range limits. This paraphyletic biological lizard species is widespread in North America and comprises four major clades connected by limited gene flow (Leaché 2009). Populations in warmer environments tend to experience greater rates of mortality (Adolph & Porter 1993) and contain individuals that mature younger at a smaller size (Angilletta *et al.* 2004) and produce more, smaller offspring (Niewiarowski, Angilletta & Leache 2004; Angilletta, Oufiero & Leache 2006). Individuals from colder environments are associated with faster embryonic growth and development (Oufiero, Angilletta & Schwenk 2006; Storm & Angilletta 2007; Du *et al.* 2010). Adaptation of the life history likely contributed to the wide range of this species; for example, a mechanistic niche model indicated that only northern phenotypes can persist in the northern portion of the range (Buckley 2008). Aspects of thermal physiology, such as the preferred body temperature and the optimal temperature for digestive performance, were similar between a northern and a southern population (Angilletta 2001). The propensity for thermoregulation by *S. undulatus* (Angilletta 2001; Angilletta, Hill & Robson 2002) may account for this conservatism of thermal physiology. This study asks whether thermal physiology is conserved throughout the geographic range and whether thermoregulatory behaviour can account for patterns of thermal niche conservatism.

We developed a quantitative model to investigate the relationship between thermoregulatory behaviour, niche conservatism and sensitivity to climate change in *S. undulatus*. First, we determined the optimal thermal physiologies throughout the geographic range corresponding to four strategies of thermoregulation. Then, we empirically characterize the thermal physiologies of eight populations of *S. undulatus* and test the predictions for the degree of thermal niche conservatism stemming from our thermoregulatory strategies; this analysis provides the first test of the Bogert effect throughout a geographic range. Finally, we showed how the conserved thermal physiologies of thermoregulators increases the incidence of thermal stress and reduces performance in future climates. Taken together, our analyses support the hypothesis that thermoregulatory behaviour can limit local adaptation of thermal physiology and heightens a species' sensitivity to climate change.

Materials and methods

OPTIMIZING PERFORMANCE CURVES

Our analysis builds on previous research using thermal performance curves to estimate how environmental conditions shape thermal physiology (Lynch & Gabriel 1987; Gilchrist 1995; Angilletta 2009; Asbury & Angilletta 2010). These curves have been used to describe many aspects of behaviour and physiology (e.g. energy assimilation or sprint speed), as well as direct measures of fitness (e.g. intrinsic rate of population growth). In *S. undulatus*, diverse types of performance are well characterized by these curves (Angilletta 2001; Angilletta, Hill & Robson 2002). A thermal performance curve characterizes the thermal limits of performance (critical thermal minimum and maximum) and the temperature that maximizes performance (thermal optimum) (see fig. 1, Huey & Stevenson 1979). Following Asbury & Angilletta (2010), we modelled performance, Z , as a nonlinear function of body temperature in kelvin, T_b :

$$Z(T_b) = \frac{[(T_b - \alpha)/b]^{(\gamma/\beta)-1} [1 - (T_b - \alpha)/b]^{[(1-\gamma)/\beta]-1} \Gamma(1/\beta)}{\Gamma(\gamma/\beta) \Gamma[(1-\gamma)/\beta]}, \quad \text{eqn 1}$$

where α , β and γ determine the mode, breadth and skewness of the performance curve, respectively. The parameter b determines the maximal breadth.

Once we estimated body temperatures experienced by a lizard across the activity season, we asked how natural selection would shape the performance curve given additive genetic variation. To do so, we searched for the values of α , β and γ that define the optimal performance curve (Asbury & Angilletta 2010). Our search was confined to values generating realistic curves ($-9 < \alpha < 5$, $0.07 < \beta < 0.17$, $\gamma = 0.7$ and $b = 43$), given the large diversity of curves observed among ectothermic animals (see Sunday *et al.* 2014). We numerically determined the curve that maximized either the sum or the product (sum of the log) of performances yielded by the distribution of body temperatures. These two optimizations bracket the potential consequences of experiencing a temperature beyond the critical thermal limits. When maximizing the sum of performance, we assumed that performance affected current fecundity and exceeding the critical thermal maximum did not affect future fecundity. When maximizing the product of performance, we assumed that performance affected survivorship and thus exceeding the critical

thermal maximum reduced the chances of future reproduction. The real cost of exceeding the critical thermal maximum probably lies somewhere between these extremes. Generally, selection favours genotypes that tolerate a higher critical thermal maximum when performance contributes to survivorship than it does when performance contributes to fecundity (Lynch & Gabriel 1987; Asbury & Angilletta 2010). Our estimates of critical thermal minima are primarily set by constraints on the breadth of performance curves because we omitted temperatures experienced at night. We set the value of performance beyond the critical thermal limits to a very low but non-zero value, corresponding to a high probability of death. We defined the thermal optimum as the body temperature that yields maximal performance and the critical thermal limits as the body temperatures that yield 1% of the maximal performance; this definition was necessary to create a specialist–generalist trade-off, because eqn 1 yields non-zero values in a fixed range of temperatures (bounded by the parameters α and b).

A growing body of evidence indicates that performance curves are also shaped by thermodynamic factors that favour a higher thermal optimum (Angilletta, Huey & Frazier 2010). Therefore, for another set of optimizations, we added an Arrhenius factor to eqn 1: e^{-E/kT_b} , where E equals the energy of activation (0.6 eV) and k equals the Boltzmann constant. This modified function mimics a thermodynamic effect that enhances performance at higher temperatures (Asbury & Angilletta 2010).

ESTIMATING OPERATIVE TEMPERATURES

We performed our analyses throughout the current range of the *Sceloporus undulatus* complex (natureserve.org). Each grid cell (343 km²) was equivalent to 10' × 10' near the equator. Our simulations were restricted to daylight hours during the months of May through September, when lizards in all parts of the range engage in surface activity. We assumed that lizards use burrows or similar refuges to buffer thermal extremes and forage minimally at other times; this behavioural buffering restricts the relevant selection to the activity season. We first translated environmental conditions into potential body temperatures using biophysical equations (Buckley 2008). These equations define the operative environmental temperature, or operative temperature, which is the equilibrium temperature of an animal with specified size, shape and colour in a given microclimate. In practice, operative temperature is calculated as the air temperature plus or minus a thermal deviation caused by radiation, convection and conduction (Bakken 1992). We calculated operative temperatures using surface or air temperature, because lizards can move between the ground and vegetation. Additionally, we bracketed the range of operative temperatures by assuming that lizards could access full shade at any time.

We used satellite-derived monthly normals (1961–1990; CRU CL 2.2) to parameterize the biophysical model with hourly air and surface temperatures and quarterly albedo (New *et al.* 2002). We modelled future climates using projections from the Coupled Model Intercomparison Project phase 3 of the World Climate Research Programme; these projections were downscaled to the size of our grid cells using a change-factor approach [http://futureclimates.conservation.org/; (Tabor & Williams 2010)]. We examined projections corresponding to the A2 scenario of the Hadley Centre's HadCM3 model and the National Center for Atmospheric Research's CCSM3.0 model. Monthly anomalies averaged over the period 2041–2060 ('2050') and 2081–2100 ('2090') were added to air and surface temperatures (more appropriate anomalies for surface temperature were unavailable). A similar analysis showed that climatic constraints on thermoregulating organisms can be captured reasonably with monthly averages of climate data (Kearney, Matzelle & Helmuth 2012).

MODELLING THERMOREGULATION

We used four scenarios to assign a body temperature within the range of potential operative temperatures: (i) lizards use microclimates randomly (thermoconformer); (ii) lizards use microclimates randomly but avoid extremes outside their critical thermal limits; (iii) lizards thermoregulate as close to their preferred temperature as possible when the benefit outweighs the cost (thermoregulation with costs); and (iv) lizards thermoregulate as close to their preferred temperature as possible without a cost (thermoregulation without costs). Since *S. undulatus* is known to thermoregulate (Angilletta 2001; Angilletta, Hill & Robson 2002), we consider the thermoconformer scenarios to be null models for testing the Bogen effect.

For a thermoconformer, we generated the distribution of body temperatures at each hour by drawing a random sample ($n = 100$) from a uniform distribution, bounded by the operative temperature in full sun and the operative temperature in full shade. For the thermoconformer that avoids extremes, we bounded three distributions [uniform; modal (normal); and bimodal (a mixture of two normal distributions)] by the mean critical thermal limits of *S. undulatus* (10.5 °C and 42.6 °C; Fig. 3) when operative temperatures were outside these limits. Using the mean critical thermal limits simplified our analysis without loss of generality, since thermal limits varied little among populations (see Results). For thermoregulation without cost, we assumed that a lizard chose microclimates to obtain a body temperature as close as possible to a preferred body temperature (32 °C, see Fig. 1a) as possible. We note that lizards tend to prefer body temperatures slightly below their thermal optimum for physiological performances (33 °C) to avoid thermal stress (Martin & Huey 2008). These assumptions enable us to see whether natural selection would alter the typical thermal physiology of *S. undulatus* given a specific strategy of thermoregulation.

For thermoregulation with costs, we started with the thermoconformer scenario and assumed that the lizard would thermoregulate whenever the performance associated with the operative temperature of a thermoregulator exceeded that of a thermoconformer (Huey & Slatkin 1976). We estimated performance using a generic curve [$Z(T_b)$] corresponding to published measurements of thermal optima [33 °C (Angilletta 2001; Angilletta, Hill & Robson 2002)] and the mean critical thermal limits (10.5 °C and 42.6 °C; Fig. 3). We imposed a cost of thermoregulation by discounting performance by 50% when calculating whether thermoconforming or thermoregulating yielded greater performance. In other words, we compared $Z(T_b)$ for a thermoconformer's body temperature to $0.5 \cdot Z(T_b)$ for a thermoregulator's body temperature, assuming that the animal flexibly switched between thermoregulating and thermoconforming based on whichever strategy offered greater performance. We examined the model's sensitivity to the cost of thermoregulation (Figs S1 and S2, Supporting information); the cost influenced the degree to which thermoregulation was beneficial, but optimal performance curves were always intermediate to the scenarios presented here. Our analysis was spatially implicit in the sense that lizards selected habitats ranging from full shade to full sun rather than moving through a matrix of habitats. However, our cost of thermoregulation relates to a spatially explicit case (e.g. Sears, Raskin & Angilletta 2011) because movements between habitats channel energy towards activity at the expense of growth or reproduction.

COMPARING THERMAL PHYSIOLOGY

To compare thermal tolerances throughout the geographic range of the *S. undulatus* complex, we collected lizards from eight populations (see Fig. 2): Gila and Pinal Counties, Arizona (33.3 N, 111.0 W; May 2007; $n = 37$); San Juan County, Utah (38.4°N,

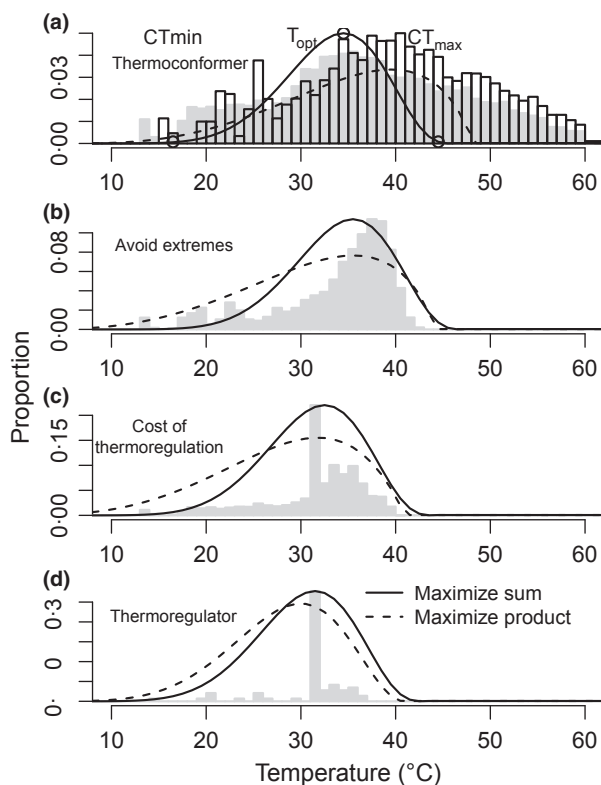


Fig. 1. Body temperatures of lizards modelled for daylight hours from May through September. A thermoregulating lizard in Texas (d) should experience a dramatically narrower distribution of body temperatures (grey bars) than does a thermoconforming lizard (a). The thermoconformer will frequently encounter body temperatures exceeding its critical thermal limits (CTmin and CTmax) and thermal optima (T_{opt}). When the thermoconformer avoids temperatures outside its critical thermal limits (b), the distribution of body temperatures is constrained, but the optimal thermal physiology is similar. When thermoregulation imposes a cost, the distribution of body temperatures should only widen slightly (d). For the thermoconformers, the optimal thermal performance is broader when maximizing the product of performance (dashed line) compared to when maximizing the sum of performance (solid line). Thermoregulation reduces the incidence of thermal extremes and selects for a lower thermal optimum. By 2090, we predict a substantial increase in the frequency of extreme body temperatures for thermoconforming lizards (white bars).

108.6°W; May 2007; $n = 42$); Burlington and Camden Counties, New Jersey (39.8°N, 74.6°W; July–August 2007; $n = 41$); Edgefield County, South Carolina (33.7°N, 82.0°W; August 2007; $n = 45$); Floyd County, Indiana (39.1°N, 86.3°W; April–May 2008; $n = 36$); Escambia County, Florida (30.9°N, 86.8°W; May 2008; $n = 45$); Keith and Garden Counties, Nebraska (41.3°N, 102.0°W; July–August 2008; $n = 44$); and Anderson County, Texas (31.9°N, 95.9°W; June 2011; $n = 5$). For each lizard, we used standard protocols to measure the preferred body temperatures and the critical thermal limits of locomotor performance (Appendix 1 in Supporting Information).

Prior to statistical analyses, we estimated phylogenetic signal in the mean values of traits for the eight populations. We used Pagel's lambda (Pagel 1999) as an index of phylogenetic signal, which outperforms other indices when applied to small samples (Münkemüller *et al.* 2012). Phylogenetic relationships were based on pruning a chronogram (Angilletta, Oufiero & Leache 2006). Analyses were performed using the *ape* (Paradis, Claude & Strim-

mer 2004), *geiger* (Harmon *et al.* 2008) and *picante* (Kembel *et al.* 2010) libraries of the R Statistical Package (R Development Core Team 2012). The value of Pagel's lambda can range from 0 to 1, with 0 reflecting no phylogenetic signal. Values for our traits were ≤ 0.002 , indicating virtually no phylogenetic signal. Therefore, we used the untransformed data to model sources of variation in thermal physiology.

General linear modelling was used to estimate the effects of body size (snout–vent length), sex and population on the preferred body temperature, critical thermal minimum and critical thermal maximum. For analyses of preferred body temperature, we also included time of day as a fixed factor and individual as a random factor. Initially, we modelled all main effects and interactions. Then, we dropped terms from the maximal model and used the Akaike information criterion to confirm the improved fit of the simplified model. We removed terms from the highest order to the lowest order until the model with the lowest AIC was obtained. All models were fit using the nlme library of the R Statistical Package.

Results

THE BOGERT EFFECT

Between sunrise and sunset, distributions of operative temperatures throughout the range enable lizards to thermoregulate effectively by shuttling between sun and shade. To illustrate this point, consider the predicted distribution of body temperatures experienced by a lizard in Texas that either thermoconforms or thermoregulates (Fig. 1). A thermoconformer would frequently exceed a body temperature of 50 °C, whereas a thermoregulator would never exceed a body temperature of 44 °C. Even thermoregulation imposes a cost, a thermoregulator would rarely exceed a body temperature of 40 °C and the maximal body temperature remains 44 °C. Thus, thermoregulation dramatically constricts the predicted range of body temperatures, which accords with observations of lizards in nature (Hertz, Huey & Stevenson 1993).

The fitness landscape for key parameters of the performance curve depends on the strategy of thermoregulation (Fig. S3, Supporting information). By reducing the incidence of high temperatures, thermoregulation results in an optimal performance curve with a lower critical thermal maximum and a lower thermal optimum. This effect exists whether maximizing the sum or the product of performance (Fig. 1, solid vs. dashed lines), but maximizing the sum selects for a narrower performance breadth. The optimal performance curve for a thermoconformer that avoids extreme temperatures resembles that of a strict thermoconformer. Given a probable scenario of climate change, a thermoconformer would experience body temperatures above 40 °C more frequently by 2090 than at present (Fig. 1, top panel).

By extending this analysis throughout the geographic range, we quantified how thermoregulation limits geographic variation in the optimal thermal physiology. Figure 2 shows results when fitness depends on the sum of performance. Without thermoregulation, optimal performance curves differ dramatically throughout the range; in fact, the thermal optima and critical thermal limits that

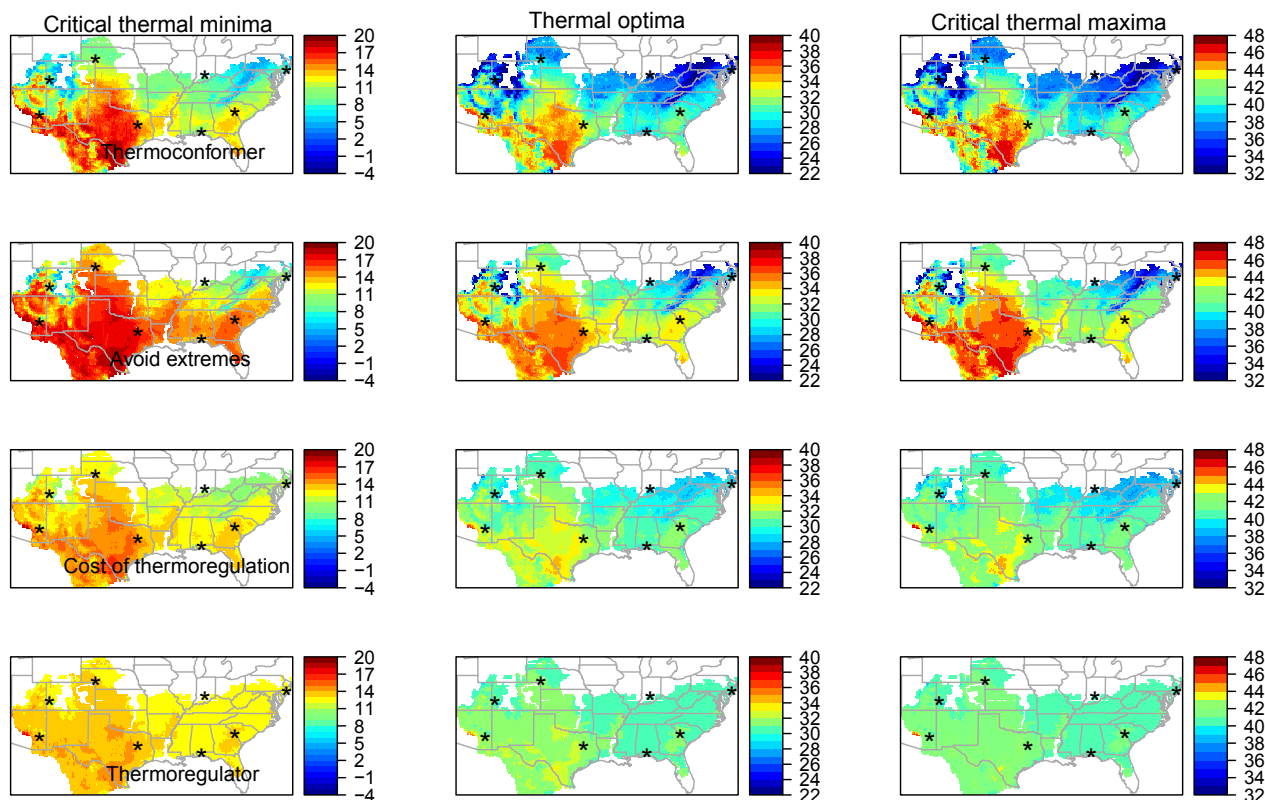


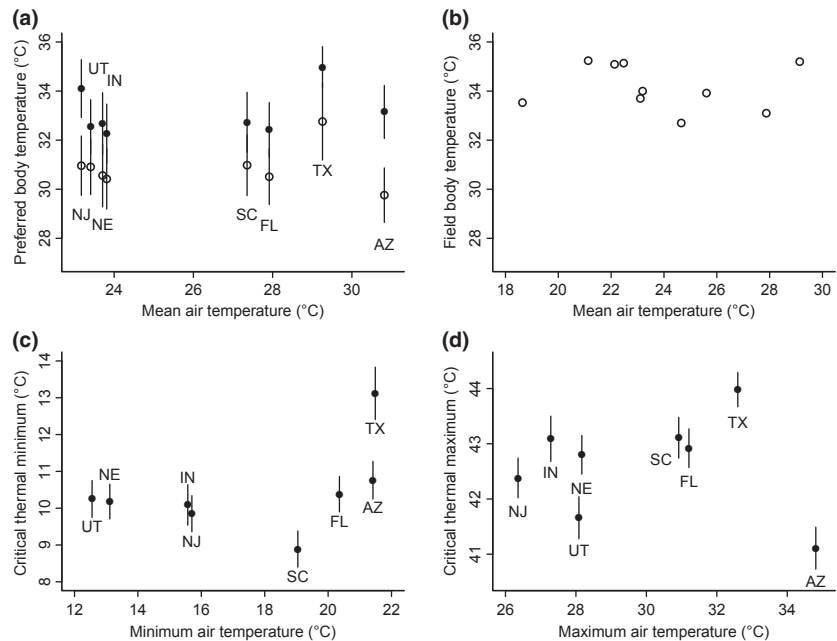
Fig. 2. Based on our model, selective pressures on thermal physiology depend on whether lizards can thermoregulate and whether they pay a cost when doing so. Greater geographic variation in critical thermal minima (CTmin, left), thermal optima (Topt, middle) and critical thermal maxima (CTmax, right) are predicted for thermoconforming lizards (whether or not they avoid thermal extremes) compared the lizards thermoregulating without costs. The predicted optimal thermal physiologies for lizards thermoregulating with an associated cost are intermediate. The colour scale is centred such that green colours correspond to the mean value observed across populations. The localities sampled for empirical studies are marked (*).

maximize fitness differ by 14 °C between the warmest and coldest sites (Fig. 2, top row). This conclusion holds for all three distributions of operative temperatures – uniform, normal and bimodal (Fig. S4, Supporting information). Interestingly, selection favours greater geographic variation in critical thermal limits for thermoconformers that avoid extreme temperatures. This pattern emerges because lizards avoid low body temperatures, relaxing constraints on the critical thermal maximum arising from its correlation with the critical thermal minimum. With behavioural thermoregulation, the critical thermal limits should vary only by 7 °C throughout the range (Fig. 2). Even when thermoregulation imposes a cost, the thermal optima and critical thermal limits that maximize fitness differ by 10 °C between the warmest and coldest sites (see Figs S1 and S2 for sensitivity to the cost of thermoregulation). For thermoconformers, the predicted variance of the thermal optima throughout the range was 28 times greater than that of thermoregulators (11.4 and 0.40, respectively, $F_{11593, 11593} = 28.94$, $P < 10^{-15}$). Although more pronounced variation in the performance curve was predicted when maximizing the product of performance, thermoregulation still substantially limited geographic variation in the optimal performance curve (Fig. S5, Supporting information). Similar results were obtained

when including a thermodynamic effect on performance (Figs S6 and S7, Supporting information), which forces a positive correlation between the thermal optimum and the maximal performance (Angilletta, Huey & Frazier 2010). These results suggest that thermoregulation reduces geographic variation in thermal physiology under a wide range of conditions.

Using lizards from eight populations (Table S1, Supporting information), we tested our model's predictions about geographic variation in thermal physiology. Despite the wide range of thermal conditions throughout the range of *S. undulatus*, lizards from all populations selected similar body temperatures in artificial thermal gradients (Fig. 3a). Mean preferred body temperatures ranged from 29.8° to 32.8 °C during the morning and 32.3° to 35.0 °C during the afternoon. These body temperatures were unrelated to the environmental temperatures experienced by these populations (morning: $F_{1,6} = 0.05$, $P = 0.83$; afternoon: $F_{1,6} = 0.58$, $P = 0.48$, Fig. 3a). In fact, the most likely statistical model omitted an effect of population (Table S2, Supporting information). Preferred body temperatures fell within the range that enables this species to sprint quickly (Angilletta, Hill & Robson 2002) and digest food rapidly (Angilletta 2001).

Fig. 3. Both (a) body temperature (means \pm 95% confidence intervals) in artificial thermal gradients in the morning (open circles) and afternoon (filled circles) and (b) body temperatures in natural environments were unrelated to mean air temperatures during daylight over the activity season. Consequently, critical thermal minima (c) and the critical thermal maxima (d) do not correspond to mean daily maximal and minimal air temperatures experienced by the populations during daylight from May through September (means \pm 95% confidence intervals). Lizards from Texas (TX) exhibit higher preferred body temperatures and critical thermal limits. The state abbreviations corresponding to each population are indicated (AZ: Arizona, FL: Florida, IN: Indiana, NJ: New Jersey, NE: Nebraska, SC: South Carolina, TX: Texas, UT: Utah). Body temperatures were compiled from the literature.



Throughout the geographic range, lizards maintain body temperatures that correspond closely to those selected in artificial thermal gradients. Among 10 populations, spanning more than 10° of latitude and 2300 m of elevation, mean body temperatures during activity ranged from 32.7° to 35.2°C and were unrelated to environmental temperatures (Fig. 3b; $F_{1,8} = 0.07$, $P = 0.79$). The close match between body temperatures selected in artificial and natural environments supports the common view that these species respond to thermal change by limiting activity to times and places that enable effective thermoregulation (Dunham, Grant & Overall 1989; Adolph & Porter 1993).

Consistent with our predictions for a thermoregulator, critical thermal limits have diverged very little among eight populations of lizards. Critical thermal minima and maxima varied only by 4.2°C (Fig. 3c) and 2.9°C (Fig. 3d), respectively. Moreover, these thermal limits were unrelated to environmental temperatures (minima: $F_{1,6} = 1.35$, $P = 0.39$; maxima: $F_{1,6} = 0.06$, $P = 0.82$). The observed variances of critical thermal limits among populations were indistinguishable from the predicted variances for thermoregulators (minima: $F_{7,7} = 0.38$, $P < 0.22$; maxima: $F_{7,7} = 0.68$, $P < 0.62$), but were less than the variances predicted for thermoconformers (minima: $F_{7,7} = 8.7$, $P = 0.01$; maxima: $F_{7,7} = 15.7$, $P = 0.002$). Similarly, the observed variances of preferred body temperatures among populations were indistinguishable from the predicted variances of field body temperatures for thermoregulators (morning preferred temperature: $F_{7,7} = 0.74$, $P < 0.70$; afternoon preferred temperature: $F_{7,7} = 0.61$, $P < 0.54$), but were less than the predicted variances for thermoconformers (morning preferred temperature: $F_{7,7} = 17.0$, $P = 0.001$; afternoon preferred temperature: $F_{7,7} = 14.2$, $P = 0.002$). These observations support our model of the Bogert effect and confirm previous claims that thermal tolerances have been conserved during the evolution of *S. undulatus* (Crowley 1985).

Our model also predicted that, even with thermoregulation, lizards in the south-western region of the United States would have higher critical thermal limits than lizards from other regions. Consistent with this prediction (Fig. 2), lizards from Texas had unusually high critical thermal limits (see Tables S1–S3, Supporting information). When the population from Texas was excluded, critical thermal limits varied by no more than 2°C among populations. Thus, large variations in environmental temperatures were not reflected in the small variations in cold and heat tolerances, except in the region where thermal limits should be higher (Texas). These unusually high critical thermal limits coupled with limited variation in critical thermal limits among other populations have a parsimonious explanation: thermoregulation reduces selective pressures on thermal physiology and slows local adaptation, except in places where lizards cannot thermoregulate effectively at all times. Phylogenetic distance among populations may constrain the potential for local adaptation (Leaché 2009), but we observed little correspondence between phylogenetic distance and thermal physiology.

IMPACTS OF CLIMATE CHANGE

How will the Bogert effect influence how species respond to climate change? In the *S. undulatus* complex, thermoregulation sufficiently buffers the current variation in thermal conditions throughout the range. To assess whether opportunities for thermoregulation will decline, consider our analysis of the climate in Texas, where lizards face some of the most extreme temperatures within the range. Based on a moderate scenario, the effectiveness of thermoregulation in this environment will decay rapidly; thermoregulators in the climate anticipated for 2070 will never exceed the critical thermal maximum of 44°C , whereas those in the climate anticipated for 2090 will do so (Fig. 4).

Consequently, selection for greater heat tolerance will also occur abruptly (as depicted in fig. 7 of Huey *et al.* 2012). Without additive genetic variation in populations, thermal adaptation would occur too slowly to prevent a loss of performance during climate warming (Huey & Kingsolver 1993; Lynch & Lande 1993). Developmental plasticity may also influence thermal physiology, but rearing of a related species suggests the plasticity of thermal physiology is limited (Buckley *et al.* 2007). Thermoregulation may also preclude adaptation of thermal tolerance by limiting genetic variation among populations. For a thermoconformer, optimal values for thermal optimum and critical thermal maxima span interquartile ranges of 5 °C (27.5–32.5 °C and 37.5–42.5 °C, respectively). However, these optimal values span interquartile ranges of only 1 °C for a thermoregulator (30.5–31.5 °C and 40.5–41.5 °C, respectively). Substantial additive genetic variation in preferred body temperature must exist for populations to adapt to anticipated changes in climate (Sinervo *et al.* 2010). In the absence of local adaptation, gene flow among populations

cannot amplify genetic variances in populations (Atkins & Travis 2010).

If thermoregulators do not adapt to climate warming, we predict median losses in performance of 5% by 2050 (range = –36–15%) and 17% by 2090 (range = –53–34%), with most the pronounced losses anticipated in south-western deserts (Fig. 5). The incidence of body temperatures exceeding the critical thermal maximum should increase slightly by 2050 (mean = 0.1%; maximum = 19%) and more dramatically by 2090 (mean = 3%; maximum = 32%). These results correspond to a moderate scenario for climate change, but results are similar when using an alternative scenario (Fig. S8, Supporting information).

Discussion

Our theoretical model demonstrates how spatial gradients in opportunities for and the effectiveness of thermoregulation can conserve thermal niches. Moreover, our empirical observations support the model of the Bogert effect and confirm previous claims that thermal tolerances have been conserved during the evolution of *S. undulatus* (Crowley 1985). Even among North American species of *Sceloporus*, lizards maintain very similar body temperatures during activity despite covering an elevational range of more than 2500 m (Andrews 1998). By contrast, Central and South American species of *Sceloporus* maintain lower body temperatures in colder environments (Andrews 1998). This greater independence between environmental temperature and body temperature for North American species indicates that these species have especially effective strategies of thermoregulation or occupy habitats with more opportunities for thermoregulation. The conservation of preferred body temperatures within multiple genera of lizards suggests that the Bogert effect has general significance for reptiles (Andrews 1998; Cruz *et al.* 2009).

Thermoregulatory behaviour can buffer a species from climate change over the short term (Kearney, Shine & Porter 2009; Clusella-Trullas & Chown 2011; Huey *et al.* 2012) but confer a risk of extinction over the long term. For ectotherms such as lizards, effective thermoregulation requires access to preferred microclimates (Hertz, Huey & Stevenson 1993). For an organism that functions within a narrow range of body temperatures, climates severely restrict activity over space and time (Sinervo *et al.* 2010; Sears, Raskin & Angilletta 2011). Such constraints are manifested as decreased activity when environments become too hot or too cold (Adolph & Porter 1993; Sears, Raskin & Angilletta 2011). If animals cool during inactivity, physiological functions such as digestion, growth and immunity proceed slowly (Angilletta 2009). In some environments, opportunities for thermoregulation have decreased to the point where populations of lizards cannot persist (Sinervo *et al.* 2010). For other environments, a slight warming could eliminate populations that persist today (Buckley *et al.* 2010; Sinervo *et al.* 2010). Even when environmental conditions permit lizards to thermoregulate,

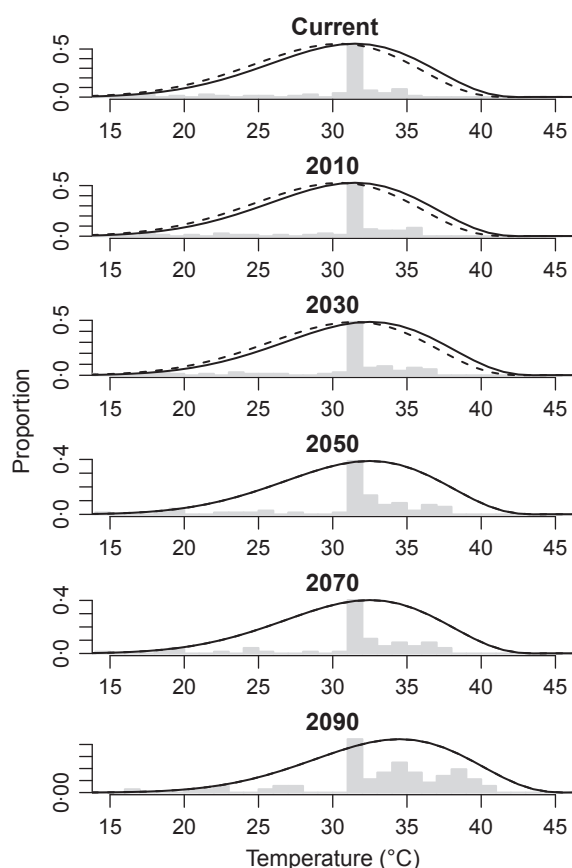


Fig. 4. Predicted body temperatures of thermoregulating lizards in Texas, during daylight hours between May and September. The distribution of body temperatures and optimal thermal physiology shift gradually with climate warming, before increasing abruptly prior to 2090. In later time periods, the optimal thermal physiology is the same regardless of whether we maximize the sum (solid line) or product (dashed line) of performance. Warming was modelled at a constant rate between points at which temperature anomalies were projected (1961–1990, 2050 and 2090).

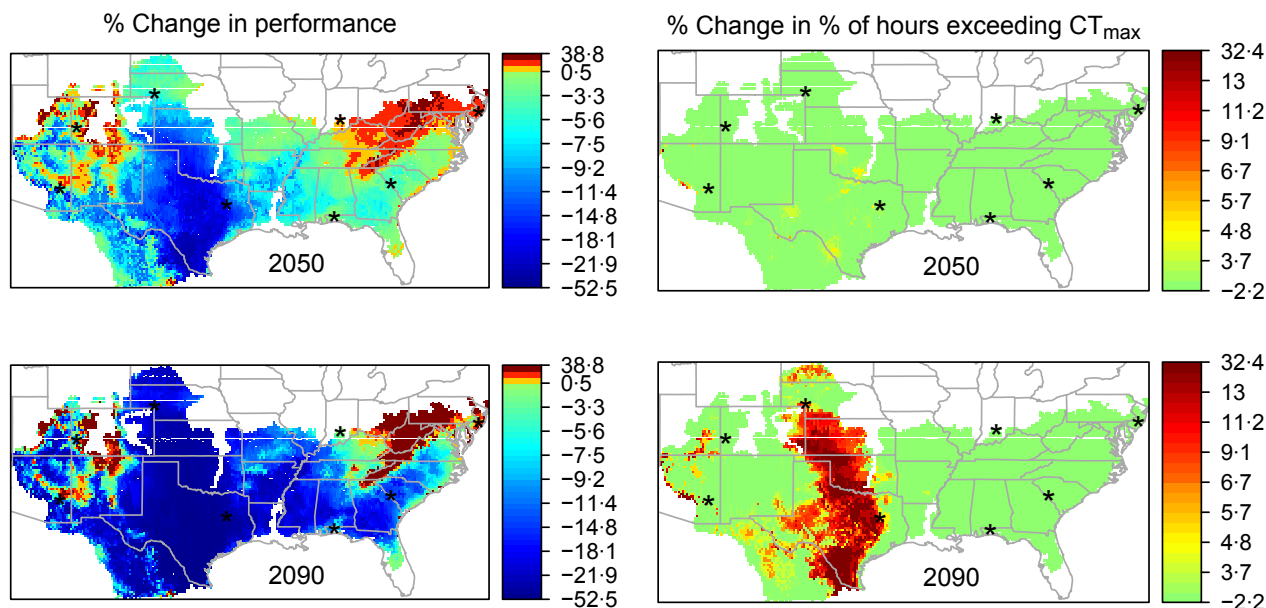


Fig. 5. Lizards exhibiting the thermal niche conservatism associated with thermoregulation are predicted to experience performance declines (left, proportion change in performance relative to the current baseline) and a greater incidence of operative temperatures exceeding CT_{max} (right, proportion change in the number of events relative to the current number) by 2050 (top) and 2090 (bottom). The climate projections correspond to a midrange climate change scenario (HadCM3 scenario A2). The colour scale depicts quantiles and is centred such that green colours indicate little or no change. The localities sampled for empirical studies are marked (*).

this behaviour requires time and energy that detracts from other functions (Huey & Slatkin 1976; Angilletta 2009). If preferred microclimates become less common or less accessible, the cost of thermoregulation might exceed the benefit (Huey & Slatkin 1976; Angilletta 2009).

A shift in thermoregulatory strategy could lessen the impact of climate change (Gvoždík 2012) if natural selection can also shift thermal physiology in the same direction. Yet we found no evidence that thermoregulatory behaviour has diverged among populations in the *S. undulatus* complex. Indeed, lizards in diverse climates preferred similar body temperatures in the laboratory and maintained similar body temperatures during activity (see Fig. 3). Given that thermoregulatory behaviour has been strongly conserved, we expect the same in the future. Still, failure to thermoregulate can expose animals to temperatures that select for a greater critical thermal maximum. The relatively high critical thermal maximum of lizards from Texas suggests that this trait can evolve if the environment warms enough to impose natural selection. Thus, our predictions about the frequency of lethal thermal stress are probably less robust than our predictions about the loss of performance. Similar analyses applied to other ectothermic taxa are needed to infer the generality of the Bogert effect and its implications for biodiversity in future climates.

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Data accessibility

Thermal tolerance and preference data are deposited in the Dryad Digital Repository (doi: 10.5061/dryad.64716) (Buckley, Ehrenberger & Angilletta 2015).

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Appendix S1 Supplementary methods.

Fig. S1 Critical thermal minima (left), thermal optima (middle), and critical thermal maxima (right) that maximize the sum of performance.

Fig. S2 Critical thermal minima (left), thermal optima (middle), and critical thermal maxima (right) that maximize the product of performance.

Fig. S3 Performance associated with the range of modes (α) and breadths (β) we considered when optimizing thermal performance curves under the four thermoregulation scenarios.

Fig. S4 Critical thermal minima (left), thermal optima (middle), and critical thermal maxima (right) that maximize the sum of performance.

Fig. S5 Critical thermal minima (left), thermal optima (middle), and critical thermal maxima (right) that maximize the product of performance.

Fig. S6 Critical thermal minima (left), thermal optima (middle), and critical thermal maxima (right) that maximize the sum of per-

formance, given a thermodynamic effect (i.e., hotter is better).

Fig. S7 Critical thermal minima (left), thermal optima (middle), and critical thermal maxima (right) that maximize the product of performance, given a thermodynamic effect (i.e., hotter is better).

Fig. S8 In future climates, a thermoregulating species, which has a highly conserved thermal niche throughout its range, would perform worse (left plots, proportion change in performance relative to the current baseline) and experience thermal stress more often (right plots, proportion change in the number of times that body temperature exceeds the critical thermal maximum relative to the current baseline).

Table S1 Thermal preferences and tolerances of lizards from eight populations of the *Sceloporus undulatus* complex.

Table S2 Inferential statistics for the most likely general linear mixed model of preferred body temperature in *Sceloporus undulatus*.

Table S3 Inferential statistics for the most likely general linear mixed model of the critical thermal minimum in *Sceloporus undulatus*.

Table S4 Inferential statistics for the most likely general linear mixed model of the critical thermal maximum in *Sceloporus undulatus*.

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