

Geographic variation in vulnerability to climate warming in a tropical Caribbean lizard

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Summary

1. Rising global temperatures are predicted to impact organisms in diverse ways. For ectotherms, recent broad-scale analyses have predicted global patterns of vulnerability to warming, with tropical species at higher risk of detrimental effects than temperate species. However, vulnerability results from complex interactions between environment, physiology and behaviour. For species that inhabit a diversity of habitat types, these interactions may change across their range.

2. We measured operative thermal environments (T_e) and body temperatures (T_b) of the tropical Caribbean lizard *Anolis cristatellus* at nine sites representing two habitat types: mesic and xeric forest. The thermal sensitivity of whole-organism physiological performance (i.e. sprint speed) of one mesic and one xeric population was also measured. Thermal and performance data were integrated to determine how habitat thermal variation, behavioural thermoregulation and thermal physiology influence current physiological performance capacity in the field. We then evaluate if habitat suitability and physiological capacity would change assuming climate warming of 3 °C over the next century.

3. The mean T_e of the xeric habitat was 4.5 °C warmer than that of the mesic habitat. However, behavioural thermoregulation by xeric lizards led to lesser differences in T_b (3.5 °C) between habitat types. The thermal sensitivity of sprint performance was similar for mesic and xeric lizards, and lizards from both habitats maintain sprint capacities near 100%. Climate warming is predicted to influence mesic and xeric lizards differently. Xeric lizards currently live in a thermal environment near their upper temperature threshold, while mesic lizards do not. As a result, the number of suitable perch sites is predicted to decrease dramatically in the xeric but not the mesic habitat. In addition, the physiological capacity of mesic lizards is predicted to increase by approximately 4%, whereas a decrease of approximately 30% is predicted for xeric lizards.

4. We characterized variation in the current biophysical and ecophysiological conditions experienced by *A. cristatellus* by integrating fine-scale measurements of thermal microhabitats with data on body temperatures and physiological performance capacities. These data allowed us to explicitly demonstrate how variation in these parameters can influence population susceptibility to climate warming across a species range and highlight the utility of a mechanistic approach in studies of global climate change.

Key-words: *Anolis*, behavioural thermoregulation, global change, Puerto Rico, thermal ecology, whole-organism performance

Introduction

Environmental temperature variation is extensive across the geographic range of many organisms. Ectotherms, which cannot produce appreciable physiological heat, are particularly sensitive to this thermal variation (Porter & Gates

1969). As such, knowledge of variation in the thermal environment throughout an ectothermic species' range can greatly contribute to our understanding of that species' ecology (Kearney & Porter 2009). For example, studies incorporating thermal variation across a species' range lay the groundwork for understanding variation in thermoregulatory patterns (Huey 1974; Adolph 1990; Freidenburg & Skelly 2004), life-history strategies (Kingsolver 1983;

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Dunham, Grant & Overall 1989; Angilletta 2001) and intra- and interspecific variation in thermal physiology (Crowley 1985; Van Damme, Bauwens & Verheyen 1990; Willett 2010).

The need to characterize the thermal niche has become increasingly relevant in light of rapid increases in global temperature associated with anthropogenic climate change (IPCC 2007). Several broad-scale analyses of terrestrial ectotherms have suggested global patterns of susceptibility to this warming (e.g. Deutsch *et al.* 2008; Huey *et al.* 2009; Kearney, Shine & Porter 2009; Dillon, Wang & Huey 2010; Sinervo *et al.* 2010; Duarte *et al.* 2012). In general, these studies predict that tropical ectotherms are more susceptible to increasing temperatures than their temperate counterparts, for two reasons (but see Bonebrake & Mastrandrea 2010; Clusella-Trullas, Blackburn & Chown 2011). First, tropical ectotherms tend to live in thermal environments closer to their upper temperature thresholds. Second, tropical ectotherms may have less potential to behaviourally buffer themselves from increasing temperatures. For example, among lizards, the thermal safety margin for physiological performance (i.e. the difference between the optimal performance temperature and environmental temperature) decreases with decreasing latitude such that tropical lizards usually have lower capacities to tolerate warming than temperate-zone lizards (Huey *et al.* 2009). Similarly, the reproductive rates of most tropical insects are predicted to decrease because of climate warming, whereas insects in temperate regions are generally predicted to experience increases in reproductive rate (Deutsch *et al.* 2008). However, because of the scale of analysis, these studies often exclude aspects of the thermal ecology of individual species that may increase or decrease their susceptibility to warming, such as fine-scale geographic variation in thermal environment and/or geographic variation in the temperature-dependence of whole-organism performance.

In recent years, characterization of the thermal niche has been carried out mostly using modelling approaches that either correlate climatic data with current distribution data (i.e. correlative models), or integrate physiological data with climatic data to estimate habitat and body temperatures to predict where organisms can occur (i.e. mechanistic models; reviewed in Kearney & Porter 2009; Buckley *et al.* 2010). These approaches have a number of benefits, as they allow estimation of climatic niches for species for which ecological and physiological data are unavailable (primarily correlative models) or can be used to predict thermal conditions and their physiological consequences for widely distributed species for which direct measurements across the range are impractical (mechanistic models). However, a limitation of those approaches is that body temperatures and operative thermal environments of the organisms in question are not directly measured. Instead, estimated temperatures are often derived from environmental measurements taken at macro-scales that do not necessarily translate to the conditions experienced by organisms in their microhabitats (Chown & Terblanche 2007; Huey *et al.* 2009; Helmuth *et al.* 2010; Sears, Raskin & Angilletta 2011). Furthermore, although behavioural thermoreg-

ulation is pervasive among ectotherms (Angilletta 2009), these methods do not measure the extent to which organisms behaviourally thermoregulate across their range, and often ignore behavioural thermoregulation or assume the degree to which it occurs.

The thermal niche can also be characterized by integrating body temperature measurements of free-ranging animals with fine-scale estimates of their operative thermal environment (Christian & Weavers 1996). Contrary to broad-scale modelling, these approaches focus on comprehensive measurement of thermal environments at the scale at which organisms experience them (Gates 1980; Helmuth *et al.* 2010), and many were explicitly developed to detect and estimate the extent of behavioural thermoregulation. Thus, these approaches provide a valuable tool with which to explore the complex interactions between thermal environment, thermal physiology and behaviour that may influence the ability of species to persist in the face of climate warming (Huey, Hertz & Sinervo 2003; Kearney, Shine & Porter 2009). Despite the advantages, studies of this kind are rarely used to evaluate the possible impacts of climate change.

Here, we implement the 'null model' approach following Hertz, Huey & Stevenson (1993) and measure geographic variation in body temperature, operative thermal environment and behavioural thermoregulation in the tropical lizard *Anolis cristatellus* (Fig. 1). *Anolis cristatellus* is an arboreal lizard that occupies two distinct habitat types on the Caribbean island of Puerto Rico: mesic (moist, closed-canopy forest) and xeric (dry, relatively open-canopy forest). Tropical



Fig. 1. A male *Anolis cristatellus* photographed at Site X4 (photograph by A.R. Gunderson).

lizards are predicted to be more vulnerable to climate change than their temperate-zone counterparts (Huey *et al.* 2009; Kearney, Shine & Porter 2009); however, within the tropics, closed-forest species are predicted to be more susceptible than open-forest species (Huey *et al.* 2009). Here we test this prediction in a species that occupies both habitat types. In doing so, we evaluate how the occupation of different habitats may influence the impacts of climate warming on tropical species.

To achieve this goal, we sampled lizard body temperatures (T_b) and estimated operative thermal environments using copper lizard models (T_e) at nine sites across Puerto Rico (four mesic and five xeric), covering a large proportion of this species' range (see Fig. S1, Supporting Information). Measurements of T_b and T_e were used to evaluate patterns of behavioural thermoregulation among these sites (Hertz, Huey & Stevenson 1993). To estimate the impact of temperature on physiological capabilities, we estimated thermal performance curves for sprint speed for *A. cristatellus* from both mesic and xeric habitats. Locomotor performance (i.e. sprint speed) is an ecologically relevant temperature-dependent performance trait (Bennett 1980; Irschick *et al.* 2008) that is commonly used as a physiological parameter to explore the impact of climate warming on ectotherms, including lizards (Buckley 2008; Kearney *et al.* 2008; Huey *et al.* 2009), and has been used as an estimate of general physiological sensitivity to temperature (Huey *et al.* 2009). We then combined data for T_e , T_b , and physiological sensitivity to temperature to estimate geographic variation in susceptibility to climate warming in *A. cristatellus* across Puerto Rico, using three metrics: (i) warming tolerance, (ii) predicted changes in the thermal suitability of each habitat type assuming a 3 °C increase in T_a and (iii) predicted changes in mean whole-organism physiological performance capacity of lizards assuming a 3 °C increase in T_a .

Materials and methods

STUDY SPECIES AND STUDY SITES

Anolis cristatellus is a small-to-medium sized grey-brown, sexually dimorphic, arboreal lizard typically found on the ground or on perches up to 2 m in height (Rand 1964). *Anolis cristatellus* is endemic to the islands of the Greater Puerto Rican Bank and was historically found from sea level to mid-elevation (< 800 m, Rand 1964) throughout the island of Puerto Rico, including both mesic and xeric habitats (Heatwole 1976; Hertz 1992b).

We collected thermal data at nine relatively undisturbed sites across Puerto Rico, four mesic and five xeric (see Fig. S1, Supporting Information for locations, see Table 1 for sample sizes). The mesic habitat was sampled at Bosque Estatal de Guajataca (M1: 18°25'236 N; 66°58'010 W; elevation 200 m), Bosque Estatal de Cambalache (M3: 18°26'998 N; 66°35'642 W; elevation 10 m), Bosque Estatal La Vega (M4: 18°24'862 N; 66°20'252 W; elevation 35 m) and a privately owned forest reserve adjacent to the Mata de Plátano field station (M2: 18°24'847 N; 66°43'697 W; elevation 135 m). The xeric habitat was sampled at two sites within the Bosque Seco de Guánica (X2: 17°56'711 N; 66°56'308 W, X3:

17°58'246 N; 66°52'236 W, elevation 5 m for both sites), Bosque Estatal de Aguirre (X4: 17°56'348 N; 66°12'100 W, elevation 2 m), Bosque Estatal de Boquerón, Morillos de Cabo Rojo area (X1: 17°57'239 N; 67°11'920 W, elevation 2 m) and a U.S. Naval base, Roosevelt Roads (X5: 18°13'660 N; 65°35'667 W, elevation 10 m). All of the mesic sites lie within Holdridge's Subtropical Moist Forest life-zone (Ewel & Whitmore 1973; see also Daly, Helmer & Quiñones 2003) and are part of a contiguous area of predominantly mesic forest that extends across most of the northern and western coastal regions of the island. Four of the xeric locations (X1–X4) are part of a continuous swath of xeric habitat that runs along much of the southern coast of Puerto Rico. The other xeric site (X5) is separated from the others by mesic habitat and is part of 'Las Cabezas de San Juan', a region of xeric habitat in the north-eastern corner of the island. All of the xeric sites lie within Holdridge's Subtropical Dry Forest life-zone (Ewel & Whitmore 1973). In general, the xeric habitat receives less rainfall than the mesic habitat, by as much as 10 cm per month (Daly, Helmer & Quiñones 2003; Brandeis *et al.* 2009).

LIZARD AND COPPER MODEL THERMAL DATA

We measured T_b and T_e (copper model temperatures) at each of the nine sites between July 7 and August 22, 2009. Thermal data were also collected at sites M3 and X4 from 14 to 21 December 2009. Each location was sampled for 3 days from 07:00 to 18:00 h, totalling 33 h of sampling effort per site (i.e. 3 h of sampling per hour of the day), per season. However, site M3 was sampled for 30 h over 3 days in July, and site X5 was sampled for 19 h over 2 days. Our sampling effort should produce a representative picture of the thermal environments experienced by lizards at each site in a given season because of the low thermal variability of tropical climates (Janzen 1967). This is evident in our data. Among sites within a given habitat type sampled in the same season (July and August), all of which were sampled on different days, pair-wise differences in mean operative temperatures were never more than 1 °C (Table 1). Previous studies in Puerto Rico have found that even within sites, maximum seasonal differences in mean air temperature are about 3 °C (Brandeis *et al.* 2009; a similar pattern was found for T_b and T_e in this study, see seasonal data in the Results). Data were not collected while it was raining because lizards are inactive. In total, the mesic and xeric habitats received 129 and 151 h of sampling effort, respectively, throughout July and August. We focused our sampling efforts during the months of July and August because this period coincides with high rates of reproductive activity of *A. cristatellus* across Puerto Rico (Gorman & Licht 1974).

At each site, a location in the forest was haphazardly chosen as a starting point for sampling for a given day. From this point, a compass direction was taken from a random number table. This compass direction was used as a transect line along which sampling occurred. The transect line was walked until an impassable barrier was reached (e.g. ocean, fence, road, cliff), at which point another random compass direction was then taken as a new transect line (under the restrictions that it moved away from the impassable barrier and, to avoid re-sampling the same individuals that had previously been disturbed, was not 180° from the previous transect line). Thus, we sampled large areas by crisscrossing the forests along multiple, randomly chosen transects.

At each site, we walked slowly along transects looking for lizards. When a lizard was spotted, we attempted to capture it by noosing to measure its T_b . We did not sample lizards that moved from either sun

Table 1. Summary statistics for *Anolis cristatellus* field thermal data from four mesic sites and five xeric sites in Puerto Rico

Month & Site	N_{lizards}	T_b (\pm SE)	P_{lizards} (\pm SE)	N_{models}	T_c (SE)	P_{models} (\pm SE)
July–August						
M1	127	28.6 (0.2)	94.3 (0.4)	127	28.5 (0.1)	94.3 (0.3)
M2	94	28.7 (0.2)	94.6 (0.4)	91	28.7 (0.2)	94.6 (0.3)
M3	96	29.2 (0.1)	95.8 (0.2)	95	29.2 (0.1)	95.9 (0.2)
M4	152	29.0 (0.1)	95.2 (0.3)	151	29.0 (0.1)	95.4 (0.3)
Mesic combined	469	28.9 (0.1)	95.0 (0.2)	464	28.9 (0.1)	95.0 (0.2)
X1	136	32.6 (0.1)	97.9 (0.3)	137	33.5 (0.2)	87.8 (2.2)
X2	140	32.6 (0.2)	96.9 (0.4)	140	33.1 (0.2)	92.0 (1.2)
X3	116	32.4 (0.2)	97.8 (0.3)	114	33.2 (0.3)	88.1 (2.2)
X4	140	32.8 (0.2)	96.9 (0.4)	138	33.9 (0.2)	85.2 (2.2)
X5	106	32.5 (0.2)	97.3 (0.4)	103	32.9 (0.2)	93.5 (1.6)
Xeric combined	638	32.6 (0.1)	97.3 (0.2)	632	33.4 (0.1)	84.7 (1.9)
December						
M3	118	26.3 (0.2)	88.4 (0.6)	117	26.2 (0.2)	88.2 (0.6)
X4	160	29.9 (0.2)	96.2 (0.8)	160	30.1 (0.2)	94.2 (0.9)

N = sample size, T_b = mean lizard body temperature ($^{\circ}\text{C}$), P = mean relative sprint performance capacity (% of maximum sprint performance), T_c = mean copper model temperature ($^{\circ}\text{C}$).

to shade or shade to sun during the capture process. Immediately upon capture, T_b was measured cloacally with a thermocouple probe connected to a digital thermocouple thermometer (Omega Engineering Inc., Stamford, CT, USA) accurate to 0.1 $^{\circ}\text{C}$. The snout-to-vent length (SVL) of each lizard was also measured, and all individuals were released at the site of capture. Both males and females were sampled and sexes did not differ in T_b in either habitat (Wilcoxon rank sum tests, both $P > 0.05$). Thus, data for males and females were pooled for all analyses. Mesic individuals had a mean (\pm SD) SVL of 47.9 ± 7.9 mm, while xeric individuals had a mean SVL of 53.3 ± 9.2 (see Table S1, Supporting information for a summary of SVL data by location and sex). After each lizard was sampled, we took a T_c measurement by recording the temperature of a copper lizard model at a random location within 8 m of the capture site. We used painted, hollow copper models with a thermocouple affixed inside and shaped with a mould of *A. cristatellus*. The models are designed to have a low specific heat capacity, and thus their temperature rapidly reaches equilibrium under field conditions (see Hertz 1992a). In practice, we concluded that a model reached equilibrium when its temperature did not change (at an accuracy of 0.1 $^{\circ}\text{C}$) for 10 s. Our models were constructed by P.E. Hertz and have been used in previous studies of *A. cristatellus* thermal ecology (see Hertz 1992a; b for a detailed description of the models). To determine the copper model location, we generated a random number table that gave random compass directions (1–360 $^{\circ}$ at one degree intervals), distances (0–8 m at 0.5 m intervals) and perch heights (0–200 cm at 1 cm intervals). Two meters was chosen as the maximum height because *A. cristatellus* is rarely found above this height (Rand 1964). We chose eight meters as the maximum distance because we have rarely observed an individual moving more than 8 m in a single bout in the field (A. R. Gunderson and M. Leal, unpublished data). Using this sampling scheme, a model temperature was taken approximately 3–4 min after each lizard temperature was collected. These model temperatures provide an estimate of the T_c distribution at each site. For each lizard and model, we also recorded the immediate weather conditions (cloudy, sun visible behind clouds, sunny) and basking status (not basking: $\leq 25\%$ of body in direct sunlight; basking: $> 25\%$ of body in direct sunlight).

Neither T_b nor T_c data were normally distributed; therefore, we used nonparametric models (Kruskal–Wallis and Wilcoxon sum rank tests) to test for differences between populations and habitats.

ESTIMATING THE EXTENT OF BEHAVIOURAL THERMOREGULATION

For each site, we calculated the extent of behavioural thermoregulation using two different metrics: E , calculated as $E = 1 - d_b/d_c$ (Hertz, Huey & Stevenson 1993), and $d_c - d_b$, or the absolute temperature difference of mean d between lizards and models (Blouin-Demers & Weatherhead 2001). The variables d_b and d_c describe the mean deviation of T_b and T_c from the preferred temperature (i.e. set point) range, respectively. Preferred temperatures, calculated as the central 50% of body temperatures chosen by lizards in a laboratory thermal gradient, were previously reported for one mesic site (approximately 10 miles north-east of our site M4, $N = 6$) and one xeric site (our site X3, $N = 6$; Huey & Webster 1976; Hertz, Huey & Stevenson 1993). The preferred temperature ranges differed slightly between populations of *A. cristatellus* (mesic preferred temperature range = 28.6–30.7 $^{\circ}\text{C}$; xeric preferred temperature range = 28.6–30.9 $^{\circ}\text{C}$). Therefore, we used the mesic preferred temperature range for d calculations at all mesic sites, and the xeric preferred temperature range for d calculations at all xeric sites.

Two complementary analyses were used to test whether lizards at a particular site are nonrandomly utilizing available thermal resources and, thus, behaviourally thermoregulating (Hertz, Huey & Stevenson 1993). First, we used Wilcoxon's sum rank tests to compare T_b to T_c within each site. Second, we conducted G-tests to determine whether basking rates differed between lizards and copper models (i.e. random perch sites).

In addition, to determine whether lizard use of available thermal resources increased their predicted whole-organism performance capacity over null expectations, we used Wilcoxon's sum rank tests to compare the predicted relative performance capacity of lizards and of copper models within a site.

TEMPERATURE-DEPENDENT WHOLE-ORGANISM PERFORMANCE

Male lizards from mesic site M3 and xeric site X3 were collected from 5 to 8 August 2010 and transported to Duke University. In the laboratory, lizards were housed individually in plastic cages ($29 \times 21 \times 21$ cm) with a wooden dowel provided as a perch in a climate-controlled growth chamber (28 $^{\circ}\text{C}$, 60% relative humidity)

under a 12L : 12D light cycle. All lizards were watered daily and fed crickets dusted with calcium powder three times per week.

We calculated sprint speed by conducting frame-by-frame video analysis of lizards running up a wooden racetrack (Husak 2006). The racetrack was 1.5 m in total length, with visible landmarks every 25 cm and was set at a 37° angle. Runs at 19.5 and 32 °C were filmed with a Canon ZR 950 camcorder (Canon USA, Inc., Lake Success, NY, USA) at 29.5 frames-per-second. Runs at all other temperatures were filmed at 120 frames-per-second using the Slow Smooth Record function on a Sony HDR-SR11 Handycam (Sony Corporation of America, New York, NY, USA).

Lizards were induced to run, if necessary, by gently tapping their tails. At each test temperature, we analysed two 'good' runs per lizard, defined as a run in which the lizard neither stopped nor jumped off of the track. Lizards were run twice per day (once in the morning and once in the afternoon). For 'good' runs, we measured sprint speed over each 25-cm interval and used the fastest interval as an individual's speed for that temperature (following Huey 1983). Each lizard was run at six temperatures: 19.5, 23, 26, 29, 32 and 35 °C in the following randomized order: 19.5, 32, 29, 23, 26 and 35 °C. The desired body temperature was attained by placing the lizards in either a climate-controlled room or incubator set to the test temperature 1 h prior to a run. We confirmed that ambient temperatures and body temperatures were equivalent at 19.5 and 35 °C and are confident that test temperatures and body temperatures are in accordance across the range temperatures used. This is expected for an ectotherm with low rates of water loss in a room with no solar radiation and little to no air flow (Gates 1980). All runs were conducted 24 h after feeding. To calculate the thermal performance curve, we only included data for individuals that were run at a minimum of five of the test temperatures (lizards were removed from trials if a portion of their tail was lost during the experiment), giving us a sample size of eight mesic and five xeric lizards.

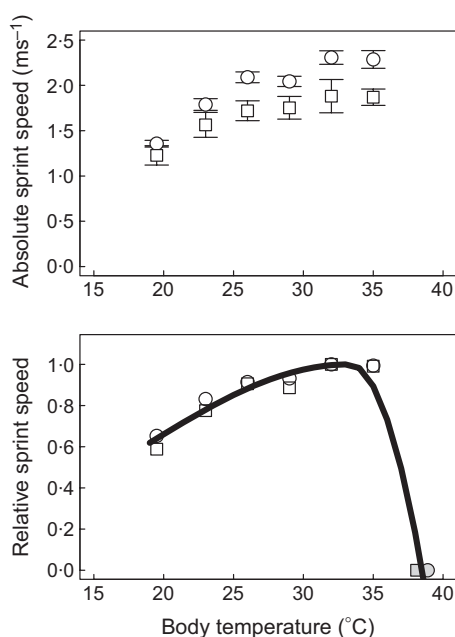


Fig. 2. Temperature-dependent sprint performance for a mesic and a xeric population of *Anolis cristatellus*. (a) Mean absolute sprint speed (\pm SE). (b) Relative sprint speed. *circles* = mesic lizards; *squares* = xeric lizards. Note: CT_{max} values (shaded symbols) were obtained from Huey & Webster (1976).

Sprint speed data were used to generate a temperature-dependent sprint performance curve (Fig. 2b). At each temperature, mesic and xeric lizards had nearly identical mean relative sprint performance (Fig. 2b). Thus, we combined data from mesic and xeric lizards to generate a single thermal performance curve that was used in all whole-organism performance analyses. Following Huey *et al.* (2009), we modelled the temperature-dependence of sprint performance by combining two different functions. For the left side of the curve, from the lowest temperature to the optimum temperature, we fitted the following function to the data: $P(T) = e^{-\left(\frac{T-T_{opt}}{2\sigma}\right)^2}$ (Huey *et al.* 2009), where P = relative sprint performance, T = temperature, T_{opt} = temperature of optimal performance, and σ is a term related to the breadth of the curve. We solved for the T_{opt} and σ terms using a nonlinear least-squares analysis implemented in the R statistical programming language. For temperatures above T_{opt} , the curve was described by the function: $P(T) = 1 - 0 - \left(\frac{T-T_{opt}}{CT_{max}-T_{opt}}\right)^2$ (Huey *et al.* 2009), where CT_{max} is the 'critical thermal maximum', or the upper body temperature at which a lizard loses the ability to right itself, which is often used as a proxy for the upper lethal temperature threshold (Huey & Stevenson 1979). We obtained the CT_{max} of *A. cristatellus* from previously published data (Mesic lizards: $N = 10$, $\bar{X} = 38.1 \pm 0.4$ °C; xeric lizards: $N = 11$, $\bar{X} = 38.9 \pm 0.3$ °C; Huey & Webster 1976).

The estimated temperature-dependent performance curve was applied to the sampled values of T_b and T_c to estimate the physiological performance consequences of thermal variation across the range of *A. cristatellus*.

SUSCEPTIBILITY TO CLIMATE WARMING

We evaluated the susceptibility of *A. cristatellus* to climate warming using three metrics. First, we calculated the 'warming tolerance' [i.e. the difference between the current mean T_c and the CT_{max} (Deutsch *et al.* 2008)] of lizards in both habitat types. We used mean CT_{max} values for *A. cristatellus* from each habitat type reported in Huey & Webster (1976). Next, we estimated whether or not the suitability of the thermal environment in each habitat will change by calculating the percentage of the available thermal environment (i.e. the T_c distribution) that will be within 2 °C of CT_{max} after climate warming. We assume a 3 °C increase in T_a (Buckley 2008; Huey *et al.* 2009; Kearney, Shine & Porter 2009; Buckley *et al.* 2010), which is within the range of predicted increases in air temperature in Puerto Rico over the next century (Christensen *et al.* 2007). Furthermore, we assumed that T_c changes at the same rate as T_a . Finally, using the thermal performance curve for sprint speed (Fig. 2b), we predicted the change in mean performance capacity of lizards in each habitat from current values, again assuming a 3 °C increase in T_a . We assumed that T_b increases with T_a in a one-to-one relationship, which has been previously demonstrated for two populations of *A. cristatellus* on Puerto Rico (Huey *et al.* 2009). We do not incorporate potential changes in wind-speed into our predictions for T_c and T_b because at present there is no reliable method to predict wind-speed changes over the next century (IPCC 2007).

STATISTICAL ANALYSES

Adjustment of the Type I error rate for multiple tests was carried out using the false-discovery rate method (Whitlock & Schluter 2009). All statistical tests were two-tailed at $\alpha = 0.05$ and were performed using

the R statistical programming language V 2.9.2 (R Development Core Team, 2009).

Results

OPERATIVE TEMPERATURE VARIATION

Mean T_e in the xeric habitat ranged from 32.9 to 33.9 °C and did not differ significantly among sites (Kruskal–Wallis sum rank test, chi-squared = 8.30, d.f. = 4, $P = 0.081$), whereas mean T_e across mesic sites ranged from 28.5 to 29.2 °C and differed significantly (Kruskal–Wallis rank sum test, chi-squared = 15.53, d.f. = 3, $P = 0.001$; Table 1). However, differences in mesic mean T_e s were small. T_e s at M1 and M2 were each cooler than T_e s at sites M3 and M4 (multiple pair-wise comparisons with false-discovery rate correction for Type I error rate, all $P < 0.05$; Table 1). Combining data within mesic and xeric sites, T_e differed between mesic and xeric habitats. During July and August, the mean T_e of the xeric habitat was significantly warmer than that of the mesic habitat, by approximately 4.5 °C (Wilcoxon sum rank test, $P < 0.001$; Table 1).

In December, mean T_e at xeric site X4 (30.1 °C) was significantly warmer than mean T_e at mesic site M3 (26.2 °C; Wilcoxon sum rank test, $P < 0.001$; Table 1). In addition, mean T_e at both sites was significantly cooler in December than in July and August (Wilcoxon sum rank tests, both $P < 0.001$; Table 1).

BODY TEMPERATURES

Across xeric sites, mean T_b ranged from 32.4 to 32.8 °C (Table 1) and did not vary significantly (Kruskal–Wallis sum rank test, chi-squared = 6.07, d.f. = 4, $P = 0.194$). Across mesic sites, mean T_b ranged only from 28.6 to 29.2 °C (Table 1) but nonetheless varied significantly (Kruskal–Wallis rank sum test, chi-squared = 12.71, d.f. = 3, $P = 0.006$). Sites M1 and M2 were each significantly cooler than sites M3 and M4 (all $P < 0.05$), a pattern that is congruent with the differences in operative temperatures between mesic sites.

The mean T_b (32.6 °C) of lizards across xeric sites in July and August was significantly cooler than the mean T_e (33.4 °C; Wilcoxon sum rank test, $P < 0.001$; Table 1). This pattern was most pronounced at midday (Fig. 3, Fig. S2, Supporting Information). Thus, xeric lizards appear to actively seek cool perch sites during the warmest portion of the day. By contrast, T_b across mesic sites did not differ from T_e ; indeed, combining data for mesic sites, lizards and copper models had identical mean temperatures (28.9 °C; Table 1). Accordingly, T_b tracked T_e throughout the day at all mesic sites (Fig. 3, Fig. S2, Supporting Information).

In accordance with the July and August data, habitat differences in lizard body temperature were also present in December. Mean T_b at xeric site X4 was 3.6 °C warmer than mean T_b at mesic site M3 (Wilcoxon sum rank test,

$P < 0.001$; Table 1, Fig. S4, Supporting Information). However, unlike the July and August data, T_b did not differ significantly from T_e at either site (Wilcoxon sum rank tests, both $P > 0.05$). In addition, mean T_b at both sites was significantly cooler in December than in July and August, by approximately 3 °C (Wilcoxon sum rank tests, both $P < 0.001$; Table 1).

WHOLE-ORGANISM PERFORMANCE CAPACITY

In terms of absolute sprint speed, on average mesic lizards ran faster than xeric lizards at all test temperatures (Fig. 2a). However, mesic and xeric lizards ran at nearly identical relative sprint speeds at all temperatures (Fig. 2b).

Across xeric sites, mean sprint performance capacity of lizards ranged from 96.9% to 97.9%. Within these populations, mean lizard performance capacity ranged from 4.9% to 11.7% higher than mean copper model performance capacity (Table 1, Fig. 3, see Fig. S3, Supporting Information for plots reporting lizard and copper model performance capacity at each site throughout the day). A closer examination reveals that the difference between lizard and copper model performance capacity was particularly marked at midday (11:00–13:00 h), when lizard mean performance capacity was 8.2–21.4% higher than that of copper models. Across mesic sites, mean sprint performance capacity ranged only from 94.3% to 95.8% (Table 1). Contrary to xeric sites, performance capacities of lizards and models were very similar under mesic conditions (Table 1).

Lizards and copper models did not differ in performance capacity at either site during December (Wilcoxon sum rank tests, both $P > 0.05$, Table 2). In addition, lizard and copper model performance capacities were significantly lower in December than in July and August for both sites (Wilcoxon sum rank tests, both $P \leq 0.001$; Table 1).

BEHAVIOURAL THERMOREGULATION

Within mesic sites, the extent of thermoregulation (E) ranged from -0.19 to -0.03 , and $d_e - d_b$ ranged from -0.09 to -0.01 (Table 2). Within xeric sites, E ranged from 0.18 to 0.32, while $d_e - d_b$ ranged from 0.41 to 0.85 (Table 2). Combined with the data on differences between T_b and T_e , these results indicate that xeric lizards behaviourally thermoregulate, while mesic lizards do not. In addition, at four of five xeric sites, lizards basked significantly less often than models (sites X2 – X5, G-tests, all $P < 0.05$), whereas basking rates of lizards and models did not differ significantly at any of the mesic sites (G-tests, all $P > 0.05$).

SUSCEPTIBILITY TO CLIMATE WARMING

Across the mesic sites, warming tolerance ranged from 8.9 to 9.6 °C ($\bar{X} = 9.3$ °C). Warming tolerance across xeric sites was lower and ranged from 5.0 to 6.0 °C ($\bar{X} = 5.6$ °C).

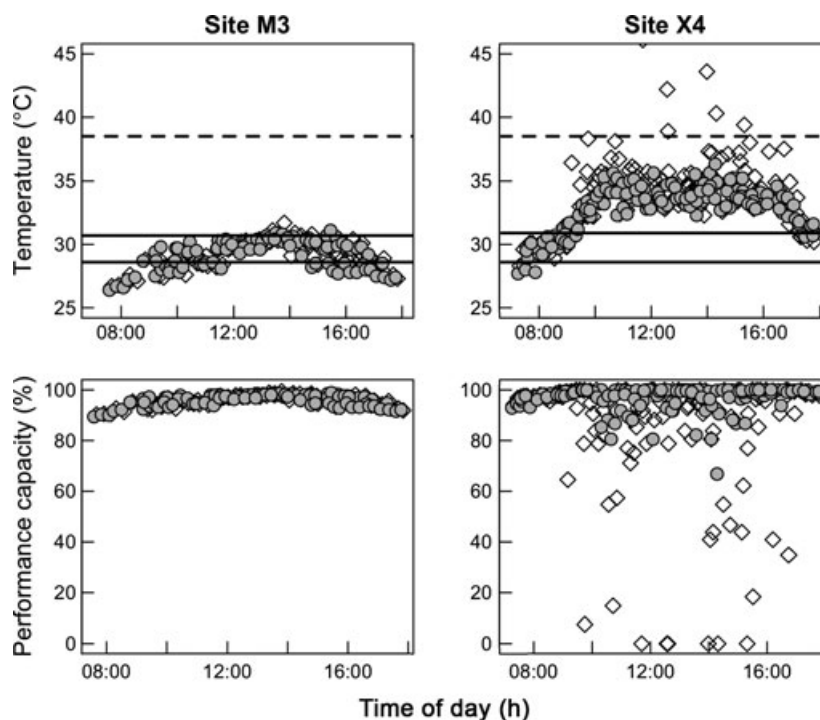


Fig. 3. Temperatures and estimated performance capacities for *Anolis cristatellus* (filled circles) and copper models (open diamonds) at one mesic and one xeric site in July and August. Dashed lines indicate the critical thermal maximum (CT_{max} ; Huey & Webster 1976). Solid lines encompass the preferred temperature range (Hertz, Huey & Stevenson 1993).

Combing data within habitat types, a 3 °C increase in T_a is predicted to impact the thermal suitability of each habitat type differently. In the xeric habitat thermal suitability is predicted to decrease, with the number of perch sites within 2 °C of CT_{max} increasing from 7% currently to 41%. In contrast, the thermal suitability of the mesic habitat is not predicted to change. We recorded no T_e values within 2 °C of CT_{max} in the current mesic habitat, and no T_e values are predicted to occur within 2 °C of CT_{max} with a 3 °C increase in T_a .

Finally, assuming a 3 °C increase in T_a , lizards in the xeric habitat are predicted to experience a decrease in mean performance capacity ranging from 26% to 32%, depending on the site (Fig. 4). In contrast, lizards in the mesic habitat are predicted to experience an increase in mean performance capacity ($\approx 3.5\%$) with the same increase in T_a (Fig. 4).

Discussion

We found that xeric and mesic habitats present two distinct thermal niches for *A. cristatellus* and that differences in thermoregulatory strategies between habitats are associated with differences in operative temperatures (T_e). Nevertheless, we found no difference in the thermal sensitivity of whole-organism performance (i.e. sprint speed) of *A. cristatellus* occupying these habitats (Fig. 2b). Furthermore, individuals from both habitats achieve high performance capacities under current conditions (Table 1); however, global warming is predicted to impact the performance capacities of mesic and xeric lizards differently.

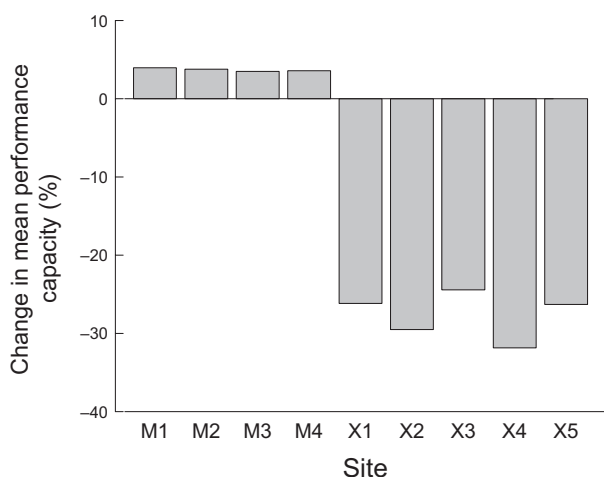
The mean T_e of the xeric habitat (33.4 °C) was 4.5 °C warmer than that of the mesic habitat (28.9 °C), and T_e s in the xeric habitat sometimes reached lethal temperatures, which we never observed in the mesic habitat. The difference between xeric and mesic habitats in T_e was also present across seasons (Table 1). Taken together these findings demonstrate that populations of *A. cristatellus* experience two distinct thermal niches, in which xeric habitats are significantly warmer than mesic habitats. Previous studies conducted throughout the Caribbean have also found that xeric and mesic habitats provide distinct thermal niches for lizards, including anoles and *Sphaerodactylus* (e.g. Ruibal 1961; Huey & Webster 1976; Hertz 1992a,b; Álvarez 1992; Knouft *et al.* 2006). In addition, mesic and xeric habitats on Puerto Rico have been shown to provide distinct physical environments with respect to hydric conditions (Gunderson, Siegel & Leal 2011) and spectral characteristics (Leal & Fleishman 2004).

The pattern observed in T_e was also present in T_b , but to a lesser degree because of behavioural thermoregulation by xeric lizards. On average, xeric lizards were 3.5 °C warmer than mesic lizards (Table 1). Additionally, mesic lizards were able to remain within their preferred temperature range for the majority of the day, whereas xeric lizards were unable to attain preferred temperatures for most of the day (Fig. 3, Fig. S2, also see Table S2, Supporting Information for mean temperature data binned by time of day). Although lizards from xeric and mesic sites had lower T_b s in December, xeric lizards remained significantly warmer than mesic lizards (Table 1). Therefore, we found that differences in T_b are

Table 2. Summary statistics evaluating the use of behavioural thermoregulation by *Anolis cristatellus* at nine sites across Puerto Rico

Month & Site	Bask _{lizards} (%)	Bask _{models} (%)	d_b	d_e	$d_e - d_b$	E
July–August						
M1	16	14	0.72	0.70	-0.02	-0.03
M2	14	8	0.69	0.60	-0.09	-0.14
M3	20	24	0.25	0.25	-0.01	-0.10
M4	13	10	0.55	0.47	-0.09	-0.19
Mesic combined	16	14	0.57	0.51	-0.06	-0.11
X1	31	48	1.86	2.71	0.85	0.31
X2	26	46	2.12	2.69	0.57	0.21
X3	14	32	1.77	2.59	0.82	0.32
X4	26	49	2.17	3.13	0.62	0.30
X5	15	36	1.86	2.27	0.41	0.18
Xeric combined	22	42	1.97	2.70	0.73	0.27
December						
M3	8	19	2.45	2.43	-0.03	-0.01
X4	37	42	1.00	1.31	0.30	0.23

Bask = frequency of observations in which over 25% of the body of the lizard (or copper model) was in direct sunlight, d_b = mean absolute deviation of lizard body temperatures from the preferred temperature range, d_e = mean absolute deviation of operative temperatures from the preferred temperature range, E = the effectiveness of behavioural thermoregulation ($1 - (d_b/d_e)$; Hertz, Huey & Stevenson 1993).

**Fig. 4.** Estimated impact of climate warming (i.e., a 3 °C increase in T_a) on mean performance capacity of *Anolis cristatellus* at nine sites across Puerto Rico. Mesic sites are designated with an ‘M’, xeric sites are designated with an ‘X’.

persistent across season, which is congruent with the results reported by Hertz (1992b).

Although mesic and xeric habitats present two distinct thermal regimes, lizards from both mesic and xeric habitats are able to achieve high physiological performance capacities (means over 90%). How is it that lizards with the same thermal sensitivity can share similarly high performance capacities despite living under distinct operative thermal

environments? Two factors can contribute to this finding: behavioural thermoregulation and the shape of the thermal sensitivity curve. Mesic lizards are thermoconformers, but xeric lizards behaviourally thermoregulate by seeking out the coolest available perch sites, thereby reducing the difference in the thermal conditions experienced by lizards in each habitat. If lizards in both habitats were thermoconformers, mean T_b s would be expected to differ by 4.5 °C, but instead differ by 3.5 °C. This pattern, known as the ‘Bogert Effect’, is commonly seen among populations occupying different climatic regions (Bogert 1949; Huey, Hertz & Sinervo 2003).

In addition, *A. cristatellus*, like most organisms (reviewed in Angilletta 2009), has a broad plateau of low thermal sensitivity at body temperatures below the optimal temperature for performance ($T_{opt} = 33.31$; Fig. 2b). Both mesic and xeric lizards experience mean T_b s below T_{opt} (Table 1) and thus the relatively large difference in T_b translates into a minor difference in physiological performance. The complex interactions between operative thermal environment, behaviour and thermal physiology underline the advantages of integrating all three of these factors when evaluating the thermal niche.

At the microhabitat level, the xeric habitat had greater variation in T_e than the mesic habitat (xeric T_e range = 21.5 °C; mesic T_e range = 8.5 °C; Fig. 3, Fig. S2, Supporting Information). A potential consequence of reduced thermal variation at mesic sites is an increase in the cost of behavioural thermoregulation, as perch sites that deviate substantially from the mean T_e are rare and require high energetic expenditures to occupy them (Huey 1974; Huey & Webster 1976; Huey & Slatkin 1976; but see Angilletta 2009 for a model of how the spatial distribution of available operative temperatures can influence thermoregulatory costs). The constraint placed on behavioural thermoregulation by low thermal variability within tropical forests has been suggested to increase the susceptibility of tropical lizards to climate warming (Huey *et al.* 2009). However, for populations of *A. cristatellus* inhabiting mesic forest, low thermal variability does not appear to pose a problem, as we predict that mesic lizards will experience a slight increase in physiological performance capacity with warming.

In contrast, the xeric habitat is more thermally variable, and thus, the cost of attaining body temperatures that deviate from the mean T_e is likely reduced. Xeric lizards do thermoregulate and, in doing so, increase their physiological performance capacity relative to a hypothetical thermoconformer (i.e. copper models) at the same site (Fig. 3, Table 1). However, we predict that *A. cristatellus* in the xeric habitat are more susceptible to climate warming than those in the mesic habitat. In the case of xeric populations, the thermal environment is already warm relative to their thermal sensitivity (Fig. 2, Table 1), a pattern predicted to be common for tropical lizards (Kearney, Shine & Porter 2009). Most likely in response to this relatively warm environment, *A. cristatellus* in the xeric habitat already utilize the coolest perches available during the warmest times of the day. Thus, behavioural thermoregulation may have limited potential to buffer xeric

lizards from increasing T_b s as environmental temperatures rise over the next century.

At present, *A. cristatellus* living in the xeric habitat have a warming tolerance that is 3.7 °C lower than the warming tolerance of lizards from the mesic habitat, and a 3 °C increase in T_a is predicted to decrease the thermal suitability of the xeric environment. In addition, xeric lizards are predicted to experience a decrease in physiological performance capacity of approximately 30% with a 3 °C increase in T_a . This drop in performance of xeric lizards would result from their body temperatures exceeding the optimal performance temperature, placing them on the steep slope on the right side of the asymmetrical sprint performance curve (Fig. 2b). As a consequence of changes in T_c and performance capacity, xeric lizards will likely be forced to be inactive in cool retreats for several hours a day, reducing rates of energy acquisition and possibly leading to population collapse (Dunham 1993; Huey *et al.* 2009; Sinervo *et al.* 2010). Furthermore, at some xeric sites, *A. cristatellus* is found sympatrically with *Anolis cooki*, a species that prefers warmer microhabitats and is more heat tolerant (Huey & Webster 1976; Hertz 1992b). These species use the same structural niche and compete for resources (Ortiz & Jenssen 1982), and thus increased inactivity of *A. cristatellus* might provide a competitive advantage to *A. cooki*.

It has been suggested that the negative effects of climate warming may be mitigated by shifts in phenology (e.g. Parmesan 2006; Bradshaw & Holzapfel 2008; Willis *et al.* 2008; Pau *et al.* 2011). For example, under climate warming periods that were previously unfavourable for activity (i.e. too cold) may become favourable, therefore buffering populations from decreased activity during times that become too warm. However, this mechanism of coping with warming is unlikely to buffer populations of *A. cristatellus* in xeric habitats, for two reasons. First, *A. cristatellus* is a diurnal lizard, and individuals are already active from sun-up to sun-down. Therefore, increasing temperatures are unlikely to affect daily start and end times for activity. Second, like many tropical organisms, *A. cristatellus* is reproductive year round (Gorman & Licht 1974). Thus, temperature change cannot affect start and end times of reproduction. In mesic habitats reproductive effort (measured as the % of females gravid in point estimates) remains high (> 65%) during the nine warmest months of the year and on average does not decrease below 30% during the coldest months (Gorman & Licht 1974). Although data for xeric *A. cristatellus* are limited, they appear to experience even less seasonal variation in reproductive effort (Gorman & Licht 1974).

The prognosis for mesic *A. cristatellus* is more positive. With a 3 °C increase in T_a , mesic lizards will still have a warming tolerance higher than the current value for xeric lizards, and the thermal suitability of the mesic habitat is not predicted to decline. In addition, because mesic lizards currently have T_b s that place them in the middle of the broad lower shoulder of the sprint performance curve (Fig. 2), a 3 °C increase in T_a is predicted to increase mean performance by approximately 3.5% (Fig. 4). Furthermore, contrary to

A. cristatellus in the xeric habitat, *A. cristatellus* in the mesic habitat are not sympatric with congeners that use the same structural niche but prefer a warmer thermal niche. If community composition stays the same, mesic *A. cristatellus* are not likely to face the potential for competitive exclusion under climate warming.

Our results reinforce the benefits of a mechanistic approach, in which physiological traits are considered in concert with operative thermal environments (Helmuth, Kingsolver & Carrington 2005; Kearney & Porter 2009). For example, our prediction that mesic and xeric *A. cristatellus* will be differentially affected by climate warming resulted from combining thermal sensitivity, body temperature and operative temperature data. In addition, we further demonstrate the advantage of direct measurements of the thermal environment and body temperatures (see also Gilman, Wethey & Helmuth 2006), as these allow one to elucidate variation in patterns of behavioural thermoregulation, which can be important for species persistence as thermal conditions change (Huey, Hertz & Sinervo 2003; Kearney, Shine & Porter 2009; Huey, Losos & Moritz 2010).

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References

- Adolph, S.C. (1990) Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology*, **71**, 315–327.
- Álvarez, H.J. (1992) *Thermal Characteristics of Sphaerodactylus Species in Puerto Rico and Their Implications for the Distribution of Species in Puerto Rico*. PhD Dissertation, University of Puerto Rico, Río Piedras.
- Angilletta, M.J. (2001) Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus undulatus*). *Ecology*, **82**, 3044–3056.
- Angilletta, M.J. (2009) *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford University Press, Oxford.
- Bennett, A.F. (1980) The thermal dependence of lizard behaviour. *Animal Behaviour*, **28**, 752–762.
- Blouin-Demers, G. & Weatherhead, P.J. (2001) Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. *Ecology*, **82**, 3025–3043.
- Bogert, C.M. (1949) Thermoregulation in reptiles, a factor in evolution. *Evolution*, **3**, 195–211.
- Bonebrake, T.C. & Mastrandrea, M.D. (2010) Tolerance adaptation and precipitation changes complicate latitudinal patterns of climate change impacts. *Proceedings of the National Academy of Sciences USA*, **107**, 12581–12586.
- Bradshaw, W.E. & Holzapfel, C.M. (2008) Genetic responses to rapid climate change: it's seasonal timing that matters. *Molecular Ecology*, **17**, 157–166.

- Brandeis, T.J., Helmer, E.H., Marcano-Vega, H. & Lugo, A.E. (2009) Climate shapes the novel plant communities that form after deforestation in Puerto Rico and the U.S. Virgin Islands. *Forest Ecology and Management*, **258**, 1704–1718.
- Buckley, L.B. (2008) Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. *The American Naturalist*, **171**, E1–E19.
- Buckley, L.B., Urban, M.C., Angilletta, M.J., Crozier, L.G., Rissler, L.J. & Sears, M.W. (2010) Can mechanism inform species' distribution models? *Ecology Letters*, **13**, 1041–1054.
- Chown, S.L. & Terblanche, J.S. (2007) Physiological diversity in insects: ecological and evolutionary contexts. *Advances in Insect Physiology*, **33**, 50–152.
- Christensen, J.H., Hewitson, B., Busuioac, A., Chen, A., Gao, X., Held, I., Jones, R., Kolli, R.K., Kwon, W.-T., Laprise, R., Magaña Rueda, V., Mearns, L., Menéndez, C.G., Räisänen, J., Rinke, A., Sarr, A. & Whetton, P. (2007) Regional climate projections. *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor & H.L. Miller), pp. 847–940. Cambridge University Press, Cambridge.
- Christian, K.A. & Weavers, B.W. (1996) Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. *Ecological Monographs*, **66**, 139–157.
- Clusella-Trullas, S., Blackburn, T.M. & Chown, S.L. (2011) Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. *The American Naturalist*, **177**, 738–751.
- Crowley, S.R. (1985) Thermal sensitivity of sprint-running in the lizard *Sceloporus undulatus*: support for a conservative view of thermal physiology. *Oecologia*, **66**, 219–225.
- Daly, C., Helmer, E.H. & Quiñones, M. (2003) Mapping the climate of Puerto Rico, Viequez and Culebra. *International Journal of Climatology*, **23**, 1359–1381.
- Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. & Martin, P.R. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences USA*, **105**, 6668–6672.
- Dillon, M.E., Wang, G. & Huey, R.B. (2010) Global metabolic impacts of recent climate warming. *Nature*, **467**, 704–707.
- Duarte, H., Tejedó, M., Katzenberger, M., Marangoni, F., Baldo, D., Beltrán, J.F., Martí, D.A., Richter-Boix, A. & Gonzalez-Voyer, A. (2012) Can amphibians take the heat? Vulnerability to climate warming in sub-tropical and temperate larval amphibian communities. *Global Change Biology*, **18**, 412–421.
- Dunham, A.E. (1993) Population responses to environmental change: operative environments, physiologically structured models, and population dynamics. *Biotic Interactions and Global Change* (eds P.M. Kareiva, J.G. Kingsolver & R.B. Huey), pp. 95–119. Sinauer Associates, Sunderland, Massachusetts, USA.
- Dunham, A.E., Grant, B.W. & Overall, K.L. (1989) Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. *Physiological Zoology*, **62**, 335–355.
- Ewel, J.J. & Whitmore, J.L. (1973) The ecological life zones of Puerto Rico and the U.S. Virgin Islands. Forest Service Research Paper ITF-18, U.S. Department of Agriculture.
- Freidenburg, L.K. & Skelly, D.K. (2004) Microgeographical variation in thermal preference by an amphibian. *Ecology Letters*, **7**, 369–373.
- Gates, D.M. (1980) *Biophysical Ecology*. Dover Publication Inc., New York.
- Gilman, S.E., Wethey, D.S. & Helmuth, B. (2006) Variation in the sensitivity of organismal body temperature to climate change over local and geographic scales. *Proceedings of the National Academy of Sciences USA*, **103**, 9560–9565.
- Gorman, G.C. & Licht, P. (1974) Seasonality in ovarian cycles among tropical *Anolis* lizards. *Ecology*, **55**, 360–369.
- Gunderson, A.R., Siegel, J. & Leal, M. (2011) Tests of the contribution of acclimation to geographic variation in water loss rates of the West Indian lizard *Anolis cristatellus*. *Journal of Comparative Physiology B*, **181**, 965–972.
- Heatwole, H. (1976) Herpetogeography of Puerto Rico VII. Geographic variation in the *Anolis cristatellus* complex in Puerto Rico and the Virgin Islands. *Occasional Papers of the Museum of Natural History University of Kansas*, **46**, 1–18.
- Helmuth, B., Kingsolver, J.G. & Carrington, E. (2005) Biophysics, physiological ecology, and climate change: does mechanism matter? *Annual Review of Physiology*, **67**, 177–201.
- Helmuth, B., Broitman, B.R., Yamane, L., Gilman, S.E., Mach, K., Mislan, K.A.S. & Denny, M.W. (2010) Organismal climatology: analyzing environmental variables at scales relevant to physiological stress. *Journal of Experimental Biology*, **213**, 995–1003.
- Hertz, P.E. (1992a) Temperature regulation in Puerto Rican *Anolis* lizards: a field test using null hypotheses. *Ecology*, **73**, 1405–1417.
- Hertz, P.E. (1992b) Evaluating thermal resource partitioning by sympatric lizards *Anolis cooki* and *A. cristatellus*: a field test using null hypotheses. *Oecologia*, **90**, 127–136.
- Hertz, P.E., Huey, R.B. & Stevenson, R.D. (1993) Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *The American Naturalist*, **142**, 796–818.
- Huey, R.B. (1974) Behavioral thermoregulation in lizards: importance of associated costs. *Science*, **184**, 1001–1003.
- Huey, R.B. (1983) Natural variation in body temperature and physiological performance in a lizard (*Anolis cristatellus*). *Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams* (eds A.G.J. Rhodin & K. Miyata), pp. 484–490. Museum of Comparative Zoology, Cambridge, Massachusetts, USA.
- Huey, R.B., Hertz, P.E. & Sinervo, B. (2003) Behavioral drive versus behavioral inertia in evolution: a null model approach. *The American Naturalist*, **161**, 357–366.
- Huey, R.B., Losos, J.B. & Moritz, C. (2010) Are lizards toast? *Science*, **328**, 832–833.
- Huey, R.B. & Slatkin, M. (1976) Cost and benefits of lizard thermoregulation. *The Quarterly Review of Biology*, **51**, 363–384.
- Huey, R.B. & Stevenson, R.D. (1979) Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *American Zoologist*, **19**, 357–366.
- Huey, R.B. & Webster, T.P. (1976) Thermal biology of *Anolis* lizards in a complex fauna: the *cristatellus* group on Puerto Rico. *Ecology*, **57**, 985–994.
- Huey, R.B., Deutsch, C.A., Tewksbury, J.J., Vitt, L.J., Hertz, P.E., Álvarez-Pérez, H.J. & Garland Jr, T. (2009) Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society of London. Series B*, **276**, 1939–1948.
- Husak, J.F. (2006) Does speed help you survive? A test with Collard lizards of different ages. *Functional Ecology*, **20**, 174–179.
- IPCC (2007) *Climate Change 2007. The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.
- Irschick, D.J., Meyers, J.J., Husak, J.F. & Le Galliard, J.-F. (2008) How does selection operate on whole-organism functional performance capacities? A review and synthesis *Evolutionary Ecology Research*, **10**, 177–196.
- Janzen, D.H. (1967) Why mountain passes are higher in the tropics. *The American Naturalist*, **101**, 233–249.
- Kearney, M. & Porter, W. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, **12**, 334–350.
- Kearney, M., Shine, R. & Porter, W.P. (2009) The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proceedings of the National Academy of Sciences USA*, **106**, 3835–3840.
- Kearney, M., Phillips, B.L., Tracy, C.R., Christian, K.A., Betts, G. & Porter, W.P. (2008) Modelling species distributions without using species distributions: the cane toad in Australia under current and future climates. *Ecography*, **31**, 423–434.
- Kingsolver, J.G. (1983) Ecological significance of flight activity in *Colias* butterflies: implications for reproductive strategy and population structure. *Ecology*, **64**, 546–551.
- Knouft, J.H., Losos, J.B., Glor, R.E. & Kolbe, J.J. (2006) Phylogenetic analysis of the evolution of the niche in lizards of the *Anolis sagrei* group. *Ecology*, **87**, S29–S38.
- Leal, M. & Fleishman, L.J. (2004) Differences in visual signal design and detectability between allopatric populations of *Anolis* lizards. *The American Naturalist*, **163**, 26–39.
- Ortiz, P.R. & Janssen, T.A. (1982) Interspecific aggression between lizard competitors, *Anolis cooki* and *Anolis cristatellus*. *Zeitschrift für Tierpsychologie*, **60**, 227–238.
- Parnesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.
- Pau, S., Wolkovich, E.M., Cook, B.I., Davies, T.J., Kraft, N.J.B., Bolmgren, K., Betancourt, J.L. & Cleland, E.E. (2011) Predicting phenology by integrating ecology, evolution, and climate science. *Global Change Biology*, **17**, 3633–3643.
- Porter, W.P. & Gates, D.M. (1969) Thermodynamic equilibria of animals with environment. *Ecological Monographs*, **39**, 227–244.
- R Development Core Team. (2009) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.

- Rand, A.S. (1964) Ecological distribution in anoline lizards of Puerto Rico. *Ecology*, **45**, 745–752.
- Ruibal, R. (1961) Thermal relations of five species of tropical lizards. *Evolution*, **15**, 98–111.
- Sears, M.W., Raskin, E. & Angilletta, M.J. (2011) The world is not flat: defining relevant thermal landscapes in the context of climate change. *Integrative and Comparative Biology*, **51**, 666–675.
- Sinervo, B., Méndez-de-la-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M.L., Meza-Lázaro, R.N., Gadsden, H., Avila, L.J., Morando, M., de la Riva, I.J., Sepulveda, P.V., Rocha, C.F.D., Ibañgüengoytia, N., Puntriano, C.A., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J. & Sites Jr, J.W. (2010) Erosion of lizard diversity by climate change and altered thermal niches. *Science*, **328**, 894–899.
- Van Damme, R., Bauwens, D. & Verheyen, R.F. (1990) Evolutionary rigidity of thermal physiology: the case of the cool temperate lizard *Lacerta vivipara*. *Oikos*, **57**, 61–67.
- Whitlock, M.C. & Schluter, D. (2009) *The Analysis of Biological Data*. Roberts and Company, Greenwood Village, Colorado, USA.
- Willett, C.S. (2010) Potential fitness trade-offs for thermal tolerance in the intertidal copepod *Tigriopus californicus*. *Evolution*, **64**, 2521–2534.
- Willis, C.G., Ruhfel, B., Primack, R.B., Miller-Rushing, A.J. & Davis, C.C. (2008) Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of the National Academy of Sciences USA*, **105**, 17029–17033.

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Supporting Information

Additional supporting material may be found in the online version of this article.

Fig. S1. Map of Puerto Rico indicating the location of the nine sites sampled in this study.

Fig. S2. Temperatures of lizards and copper models at each site during July and August.

Fig. S3. Estimated performance capacity of *A. cristatellus* and copper models throughout the day at each site in July and August.

Fig. S4. Temperature and performance data for lizards and copper models in December.

Table S1. Mean snout-to-vent length, by sex, of *A. cristatellus* sampled for body temperature at each site.

Table S2. Summary of the body temperatures of *A. cristatellus* at each of the sites in July and August throughout the day.

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