

The impact of climate change measured at relevant spatial scales: new hope for tropical lizards

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Abstract

Much attention has been given to recent predictions that widespread extinctions of tropical ectotherms, and tropical forest lizards in particular, will result from anthropogenic climate change. Most of these predictions, however, are based on environmental temperature data measured at a maximum resolution of 1 km², whereas individuals of most species experience thermal variation on a much finer scale. To address this disconnect, we combined thermal performance curves for five populations of *Anolis* lizard from the Bay Islands of Honduras with high-resolution temperature distributions generated from physical models. Previous research has suggested that open-habitat species are likely to invade forest habitat and drive forest species to extinction. We test this hypothesis, and compare the vulnerabilities of closely related, but allopatric, forest species. Our data suggest that the open-habitat populations we studied will not invade forest habitat and may actually benefit from predicted warming for many decades. Conversely, one of the forest species we studied should experience reduced activity time as a result of warming, while two others are unlikely to experience a significant decline in performance. Our results suggest that global-scale predictions generated using low-resolution temperature data may overestimate the vulnerability of many tropical ectotherms to climate change.

Keywords: *Anolis*, Bay Islands, Cayos Cochinos, *Norops*, thermal performance curve, thermoregulation

Received 25 March 2013 and accepted 25 April 2013

Introduction

Global air temperatures are predicted to rise by as much as 5 °C over the next century (IPCC, 2007), and this has led to numerous dire predictions for the planet's fauna and flora. However, these predictions are not uniformly bleak across latitude. Historically, models have suggested that major shifts in range or phenology would be most dramatic for temperate species (Root *et al.*, 2003; Parmesan, 2007). These predictions were not necessarily surprising as the greatest increases in temperature are expected to occur at temperate latitudes (IPCC, 2007). More recently, however, researchers have begun to apply a mechanistic approach to the study of climate change-responses (Kearney & Porter, 2004; Tewksbury *et al.*, 2008; Kearney *et al.*, 2009a,b; Buckley *et al.*, 2010). This approach, based on the thermal physiology of individuals and populations, has led to a reversal in latitude-based predictions for the response to climate change (Deutsch *et al.*, 2008). Evidence is now mounting that tropical ectotherms will be the hardest hit from warming, and studies have warned that tropical forest lizards, in par-

particular, are in danger of extinction (Tewksbury *et al.*, 2008; Huey *et al.*, 2009, 2012).

Several recent studies have used data from lizards and other tropical ectotherms to predict global extinctions of tropical forest lizards driven by climate change (Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008; Huey & Tewksbury, 2009; Huey *et al.*, 2009, 2012; Kearney *et al.*, 2009a,b; Bonebrake & Mastrandrea, 2010; Dillon *et al.*, 2010; Sinervo *et al.*, 2010; Urban *et al.*, 2012). Because tropical forest lizards are thought to have evolved in an environment that is thermally homogeneous in both space and time, they are assumed to be 'thermal specialists' that cannot withstand even small increases in ambient temperature (relative to organisms at more temperate latitudes). Moreover, tropical forests represent the coolest part of the tropical landscape, and lizards already living in this environment may therefore have nowhere to go to escape warming. For example, Huey *et al.* (2009) suggested that open-habitat lizards in the tropics may invade forest habitat as forest temperatures approach their preferred range. One result of this 'invasion hypothesis' could be competitive exclusion of forest lizards, who are themselves already experiencing reduced performance due to warming alone.

Making global predictions regarding responses to climate change requires the use of temperature data

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collected on a broad geographic scale. However, owing to current technological constraints, these data are only available at a maximum resolution of about 1 km², whereas the vast majority of ectotherms experience variation in temperature at a much smaller scale (often less than 5 m²; Barlett & Gates, 1967; Sears *et al.*, 2011). Moreover, global predictions use ambient temperature data gathered from weather stations, but the body temperatures of ectotherms result from a complex interplay among many biophysical parameters (including convection, conduction, and radiation) and thus consistently deviate from ambient conditions (Bakken, 1992). As such, a clear understanding of the response of ectotherms to climate change will depend critically on the fine-scale spatial and temporal structure of their thermal environments, and measurements of operative temperature (T_e) that reflect the physics of heat transfer into and out of living organisms. In other words, accurate climate change forecasts will require biologically relevant measures of thermal heterogeneity.

Here, we integrate data on lizard physiology with fine-scale measures of the thermal environment generated from species-specific physical models to estimate how a predicted 3 °C rise in ambient temperature will affect physiological performance. Our study focuses on four species of *Anolis* lizard (*Anolis lemurinus*, *Anolis bicaorum*, and *Anolis roatanensis*, three closely related forest species, and *A. allisoni*, an open-habitat species) from the Bay Islands of Honduras. While *A. lemurinus* and *A. allisoni* are found in other regions of the New World tropics, *A. bicaorum* and *A. roatanensis* are endemic to the islands of Utila and Roatan, respectively. We hypothesized that differences in thermal heterogeneity among islands and habitat types would translate into differences in thermal physiology among species, which would in turn lead to variation in their predicted responses to climate change. We discuss our results in terms of the 'invasion hypothesis' that Huey *et al.* (2009) proposed would play out in regions containing both open-habitat and forest species.

Materials and methods

Study site and sampling timeline

The islands of Cayo Menor, Utila, and Roatan are separated by less than 42 km, but differ dramatically in topography. Whereas Utila is extremely flat and almost entirely at sea level (with one small hill located in the northeastern corner of the island), Cayo Menor and Roatan are composed of numerous valleys, steep slopes, and ridges. On the tiny island of Cayo Menor, for example, the only flat land is represented by beaches around the perimeter of the island.

Lizards were captured on Cayo Menor from June to August of 2008, 2010, and 2011, on Utila from June to July of 2010 and

2011, and on Roatan from June to July, 2012. Only adults were included in analyses. Field-active body temperatures (T_b) were collected during all years, and operative temperatures (T_e) were collected during 2010 and 2011 for lizards from Cayo Menor and Utila, and during 2012 for lizards from Roatan. Thermal performance data were collected during 2010 for populations on Cayo Menor and Utila, and during 2012 for populations on Roatan. Lizards were captured by noosing or by hand, and were toe-clipped for individual identification prior to their release. Individuals were never kept in captivity for longer than 48 h, and all were released at their precise spot of capture.

Thermal physiology

Lizard field-active body temperatures (T_b s) were collected by hand immediately after capture using an Omega[®] (Stamford, CT, USA) type-K thermocouple thermometer (inserted into the cloaca). We compared T_b among populations (pooled across all individuals captured between 0700 and 1700 h) using an ANOVA with a Tukey's post hoc comparison.

On Cayo Menor and Utila, all lizards were taken back to a field station and a subset of eight individuals (four males and four females) were chosen randomly from each day's capture effort to construct thermal performance curves (TPCs). On Roatan, we constructed TPCs from all captured individuals. We gauged physiological performance by measuring maximum running speed, a trait known to be ecologically important for anoles and other lizards (Van Berkum, 1986; Husak & Fox, 2006; Calsbeek & Irschick, 2007). Running speed is the cumulative result of myriad underlying physiological processes and therefore reflects whole-organism physiological performance (Angilletta, 2009). After capture in the field, lizards were given 24 h to fast in the lab prior to physiological trials. Immediately (<5 min) before each running speed trial, lizards were heated or cooled to six different temperatures spanning their tolerance ranges (*A. lemurinus*, *A. bicaorum*, and *A. roatanensis* to 19, 22, 25, 28, 31, and 33 °C; *A. allisoni* to 19, 22, 26, 30, 33, and 36 °C) using a field-portable incubator. The order of body temperatures was chosen at random for each individual, and they were run once at each temperature. We verified that each lizard had achieved its target T_b using an Omega[®] type-K cloacal thermometer, and then motivated it to run along a wooden dowel rod (2.5 cm diameter with 10 cm graduations). The dowel rod was inclined at 20° to discourage lizards from hopping. Trials were filmed at 60 fps using a digital video camera. If we were not able to obtain a suitable run (where the lizard did not fall off the dowel rod or spin around to the other side) before 30 s had elapsed, we did not include the trial in further analyses. Lizards were given a minimum of 1 h resting time between trials at different temperatures. Between trials, lizards were maintained in ventilated, quart-sized plastic containers, isolated from one another, and kept in a room with minimal foot traffic (to create a low-stress environment). Ambient temperature in the room ranged from 24 to 28 °C. Lizards were not fed in captivity, but were given drinking water *ad libitum* using a spray bottle.

For each individual, maximal running speed over 10 cm at each temperature was estimated using frame-by-frame

analysis in the software program Eagle Eye ProViewer. Due to failed trials, sample sizes varied among temperatures and species. Sample sizes for each temperature (in order of increasing temperature) were 22, 27, 28, 29, 30, and 31 for *A. lemurinus*, 15, 28, 30, 34, 35, and 38 for *A. bicaorum*, 23, 16, 19, 19, 22, and 22 for *A. roatanensis*, 38, 33, 37, 39, 37, and 35 for *A. allisoni* on Cayo Menor, and 21, 20, 21, 20, 20, and 21 for *A. allisoni* on Roatan.

To construct TPCs, we fit the raw performance data to a set of 25 asymmetrical 'peak' functions (chosen based on the typical structure of TPCs, see 'Response to climate change' below) built into the statistical program TableCurve 2.0 (Angilletta, 2006). We then selected the best fit among these functions using Akaike's Information Criterion (AIC). Specifically, curve fits that differed in their AIC score by more than two ($\Delta\text{AIC} > 2$) were considered significantly different from one another (Burnham & Anderson, 2002; Angilletta, 2006). Functions that did not differ in AIC score were differentiated by their respective r^2 values. Using the assigned functions (Table S1, Supporting information), we then extracted the optimal temperature for performance (T_o), maximal performance (P_{max}), the critical thermal maximum (CT_{max} ; the upper temperature at which performance drops to zero), and the 80% and 95% performance breadths (B_{80} and B_{95} , respectively; the range of temperatures at which lizards can perform at 80% or 95% of P_{max}) for each species (Angilletta, 2009).

Operative temperatures

Operative temperature models (OTMs) were designed to have high conductivity of heat and thus rapidly equilibrate to thermal conditions in each habitat (Bakken, 1992; Angilletta, 2009). They were constructed from type-M (thin-walled) copper piping cut to the mean length of adults of each species (6 cm for *A. lemurinus*, *A. bicaorum*, and *A. roatanensis*, and 8 cm for *A. allisoni*; Dzialowski, 2005). Models were painted to match the color hue of each species, and we therefore assumed that they approximated the appropriate photospectrum absorbances. Ibutton™ (Embedded Data Systems, Lawrenceburg, KY, USA) temperature loggers were suspended in non conductive acrylic mesh inside of each model, and recorded temperatures every 10 min in 2010 and every 15 min in 2011 and 2012.

Operative temperature models were deployed at 425 randomized locations along fifteen 50 m transects that were haphazardly distributed in typical habitat for each species (ca. 30 OTMs per transect; Table S2, Supporting information). Transect locations on Cayo Menor and Utila were chosen to maximize coverage of each habitat type. Given the small total area of Cayo Menor (0.64 km²) and suitable *A. bicaorum* habitat on Utila (ca. 1.5 km² on the eastern edge of the island), OTM transects covered a substantial portion of the habitat that is likely to be used by anoles on each island. The island of Roatan was too large for comprehensive coverage by our OTMs. We therefore deployed our transects in typical habitat and in known areas of occurrence for each species. Along each transect, models were placed by randomly selecting an orthogonal distance from the transect (0, 1, 2, or 3 m), and height in the vegetation (0.5, 1, 2, or 3 m). In forest habitat on Cayo Menor, Utila, and Roatan, OTMs were deployed for a total of 62, 38,

and 21 days, respectively. In open habitat on Cayo Menor and Roatan, OTMs were deployed for a total of 62 and 21 days, respectively. This intensive sampling effort produced more than 49 000 OTM-hours in forest habitat and more than 35 000 OTM-hours in open habitat. Our 3-year T_e data set consisted of more than 380 000 individual temperature measurements.

For all analyses involving T_e data, we averaged the temperatures logged by each OTM for each hour period of the day between 600 and 1800 h across the study period, and then averaged those values to get an average temperature for each model. To examine variation in temporal T_e distributions, we computed the average number of hours each OTM took to reach its average peak temperature, and then compared the heating rate and maximum T_e among islands and habitat types using ANOVA. To detect differences in the spatial heterogeneity of T_e distributions, we compared their variances using Levene's test.

Response to climate change

Changes in distributions of T_e as a result of climate change have been proposed as a mechanism that may drive lizard populations to extinction (Sinervo *et al.*, 2010; Huey *et al.*, 2012). One means by which this may occur is through a reduction in the number of hours during the day that a lizard can remain active (Grant & Dunham, 1988; Sinervo *et al.*, 2010). As temperatures rise and performance declines, lizards are forced into shaded refuges. This constrains opportunities for foraging and mating, both of which ultimately reduce population growth (Dunham, 1993). With this in mind, we modeled changes in the temporal availability of optimal temperatures by projecting a 3 °C increase in T_e onto the mean diel T_e range (taken from hourly means pooled across all OTMs) in the year 2012. Our temperature projections were based on the IPCC (2007) prediction of a 3 °C increase in ambient temperature by the year 2100 for the Caribbean. Thus, we assumed that T_e scales linearly with ambient temperature (Gunderson & Leal, 2012).

Warming could also affect lizards by reducing the frequency of optimal T_e s at any given time of the day (reducing the total amount of habitat available to the population or the percentage of a lizard's territory that could be used effectively). We therefore projected the change in the proportion of T_e s falling within the performance breadth of each species as a function of time of day in the year 2100. Finally, we calculated two indices of vulnerability to climate warming, the 'thermal safety margin' and 'warming tolerance', for each species (Deutsch *et al.*, 2008). The thermal safety margin is the difference between T_o and mean T_e . Because thermal performance curves follow a typical shape whereby performance increases with temperature to an optimum, and then falls off precipitously beyond that optimum (Martin & Huey, 2008), the thermal safety margin gives the change in T_e that can be tolerated by a species before this rapid drop in performance is likely to occur. Warming tolerance is the difference between CT_{max} and mean T_e , and therefore gives the change in T_e that can occur before performance drops to zero—the equivalent of extinction.

Results

T_e distributions

Mean T_e was 28.1 °C (± 0.08 SEM), 29.1 °C (± 0.05 SEM), 28.4 (± 0.06 SEM), 29.9 °C (± 0.06 SEM), and 29.8 °C (± 0.13 SEM) for forest on Cayo Menor, forest on Utila, forest on Roatan, open habitat on Cayo Menor, and open habitat on Roatan, respectively. Mean T_e of forest habitat differed significantly among islands and from open habitat (ANOVA with Tukey's post hoc comparisons; $F_{4,420} = 125.352$, $P < 0.001$); however, open habitat on Cayo Menor and Roatan did not differ significantly from one another ($F_{4,420} = 125.352$, $P = 0.832$).

Temporal distributions of T_e also differed among islands and habitat types (Fig. 1). On Cayo Menor, individual OTMs in open-habitat achieved their peak T_e s at a faster rate in the morning compared to forest OTMs (ANOVA; $F_{4,420} = 61.364$, $P < 0.001$). Averaged across all OTMs for each hour of the day, open habitat on Cayo Menor reached peak T_e (31.9 °C) by 1000 h (an average increase of 1.2 °C per hour), while forest on Cayo Menor reached average peak T_e (29.3 °C) by 1300 h (an average increase of 0.5 °C per hour). On Roatan, individual OTMs in forest habitat achieved their peak T_e s at a faster rate in the morning than they did in open habitat (ANOVA; $F_{4,420} = 61.364$, $P = 0.003$). However, when averaged across all OTMs for each hour of the day, peak T_e on Roatan was higher in open habitat. Thus, peak T_e (31.6 °C) occurred by 1300 h (an average increase of 0.7 °C per hour) while in forest habitat, peak T_e (29.4 °C) occurred by 1100 h (an average increase of 0.6 °C per hour). Among habitat types, individual OTMs achieved their peak T_e s at a faster rate in open habitat than in forest habitat (ANOVA with Tukey's post hoc comparisons; $F_{4,420} = 125.517$, $P < 0.001$). Among

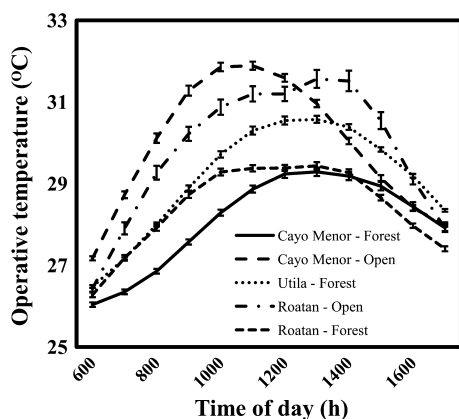


Fig. 1 Temporal T_e distributions among islands and habitat types. The data displayed are means across all OTMs for each 1-h interval from 0600 to 1800 in typical habitat for each population. Data from all years are pooled. Error bars represent SE.

islands, individual OTMs in forest habitat on Roatan achieved their peak T_e s significantly faster (ANOVA with Tukey's post hoc comparisons; $F_{4,420} = 61.364$, $P < 0.001$) than OTMs in forest habitat on Utila or Cayo Menor (which reached peak T_e s at similar rates: ANOVA; $F_{1,198} = 0.000$, $P = 0.987$). However, averaged across all OTMs for each hour of the day, forest on Utila reached a peak temperature of 30.6 °C by 1300 h (an average increase of 0.6 °C per hour), which is similar to the average rates for forest habitat on both Roatan and Cayo Menor.

Spatial variance in T_e differed among islands, as well as between habitat types within islands (Levene's test for equality of variances, $F_{4,420} = 9.016$, $P < 0.001$). In general, forest on Cayo Menor and open habitat on Roatan had the broadest (most variable) T_e frequency distributions, while forest on Utila and Roatan had the narrowest distributions (Fig. 2). Moreover, T_e distributions for transects deployed in forest habitat on Cayo Menor overlapped minimally (transect means ranged from 26.9 to 29.1 °C), whereas those on Utila overlapped greatly (transect means ranged from 28.5 to 29.4 °C).

Thermal physiology

Body temperatures differed significantly between forest and open-habitat species, and open-habitat populations differed significantly from one another (ANOVA with Tukey's post hoc comparisons; $F_{4,449} = 98.235$, $P < 0.001$; Means of 28.8 [± 0.09 SEM], 29.9 [± 0.11 SEM], 29.3 [± 0.16 SEM], 31.2 [± 0.22 SEM], and 34.2 [± 0.44 SEM] for *A. lemurinus* [$N = 202$], *A. bicaorum* [$N = 142$], *A. roatanensis* [$N = 23$], *A. allisoni* from Cayo Menor [$N = 66$], and *A. allisoni* from Roatan [$N = 21$], respectively). Among forest species, *A. lemurinus* had a significantly lower mean T_b than *A. bicaorum*, but neither differed significantly from *A. roatanensis*.

Populations also appeared to differ in the characteristic values that describe the shape of their TPCs. *A. allisoni* from Cayo Menor had the greatest P_{max} , *A. roatanensis* had the broadest performance breadth (for both B_{80} and B_{95}), and *A. allisoni* from Roatan had the highest T_o and CT_{max} (Table 1).

Response to climate change

The warming tolerances (range = 7.8–3.1) and thermal safety margins (range = 5.5–1.5) differed substantially among populations (Table 2). *A. bicaorum* had the lowest warming tolerance, while *A. lemurinus* had the lowest thermal safety margin.

The time available for activity near maximum performance is predicted to be substantially reduced

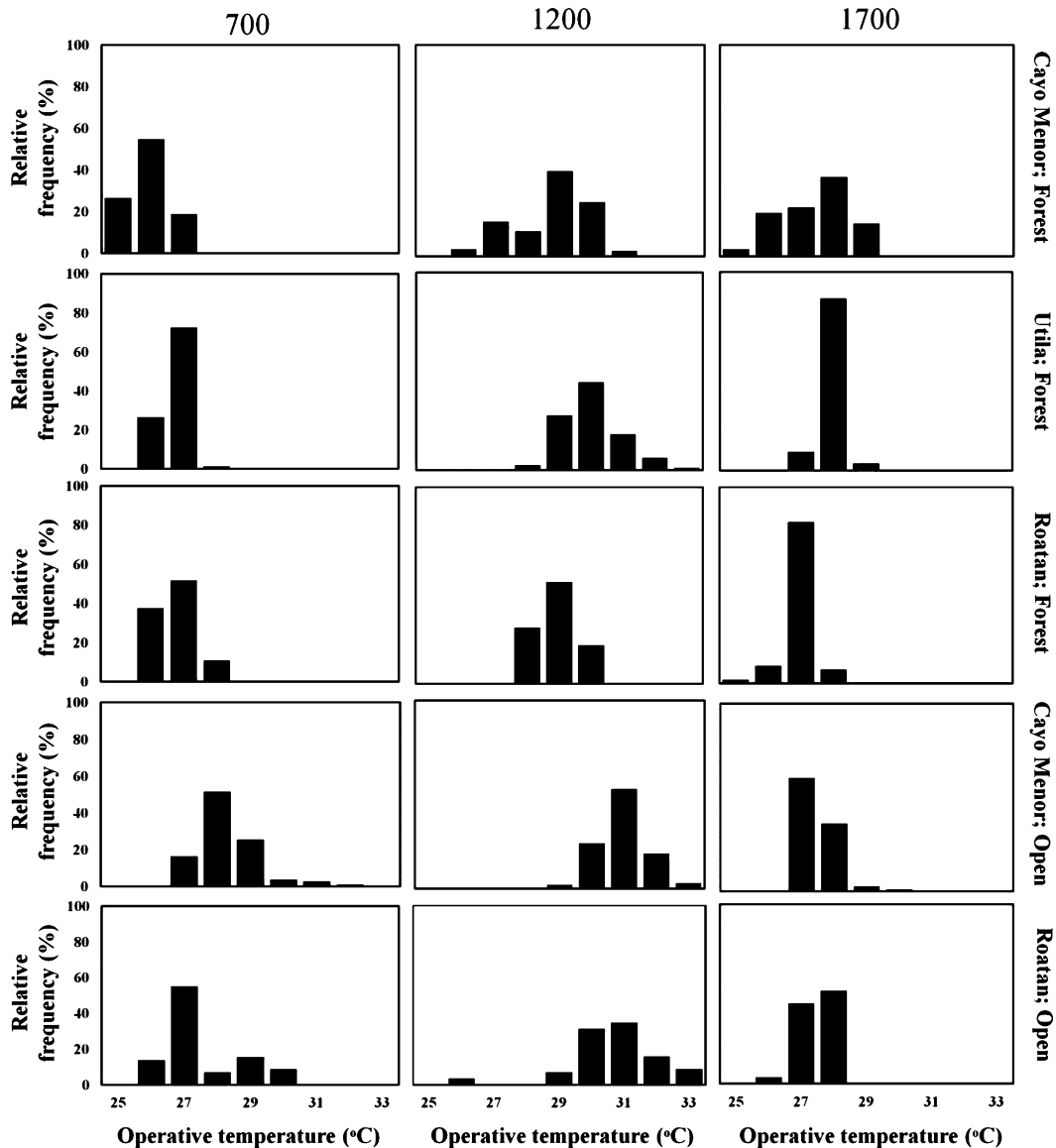


Fig. 2 Frequency distributions for T_e among islands and habitat types. Each observation represents the mean temperature logged by an OTM during a particular time interval (0700–0800, 1200–1300, or 1700–1800) averaged across the entire study period. Data from all transects in each habitat type are pooled.

for *A. lemurinus*, slightly reduced for *A. bicaorum*, and to stay the same or increase for *A. roatanensis* and both populations of *A. allisoni* (Table 3, Fig. 3). For *A. lemurinus*, in 2012, mean T_e over the entire day fell within their B_{80} , and T_{es} fell within B_{95} between the morning hours of 600 and 1100 and the late afternoon hours of 1600 and 1800. However, in 2100, mean T_e will rise above the upper bound of B_{80} during the afternoon (1100–1500), and T_{es} within B_{95} will shift to the morning (600–1000) and evening (1700–1800) hours. For *A. bicaorum*, mean hourly T_e falls within B_{80} for the majority of the day (800–1800) in 2012, but warming will reduce the total number of hours falling within B_{80}

and shift them to the morning (600–1000) and late afternoon (1600–1800) in the year 2100. Conversely, warming will not reduce the number of hours falling within B_{95} for *A. bicaorum*, but will simply shift them to earlier (800–1000) and later (1600–1800) in the day. In contrast to the forest species *A. lemurinus* and *A. bicaorum*, warming will not change the number of hours during the day providing near-optimal T_{es} for the forest species *A. roatanensis*, and will actually increase the number of hours during the day when mean T_e falls within both B_{80} and B_{95} for both populations of the open-habitat species *A. allisoni*. At present, in open-habitat on Cayo Menor, mean T_e falls within the B_{80} of

Table 1 The characteristic values that describe the shape of the thermal performance curves for each population. Values were extracted from asymmetrical peak functions fit to raw running speed data using the statistical program TableCurve 2.0. The best fit equation for each species was chosen using AIC criteria

Species	T _o (°C)	P _{max} (m s ⁻¹)	B ₈₀ (°C)	B ₉₅ (°C)	CT _{max} (°C)
<i>Anolis lemurinus</i>	29.6	0.72	24.8–31.7	27.7–30.9	33.6
<i>Anolis bicaorum</i>	31.6	0.77	27.8–32.6	30.3–32.2	33.2
<i>Anolis roatanensis</i>	31.8	0.73	21.4–33.0	22.9–32.9	33.9
<i>Anolis allisoni</i> (Roatan)	35.3	0.59	28.8–36.4	33.3–36.0	37.6
<i>Anolis allisoni</i> (CM)	33.9	0.88	29.6–35.3	32.6–34.7	37.4

Table 2 Warming tolerance and thermal safety margins for each population. Warming tolerances were calculated as the difference between CT_{max} and mean T_e. Thermal safety margins were calculated as the difference between T_o and mean T_e

Species	Warming tolerance (°C)	Thermal safety margin (°C)
<i>Anolis lemurinus</i>	5.5	1.5
<i>Anolis bicaorum</i>	3.1	2.5
<i>Anolis roatanensis</i>	5.5	3.4
<i>Anolis allisoni</i> (Roatan)	7.8	5.5
<i>Anolis allisoni</i> (CM)	7.5	4.0

Table 3 The projected change in the number of daylight hours when mean T_e falls within B₈₀ and B₉₅ (first two data columns), and the projected change in the total daily percentage of T_es (between 600 and 1800 h) falling within B₈₀ and B₉₅ for each species (second two data columns) as a result of climate change. For each OTM, T_es were averaged for every 1-h interval from 0600 to 1800 h across the entire study period, resulting in 12 data points per OTM

Species	Change in number of hours		% Change in habitat	
	B ₈₀	B ₉₅	B ₈₀	B ₉₅
<i>Anolis lemurinus</i>	-5	-3	-13	+6
<i>Anolis bicaorum</i>	-4	No change	+3	+23
<i>Anolis roatanensis</i>	No change	No change	-6	-8
<i>Anolis allisoni</i> (Roatan)	+3	+6	+28	+37
<i>Anolis allisoni</i> (CM)	+5	+5	+34	+30

A. allisoni between the hours of 800 and 1500, but by 2100 all hours of the day are projected to fall within the B₈₀ of this species. Likewise, none of the hourly mean

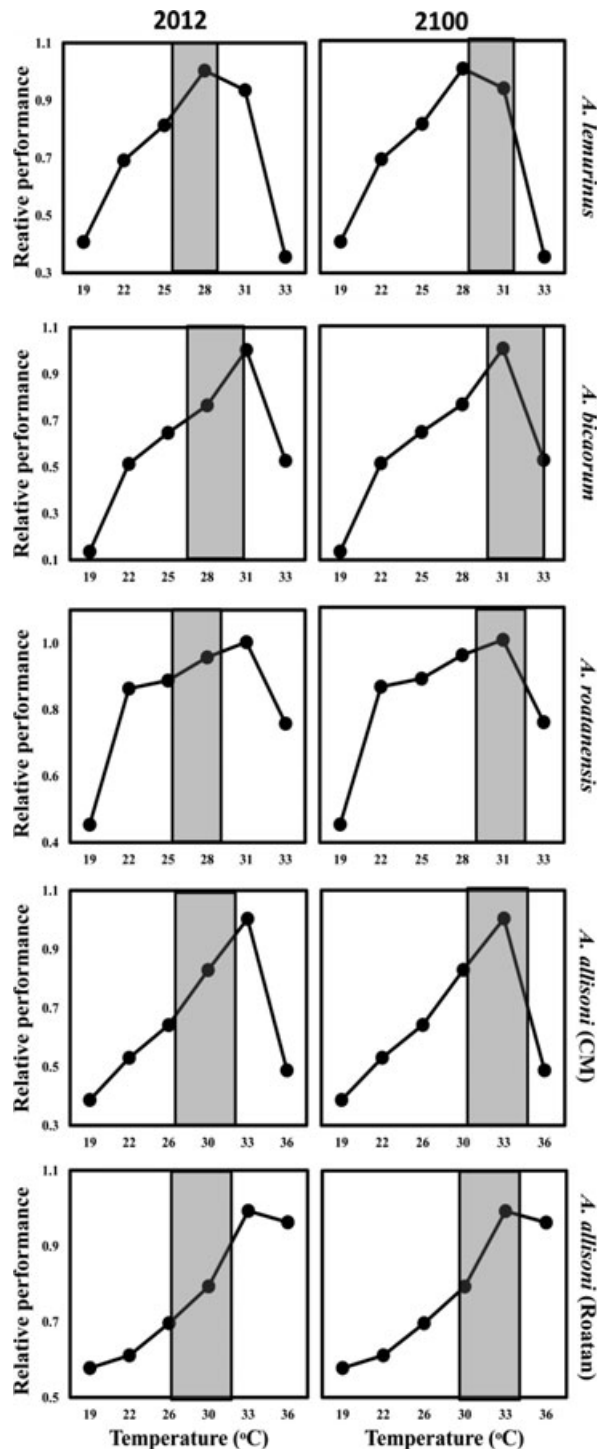


Fig. 3 Climate change projections and thermal performance curves for *Anolis lemurinus* (first row), *A. bicaorum* (second row), *A. roatanensis* (third row), *A. allisoni* from Cayo Menor (fourth row), and *A. allisoni* from Roatan (fifth row). Thermal performance curves are shown with the approximate mean diel range of operative temperatures (shaded regions) for the year 2012 (first column) and projected for the year 2100 (second column). Temperature projections of 3 °C are based on IPCC (2007) estimates for the Caribbean.

temperatures fell within B_{95} for *A. allisoni* in 2011, but in 2100, the means for several hours in the morning (800–1000), and afternoon (1200–1500) are projected to fall within the B_{95} of this species. These patterns are similar for *A. allisoni* on Roatan.

For four out of five populations, as a result of warming, the total percentage of T_e s (summed across all OTMs during each hour period, then over all hours of the day) falling within B_{95} over the course of the day is projected to increase (from 6 to 37% depending on species; Table 3, Fig. 4). The percentage change in T_e s falling within B_{80} is predicted to increase for *A. bicaorum* and both populations of *A. allisoni*, but decrease for *A. lemurinus* and *A. roatanensis*.

Discussion

Fine-scale variation in T_e

Recent studies that posit dire consequences for the Earth's tropical forest ectotherms assume that these environments are thermally homogeneous (Huey *et al.*, 2009, 2012; but see Bonebrake & Deutsch, 2012). Our results stand in contrast to this assumption. We have shown that operative thermal environments differ markedly among islands and habitat types, and this is likely due to differences in island size, shape, and topographic complexity. Although the mean and variance in T_e was generally higher in open-habitat, both temporal and spatial T_e distributions of forest habitat differed to a surprising degree among islands. For example, forest habitat on Cayo Menor displayed a remarkably high spatial variance (indeed, several transects did not overlap at all in their distributions) while forest on Utila and Roatan appeared comparatively homogeneous. However, it should be noted that we were not able to comprehensively sample T_e distributions on Roatan due to the island's large size, and given that its topographic complexity rivals that of Cayo Menor, it is likely that Roatan is much more thermally heterogeneous than we observed. Nevertheless, this high degree of geographic variation in T_e at the archipelago scale suggests that climate change will affect forest habitat on these islands in different ways, a pattern which could not have been elucidated by low-resolution environmental temperature data gleaned from weather stations. More generally, these data suggest that previous assumptions of thermal homogeneity in tropical forests have been overstated.

Thermal physiology

Due to logistical constraints associated with working in remote regions, we chose running speed as the

performance measure by which to base our climate change predictions. While ecologically relevant, running speed may be less thermally sensitive than other measures of performance such as digestive efficiency, and therefore future work should consider additional measures of performance. Nevertheless, the thermal sensitivity of running speed differed among species in ways consistent with expectations from theory (Huey & Hertz, 1984; Lynch & Gabriel, 1987; Garland *et al.*, 1991; Gilchrist, 1995; Gilchrist *et al.*, 1997; Angilletta, 2009), suggesting that it was a suitable proxy for fitness. For example, populations of *A. allisoni* occupy the habitat type with the highest mean T_e , and these populations also had the highest T_o . Likewise, *A. lemurinus* occurred in the habitat with the lowest mean T_e and had the lowest T_o . Moreover, with the exception of *A. allisoni* from Roatan, T_o scaled positively with P_{max} among species, which is consistent with the 'thermodynamic effect' (Knies *et al.*, 2009; Angilletta *et al.*, 2010). Finally, performance breadths (B_{80} and B_{95}) were higher on average for forest species than they were for open-habitat populations, consistent with the high cost of behavioral thermoregulation in forest habitat (Huey, 1974; Huey & Slatkin, 1976). Interestingly, performance breadths for the species living on the flat island of Utila, *A. bicaorum* (a forest-dwelling thermoconformer), were narrower than for any other population. We speculate that the broader performance breadths of populations on Cayo Menor and Roatan may be due to the greater topographic complexity of those islands. This pattern could result from gene flow among partially differentiated subpopulations experiencing divergent local selection pressures. On a broader geographic scale, differences in thermal sensitivity among species occupying geographically proximate islands suggest that the response to climate change will not be uniform across the archipelago.

Response to climate change

Huey *et al.* (2009) predicted that, as a result of increasing temperatures in open habitat, the Puerto Rican lizard *A. cristatellus* should be encroaching on forest habitat and beginning to compete with the forest species *A. gundlachi* by the year 2009. More generally, they suggested that this 'invasion hypothesis' may play out in many tropical regions where open-habitat and forest species live sympatrically. In the Bay Islands, this dynamic would have the potential to drive the endemic *A. roatanensis* to extinction. We found little evidence to support the invasion hypothesis on either of the two islands we studied where an open-habitat and forest species occur sympatrically. Indeed, we did not observe a single individual *A. allisoni* in forest habitat on Cayo

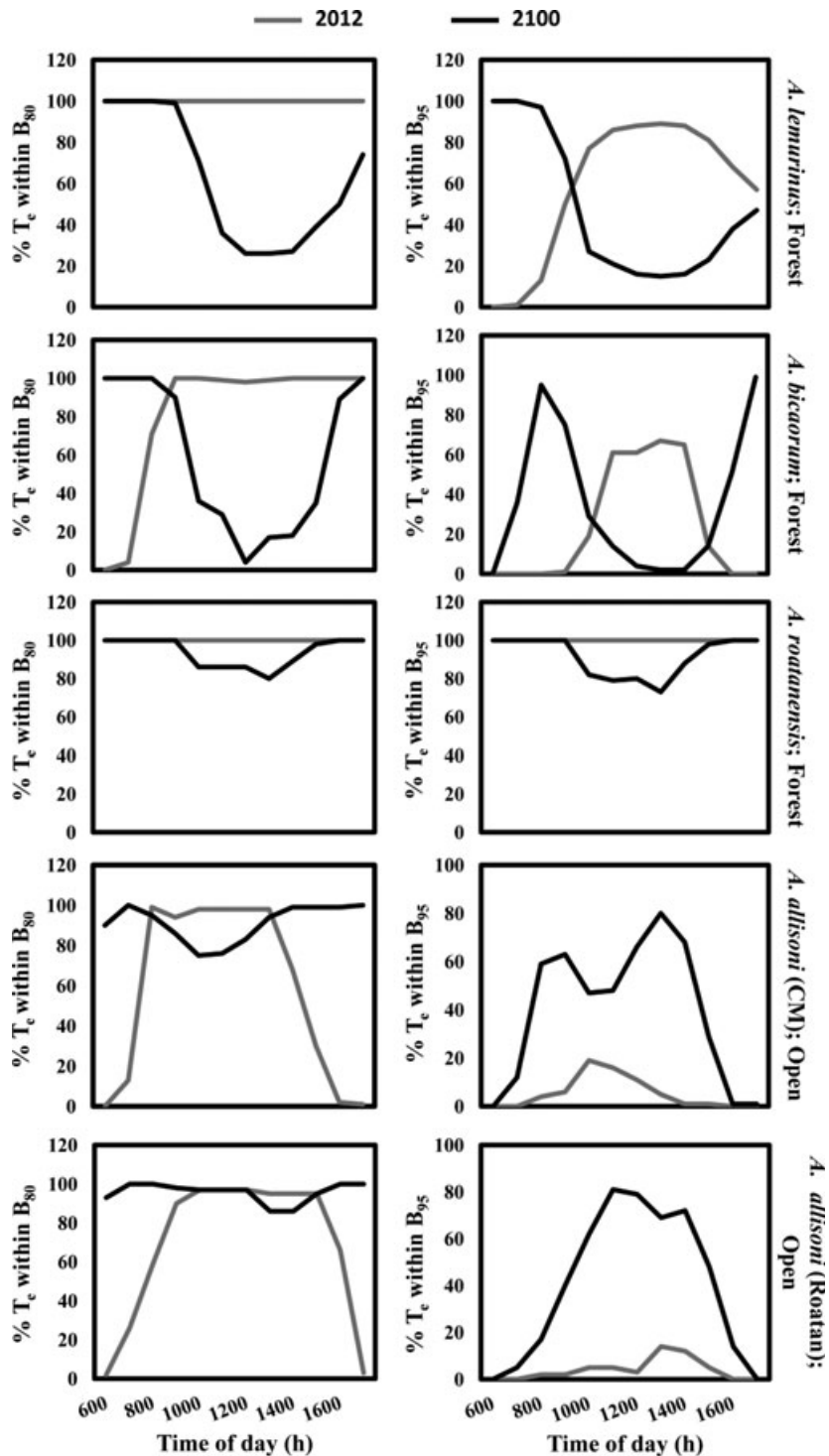


Fig. 4 The percentage of T_c s falling within the 80 (first column) and 95% (second column) performance breadths of each species over a typical day in 2012 and projected for 90 years of climate change.

Menor or Roatan during our 4 years of sampling. Moreover, the thermal physiology of *A. allisoni* populations suggests that they may experience an increase in performance capacity as temperature rises over the coming century. For example, the average diel

operative temperature ranges in open habitat on Cayo Menor and Roatan will begin to converge on the peak performance of *A. allisoni* by the year 2100 (Fig. 3). In addition, by the year 2100, ca. 30% more of the habitat will provide operative temperatures within the 80 and

95% performance breadths of *A. allisoni* (Table 3). It therefore seems unlikely that the open-habitat species in the Bay Islands will benefit from invading forest habitat. Similarly, our analyses suggest that the forest species on Roatan, *A. roatanensis*, will experience trivial reductions in performance by the year 2100. The potential impact of warming appears to be partially mitigated by their broad performance breadth. Similarly, while the forest species on Cayo Menor, *A. lemurinus*, should experience a small reduction in performance, they do not appear extremely vulnerable as their response to climate change is mediated by their relatively broad performance breadth and the existence of thermal refugia within their habitat.

For the forest species on Utila, *A. bicaorum*, our data suggest that climate change could reduce the total number of daylight hours during which lizards can perform optimally, while simultaneously producing more thermally optimal habitat in the mornings and evenings. This occurs because there is overcompensation in the morning and late-afternoon hours where the comparative increase in the frequency of optimal $T_{e,s}$ is greater than the decrease that occurs during midday (Fig. 4). The projected 23% increase in the proportion of $T_{e,s}$ falling within B_{95} for *A. bicaorum* contradicts the assertion that all tropical forest lizards are extremely vulnerable to warming, and highlights the importance of considering time-dependent changes in the frequencies of operative temperatures, in addition to changes in means (Clusella-Trullas & Chown, 2011; Clusella-Trullas *et al.*, 2011). It is not clear how these conflicting spatial and temporal patterns will affect lizards on Utila, although it is possible that reduced activity time in the middle of the day will negatively impact foraging and mating success, and could therefore negatively affect the population dynamics of this species (Sinervo *et al.*, 2010).

In addition, while *A. bicaorum* had a slightly higher thermal safety margin than *A. lemurinus*, it also had a much lower warming tolerance, suggesting that while it may start to experience a loss in performance after *A. lemurinus*, performance should decrease at a faster rate. This appears to be the case despite the fact that the T_o for *A. bicaorum* is 2 °C higher than the T_o of *A. lemurinus*. The relatively high thermal safety margin and warming tolerance of *A. roatanensis* suggest that it will be the last to experience a loss in performance among forest species, and once it does, its rate of performance loss will be relatively slow.

Summary

Our operative temperature models deployed at extremely high spatial resolution in the Bay Islands of

Honduras revealed marked differences in thermal heterogeneity among islands and habitat types. It does not appear that the 'invasion hypothesis' proposed by Huey *et al.* (2009) is likely to occur on these islands, where the open-habitat species is expected to benefit from climate change (at least for the next few decades), and the forest species is only expected to undergo a relatively minor net change in performance by the year 2100. Moreover, the projected response to climate change differs among the forest species in this study despite the fact that they occupy structurally similar lowland forested habitat and share a common ancestor that existed less than 12 000 years ago (Klutsch *et al.*, 2007; Logan *et al.*, 2012). Nevertheless, it should be noted that we based predictions on changes in mean temperature alone, yet changes in temperature variability, precipitation, and cloud cover may also be important for population stability (Hare & Cree, 2010; Clusella-Trullas *et al.*, 2011). Unfortunately, current climate models for changes in these latter two variables contain a high degree of uncertainty, and therefore incorporating them into biological models seems premature at present.

Whereas studies conducted to date have made uniformly bleak predictions for the survival of tropical forest lizards around the globe, our data show that four congeneric species, occurring in the same geographic region, differ markedly in their vulnerabilities to climate warming. Moreover, none appear to be on the brink of extinction. Considering that these populations occur over extremely small geographic ranges, it is possible that many tropical forest lizards (which range over much wider areas) may have even greater opportunity to escape warming. We suggest that topographical complexity is a major contributor to this variation, and that future attempts to forecast population responses to climate change combine holistic measures of thermal physiology with T_e distributions measured at appropriate scales.

Acknowledgements

Our methods were approved by the Dartmouth College Institutional Animal Care and Use Committee (protocol 07-02-03), and by the Instituto Nacional de Conservacion y Desarrollo Forestal of Honduras (permit DVS-ICF-062-2010). Funding for this project was provided by Operation Wallacea, the Dartmouth College Cramer Fund, and the Phi Sigma Biological Society. The authors thank the Honduran Coral Reef Foundation, the Bay Islands Foundation, the Bay Islands Conservation Association, J. Pearson, L. Horncastle, S. Fernandez, M. Stanton, S. Green, T. Coles, T. Fey, H. Lam, A. Tozer, D. Exton, A. Oviedo, C. Montgomery, A. Martinez, and S. Hopes. They also thank M. Angilletta, S. Fey, B. Calsbeek, and three anonymous reviewers for comments that helped them improve the manuscript.

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Supporting Information

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

Table S1. Final models chosen for the thermal performance curves of each population, with associated AIC scores.

Table S2. Description of operative temperature model (OTM) transects deployed during the study period.