

Abiotic constraints on the activity of tropical lizards

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Summary

1. Many tropical ectotherms are considered vulnerable to anthropogenic climate change because they have evolved to become thermal specialists. Indeed, several recent studies have suggested that even small increases in mean operative temperature may lead to a reduction in activity and the subsequent extinction of populations. Within the tropics, lizards are considered particularly vulnerable due to the potential for climate change to directly impact physiology and alter community interactions. However, models usually focus on the effects of mean operative temperature at the expense of other climate variables that may also affect lizard physiology.

2. We used daily variation in operative temperature, humidity and wind speed to examine how changes in climate influence activity in two species of lizards from the island of Cayo Menor, Honduras. *Anolis lemurinus* is a forest species, whereas *A. allisoni* is an open-habitat species. We conducted daily surveys for active lizards in habitat typical to each species, while simultaneously measuring operative thermal environments with physical models. The effects of the thermal environment were considered in the context of the thermal sensitivity of locomotor performance for each species and compared with the effects of the hydric (humidity) and convective (wind) environments.

3. When all surveys were combined into a single analysis, the activity of the forest species *Anolis lemurinus* was positively correlated with wind speed, the spatial heterogeneity of operative temperature, and the mismatch between mean operative temperature and the optimal temperature for sprint performance. Mean operative temperature did significantly affect *Anolis lemurinus* activity, but only when it was above their thermal optimum. Activity of the open-habitat species *A. allisoni* was negatively correlated with wind speed, but was not related to any other climate variable.

4. Whereas the mismatch between mean operative temperature and the thermal optimum for performance predicted the activity level of the forest species in ways partially consistent with its use in models for the response of lizards to climate change, the effects of the abiotic environment were habitat dependent. Our results suggest that successfully predicting the biological impacts of climate change will require holistic models that account for more than changes in mean temperature alone.

Key-words: *Anolis*, Bay Islands, Cayos Cochinos, climate change, Honduras, operative temperature, thermal performance curve, thermoregulation

Introduction

In the tropics, variation in daily and seasonal temperature is small compared to temperate regions. As a result, tropical ectotherms have evolved to maximize performance over a narrow temperature range and may be particularly vulnerable to climate change since even small perturbations in ambient temperature can lead to large decreases in fitness (Tewksbury, Huey & Deutsch 2008). Indeed, several recent

studies have suggested that climate change is impacting tropical species much more heavily than those in the temperate zone (Deutsch *et al.* 2008; Tewksbury, Huey & Deutsch 2008; Huey & Tewksbury 2009; Huey *et al.* 2009, 2012; Sinervo *et al.* 2010; Urban, Tewksbury & Sheldon 2012).

Among tropical ectotherms, forest lizards are thought to be particularly vulnerable to warming for two reasons: first, they already occur in the coolest part of the tropical landscape, so they cannot disperse to cooler areas. Warming may therefore rapidly push them past their thermal

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optimum and depress performance to critically low levels (Huey *et al.* 2009, 2012; Pike 2014). Secondly, although many forest-dwelling lizard species presently co-occur with open-habitat species, they minimize competition by partitioning the habitat along a climate niche axis (Rand 1964; Losos 2009). Global warming could break down this axis by increasing the temperature of forest environments until they become ideal for open-habitat species. Open-habitat species may then ‘invade’ forest habitat and compete with forest species, driving them to extinction if the forest species are already experiencing performance declines due to the effects of temperature alone (Huey *et al.* 2009). As a result of these dynamics, several recent studies have suggested that mass extinctions of tropical lizards may be on the horizon (Tewksbury, Huey & Deutsch 2008; Huey *et al.* 2009, 2012; Sinervo *et al.* 2010).

To date, most attempts to model the response of tropical ectotherms to climate change have relied on low-resolution environmental temperature data gathered from weather stations (Logan *et al.* 2013). However, the equilibrium body temperatures of small terrestrial ectotherms result from a combination of biophysical variables such as convection, conduction and radiation and often deviate from ambient conditions (Bakken 1989). Environmental temperatures gathered from weather stations are therefore unlikely to represent biologically relevant operative temperature (T_e) distributions (Sears, Raskin & Angilletta 2011; Potter, Woods & Pincebourde 2013). To account for this shortcoming, several other studies have included fine-scale measurements of T_e in models for the response of tropical lizards to climate change (Gunderson & Leal 2012; Logan *et al.* 2013; Sunday *et al.* 2014). These studies suggest that lowland tropical environments might be more thermally heterogeneous than previously thought and that some lizard taxa may be resilient to warming.

Whether they include broad-scale ambient temperatures or fine-scale T_e distributions, the predictions of nearly all studies to date are based on the effects of increases in mean temperature. They largely ignore the potential impact of changes in temperature variation, precipitation and wind speed. This is at least partly because IPCC projections are most reliable and modelling procedures are much simpler when considering only changes in mean temperature (Huey *et al.* 2012; IPCC 2013). More importantly, one proposed mechanism for population extinction in lizards is that increases in mean T_e will reduce physiological performance and force individuals to spend more time in shaded retreat sites, thereby limiting the time available for energy intake and investment in reproduction (Sinervo *et al.* 2010; Logan *et al.* 2013). However, it is unlikely that mean T_e is the only climate variable affecting the population dynamics of tropical lizards. Recent work has suggested that mean T_e may even be relatively unimportant, since the thermal physiology of squamate reptiles appears to be more closely linked to T_e variation and precipitation (Clusella-Trullas, Blackburn & Chown 2011). Despite its ubiquity in models for the response of tropical

lizards to climate change, the match between mean T_e and lizard physiology has not been directly linked to changes in population abundance or activity levels.

Here, we use daily variation in T_e , humidity and wind speed to evaluate the role these factors play in controlling the activity levels of two species of tropical lizards from the island of Cayo Menor in Honduras (Fig. 1). *Anolis lemurinus* occurs in deep forest habitat, whereas *Anolis allisoni* is found in open or edge habitat (Fig. S1). We examine activity patterns in the context of each species’ thermal physiology and discuss the implications of our data for models that project the impacts of climate change on tropical ectotherms.

Materials and methods

THERMAL PERFORMANCE CURVES

We measured the thermal sensitivity of sprint speed of *A. lemurinus* and *A. allisoni* from June through August, 2010. Sprint speed is an ecologically relevant measure of performance that has been linked to fitness in lizards (Miles 2004; Calsbeek & Irschick 2007; Logan, Cox & Calsbeek 2014). Four males and four females were chosen randomly from each day’s capture effort and were maintained for 24 h in stable field station conditions prior to the start

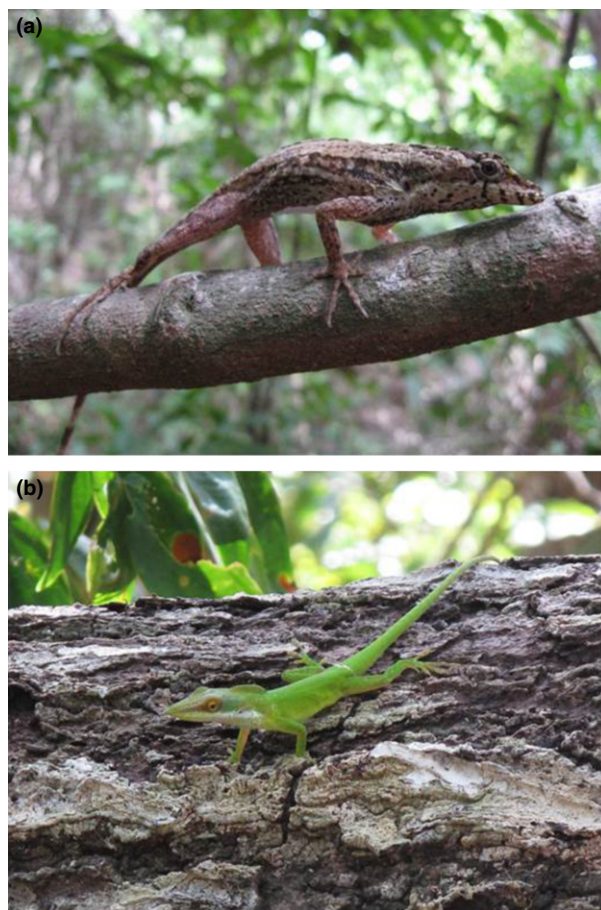


Fig. 1. The two study species. (a) *Anolis lemurinus* is a forest-dwelling species, whereas (b) *A. allisoni* occurs in open (or edge) habitat.

of trials. During this time, they were given water *ad libitum*, but were not fed. Individuals were heated or cooled to each of six temperatures that spanned their critical thermal limits (*A. lemurinus*: 19, 22, 25, 28, 31 and 33 °C; *A. allisoni*: 19, 22, 26, 30, 33, 36 °C) in field portable incubators. Each lizard was incubated for the minimum time necessary to achieve the target body temperature (usually < 10 min). We used 6 pilot runs per species to determine the lower and upper temperatures at which sprint performance declined dramatically prior to performing trials for analysis (individuals used to establish thermal windows were not included in further analyses). For sprint trials included in analyses, we verified that each individual had achieved the target temperature using a cloacal thermometer (Omega Engineering, Inc., Stamford, CT, USA), then motivated them to run along a 3-cm-diameter wooden dowel (positioned at a 20° angle to discourage hopping) and filmed with high-speed (60 fps) digital video. Each lizard was run once at each temperature and was given a minimum of 2 h rest between temperatures (no animal was kept in captivity for more than 48 h). The order of temperatures was randomized for each individual. We recorded maximum sprint speed over a 10 cm section of track using frame-by-frame analysis in the software program Eagle Eye Proviewer (Eagle Eye Proviewer Software, Roseville, MN, USA). Trials in which individuals fell off the dowel or spun around to the opposite side were excluded from further analysis. As a result, final sample sizes differed among species and temperatures (in order of increasing temperature, for *A. lemurinus*: $N = 22, 27, 28, 29, 30$ and 41 ; for *A. allisoni*: $N = 38, 33, 37, 39, 37$ and 35).

To construct thermal performance curves (TPCs) for each species, a set of asymmetrical, parabolic equations built into the statistical program TableCurve 2.0 were fit to the raw sprint data (Angilletta 2006; Logan *et al.* 2013). This model set was chosen based on the typical shape of TPCs (left skewed with a rapid decline after the optimum) (Angilletta 2009). The best fit for each species was chosen using Akaike information criterion (AIC). Specifically, equations that differed in AIC score by more than 2 were considered significantly different from one another (Akaike 1987). If multiple equations could not be distinguished using AIC, we chose the one with the highest r^2 value. We extracted the thermal optimum for performance (T_{opt} , the body temperature at which sprint speed was maximal) from the best model fit for each species.

LIZARD ACTIVITY SURVEYS

During 2011 (9 July–14 August) and 2012 (18 July–3 August), we conducted visual surveys along 50-m transects that were placed haphazardly in habitat typical to each species (Fig. S1, Supporting information). We conducted surveys along 4 transects (two per habitat type) during 2011 and 2 transects (one per habitat type) during 2012. On a given day, we chose a random time between the hours of 07.00 and 17.00 and walked each transect once in a random order. We required between 15 and 20 min to walk the length of each transect. We conducted a total of 68 activity surveys over the course of the study (34 for each species), permitting us to capture a broad range of environmental and climatic conditions.

Operative temperature models (OTMs) built to mimic the conductive and reflective properties of each species (Bakken 1992) were simultaneously deployed at high resolution along each transect. We placed 28–30 models at random positions along each transect. The position in space of an individual OTM was defined by three randomly chosen quantities: a distance along the length of the transect (from 0 to 50 m, in 1 m increments), a perpendicular distance away from the transect to the left or the right (0–3 m, in 1 m increments) and a height in the vegetation (0–3 m, in 0.5 m increments). OTMs were made using type-M (thin-walled) copper

pipings which has high heat conductivity and reaches thermal equilibrium rapidly (Angilletta 2009). Models were painted to match the average skin colour for each species, and we assumed that they approximated the appropriate photospectrum absorbencies. Temperature logging iButtons (Embedded Data Systems, Lawrenceburg, KY, USA), set to record temperature every 10 min, were suspended within each model in non-conductive acrylic mesh. At the beginning and end of each survey of a particular transect, we recorded point measurements of absolute humidity and wind speed (at 3 m above ground level) using a Kestrel® portable weather station.

ANALYSES

We evaluated the extent to which the spatial heterogeneity of T_e , the mismatch between mean T_e and T_{opt} , wind speed and humidity affected the total number of lizards active during surveys. We used the total number of lizards observed during each survey as our index of activity because per-survey sample sizes were not sufficient for absolute abundance measurements (e.g. distance sampling). Thus, we interpret our results in terms of relative lizard activity. Additionally, because all visual surveys were conducted by the same individual (MLL), we assume that detection probability remained relatively constant over the study period.

For all statistical analyses, we used the mean T_e of each OTM (rather than raw OTM data) because temperatures recorded by a single OTM were autocorrelated. Hereafter, 'mean T_e ' refers to the average of all OTM means during a particular survey. 'Spatial heterogeneity in T_e ' is the variance of OTM means. For any given abundance survey, we consider the influence of mean T_e by examining the degree to which it matched T_{opt} , as this is thought to be an index of the quality of the thermal environment for lizards (Hertz, Huey & Stevenson 1993) and is the primary mechanism by which climate change is predicted to drive extinction events (Sinervo *et al.* 2010). We also used mean values for all analyses of wind speed and humidity.

To explore the effects of the abiotic environment on each species, abiotic variables were included in separate multivariate regressions for each species with the total number of lizards active per survey as the dependent variable (data from all years were pooled). Additionally, because the drop off in performance is much greater above T_{opt} than below (TPCs are left-skewed), we compared the relationship between activity and the mismatch between T_e and T_{opt} on days when T_e was below T_{opt} versus days when it was above T_{opt} ; because mean T_e never exceeded T_{opt} in open habitat, we conducted this analysis for the forest species only. We also examined correlations between mean T_e and activity for *A. allisoni* in the presence and absence of wind. Lastly, we pooled data from both species into a single general linear model (GLM) with two-way interaction terms to test for differences in the effects of the abiotic environment among habitat types. Higher order interactions were not included in this model because of insufficient sample sizes.

Results

THERMAL PHYSIOLOGY

Mean T_{eS} in forest and open habitat on Cayo Menor were 28.1 and 29.9 °C, respectively. The mean field-active body temperatures of *Anolis lemurinus* and *A. allisoni* were 28.8 and 31.2 °C, respectively. The T_{opt} of *A. lemurinus* and *A. allisoni* was 29.6 and 33.9 °C, respectively (Fig. 2). Other differences in shape between the TPCs of these species along with in-depth comparisons between the T_e

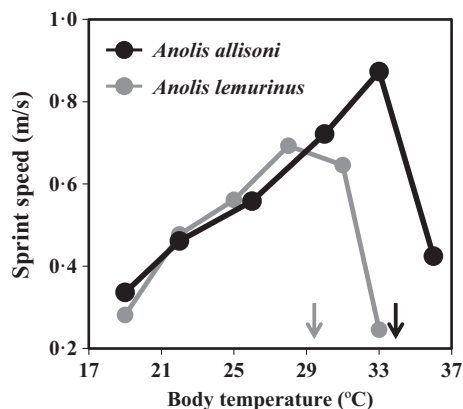


Fig. 2. Thermal performance curves for *Anolis lemuringus* (forest species) and *A. allisoni* (open-habitat species). Arrows specify the thermal optimum (T_{opt}) for each species.

distributions of forest and open habitat on Cayo Menor are reported and discussed elsewhere (Logan *et al.* 2013).

ABIOTIC CONDITIONS AND LIZARD ACTIVITY

Correlations between abiotic variables differed among habitat types (Tables S1 and S2, Supporting information). For multiple regressions partitioned by habitat type, the activity of the forest species *A. lemuringus* was positively correlated with the mismatch between mean T_e and T_{opt} ($\beta = 0.98 \pm 0.47$; $P = 0.047$), the degree of spatial heterogeneity in T_e ($\beta = 2.98 \pm 0.87$; $P = 0.002$) and wind speed ($\beta = 3.21 \pm 1.28$; $P = 0.020$) (Table 1). In open habitat, by contrast, *A. allisoni* activity was negatively correlated with wind speed ($\beta = -2.79 \pm 0.97$; $P = 0.008$), but was not correlated with any other variable (Fig. 3, Table 1). More of the variance in *A. allisoni* activity was explained by the mismatch between T_e and T_{opt} when wind was absent (although this correlation was not statistically significant: Pearson coefficient = -0.56 ; $P = 0.115$; Fig. 4). Activity levels were not correlated with humidity for either species (Fig. 3, Table 1). A GLM of the pooled data set that included data from both species revealed significant differences in the effects of two abiotic variables on activity levels in forest versus open habitats. We measured significant habitat \times wind speed ($F_{1,45} = 9.862$; $P = 0.003$) and habitat \times heterogeneity in T_e ($F_{1,45} = 4.796$; $P = 0.034$) interactions.

Table 1. Partial regression coefficients reveal strong habitat dependence of abiotic factors on the activity of two species, *Anolis lemuringus* and *A. allisoni*. 'Spatial heterogeneity in T_e ' is the variance in OTM means. Significant P -values are in bold

Effect	<i>A. lemuringus</i> (forest)			<i>A. allisoni</i> (open habitat)		
	Coefficient	t -value	P	Coefficient	t -value	P
Mismatch between T_e and T_{opt}	0.984	2.104	0.047	0.266	0.482	0.634
Spatial heterogeneity in T_e	2.981	3.438	0.002	-0.320	-0.283	0.780
Humidity	0.057	0.860	0.399	-0.021	-0.146	0.885
Wind speed	3.212	2.512	0.020	-2.785	-2.885	0.008

For *A. lemuringus*, activity was not related to the mismatch between T_e and T_{opt} when T_e was below T_{opt} (Pearson coefficient = 0.161 , $P = 0.433$; Fig. 5a). However, activity decreased rapidly with the mismatch between T_e and T_{opt} when T_e was above T_{opt} (Pearson coefficient = -0.716 , $P = 0.046$; Fig. 5b).

Discussion

A growing body of research uses changes in mean operative temperature modelled at broad geographic scales to project the impacts of climate change on tropical ectotherms (Deutsch *et al.* 2008; Tewksbury, Huey & Deutsch 2008; Huey & Tewksbury 2009; Huey *et al.* 2009, 2012; Sinervo *et al.* 2010). This work has led to the now dominant view that tropical ectotherms are particularly vulnerable to climate change relative to temperate species (Deutsch *et al.* 2008; Tewksbury, Huey & Deutsch 2008; Huey *et al.* 2012; Zeh *et al.* 2012). However, several recent studies have modelled changes in temperature at much finer spatial scales (Gunderson & Leal 2012; Logan *et al.* 2013; Sunday *et al.* 2014) or have included the effects of temporal variation in temperature in addition to changes in the mean (Raffel *et al.* 2012; Kingsolver, Diamond & Buckley 2013; Vasseur *et al.* 2014). These studies have complicated the picture by concluding that tropical species vary geographically in their susceptibility to climate warming or even that they may be less vulnerable on average compared to temperate species. With few exceptions (but see Kingsolver, Diamond & Buckley 2013; Vasseur *et al.* 2014), these models are predicated on the degree to which mean T_e matches T_{opt} (or other physiological indices meant to approximate thermally optimal conditions). As this mismatch increases, fitness (e.g. population growth) is expected to decrease owing to a loss of activity time caused by thermal stress (Sinervo *et al.* 2010). As the environment warms, lizards are forced into shaded retreat sites where they can no longer consume prey or locate mates. When individuals can no longer maintain energy balance or reproduce, population growth will decline. Despite the presumed importance of this mechanism, data demonstrating that variation in mean T_e affects the activity levels of tropical lizards are surprisingly sparse.

Contrary to predictions, neither *A. allisoni* nor *A. lemuringus* were more active when mean operative temperature

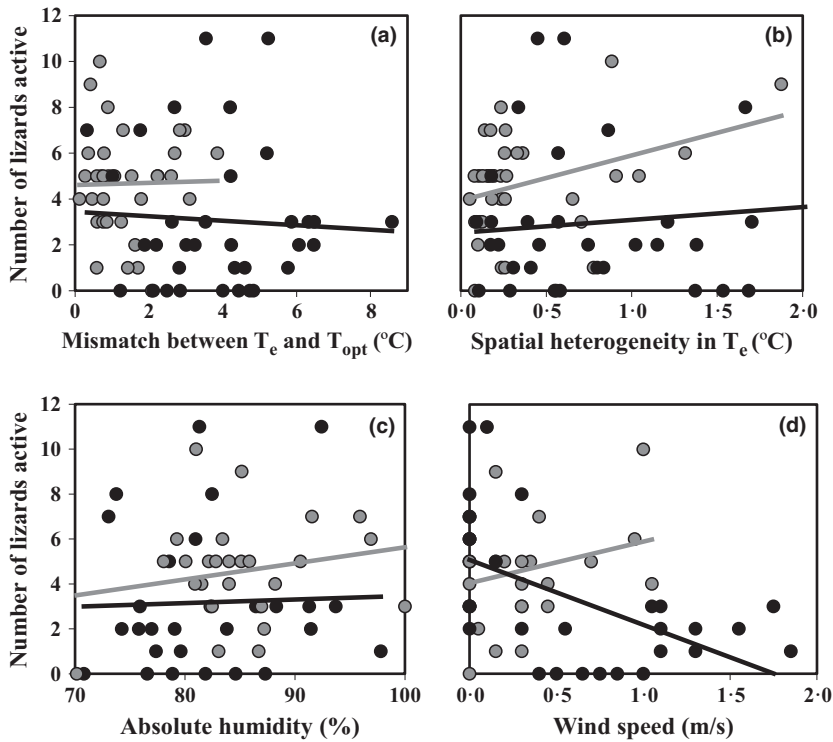


Fig. 3. Correlations between climate variables and the activity of a forest species, *Anolis lemurinus* (grey), and an open-habitat species, *A. allisoni* (black), revealed differences in the effects of abiotic variables in the two habitats. The activity of *A. lemurinus* was positively correlated with the mismatch between T_e and T_{opt} , the spatial heterogeneity of T_e and wind speed (a, b, and d, respectively). *A. allisoni* activity was negatively correlated with wind speed (d) but was not related to any other variable (a–c). Neither species' activity was correlated with humidity (c). Multivariate regressions revealed significant interactions between b) habitat \times spatial heterogeneity in T_e and d) habitat \times wind speed.

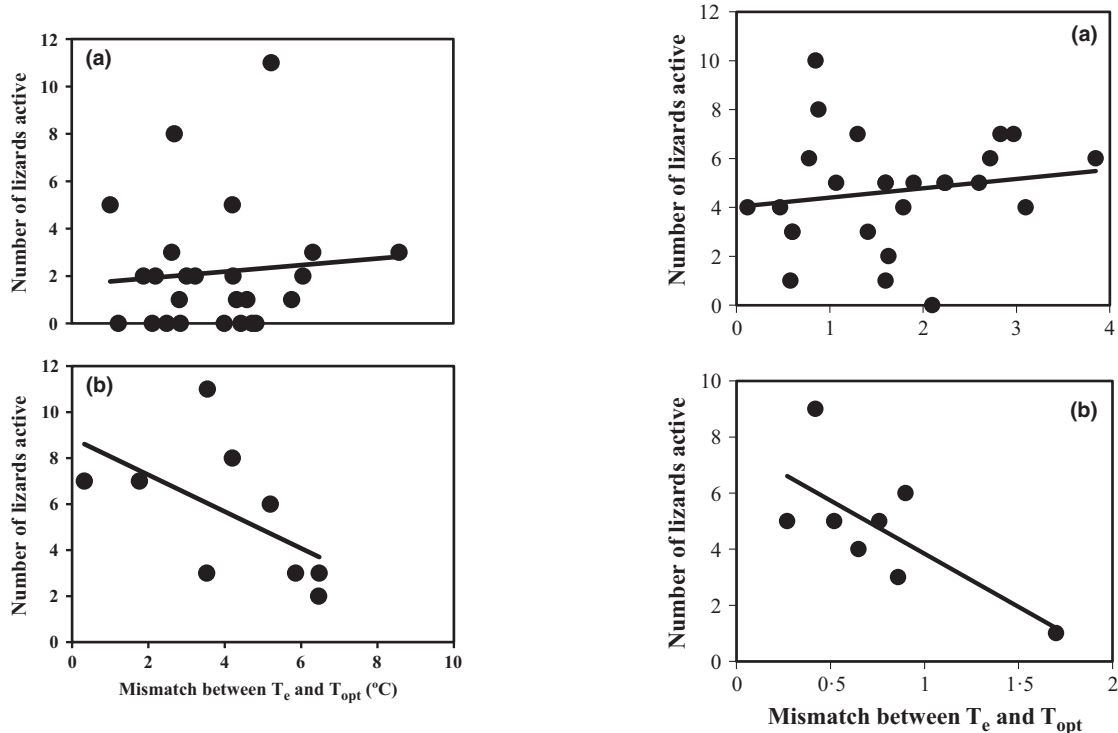


Fig. 4. A lower proportion of the variance in *A. allisoni* activity was explained by the mismatch between mean T_e and T_{opt} on a) windy days (wind speed $> 0 \text{ m s}^{-1}$) then it was on b) calm days (no wind), although neither relationship was statistically significant.

Fig. 5. *Anolis lemurinus* activity was not related to the mismatch between T_e and T_{opt} when (a) T_e was below T_{opt} , but activity decreased sharply with the mismatch between T_e and T_{opt} when (b) T_e was above T_{opt} .

matched their thermal optimum for locomotor performance. In fact, the opposite was true for the forest species, *A. lemurinus*. As mean T_e in the forest approached T_{opt} ,

A. lemurinus became less active. However, most of our surveys in forest habitat occurred when mean T_e was below the T_{opt} of *A. lemurinus*. Previous studies that model cli-

mate change effects on ectotherm activity focus on the impact of warmer, rather than cooler, temperatures (Deutsch *et al.* 2008; Sinervo *et al.* 2010). Thermal performance curves are asymmetric, such that the temperatures above T_{opt} are expected to impact lizard populations more severely than temperatures below T_{opt} (Martin & Huey 2008). Indeed, *A. lemurinus* activity did not respond to changes in operative temperature when these temperatures were below their thermal optimum, but activity decreased sharply when operative temperatures were above their thermal optimum (Fig. 5). The positive effect of the mismatch between T_e and T_{opt} on *A. lemurinus* activity in our general analysis may therefore have resulted from the majority of our surveys being conducted when mean T_e was below T_{opt} . Of a total of 34 surveys conducted in forest habitat, only nine occurred during days and times when mean T_e exceeded the T_{opt} of *A. lemurinus*. Interestingly, on the warmest days when T_e exceeded T_{opt} by nearly 2 °C (resulting in operative temperatures that were close to the critical thermal maximum of *A. lemurinus*), we still detected several active individuals. This pattern suggests either that thermally suitable areas persisted within the habitat or that there was significant variation among individuals in thermal tolerance.

A. lemurinus was more abundant when wind speed was high. Wind reduces operative temperatures through convection. However, the cooling effect of wind is unlikely to explain the positive correlation between *A. lemurinus* activity and wind speed because operative temperatures were measured with physical models that take convection into account. It is possible that wind reduces predation (or increases prey availability) by creating movement in the vegetation, although more research is needed to understand this pattern.

Forest lizards are thought to be thermoconformers whose body temperatures track ambient conditions (Huey *et al.* 2009). This is because T_e tends to be spatially homogeneous in closed canopy habitats, which makes behavioural thermoregulation difficult (Huey 1974; Huey & Slatkin 1976). Considered in this context, the positive effect of increased spatial heterogeneity in T_e (variance among OTM means) on *A. lemurinus* abundance was surprising and suggests either that forest lizards behaviourally thermoregulate more than previous thought or that spatial variation in T_e permits lizards to be active in isolated pockets of habitat (e.g. those individuals with cooler territories are able to remain active).

In contrast to its effect in forest habitat, wind speed was negatively correlated with lizard activity in open habitat. Indeed, wind speed was the only significant predictor of *A. allisoni* activity; individuals were much less likely to be active on days when wind speeds were above approximately 0.5 m s⁻¹. This was true even when mean T_e closely matched T_{opt} . In open habitat, which had higher absolute wind speeds and was drier than forest (Fig. 3), convection from wind likely caused rapid cutaneous water loss in *A. allisoni*. It is possible

that wind speed has such a strong effect on activity because a trade-off occurs between the ability to maintain optimal body temperatures through basking and the ability to maintain water balance (Calsbeek, Knouft & Smith 2006). This effect should be much less pronounced in forest habitat, where humidity is higher (and more temporally stable) and maximum wind speed is lower. However, it should be noted that wind speed was over 0.5 m s⁻¹ for nearly 70% of the surveys we conducted in open habitat, and we therefore had small sample sizes for the effects of temperature on activity during calm days. The mismatch between mean T_e and T_{opt} explained a larger proportion of the variance in activity when only these calm days were considered (although the trend was not significant). Additionally, none of our activity surveys occurred at times when T_e exceeded the T_{opt} of *A. allisoni*. As with *A. lemurinus*, the mismatch between T_e and T_{opt} might have explained more of the variance in *A. allisoni* activity had operative temperatures been closer to their critical thermal maximum. Thus, while wind appears to be a stronger constraint on *A. allisoni* activity compared to mean T_e , the latter may also play a role.

Most models for the response of tropical lizards to climate change are predicated on the assumption that a mismatch between mean operative temperature and the thermal optimum for performance reduces activity time and precipitates extinction. However, for the open-habitat species we studied (*A. allisoni*), this mismatch did not predict variation in activity (with the several caveats mentioned above). Indeed, wind speed, which is also expected to shift with climate change (IPCC 2013), was a more important constraint. For the forest species, activity did appear to depend on the mismatch between mean T_e and T_{opt} , but only when T_e exceeded T_{opt} . In contrast to *A. allisoni*, wind speed and the spatial heterogeneity of T_e were both positively correlated with *A. lemurinus* activity. The latter variable may be correlated with cloud cover, which is likely to change as climates warm (IPCC 2013).

Our results highlight the importance of climate variables other than mean operative temperature in constraining the activity levels of tropical lizards and show that the effects of the abiotic environment are habitat specific. Predictions for the response of tropical ectotherms to climate change based on models that do not consider habitat-specific effects and only include changes in mean temperature are likely to be inaccurate.

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Data accessibility

All data associated with this study are deposited in the Dryad Digital Repository: <http://10.5061/dryad.f950c> (Logan, Fernandez & Calsbeek 2014).

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Supporting Information

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

- Fig. S1.** Photographs of forest and open habitat on Cayo Menor.
Table S1. Correlations among abiotic variables in forest habitat.
Table S2. Correlations among abiotic variables in open habitat.