

Turn up the heat: thermal tolerances of lizards at La Selva, Costa Rica

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Abstract Global temperature increases over the next century are predicted to contribute to the extinction of a number of taxa, including up to 40 % of all lizard species. Lizards adapted to living in lowland tropical areas are especially vulnerable because of their dependence on specific microhabitats, low vagility, and a reduced capacity to physiologically adjust to environmental change. To assess the potential effects of climate change on lizards in the lowland tropics, we measured the critical thermal maximum (CT_{max}) of ten species from La Selva, Costa Rica. We also examined how well body size, microhabitat type, and species predicted the CT_{max}. We used current temperature data along with projected temperature increases for 2080

to predict which species may be at the greatest risk at La Selva. Of the ten species sampled, four are at serious risk of lowland extirpation and three others might also be at risk under the highest predicted temperature-increase models. Forest floor lizards at La Selva have already experienced significant population declines over the past 40 years, and we found that each of the forest floor species we studied is at serious risk of local extirpation. We also found that microhabitat type is the strongest predictor of CT_{max}, demonstrating the profound impact habitat specialization has on the thermal limits of tropical lizards.

Keywords Thermal physiology · Conservation · Lowland tropics · Habitat specialization · Critical thermal maximum

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This study and paper represent my senior undergraduate thesis, and gave me the opportunity to experience the scientific process, from start to finish, first hand. I am extremely proud of this work and believe it should be considered for the “Highlighted Student Research” section. I am eternally grateful to my coauthors and the Organization for Tropical Studies Research Experience for Undergraduates program for giving me this opportunity.

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Introduction

Climate change is one of the greatest threats to terrestrial biodiversity in the twenty-first century (Intergovernmental Panel on Climate Change 2014). Increasing average temperatures could contribute to the extinction of 18 % of all species by 2050 (Thomas et al. 2004), and almost 40 % of all lizard species could be extinct by 2080 (Sinervo et al. 2010). As ectotherms, squamates are especially vulnerable to temperature increases and are predicted to decline at higher rates than other organisms (Maes et al. 2010). Population declines in squamates resulting from anthropogenic activities are already widespread, and have been linked to habitat fragmentation, pollution, invasive species, increasing temperatures, as well as other drivers associated with global climate change (Munguia-Vega et al. 2013; Sheldon et al. 2011; Chown 2012; Dukes and Mooney 1999; Cadby et al. 2010). Particularly well studied in terms of thermal biology are the “lizards” (Squamata exclusive of

amphisbaenians and snakes) (Andrews and Schwarzkopf 2012; Angilletta et al. 2002a, b; Clusella-Trullas et al. 2011; Seebacher and Franklin 2005). Of all the anthropogenic risk factors threatening lizard species globally, temperature increases from climate change are predicted to have one of the most pronounced detrimental effects (Zeh et al. 2012).

Although models predicting future climate change show only modest temperature changes in the tropics relative to temperate zones (Magrin et al. 2007), the effects of even small increases in temperature are compounded in tropical species because of a variety of biotic and abiotic factors (Dillon et al. 2010). Compared to species living in northern latitudes, tropical species have reduced ranges of physiological tolerance and weaker ability to behaviorally thermoregulate because they evolved in areas with little climatic variation (Addo-Bediako et al. 2000; Feder and Lynch 1982; Janzen 1967; van Berkum 1988). Adapted to these conditions, tropical lizards do not readily acclimatize to changing temperatures; therefore any small changes have a much greater effect on the fitness of tropical lizards than on those species living in higher latitudes (Huey et al. 2009; Feder 1978). Species adapted to living in lowland tropical environments face further challenges because they have restricted geographic ranges, relatively low vagility, and a limited ability to move away from their particular microhabitats (Navas 1996; Becker and Zamudio 2011). Lizard species living in environments that are getting hotter can adapt to the change, move to higher elevations and lower temperatures, or become extinct (Miles 1994). Whereas lizards in northern latitudes have demonstrated the ability to shift their geographic ranges poleward to combat negative effects of increasing global temperatures (Walters et al. 2012), lowland tropical species may not have the ability to move to nearby thermal habitats due to a combination of climate and land use changes that may detrimentally affect gene flow and the species' ability to adapt or migrate to other areas (Davis and Shaw 2001). A seminal hypothesis about tropical species' ability to migrate states that mountains are "higher" in the tropics because animals adjusted to a relatively constant temperature are not able to withstand short-term temperature shifts when attempting to cross mountain ranges during migration events (Janzen 1967). Even if species in the tropics are able to migrate to higher elevations to escape increasing temperatures, this net loss of biodiversity in tropical lowlands may lead to biotic attrition in which the number of species emigrating or becoming locally extinct exceeds the number of species immigrating into the area (Colwell et al. 2008; Feeley and Silman 2010).

With a dependence on specific habitats and microhabitats, a low vagility, a reliance on relatively stable temperatures, and a weak ability to make physiological

adjustments to their environments, there is a plethora of risks to tropical lizards with any temperature increase (Gunderson and Leal 2012; Huey et al. 2010). Similar risk factors have been found in other parts of the world, and increasing temperatures are similarly implicated in these declines (Huey et al. 2012). In the tropics, Whitfield et al. (2007) documented a gradual decline of amphibians and lizards in the lowlands of Costa Rica since 1970. While a number of mechanisms have been suggested to explain these population declines, the drivers of these decreases remain controversial. Exploration of the effects of microhabitats inhabited by animals, ability to disperse poleward and increase in elevation, and physiological effects of temperature changes may help elucidate reasons for past declines and aid in predictions of species most at risk of future declines.

Many tropical species of lizards are habitat specialists and rely on the conditions and resources of specific microhabitats for their survival (Kearney and Porter 2004). The importance of habitat specialization should not be underestimated, especially in the tropics where thermoregulatory behaviors primarily prevent overheating (Vickers et al. 2011), whereas in northern latitudes similar behaviors are used mainly to gain heat (Kearney et al. 2009). Differences in body size may also have a pronounced effect on a lizard's ability to tolerate increased temperatures. Larger-bodied individuals have a wider range of available daily temperatures, although smaller individuals have a lower heat capacity and therefore an increased ability to use thermoregulation to sustain optimal temperatures (Stevenson 1985). However, depending on the type of thermal environment a lizard lives in (e.g., distance between hotter and colder microenvironments), the effect of body size may be offset by the relative cost of maintaining a preferred temperature by thermoregulating (Huey and Slatkin 1976). Microhabitat type and body size might both be crucial factors affecting the ability of lowland tropical lizard species to tolerate increasing temperatures.

The goal of this study was to assess the potential effects of future climate change on lizards in the lowland tropics. Based on predicted rates of temperature increase in Latin America (Magrin et al. 2007), we tested the hypothesis that projected temperature increases in the tropics will limit the amount of activity time available to many species of lizards in their specific microhabitats. We examined the effects of body size and microhabitat type on the critical thermal maximum (CT_{max}) values for ten species of lizards, collected field body temperature (T_b) data (temperature of individual organisms at the time of capture), and calculated the warming tolerance (WT; difference between CT_{max} and T_b) for each species. We used operative temperature (T_o) models (OTMs) to collect data on the temperatures available to lizards in each of several microhabitat types, and

examined how projected temperature increases in the tropics will limit the activity times of tropical lizards.

Materials and methods

Study site and species

We conducted this study in July and August 2013 at La Selva Biological Station, Costa Rica (hereafter, “La Selva”). La Selva is a lowland tropical wet forest reserve that comprises primary and secondary forest (McDade et al. 1994). Ten families of lizards are found at La Selva (Donnelly 1994; Guyer 1994); we collected data from a total of 176 individuals from ten species of nine families representing a wide range of body sizes, microhabitat types, and thermal tolerances across multiple phylogenetic lineages (Table 1).

We classified species’ microhabitat types as one of the following: forest floor (closed canopy of primary or secondary forest, from forest floor to 1 m up tree trunks), open area (open fields or pastures), leaf litter (inside or under forest leaf litter), or buildings (manmade structures, used or abandoned). Species were classified into one of the four microhabitat types based on where they were consistently found and captured in the field (e.g., *Sphenomorphus cherriei* were only ever seen and captured buried under leaf litter), along with their natural histories (Guyer 1994). All ten species are listed under “least concern” by the International Union for Conservation of Nature (IUCN) (Solís et al. 2012). In Latin America these species are not considered threatened; Whitfield et al. (2007), however, found that six of the lizard species sampled here showed population declines, and specifically found that *Ameiva festiva*, *Norops humilis*, *Norops limifrons*, and *S. cherriei* have experienced a gradual decline over the last 35 years at La Selva.

Thermal measurements

We measured T_b of lizards in the field using a Master cool infrared thermometer from a distance of ≤ 60 cm (model 52224-A; ± 2 °C; distance:area measured = 30 cm:2.5 cm²). We measured T_b from lizards in the field upon initial observation by using the thermometer before capture. We then captured each lizard by hand or noose, and transported it to the lab in small, perforated plastic containers. We did not capture lizards if we were unable to record a stable T_b measurement or were unable to take a temperature reading from a minimum distance of ≤ 60 cm. We held lizards in their containers at ambient temperature (T_a ; ~23–29 °C) for 24 h prior to CT_{max} trials. We measured the lizards’ snout-vent length (SVL), transferred the lizards to individual perforated plastic containers of varying sizes (depending on SVL of the lizard), and then placed the containers into a large plastic container (40 cm width \times 55 cm length \times 20 cm height) filled with ~1.5 cm of water at 27.3 °C. We administered gradual temperature increases of ~0.5 °C every 3 min by adding ~15–30 mL of water heated to 100 °C using a Proctor-Silex 1-L electric kettle (model K2070Y). Water temperature increases were monitored using an infrared thermometer and an in-water Taylor thermometer (model 21418-1 J). After each 0.5 °C temperature increase, we made attempts to place the animals onto their backs three times. Normally lizards can right themselves immediately; when they failed to do so for a 5-s period, we recorded the water temperature as the individual lizard’s CT_{max} (Lutterschmidt and Hutchison 1997). We performed control trials to ensure the loss of righting reflex was due to temperature increase and not stress or habituation from the experiment, where we kept four individuals of each species at a constant temperature (27.3 °C) and placed them on their backs repeatedly for ~30 min. No individuals showed loss of righting reflex from the control tests alone.

Table 1 Descriptive statistics (means \pm 1 SEM) of critical thermal maxima (CT_{max}), body temperature (T_b), and size [snout-vent length (SVL)] of all lizard species captured during this study at La Selva Biological Station (Costa Rica)

Family	Species	Microhabitat type	CT_{max} (°C)	T_b (°C)	SVL (mm)
Dactyloidae	<i>Norops humilis</i> (n = 20)	Forest floor	27.96 \pm 0.08	25.70 \pm 0.15	18.4 \pm 10.2
Dactyloidae	<i>Norops limifrons</i> (n = 20)	Forest floor	28.84 \pm 0.20	26.12 \pm 0.18	24.9 \pm 10.2
Scincidae	<i>Sphenomorphus cherriei</i> (n = 16)	Leaf litter	31.36 \pm 0.17	28.01 \pm 0.28	24.7 \pm 6.2
Xantusiidae	<i>Lepidophyma flavimaculatum</i> (n = 20)	Forest floor	32.02 \pm 0.31	26.42 \pm 0.23	18.4 \pm 10.2
Sphaerodactylidae	<i>Gonatodes albogularis</i> (n = 20)	Building	37.55 \pm 0.24	27.24 \pm 0.24	34.3 \pm 7.7
Gekkonidae	<i>Hemidactylus frenatus</i> (n = 20)	Building	36.48 \pm 0.35	26.28 \pm 0.19	40.1 \pm 8.9
Phyllodactylidae	<i>Thecadactylus rapicauda</i> (n = 16)	Building	37.44 \pm 0.19	27.13 \pm 0.19	103.8 \pm 25.9
Teiidae	<i>Ameiva festiva</i> (n = 20)	Open	39.78 \pm 0.30	34.35 \pm 0.99	62.9 \pm 14.1
Iguanidae	<i>Iguana iguana</i> (n = 12)	Open	40.58 \pm 0.18	32.99 \pm 0.75	76.6 \pm 22.1
Corytophanidae	<i>Basiliscus vittatus</i> (n = 11)	Open	42.48 \pm 0.19	35.86 \pm 0.55	112.3 \pm 33.9

T_o models

We constructed hollow, cylindrical, copper OTMs following Dzialowski (2005) to simulate lizard thermal capacities over 72-h periods. We fabricated a total of ten lizard models for field use. We calibrated Thermochron iButtons (DS1921G-F5; Maxim/Dallas Semiconductor, Dallas, TX) using methods established by Hasegawa et al. (2005), placed iButtons inside the OTMs, and set the iButtons to record temperature at 10-min intervals over a 72-h period. We placed OTMs in the field in locations where the lizard species in this study were most regularly observed and captured. In each location, we placed a small model (60 mm length \times 15 mm diameter) and a large model (246 mm length \times 15 mm diameter) within 20 cm of each other (Shine and Kearney 2001); we placed a total of five pairs of models (a pair of models represents a large and small model) in each microhabitat type within \sim 5 m of each other. We used small OTMs to simulate *N. humilis*, *N. limifrons*, *Lepidophyma flavimaculatum*, *S. cherriei*, *Gonatodes albogularis*, and *Hemidactylus frenatus* based on their average SVL (<60 mm), and large OTMs to simulate *A. festiva*, *Iguana iguana*, *Basiliscus vittatus*, and *Thecadactylus rapicauda* (SVL >60 mm). We averaged T_o data over 72 h from the five sets of models within each microhabitat type (buildings, open, leaf litter, and forest floor) and each model type (small model and large model). We downloaded T_a data for the same 72-h periods from the La Selva meteorological station (Sarapiquí, Heredia, Costa Rica), which records minimum, maximum, and average air temperatures from an open site at the base of a radio tower at La Selva Biological Station (10°25'53.14"N, 84°0'10.51"W).

For each species, we calculated WT by subtracting average T_b of all individuals per species during field capture from CT_{max} . This figure establishes the temperature change an animal can tolerate before the environment is no longer suitable (Deutsch et al. 2008); the lower an animal's WT, the less temperature increase it can tolerate.

To explore the effects of global warming, we used two predicted temperature changes by the year 2080 (Magrin et al. 2007): a conservative (low) estimate based on a predicted average 1.15 °C increase, and a more extreme (high) estimate based on a predicted average 5.8 °C increase. Because the future T_o s in the various microhabitats are not all expected to increase specifically by 1.15 or 5.80 °C due to differences in exposure to solar radiation and other factors, we calculated predicted operative temperatures (T_{adj}) for each microhabitat type to reflect the projected temperatures available to lizards by 2080 in specific microhabitats and to correct for any temperature variation between ambient air temperature from the meteorological station (T_a) and T_o collected from each of the four microhabitat types sampled. We calculated the T_{adj} as:

$$T_{adj} = \frac{T_o \times (T_a + 1.15 \text{ or } 5.80)}{T_a}$$

For both the low and high estimates, we calculated the number of hours per day that T_{adj} would exceed the species' CT_{max} in their specific microhabitat. Number of hours per day currently available subtracted from predicted hours available in 2080 gave two estimates of the projected activity time lost in the future due to climate change.

Data analysis

Our data did not meet the assumptions for parametric testing, so we tested the effects of microhabitat type (fixed effect) and SVL and species (random effects) on CT_{max} using a generalized linear mixed model (GLMM) with the package nlme (Pinheiro et al. 2013) in R (R Development Core Team 2012). A separate GLMM with microhabitat type and SVL as fixed effects and species as a random effect was performed to examine the relative importance of SVL and microhabitat type as predictors of CT_{max} . Using methods described by Nakagawa and Schielzeth (2013), we calculated a general measure of R^2 , marginal R^2 (R^2_{GLMM}), from this model to estimate the variance explained by microhabitat type and SVL. Because two of the selected microhabitats (leaf litter and forest floor) only had one species representative each, we used phylogenetic independent contrasts to assess the effect of microhabitat type on CT_{max} independent of phylogeny using a tree inferred from 29 nuclear loci and C-mos nuclear DNA sequences (Townsend et al. 2011; Han et al. 2004).

Results

CT_{max} was highest in lizards living in open microhabitats, followed by buildings, and then forest floor and leaf litter (Fig. 1). Microhabitat type had a significant effect on CT_{max} ($F_3 = 469.5$, $p < 0.001$), as did SVL ($F_1 = 185.4$, $p < 0.001$), with 38 % of the variation in CT_{max} being explained by microhabitat type ($R^2_{GLMM} = 0.38$) and 8 % of the variation explained by SVL ($R^2_{GLMM} = 0.08$). The effect of microhabitat type was greatest for the forest floor lizards ($t = 38.12$, $p < 0.001$), followed by open microhabitat ($t = 8.58$, $p < 0.001$), building ($t = 6.21$, $p < 0.001$), and leaf litter ($t = 1.38$, $p = 0.02$) lizards. Results from phylogenetic independent contrasts showed a significant relationship between CT_{max} and microhabitat type, independent from phylogeny [$R^2 = 0.40$, $R^2(\text{adj}) = 0.33$, $F_{1,8} = 5.38$, $p = 0.048$].

WT also varied across species, and can be grouped into three categories: high (>10 °C; *T. rapicauda*, *G. albogularis*, and *H. frenatus*), medium (5–8 °C; *L. flavimaculatum*,

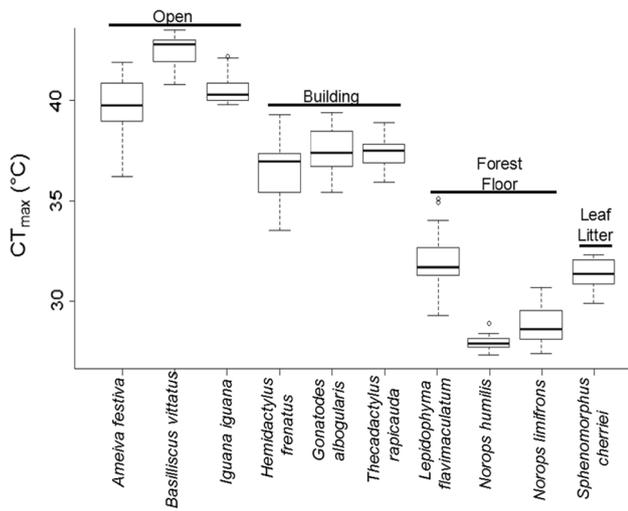


Fig. 1 Comparison of critical thermal maxima (CT_{max} ; °C) of ten species of tropical lowland lizards from La Selva Biological Station (Costa Rica), grouped by microhabitat type. *Open circles* represent outlying individuals

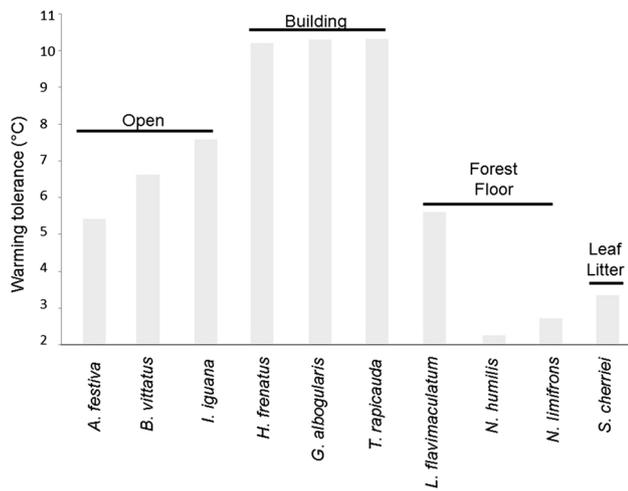


Fig. 2 Warming tolerance (CT_{max} minus body temperature; °C) for ten species of tropical lowland lizards from La Selva Biological Station

A. festiva, *I. iguana*, and *B. vittatus*) and low (<5 °C; *N. limifrons*, *N. humilis*, and *S. cherriei*) (Fig. 2). Even at the highest predicted temperature changes, the lizards found in buildings—*G. albogularis*, *H. frenatus*, and *T. rapicauda*—will not lose any daily activity time (Fig. 3) because their WT is so high. In contrast, lizards in each of the other three microhabitat types (Figs. 4, 5, 6) will experience temperatures above their CT_{max} .

Four species of lizards are currently living in environments with temperatures that exceed their CT_{max} for portions of a 24-h period (*A. festiva*, *N. limifrons*, *N. humilis*, and *I. iguana*;

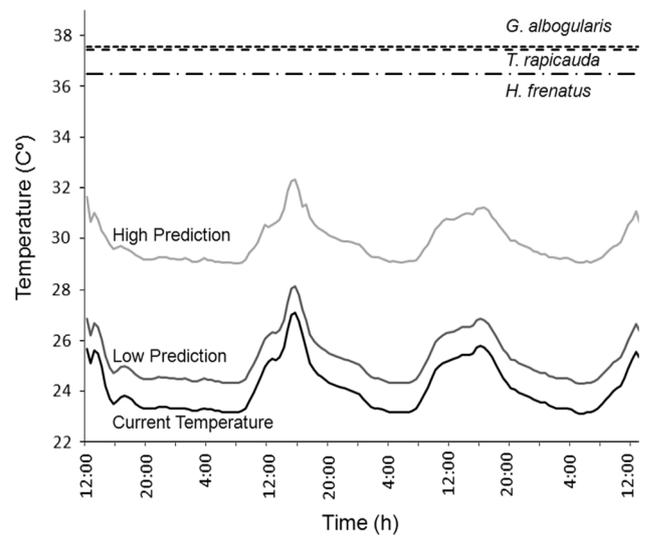


Fig. 3 Lizards inhabiting building surfaces at La Selva Biological Station are not at risk of extinction from rising temperatures because projected ambient temperatures will not exceed their CT_{max} . *Solid lines* show 72-h average temperature fluctuations (°C) of building surfaces: currently, under “low” climate change predictions (+1.15 °C), and under “high” climate change predictions (+5.8 °C). *Dashed lines* show CT_{max} of *G. albogularis* ($n = 20$), *T. rapicauda* ($n = 16$), and *H. frenatus* ($n = 20$)

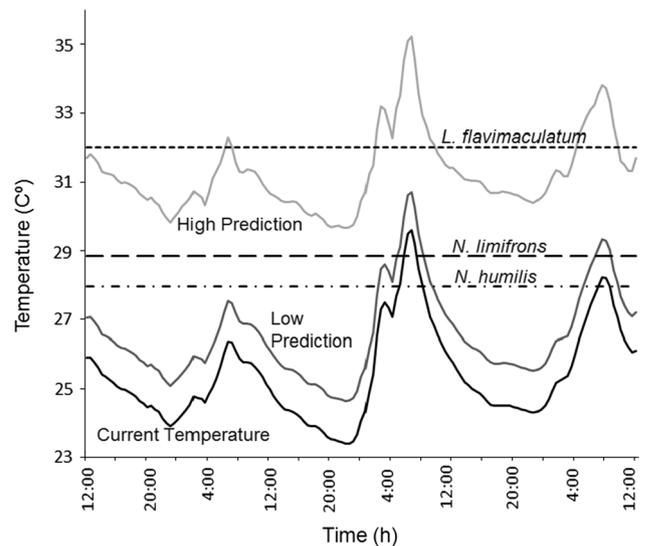


Fig. 4 Lizards inhabiting the forest floor at La Selva Biological Station will experience at least some reduction in activity time because future ambient temperatures will exceed their CT_{max} . *Solid lines* show 72-h average temperature fluctuations (°C) of the forest floor: currently, under low climate change predictions (+1.15 °C), and under high climate change predictions (+5.8 °C). *Dashed lines* show CT_{max} of *L. flavimaculatum* ($n = 20$), *N. limifrons* ($n = 20$), and *N. humilis* ($n = 20$)

Table 2). Taking into account the most conservative predictions of a climate change model, three species (*A. festiva*, *N. humilis*, and *N. limifrons*) will lose more than one additional hour of daily

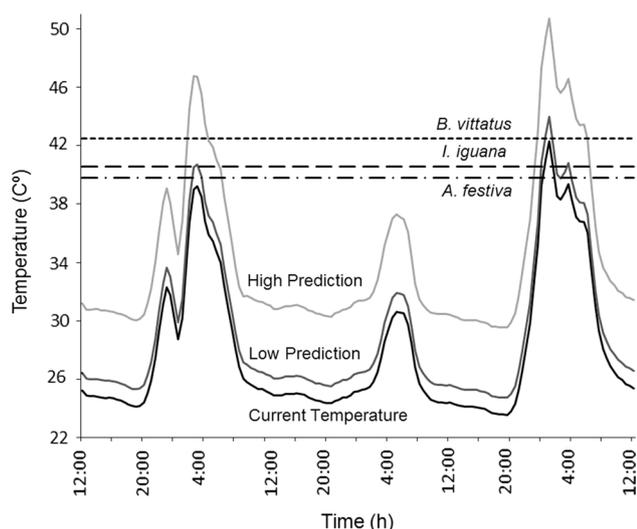


Fig. 5 Lizards inhabiting open spaces at La Selva Biological Station will experience at least some reduction in activity time because future ambient temperatures will exceed their CT_{max} . Solid lines show 72-h average temperature fluctuations ($^{\circ}C$) of the open spaces: currently, under low climate change predictions (+1.15 $^{\circ}C$), and under high climate change predictions (+5.8 $^{\circ}C$). Dashed lines show CT_{max} of *B. vittatus* ($n = 11$), *I. iguana* ($n = 12$), and *A. festiva* ($n = 20$)

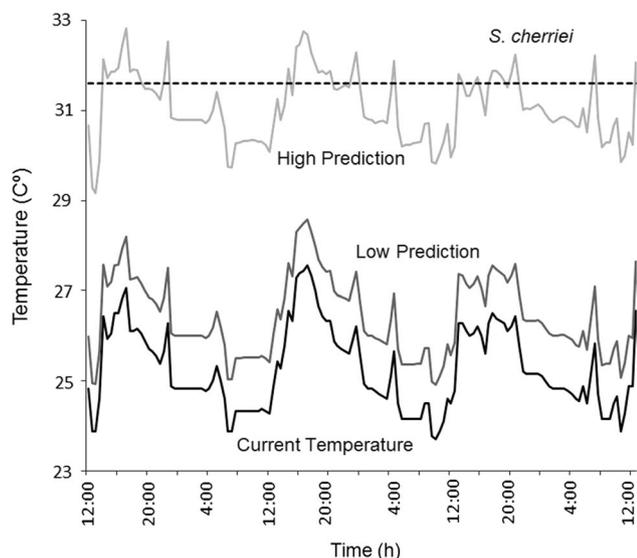


Fig. 6 A lizard species (*S. cherriei*) inhabiting leaf litter at La Selva Biological Station will experience at least some reduction in activity time because future ambient temperatures will exceed its CT_{max} . Solid lines show 72-h average temperature fluctuations ($^{\circ}C$) of the leaf litter: currently, under low climate change predictions (+1.15 $^{\circ}C$), and under high climate change predictions (+5.8 $^{\circ}C$). Dashed lines show CT_{max} of *S. cherriei* ($n = 16$)

activity time. All but three lizard species will lose more than 1 h of daily activity time under the highest predicted temperature-change model; five species will lose more than 4 h day^{-1} .

Discussion

Our hypothesis that lizard species at La Selva will experience a decrease in available daily activity time in accordance with both low and high models of climate change by 2080 (Magrin et al. 2007) was supported for some but not all species. CT_{max} varied among species and was highest in species occupying open areas and lowest in forest- and leaf litter-dwelling species. Species with the lowest CT_{max} also had the lowest WT (*S. cherriei*, *N. humilis*, *N. limifrons*); however, those species with the highest CT_{max} (*B. vittatus*, *I. iguana*, *A. festiva*) did not have the highest WT. Instead, lizards living around buildings (*G. albogularis*, *H. frenatus*, *T. rapicauda*) had the highest WT values but only a moderate CT_{max} (Fig. 4).

We found that some of the lizard species tested are currently living in microhabitats that exceed their CT_{max} for portions of the day (Table 2), meaning that they cannot be active all day long. These same species are predicted to lose further daily activity time under even the conservative, low model of predicted climate change. We also found that all but three lizard species would lose some daily available activity time under models predicting the highest temperature increases by 2080. Sinervo et al. (2010) suggested that a loss of ≥ 3.85 h day^{-1} is associated with the risk of extinction. According to this metric, four species in this study (*S. cherriei*, *N. limifrons*, *L. flavimaculatum*, and *N. humilis*) are at serious risk of population decline and local extirpation at La Selva and potentially beyond if the extreme scenario of climate change is realized because they will lose over 8 h of available daily activity time. Additionally, three other species might be at serious risk of lowland extirpation under models predicting the highest temperature increase, as their predicted time losses approach the extinction threshold suggested by Sinervo et al. (*A. festiva*, 3.67 h; *B. vittatus*, 3 h; and *I. iguana*, 3.5 h). Interestingly, the four most susceptible species all live in leaf litter or on the forest floor, suggesting that of all microhabitats sampled, those living in the forest are most susceptible to detrimental impacts from future temperature increases. Species that inhabit open areas may also be susceptible to detrimental effects of temperature increases. Assuming no physiological changes, *N. humilis* and *N. limifrons* are at the greatest risk of local extinction under the high temperature-increase scenario because temperatures in the environment will exceed their CT_{max} for the entire day.

Our assessment of temperatures available to animals in each of the microhabitat types (T_o) was based on stationary models in an attempt to simulate lizard thermal capacities (Dzialowski 2005). Lizards in the wild can move through their environment to maintain preferred T_b s. We attempted to avoid temperature bias due to stationary models by placing multiple sets of OTMs throughout each of

Table 2 Average time (h) in a 24-h period unavailable to lowland tropical lizard species from La Selva Biological Station because ambient temperatures exceed species-specific CT_{max} ; the table shows

Species	Time unavailable under current temperatures (h day ⁻¹)	Time unavailable under low prediction (h day ⁻¹)	Time unavailable under high prediction (h day ⁻¹)
<i>A. festiva</i>	0.5	1.67	4.17
<i>B. vittatus</i>	0	0.33	3
<i>I. iguana</i>	0.33	1.0	3.83
<i>S. cherriei</i>	0	0	9.5
<i>L. flavimaculatum</i>	0	0	4.83
<i>N. humilis</i>	1.83	3.8	24
<i>N. limifrons</i>	0.67	1.8	24
<i>G. albogularis</i>	0	0	0
<i>H. frenatus</i>	0	0	0
<i>T. rapicauda</i>	0	0	0

current environmental temperatures, “low” climate change predictions, and “high” climate change predictions

the microhabitat types where the lizard species were found. By averaging the temperature readings from all the OTMs in each microhabitat, we attempted to create an overall representation of temperatures available to the animals. In an effort to remain consistent we took temperature measurements and placed OTMs in areas where animals were most frequently observed and, more importantly, easily captured. Two species in our study, *I. iguana* and *B. vittatus*, were most frequently captured and available for stable thermal measurements in open areas and were therefore classified as “open” microhabitat specialists. Both species, however, are known to inhabit the forest floor and *I. iguana* frequently basks in the forest canopy (Guyer 1994). Future studies should look to further remove bias from stationary models and attempt to capture a precise thermal regime for animals inhabiting diverse locations in primary and secondary forests.

In contrast to the at-risk species, none of the three species of lizards found on buildings (*G. albogularis*, *H. frenatus*, and *T. rapicauda*) will lose activity time by 2080, even under the highest temperature-increase models. Why are these species seemingly robust to temperature increases (e.g., high WT)? While these three species belong to different families, they are all geckos (infraorder Gekkota). Huey et al. (1989) found that many species of nocturnal geckos experience relatively low T_b s when active but have high CT_{max} levels, similar to those of diurnal lizards. They suggest that geckos are adapted to survive high T_b s that may occur during the day when cool diurnal retreats are unavailable. *H. frenatus* and *T. rapicauda* are both nocturnal, while *G. albogularis* is diurnal (Guyer 1994). Despite this difference in daily activity patterns, there was little difference in body temperatures among the three species (Table 1). However, we never captured a nocturnal species during the daytime, nor did we find their daytime retreats, which might

have biased our T_b measurements for these species resulting in unusually large WT values. An additional life history trait to consider is that *G. albogularis* and *T. rapicauda* are both native to Costa Rica, while *H. frenatus* is an introduced species (Guyer 1994). We found all three species exclusively on buildings, and not in forest, so it may be that their WT are so large because we did not find them in their natural habitat, especially the two native species that were adapted to living in La Selva long before buildings were present. Future studies should look for these three animals in the primary forest and examine the body temperatures they experience there, which may give a more accurate WT description.

Our examination of the effects of microhabitat type, species, and SVL revealed that microhabitat type is the strongest predictor of CT_{max} . This suggests that, regardless of size or evolutionary relationship, the microhabitat type utilized is an important predictor of the maximum temperature a tropical lizard can tolerate. This demonstrates the profound impact habitat specialization has on the thermal limits of tropical lizards. Despite considerable phylogenetic distances, *Norops* spp. (Dactyloidae), *S. cherriei* (Scincidae) and *L. flavimaculatum* (Xantusiidae) have similar CT_{max} (Fig. 1) and all inhabit the forest floor or leaf litter. Second, despite marked size differences in species occupying the same microhabitat type, CT_{max} did not vary considerably. For example, *T. rapicauda* and *G. albogularis* showed nearly identical CT_{max} (37.6 ± 0.2 and 37.4 ± 0.2 °C, respectively) but differed dramatically in size (SVL 104 ± 26 vs. 34 ± 8 mm). The effect of SVL on CT_{max} was not as strong as the effect of microhabitat type on CT_{max} , suggesting that, contrary to previous findings, size is not the greatest predictor of habitat specialization and thermal tolerance (Jenssen et al. 1998), but that other physiological constraints may instead lead to the

microhabitat type an animal inhabits. Also, while previous studies have suggested that larger lizards are at a greater risk of extinction from increasing temperatures (Meiri 2008), we found that the smallest lizard species sampled, *N. humilis*, has the highest risk of local extinction as predicted by total number of daily hours lost (Sinervo et al. 2010). Studies outside of the tropics have demonstrated the fundamental importance of lizards' ability to behaviorally thermoregulate in maintaining optimal body temperatures and for selecting microhabitats (Angilletta et al. 2002a, b; Grover 1996; Belliure et al. 1996). The environmental constraints from a low CT_{max} in species like *N. humilis* further validate findings that tropical species, compared to similarly sized lizards in northern latitudes, have a decreased ability to disperse along altitudinal gradients due to physiological thermal limits that prevent movement outside of their microhabitats (Ghalambor et al. 2006).

There is still ongoing debate as to exactly how global populations will respond to climate change (Walters et al. 2012). Some studies suggest "hotter is better," meaning that animals will have greater physical performance abilities with increased temperature (Angilletta et al. 2010; Asbury and Angilletta 2010), other studies propose that effects will vary among taxa and may be unpredictable (Frazier et al. 2006), and other groups suggest we are currently in the midst of a sixth mass extinction event brought about by climate change (Wake and Vredenburg 2008). Unfortunately, most climate change models predict dire outcomes for global lizard populations (Thomas et al. 2004; Sinervo et al. 2010; Huey et al. 2010). Two important considerations in these assessments are how close the lizards are to their CT_{max} in nature and how good they are at acclimatizing or adapting to changing temperatures (Stillman 2003). In northern latitudes, species under rising temperature pressures were forced to switch from diurnal to nocturnal activity patterns (Vasconcelos et al. 2012). In other parts of the world, acclimatization, and eventually heritable changes in thermal tolerances, happened in a relatively short time (Leal and Gunderson 2012). In this study, we made no attempt to quantify if or how these species will be able to acclimatize or adapt to increasing temperatures. Future research on lowland tropical species should focus attention on species' relative ability to adjust to changing temperatures in both long- and short-term warming scenarios.

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Author contribution statement G. A. B. and S. M. W. conceived and designed the experiments. G. A. B. and S. M. W. conducted fieldwork and performed the experiments. G. A. B. and E. N. T. analyzed the data. G. A. B., E. N. T., and S. M. W. wrote the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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