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Ecology

Using microhabitat thermal heterogeneity to avoid lethal overheating: an empirical approximation in reproductive oviparous and viviparous lizards

Usando la heterogeneidad térmica a nivel microhábitat para evitar el sobrecalentamiento letal: una aproximación empírica en lagartijas ovíparas y vivíparas

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Abstract

Global warming has been recognized as a great threat for biodiversity. Particularly, it has been predicted that temperature raise could be lethal for ectothermic species in tropical regions, because their physiological and ecological traits are linked to specific ranges of environmental temperatures. However, some species may have been exposed for decades at temperatures exceeding their maximum thermal limit for embryonic development. Understanding how these organisms have faced historical extreme temperatures will allow us to improve inferences of species responses to the expected temperature increase. Here, we assessed whether 2 lizards, *Sceloporus horridus* (oviparous) and *Sceloporus stejnegeri* (viviparous) have been exposed to potential lethal thermal regimes where they inhabit, and whether behavioral use of microhabitat thermal heterogeneity has enabled them to avoid overheating on their offspring. We found that historical, current, and future environmental temperatures exceed the maximum limit tolerated by developing embryos of both species. However, the available temperature at microhabitat level for viviparous and potential nesting places for oviparous lizards offer thermal refuges with temperatures lower than maximum threshold tolerated. Our data suggest that thermoregulatory behavior and nesting adjustments, jointly with microhabitat thermal heterogeneity might buffer damages of warmest environmental temperature expected on developing offspring of these 2 lizards.
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Keywords: Behavioral and nesting responses; Overheating; Temperature rise; Thermal heterogeneity; Reproductive mode

Resumen

El calentamiento global es reconocido como una amenaza a la biodiversidad. En particular, se pronostica que el aumento de temperatura será letal para especies ectotérmicas en los trópicos, pues sus rasgos biológicos y ecológicos funcionan en intervalos específicos de temperatura. Sin embargo, algunas especies podrían haber enfrentado por décadas temperaturas que exceden los límites térmicos para ciertos rasgos, como el desarrollo embrionario. Entender cómo estos organismos han enfrentado estas temperaturas permitirá mejorar las inferencias sobre sus posibles respuestas al incremento de la temperatura. Aquí evaluamos si 2 lagartijas, *Sceloporus horridus* (ovípara) y *Sceloporus stejnegeri* (vivípara), han estado expuestas a temperaturas históricas deletéreas y si el uso de la heterogeneidad térmica del microhábitat ha evitado un impacto negativo en

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el desarrollo embrionario. Nuestros resultados muestran que la temperatura histórica, actual y futura excede el umbral térmico para el desarrollo embrionario en ambas especies, sin embargo, la temperatura a nivel de microhábitat para lagartijas vivíparas y los sitios potenciales de anidación para ovíparas ofrecen refugios térmicos para el desarrollo de sus embriones. Nuestros datos indican que el comportamiento termorregulador y de anidación, junto con la heterogeneidad térmica del microhábitat, podrían amortiguar los impactos del incremento de la temperatura para estas 2 especies.

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Palabras clave: Respuestas termorreguladoras y de anidación; Sobrecalentamiento; Incremento de temperatura; Heterogeneidad térmica; Modo reproductor

Introduction

Global warming has been considered one of the major contemporary threats to biodiversity and survival of terrestrial ectothermic species in the tropics (Huey & Tewksbury, 2009; Williams, Jackson, & Kutzbach, 2007), where most of these organisms operate at environmental temperatures closer to their thermal tolerance limits for suitable performance of key physiological processes such as feeding, water balance, locomotion and breeding (Andrews, Mathies, & Warner, 2000). Therefore, even a slight temperature increase could lead the local extirpation of populations (Huey & Tewksbury, 2009; Sinervo et al., 2010). Furthermore, some ectothermic species such as lizards exhibit low dispersion capacities to migrate in short term to localities with suitable thermal conditions (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011). In consequence, lizards in tropic latitudes could be more vulnerable to the effects of global warming than species of temperate latitudes (Deutsch et al., 2008; Huey et al., 2009).

However, before considering the inexorable negative effects of rising temperatures expected on the persistence of populations, it is important to regard that some populations might have experienced extreme heat for over several decades during their respective reproductive periods. The fact that such populations remain, shows that lizards are able to avoid deleterious effects of damaging temperatures on developing offspring and themselves, possibly by means of using thermal heterogeneity of microhabitat behaviorally (Huey et al., 2012; Scheffers, Edwards, Diesmos, Williams, & Evans, 2014). Thus, 2 main questions arise: (1) which are the specific behavioral mechanisms that have enabled small *Sceloporus* lizards to achieve and maintain suitable temperature ranges for their developing offspring and themselves? and (2) can behavioral mechanisms be useful to lizard populations persistence in a global warming context? Therefore, a main goal in the short term should be to describe and understand how species have used the thermal heterogeneity at the microhabitat level and how these have allowed them to deal with historic high macroclimatic thermal regimes. We hypothesize that both viviparous and oviparous sceloporine tropical lizards attain suitable body temperatures for their offspring, modulating specific thermoregulatory mechanism as microhabitat selection and shuttling between microhabitats in the case of viviparous species, and accurate selection of nesting sites of oviparous species. To test the above ideas may allow us to generate inferences on their future persistence and distribution in a global warming context.

Here, we aimed to assess whether 2 lizard species, with different parity mode, have historically been exposed to temperatures close or above their thermal tolerance limits for a successful embryonic development (34 °C; Beuchat, 1986; Mathies & Andrews, 1997), and if so, which behavioral mechanisms have enabled them to face these thermal regimes. For viviparous *Sceloporus stejnegeri*, we characterized the current operative temperature (T_e) available, as well as relevant traits of its thermoregulatory behavior. For oviparous *Sceloporus horridus*, we characterized the temperature available at potential nesting sites. By using 2 species with different reproductive modes allowed us to understand how these species have avoided overheating and discuss if behavioral abilities such as thermoregulatory traits and nesting site selection will enable them to successfully face heat stress in a future scenario of temperature rise.

Materials and methods

Viviparous lizard *Sceloporus stejnegeri* (Stejneger's spiny lizard) breeds from fall to winter. Studied population inhabit the tropical dry forest at 350 m in elevation (type locality) at Tierra Colorada, Guerrero (16°27′36″ N, −98°39′ W) (Bell, Smith, & Chiszar, 2003; Wiens & Reeder, 1997). Oviparous *S. horridus* (Southern rough lizard), breeds from spring to summer. Our study population is located in tropical dry forest at 520 m asl (Sites, Archie, Cole, & Flores-Villela, 1992; Valencia-Limón, Castro-Franco, & Bustos-Zagal, 2014) at Xalitla, Guerrero (17°59′24″ N, −99°32′24″ W). Both localities are located in the middle section of the Balsas River basin. Embryonic development of both species tolerated a maximum thermal threshold of 34 °C under laboratory treatments (Beuchat, 1986; Mathies & Andrews, 1997) and when this boundary is exceeded, embryos may exhibit physical abnormalities which increase their mortality (Beuchat, 1988; Beuchat & Ellner, 1987).

We obtained and analyzed the trend of historical maximum environmental temperature (T_{hmax}) for both localities during the reproductive season of each studied species: from October to March for *S. stejnegeri* (Ramírez-Pinilla, Calderón-Espinosa, Flores-Villela, Muñoz-Alonso, & Méndez-de la Cruz, 2009) in Tierra Colorada and from March to September for *S. horridus* in Xalitla (Valdéz-González & Ramírez-Bautista, 2002). Historical maximum environmental temperature values (T_{hmax}) were obtained from 3 meteorological stations situated near (around 1 km) each locality (Comisión Nacional del Agua [Conagua]

http://smn.cna.gob.mx/es/climatologia/informacion-climatologica; temperature records ranging from 1953 to 2000). With these data we are able to sketch the macroclimatic temperature regime experienced by both lizard populations over the past decades in each locality.

Values of maximum environmental temperature (T_{fmax}) forecasted by using climate model outputs were obtained, from the Centro de Ciencias de la Atmósfera (Universidad Nacional Autónoma de México [UNAM]; www.atmosfera.unam.mx). Climate projections were derived for 2030 and 2050 ECHAM5/MPI climate model. Climate anomalies were scaled based on the A2 scenario, which describes a heterogeneous world regionally oriented to the economic development. The *per capita* economic growth and technological change are slower than in the other scenarios. Global concentrations of CO_2 shall increase from 380 ppm in 2000 to 700 ppm in 2080, and temperature will rise by 2.8 °C according to suggested by the Intergovernmental Panel on Climate Change (IPCC, 2013).

Fieldwork in Xalitla in July was carried out, which corresponds to the organogenesis stage development for *S. horridus* embryos (Valdéz-González & Ramírez-Bautista, 2002). Because it is difficult to locate lizard nests, we characterized soil temperature for several depths of potential nesting. Egg temperature is regulated by the temperature of the surrounding soil therefore, measurement of soil temperature represents a good proxy for the temperature experienced by embryos within the nest (Ackerman & Lott, 2004). Potential nesting places were located under canopy covered areas (i.e. shade conditions) where gravid adult females were observed, and at contiguous open sandy areas (i.e. full sun conditions) potentially used by nesting females (Angilletta, Sears, & Pringle, 2009). Potential nesting places were separated by 5 lineal meters from each other.

We dug 18 nests perpendicularly to ground surface and set Dataloggers (Hobo pendant® UA-002-08; 0–50 °C ± 0.53 °C at 0–50 °C calibration) in each hypothetical nest. Datalogger sensors were placed as follows: 6 inside hypothetic nests at the known nesting depth under shade microhabitats (4.7 cm; Warner & Andrews, 2002), 6 inside hypothetic nests at the known nesting depth under full sun conditions (6.4 cm; Angilletta et al., 2009), and finally 6 inside hypothetical nests built at experimental depths (8.4 cm) under full sun. Further, one Datalogger was used to record current air temperature (T_{cenv}) at 1 cm above the ground in sun-exposed sites. Temperature was recorded every 30 min from 08:00 to 18:00 h for 6 consecutive days in July. We compared temperatures between nest in shaded and full sun microhabitats and among nests depths via nested Anova test, because both variables are changed at the same time (Logan, 2011). Additionally, we used a linear regression between nests at 6.4 cm in depth and T_{cenv} to test whether there is a relationship between them, as a way to connect nest temperature data with historical temperature data.

Fieldwork in Tierra Colorada was carried out in November, which corresponds to organogenesis stage development of embryos for *S. stejnegeri* (Ramírez-Pinilla et al., 2009). To record operative temperature (T_e) experienced by adult females, we built hollow copper models (85 mm and 31.8 mm in diameter) that mimic the morphology and absorptivity of *S. stejnegeri* lizards. Models were calibrated outdoors in the Tierra Colorada locality using restrained live lizards to observe if their T_b and temperature of models varies jointly and attains the same equilibrium temperatures. We measured simultaneously, body temperature (T_b) of 3 restrained live lizards and 3 copper models temperatures attached to a digital thermocouple thermometer. A pair composed of a copper model and a restrained live lizard were placed under solar radiation loads available at each of the microhabitats deep shade (*Dsh*), filtered sun (*FS*) and complete sun (*CS*), we simultaneously measured both temperatures every 60 s for 10 min, during midday when the heat loads tend to reach their maximum intensity in the Tierra Colorada locality.

We validated if model temperatures accurately simulate T_b of lizards by a regression analysis (a significant correlation between T_e models and T_b lizard was detected $F_{1,9} = 177.58$; $R^2 = 0.957$; $p = <0.001$ in *Dsh*; $F_{1,9} = 72.90$; $R^2 = 0.901$; $p = <0.001$ in *FS* and $F_{1,9} = 112.19$; $R^2 = 0.933$; $p = <0.001$ in *CS*). This procedure is appropriate for small animals [≤30 g and100 mm of snout-vent length (SVL)] with negligible heat capacity (Bakken, 1992; Bauwens, Hertz, & Castilla, 1996; Díaz, 1997; Dzialowski, 2005; Hertz, Huey, & Stevenson, 1993). After calibration, we plugged an external thermocouple Hobo U23 Pro v2 external temperature® Datalogger (−40 to 70 °C ± 0.2 °C at 0° to 50 °C calibration) to the copper model's central cavity (Dzialowski, 2005; Hertz, 1992; Hertz et al., 1993). In each microhabitat 10 copper models ($n = 30$) were placed, with the same location and orientation when lizards were observed in the field (see Grant & Dunham, 1988; Hertz, 1992). Then, we recorded every 30 min from 08:00 to 18:00 h for 6 consecutive days (Bakken, 1992). Current air temperature (T_{cenv}) at 1 cm above the ground was also recorded with one Datalogger in *CS* microhabitat. Both, female gravid and viviparous pregnant lizards were captured to record their T_b using a Miller and Weber® cloacal rapid reading thermometer Schultheis model (0–50 °C). We compared T_e values between microhabitats with a non-parametrical analysis (Kruskal–Wallis test) using localities and microhabitats as factors.

Additionally, when an individual was sighted out of their shelter the following thermoregulatory traits were registered: (1) microhabitat occupied to determine which is the most frequented by lizards, and (2) basking time (*BT*), in seconds, that lizards spent in a specific microhabitat, which was compared between microhabitats via one-way Anova. Chi square test with Monte Carlo simulations (5,000) and post hoc Marascuilo procedure was used to test significant differences in the frequency in which active lizards were observed on each microhabitat (Agresti, 1990). Statistical analyses were implemented with α of 0.05 in R (R Development Core Team, 2013).

Results

For both study sites, we found that T_{hmax} was higher than 34 °C for most of the months, during the reproductive season for both species, in the last 50 years. For *S. stejegeri* warmer months were November–March and for *S. horridus* were March–August

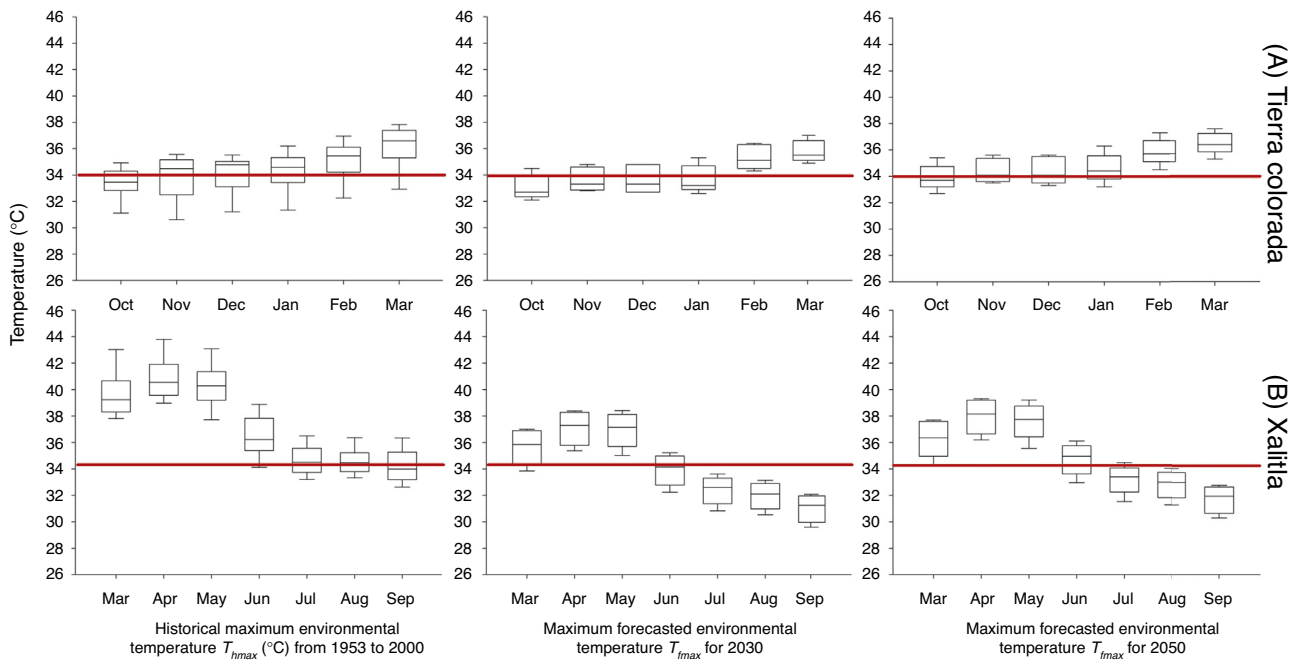

Figure 1. Historic mean monthly maximum environmental temperatures available in the localities inhabit by *Sceloporus stejnegeri* in Tierra Colorada (A) and *S. horridus* in Xalitla (B), in their respective reproductive season months from 1953 to 2000 and forecasts for 2030 and 2050. The red line shows the critical thermal maximum for developing embryos.

(Fig. 1). In Tierra Colorada, T_{hmax} average was 34.4 ± 0.23 °C and did not show statistical differences ($F_{2,\,400} = 2.38$; $p = 0.093$) with maximum forecasted environmental temperature (T_{fmax}) to 2030 ($\tilde{X} = 34.1 \pm 1.3$ °C) and 2050 ($\tilde{X} = 34.9 \pm 1.2$ °C). In Xalitla, T_{hmax} average was 37.2 ± 1.5 °C. In this case, T_{hmax} was significantly higher ($F_{2,\,501} = 51.0$; $p < 0.05$; Tukey's hsd test $p < 0.05$) than maximum forecasted environmental temperature (T_{fmax}) to 2030 ($\tilde{X} = 34.1 \pm 2.53$ °C) and 2050 ($\tilde{X} = 34.8 \pm 2.53$ °C; Fig. 1).

In Tierra Colorada, we found statistical differences for current operative temperature (T_e) at microhabitat level ($H_2 = 9.961$; $p < 0.05$, $n = 33$), where lowest values were recorded in *Dsh* ($\tilde{X} = 31.9 \pm 2.8$ °C) than *FS* ($\tilde{X} = 33.6 \pm 3.4$ °C) and *CS* ($\tilde{X} = 36.3 \pm 3.2$ °C) microhabitats (Dunn's test $p < 0.05$, Fig. 2A). T_e in *Dsh* microhabitat exceeds the maximum tolerated threshold of 34 °C for developing embryos for only 2 h a day (14:00–16:00 h). Conversely, in *FS* and *CS* microhabitats, T_e exceeded the tolerated threshold several hours a day (Fig. 2B).

For basking time of *S. stejnegeri* we observed active individuals spending significantly more time in *Dsh* ($\tilde{X} = 12.5 \pm 0.4$ s) than in *CS* ($\tilde{X} = 8.5 \pm 0.5$ s), and *FS* ($\tilde{X} = 10.6 \pm 0.9$ s) microhabitats ($F_{2,\,18} = 58.78$; $p < 0.05$; Tukey test $p < 0.05$). Moreover, we found statistical differences in the number of individuals observed by microhabitats ($\chi^2 = 6.45$; $p < 0.05$). The Marascuilo procedure post hoc indicated that the proportion of lizards sighted on *Dsh* ($n = 14$) is significantly higher than observed on *FS* ($n = 4$) and *CS* ($n = 2$) (Table 1).

At Xalitla, current air temperature (T_{cenv}) determines heavily the temperature available in artificial nests at 6.4 cm depth, according to linear regression analysis ($F_{1,\,131} = 356.76$; $R^2 = 0.733$; $p < 0.05$). Also, the current temperature values in nests built in shade microhabitat at 4.7 cm depth ($\tilde{X} = 30.22 \pm 0.6$ °C) were significantly lower than the temperature recorded in nests at a depth of 8.4 cm ($\tilde{X} = 35.46 \pm 4.8$ °C) and 6.4 cm ($\tilde{X} = 36.70 \pm 5.4$ °C) exposed to full sun (nested Anova test, $F_{1,\,132} = 52.40$; $p < 0.05$; Fig. 2C). However, between 6.4 and 8.4 cm depths in nest exposed to full sun, there are no statistical differences (nested Anova test, $F_{1,\,132} = 0.12$; $p = 0.7274$; Fig. 2C). Temperatures inside nests at 4.7 cm depth under shade did not exceed the maximum tolerated threshold for developing embryos (34 °C) throughout the day, contrary to what happens inside nests at 6.4 and 8.4 cm depth (Fig. 2D). Finally, lizards of both species showed a T_b average that did not exceed the deleterious threshold for embryos (gravid *S. horridus* $\tilde{X} = 33.2 \pm 1.22$ °C and pregnant *S. stejnegeri* $\tilde{X} = 31.4 \pm 0.97$ °C).

Table 1
Absolute differences and critical values that denote statistically significant when absolute difference is greater that the critical range, between pairs of microhabitats where lizard's proportions were evaluated by Marascuilo procedure, implemented for positive Chi-square test.

Microhabitats contrast	Absolute differences	Critical value	Significant
$\lvert p(Dsh) - p(FS)\rvert$	0.5000	0.3329	Yes
$\lvert p(Dsh) - p(CS)\rvert$	0.6000	0.2998	Yes
$\lvert p(FS) - p(CS)\rvert$	0.1000	0.2737	No

Discussion

Ectothermic species can show different biological responses to climate change, from hereditary genetic changes (Bradshaw & Holzapfel, 2006; Logan, Cox, & Calsbeek, 2014; Moritz et al., 2012) to phenotypic plasticity (Pigliucci, Murren, & Schlichting, 2006). The evidence in literature suggests that the

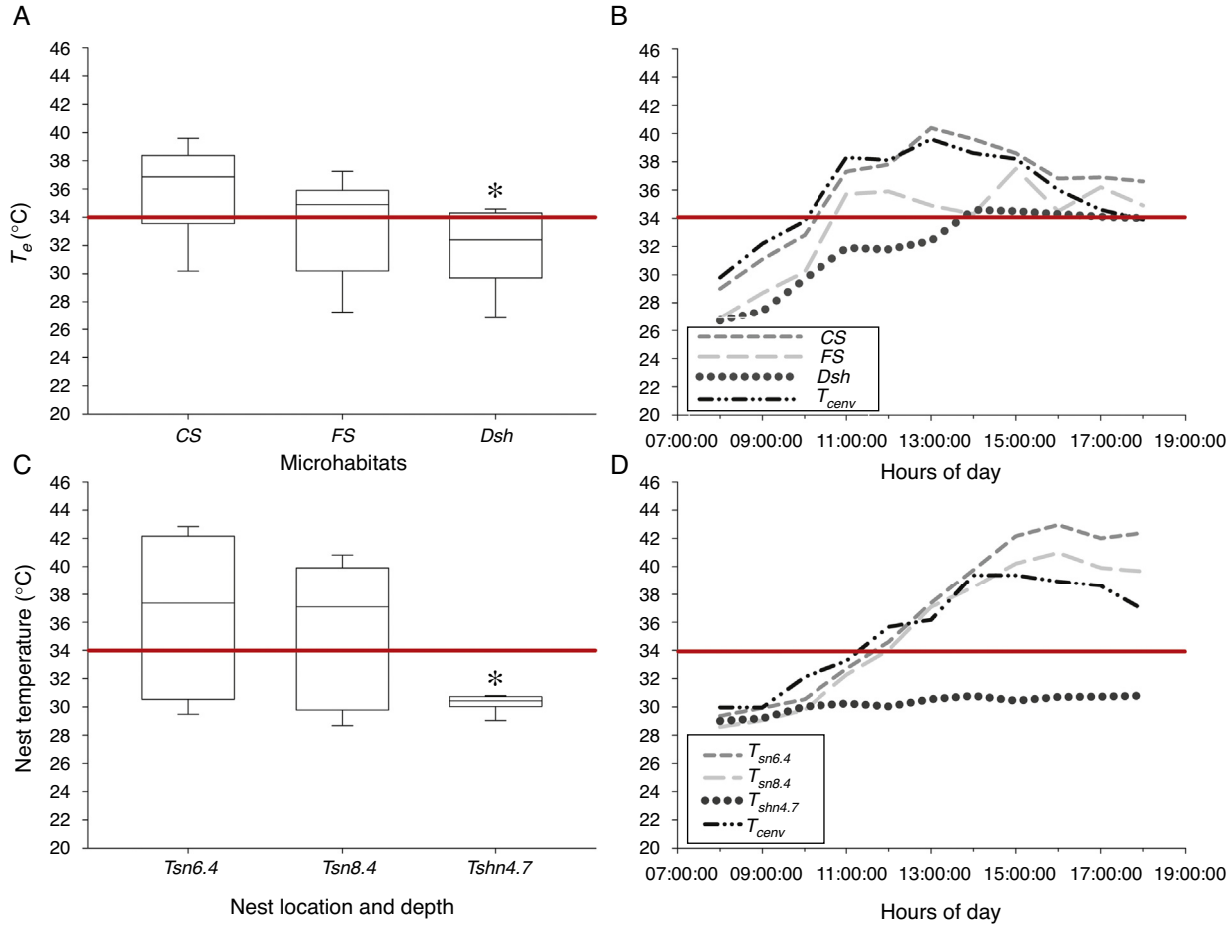

Figure 2. (A) Operative temperatures (T_e) measured at complete sun (*CS*), filtered sun (*FS*) and deep shade (*Dsh*) microhabitats; (B) current air (T_{cenv}) and microhabitats temperature variation through the day at each microhabitat used by pregnant *Sceloporus stejnegeri* lizards at Tierra Colorada, Guerrero; (C) representative temperatures at different soil depths in full sun and shade conditions, and (D) current air temperature (T_{cenv}) and nest variation through the day for *Sceloporus horridus* lizards in Xalitla, Guerrero. The red line is the critical thermal maximum to development embryos of both *Sceloporus* lizards' species (34 °C). Asterisk denotes significance at $p < 0.05$ level.

most straightforward modification under climate change could be behavioral issues. For example, switching time of activity and choosing cool shaded microhabitats as thermal refuges could prevent lizards from being exposed to lethal temperatures (Huey, Hertz, & Sinervo, 2003; Kearney, 2013; Kearney, Shine, & Porter, 2009; Scheffers et al., 2014; Sunday et al., 2014).

Although adults of some species belonging to the *Sceloporus* genus might tolerate temperatures up to 40 °C (Angilletta, Zelic, Adrian, Hurliman, & Smith, 2013; Clusella-Trullas, Blackburn, & Chown, 2011; Clusella-Trullas & Chown, 2014), here we focused on thermal threshold for a successfully embryonic development (34 °C; Beuchat, 1986; Mathies & Andrews, 1997). Our analyses of historical macroclimatic temperature showed that maximum temperature has frequently exceeded the tolerated threshold of 34 °C for successful embryonic development for both *Sceloporus* lizard species. This fact suggests that *S. horridus* and *S. stejnegeri* have effectively used the thermal heterogeneity available at microhabitat level to avoid lethal overheating. This heterogeneity is provided by vegetation and local orography, which has enabled them to avoid the potential lethal effects of high environmental temperatures via regulating behavioral traits to attain suitable temperature ranges to their developing offspring (Goller, Goller, & French, 2014; Sears, Raskin, & Angilletta, 2011).

We found that pregnant viviparous *S. stejnegeri* lizards attained a suitable temperature range for themselves and their offspring mainly by choosing microhabitats with cooler conditions under canopy, moreover, rocky substrates with crevices available would be useful for lizards to avoid the exposure to lethal temperatures in the warmest microhabitats for longer times (Scheffers et al., 2014; Sears et al., 2011). On the other hand, oviparous *S. horridus* might be choosing potential nesting sites with appropriate thermal conditions to lay their eggs.

Together, thermal heterogeneity of microhabitat and behavioral abilities of lizards seems to buffer the negative effects of extreme local heat conditions on developing embryos. Pregnant *S. stejnegeri* lizards are active mostly on *Dsh* microhabitat provided by vegetal cover available, because T_e on *FS* and *CS* microhabitats exceed embryo's thermal tolerated threshold (34 °C) throughout the day. Additionally, these lizards move between different microhabitats, which allow them to be active for several hours for feeding, exploration, and social interactions

(Bauwens et al., 1996; Carrascal, López, Martín, & Salvador, 1992; Kearney et al., 2009).

Gravid females of oviparous *S. horridus* have the availability of soil under shade with the physical characteristics (sandy and relatively near to water) described as suitable for nesting for other species belonging to *Sceloporus* genus (Warner & Andrews, 2002). Shaded places are facilitated by canopy that covers almost 100% of direct sunlight (Parker, Tinoco-Ojanguren, Martínez-Yrízar, & Maass, 2005). The data obtained in artificial/hypothetical nests suggest that these lizards could buffer negative impact of high environmental temperatures on their offspring by simply being active and nesting under the shade provided by vegetal cover (Angilletta, 2009; Doody, 2009; Telemeco, Elphick, & Shine, 2009), rather than digging deeper nests in full sun where temperatures exceeds the maximum threshold tolerated by *S. horridus* offspring. Data from artificial/hypothetical nests are a good indicator for the temperatures at which embryos can be exposed because like natural nests, their temperature is regulated by the temperature of the surrounding soil (Brown & Shine, 2004; Campbell & Norman, 1998). Therefore, the behavioral selection of appropriate nesting sites under the canopy could be the most plausible strategy for embryos to avoid extreme heat at the Xalitla locality.

We suggest that the specific behavioral mechanisms described here are the potential strategies that have allowed the 2 studied *Sceloporus* species to achieve suitable temperature regimes for healthy development of their offspring, and perhaps for the suitable performance of their own physiological processes, in our study localities, which have presented historical and current temperatures above the critical thermal threshold. Therefore, exploiting thermal heterogeneity of microhabitat by behavioral mechanisms, could be crucial to population's persistence in sites with historic and current warmer temperatures (Goller et al., 2014; Sears et al., 2011; Sunday et al., 2014). Furthermore, for future temperature rise scenarios we found that thermal regimes remain similar to the historical and current temperature ranges therefore, behavioral responses could be useful to lizard populations and do not face a threat of erosion caused for a stressful warming in the future; however, it depends on the fact that microhabitat heterogeneity is not modified by human activities (Scheffers et al., 2014; Sunday et al., 2014). Thus, the availability of shaded areas for tropical ectothermic organisms becomes a key resource for them to buffer the impacts of macroclimatic higher temperatures (Huey & Tewksbury, 2009; Kearney, 2013; Kearney et al., 2009; Scheffers et al., 2014).

Here, we provide empiric evidence that lizards, as well as other species are not inert biological entities unable to respond to environmental changes as previous studies suggest (Sinervo et al., 2010). However, there is a need to integrate such information in studies on the effects of climate change on biodiversity for a better understanding of potential species responses to face global warming. Future research should explore other potential ways of organismic adaptation to a rapid environmental warming, such as genetically regulated changes in ranges of physiological tolerances (Leal & Gunderson, 2012; Moritz et al., 2012), biomolecular development of mechanisms of protein production at the cellular level that provide full corporal adaptation to hyperthermia (Evgen'ev, Garbuz, Shilova, & Zatsepina, 2007), phenotypic plasticity in thermal physiology traits (Niehaus, Angilletta, Sears, Franklin, & Wilson, 2012), and to evaluate the rate at which this changes occurs (Huey et al., 2012).

With this in hand, we will have a broader overview to understand the potential effects of global warming on species and their potential responses. Even though, behavioral strategies can be useful to buffer the negative impact of the temperature rise, but could be not enough to cope with a fast extreme warming or unpredictable and longer drought periods and landscape fragmentation. In some cases, behavior could limit local adaptation of thermal physiology required to deal with this phenomenon (Barrows, Rotenberry, & Allen, 2010; Buckley, Ehrenberger, & Angilletta, 2015; Huey et al., 2003; Sinervo et al., 2010).

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References

Ackerman, R. A., & Lott, D. B. (2004). Thermal hydric and respiratory climate of nests. In D. C. Deeming (Ed.), *Reptilian incubation: environment, evolution, and behavior* (pp. 15–43). London: Nottingham University Press.

Agresti, A. (1990). *Categorical data analysis*. New York: John Wiley & Sons.

Andrews, R. M., Mathies, T., & Warner, D. (2000). Effect of incubation temperature on morphology, growth, and survival of juvenile *Sceloporus undulatus*. *Herpetological Monographs*, *14*, 420–431.

Angilletta, M. J. (2009). *Thermal adaptation: a theoretical and empirical synthesis*. Oxford: Oxford University Press.

Angilletta, M. J., Sears, W. S., & Pringle, M. P. (2009). Spatial dynamics of nesting behavior: lizards shift microhabitats to construct nest with beneficial thermal properties. *Ecology*, *23*, 231–232.

Angilletta, M. J., Zelic, M. H., Adrian, G. J., Hurliman, A. M., & Smith, C. D. (2013). Heat tolerance during embryonic development has not diverged among populations of a widespread species (*Sceloporus undulatus*). *Conservation Physiology*, *1*, 1–9.

Bakken, G. S. (1992). Measurement and application of operative and standard operative temperatures in ecology. *American Zoologist*, *32*, 194–216.

Barrows, C. W., Rotenberry, J. T., & Allen, M. F. (2010). Assessing sensitivity to climate change and drought variability of a sand dune endemic lizard. *Biological Conservation*, *143*, 731–736.

Bauwens, D. P., Hertz, H., & Castilla, A. M. (1996). Thermorregulation in lacertid lizard: the relative contributions of distinct behavioral mechanisms. *Ecology*, *77*, 1818–1830.

Bell, E. L., Smith, H. M., & Chiszar, D. (2003). An annotated list of the species-group names applied to the lizard genus *Sceloporus*. *Acta Zoologica Mexicana*, *90*, 103–174.

Beuchat, C. A. (1986). Reproductive influences on the thermoregulatory behavior of a live-bearing lizard. *Copeia*, *4*, 971–979.

Beuchat, C. A. (1988). Temperature effects during gestation in a viviparous lizard. *Journal of Thermal Biology*, *13*, 135–142.

Beuchat, C. A., & Ellner, S. (1987). A quantitative test of life history theory: thermoregulation by viviparous lizard. *Ecological Monographs*, *57*, 45–60.

Bradshaw, W. E., & Holzapfel, C. M. (2006). Evolutionary response to rapid climate change. *Science*, *312*, 1477–1478.

Brown, G. P., & Shine, R. (2004). Maternal nest-site choice and offspring fitness in a tropical snake (*Tropidonophis mairii* Colubridae). *Ecology*, *85*, 1627–1634.

Buckley, L. B., Ehrenberger, J. C., & Angilletta, M. J. (2015). Thermoregulatory behavior limits local adaptation of thermal niches and confers sensitivity to climate change. *Functional Ecology*, *29*, 1038–1047.

Campbell, G. S., & Norman, J. M. (1998). *An introduction to environmental biophysics*. New York: Springer.

Carrascal, L. M., López, P., Martín, J., & Salvador, A. (1992). Basking and antipredator behaviour in a high altitude lizard: implications of heat-exchange rate. *Ethology*, *92*, 43–154.

Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, *333*, 1024.

Clusella-Trullas, S., Blackburn, T. M., & Chown, S. L. (2011). Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. *The American Naturalist*, *177*, 738–751.

Clusella-Trullas, S., & Chown, S. L. (2014). Lizard thermal trait variation at multiple scales: a review. *Journal of Comparative Physiology B*, *184*, 5–21.

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K., Ghalambor, C. K., Haak, D. C., et al. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 6668–6672.

Díaz, J. A. (1997). Ecological correlates of the thermal quality of an ectotherm's habitat: a comparison between two temperate lizard populations. *Functional Ecology*, *11*, 79–89.

Doody, J. S. (2009). Superficial lizards in cold climates: nest site choice along an elevational gradient. *Austral Ecology*, *34*, 773–779.

Dzialowski, E. (2005). Use of operative temperature and standard operative temperature models in thermal biology. *Journal of Thermal Biology*, *30*, 317–334.

Evgen'ev, M. B., Garbuz, D. G., Shilova, V. Y., & Zatsepina, O. G. (2007). Molecular mechanism underlying adaptation of xeric animals. *Journal of Bioscience*, *32*, 489–499.

Goller, M., Goller, F., & French, S. S. (2014). A heterogeneous thermal environment enables remarkable behavioral thermoregulation in *Uta stansburiana*. *Ecology and Evolution*, *4*, 3319–3329.

Grant, B. W., & Dunham, A. E. (1988). Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology*, *69*, 167–176.

Hertz, P. E. (1992). Temperature regulation in Puerto Rican *Anolis* lizards: a field test using null hypotheses. *Ecology*, *73*, 1405–1417.

Hertz, P. E., Huey, R. B., & Stevenson, R. (1993). Evaluating temperature regulation by field active ectotherms: the fallacy of the inappropriate question. *American Naturalist*, *142*, 796–818.

Huey, R. B., Hertz, P. E., & Sinervo, B. (2003). Behavioral drive versus behavioral inertia in evolution: a null model approach. *American Naturalist*, *161*, 357–365.

Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A., Jess, M., & Williams, S. E. (2012). Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *367*, 1665–1679.

Huey, R. B., & Tewksbury, J. J. (2009). Can behavior douse the fire of climate warming? *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 3647–3648.

Huey, R. B., Tewksbury, J. J., Deutsch, C. A., Vitt, L. J., Hertz, P. E., Pérez, H. J. A., et al. (2009). Why tropical forest lizard are vulnerable to climate warming? *Proceedings of the Royal Society of London B: Biological Sciences*, *276*, 1939–1948.

IPCC (Intergovernmental Panel on Climate Change). (2013). *Climate change 2013: the physical science basis, IPCC*. New York: Cambridge University Press.

Kearney, M. (2013). Activity restriction and the mechanistic basis for extinctions under climate warming. *Ecology Letters*, *16*, 1470–1479.

Kearney, M., Shine, R., & Porter, W. P. (2009). The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 3835–3840.

Leal, M., & Gunderson, A. R. (2012). Rapid change in the thermal tolerance of a tropical lizard. *American Naturalist*, *180*, 815–822.

Logan, M. (2011). *Biostatistical design and analysis using R: a practical guide*. London: John Wiley & Sons.

Logan, M. L., Cox, R. M., & Calsbeek, R. (2014). Natural selection on thermal performance in a novel thermal environment. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 14165–14169.

Mathies, T., & Andrews, R. M. (1997). Influence of pregnancy on the thermal biology of the lizard *Sceloporus jarrovi*: why do pregnant females exhibit low body temperatures? *Functional Ecology*, *11*, 498–507.

Moritz, C., Langham, G., Kearney, M., Krockenberger, A., VanDerWal, J., & Williams, S. (2012). Integrating phylogeography and physiology reveals divergence of thermal traits between central and peripheral lineages of tropical rainforest lizards. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *367*, 1680–1687.

Niehaus, A. C., Angilletta, M. J., Sears, M. W., Franklin, C. E., & Wilson, R. S. (2012). Predicting the physiological performance of ectotherms in fluctuating thermal environments. *Journal of Experimental Biology*, *215*, 694–701.

Parker, G., Tinoco-Ojanguren, C., Martínez-Yrízar, A., & Maass, M. (2005). Seasonal balance and vertical pattern of photosynthetically active radiation within canopies of a tropical dry deciduous forest ecosystem in Mexico. *Journal of Tropical Ecology*, *21*, 283–295.

Pigliucci, M., Murren, C. J., & Schlichting, C. D. (2006). Phenotypic plasticity and evolution by genetic assimilation. *Journal of Experimental Biology*, *9*, 2362–2367.

R Development Core Team. (2013). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available online at http://www.R-project.org

Ramírez-Pinilla, M. P., Calderón-Espinosa, M. L., Flores-Villela, O., Muñoz-Alonso, A., & Méndez-de la Cruz, F. R. (2009). Reproductive activity of three sympatric viviparous lizards at Omiltemi, Guerrero, Sierra Madre del Sur, Mexico. *Journal of Herpetology*, *43*, 409–420.

Scheffers, B. R., Edwards, D. P., Diesmos, A., Williams, S. E., & Evans, T. A. (2014). Microhabitats reduce animal's exposure to climate extremes. *Global Change Biology*, *20*, 495–503.

Sears, M. W., Raskin, E., & Angilletta, M. J. (2011). The world is not flat: defining relevant thermal landscapes in the context of climate change. *Integrative and Comparative Biology*, *51*, 666–675.

Sinervo, B., Méndez-de la Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagran-Santa Cruz, M., et al. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science*, *328*, 894–899.

Sites, J. W., Archie, J. W., Cole, C. J., & Flores-Villela, O. (1992). *A review of phylogenetic hypothesis for lizards of the genus* Sceloporus *(Phrynosomatidae): implications for ecological and evolutionary studies*. New York: American Museum of Natural History.

Sunday, J. M., Bates, A. E., Kearney, M. R., Colwell, R. K., Dulvy, N. K., Longino, J. T., et al. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 5610–5615.

Telemeco, R. S., Elphick, M. J., & Shine, R. (2009). Nesting lizards (*Bassiana duperreyi*) compensate partly, but not completely, for climate change. *Ecology*, *90*, 17–22.

Valdéz-González, M. A., & Ramírez-Bautista, A. (2002). Reproductive characteristics of the spiny lizards *Sceloporus horridus* (Squamata: Phrynosomatidae) from México. *Journal of Herpetology*, *36*, 36–46.

Valencia-Limón, E. R., Castro-Franco, R., & Bustos-Zagal, G. M. (2014). Dimorfismo sexual y ciclo reproductor de *Sceloporus horridus horridus* (Wiegmann 1939) (Sauria: Phrynosomatidae). *Acta Zoologica Mexicana*, *30*, 91–105.

Warner, D. A., & Andrews, R. M. (2002). Nest-site selection in relation to temperature and moisture by the lizard *Sceloporus undulatus*. *Herpetologica*, *58*, 399–407.

Wiens, J. J., & Reeder, T. W. (1997). Phylogeny of the spiny lizards (*Sceloporus*) based on molecular and morphological evidence. *Herpetological Monographs*, *11*, 1–101.

Williams, J. W., Jackson, S. T., & Kutzbach, J. E. (2007). Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 5738–5742.