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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

Saúl López-Alcaide [a], Constantino González-Salazar [b,c,*], Rodrigo Macip-Ríos [d], Enrique Martínez-Meyer [a]

[a] *Instituto de Biología, Universidad Nacional Autónoma de México, Tercer Circuito Exterior s/n, Ciudad Universitaria, 04510 Mexico City, Mexico*
[b] *Departamento de Ciencias Ambientales, CBS Universidad Autónoma Metropolitana, Unidad Lerma, Hidalgo Pte. 46, 52006 Lerma, Estado de México, Mexico*
[c] *C3 – Centro de Ciencias de la Complejidad, Universidad Nacional Autónoma de México, Circuito Centro Cultural s/n, Ciudad Universitaria, 04510 Mexico City, Mexico*
[d] *Escuela Nacional de Estudios Superiores, Unidad Morelia, Universidad Nacional Autónoma de México, Antigua Carretera a Pátzcuaro 8701, Ex Hacienda de San José de la Huerta, 59190 Morelia, Michoacán, Mexico*

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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.

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

* Corresponding author.
E-mail address: cgsalazar7@gmail.com (C. González-Salazar).
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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.

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]

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