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ESTRATEGIAS CONDUCTUALES Y SUS MECANISMOS
NEUROFISIOLÓGICOS SUBYACENTES EN *Sceloporus aeneus* (SQUAMATA:
PHRYNOSOMATIDAE)

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DEDICATORIAS

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RESUMEN

La variedad de conductas que pueden ser observadas en los vertebrados es amplia y se puede dividir en aquellas conductas expresadas de manera individual y las conductas características a un grupo. En relación con las diferencias individuales en la conducta, se ha determinado que estas son consistentes a lo largo del tiempo y de distintos contextos y de manera particular se les ha denominado estrategias conductuales. Por otro lado, dentro de las expresiones conductuales características a un grupo de individuos, los ectotermos se caracterizan por presentar un conjunto de conductas que les permiten alcanzar una temperatura óptima para realizar sus actividades cotidianas. Esta conducta de termorregulación ha llamado recientemente la atención de los investigadores debido a los efectos que el incremento en la temperatura ambiental, consecuencia del cambio climático global, puede tener sobre los organismos ectotermos. El éxito de un individuo en un ambiente determinado puede estar asociado al tipo de conducta que exprese así como su habilidad de modificarla y ajustarla a las condiciones prevalentes al momento; la capacidad de un individuo de modificar su conducta parece estar relacionada con varios mecanismos neurológicos y fisiológicos que la modulan. Por lo anterior, el objetivo principal del presente estudio fue evaluar las estrategias conductuales entre hembras y machos, la conducta de termorregulación de machos bajo distintos escenarios térmicos e investigar sobre los posibles mecanismos neurofisiológicos que subyacen la expresión de dichas conductas. Para ello, se estudió a la lagartija endémica a México *Sceloporus aeneus*, cuyas diferencias conductuales entre sexos, así como su conducta de termorregulación, han sido escasamente estudiadas.

En el capítulo I se abordan aspectos generales acerca de las diferencias individuales en la conducta, las características de los tipos de estrategias conductuales y de la conducta de termorregulación. Asimismo, se ofrece un panorama general de los posibles efectos que tienen la testosterona, serotonina, dopamina y el tamaño del cerebro sobre la conducta de los organismos. En el capítulo II se detalla como la temporada de reproducción puede ser un factor que promueve las diferencias conductuales entre hembras y machos de la especie en estudio. Se evaluaron los niveles de intrepidez, actividad y agresividad entre sexos así como su consistencia. Los resultados indican que los machos son más intrépidos y activos que las hembras; sin embargo, los niveles de agresividad son similares. Lo anterior puede sugerir que los machos pueden incurrir en

un mayor tasa de depredación a cambio de un mayor éxito reproductivo mientras que las hembras parecen actuar con más cautela, pero con altos niveles de agresividad ante otras hembras, para competir por recursos necesarios durante la temporada de reproducción.

Si bien existen distintos estudios que indican la importancia que representa una conducta de termorregulación flexible como mecanismo que permita amortiguar los efectos del calentamiento global en organismos ectotermos, son escasos los estudios que han observado este mecanismo de forma empírica y bajo condiciones controladas. Esta problemática es abordada en el capítulo III, donde se evaluó la conducta de termorregulación en machos de *S. aeneus*. Se reporta que la conducta de termorregulación es flexible, caracterizada por una variación en las frecuencias de posturas corporales, la selección de microhábitats térmicos y los cambios en la exposición entre calor y frío dependen de la temperatura ambiental en la cual se encuentran los individuos. De igual forma, se observó que, a pesar de ser expuestos a altas temperaturas, el umbral de la temperatura crítica máxima no fue rebasado por los individuos, por lo que la conducta de termorregulación favorece la supervivencia de la especie ante un escenario de temperaturas ambientales hostiles. Por otra parte, en el capítulo IV se realizó una revisión bibliográfica acerca de las implicaciones que representa a la conducta en distintos vertebrados, la actividad del sistema HPG, del sistema dopaminérgico y serotoninérgico, así como el tamaño del cerebro en relación al tamaño de los individuos. La literatura sugiere que la actividad de la serotonina y la testosterona pueden ser los principales factores que modulan la conducta agresiva, mientras que la actividad de la dopamina esta involucrada en regular la conducta de recompensa. En conjunto, el sistema dopaminérgico y serotoninérgico pueden estar actuando sobre el área pre-óptica del hipotálamo permitiendo una mayor sensibilidad del ambiente térmico y a su vez modificando la conducta de termorregulación. Asimismo, se plantea que los individuos con cerebros más grandes pueden estar asociados con el fenotipo reactivo al presentar una mayor flexibilidad conductual; sin embargo, la literatura disponible no es concluyente por lo que es necesario llevar a cabo estudios que puedan ayudar a esclarecer esta relación. Finalmente, en el capítulo V los resultados derivados del presente estudio son integrados y se discuten a la luz de la literatura más reciente.

Capítulo 1

Introducción general



La ecología conductual es un campo de investigación que emplea distintos enfoques para estudiar las bases ecológicas y evolutivas de la conducta animal. Lo anterior ha permitido reconocer que los organismos de una población presentan diferencias individuales en la conducta las cuales son consistentes a lo largo del tiempo y de distintos contextos. Estas diferencias individuales han sido categorizadas como personalidad animal (Gosling 2001), temperamento (Réale *et al.* 2007) o estrategias conductuales o de afrontamiento (Koolhaas *et al.* 1999). Las estrategias conductuales pueden estar formadas por cinco rasgos o caracteres de acuerdo a Réale y colaboradores (2007): (1) intrepidez/timidez, (2) exploración/escape, (3) actividad, (4) agresividad y (5) sociabilidad. De manera general, se han descrito dos fenotipos de respuesta dentro del continuo de las estrategias conductuales de acuerdo a los niveles que presentan en los caracteres conductuales y su actividad neurofisiológica. Por un lado, los individuos *proactivos*, conductualmente presentan una respuesta ataque-huida (fight-flight), son agresivos e intrépidos y muestran una alta tendencia a formar rutinas. Por otro lado, los animales *reactivos* se caracterizan conductualmente por una respuesta de inmovilidad, son tímidos, poco agresivos y presentan una mayor flexibilidad conductual (Koolhaas *et al.* 1999; Ruiz-Gómez *et al.* 2011). La conducta de ambos fenotipos parece estar modulada principalmente por la actividad del eje hipotalámico-pituitario-gonadal (HPG), así como la actividad del córtex prefrontal que recibe gran aporte del sistema serotoninérgico y dopaminérgico (Coopens *et al.* 2010; Koolhaas *et al.* 2010). Las diferencias en la actividad de estos sistemas parecen ser las responsables de los contrastes en las estrategias conductuales individuales. Asimismo, se ha observado en distintos grupos taxonómicos diferencias en el tamaño del cerebro en proporción con el tamaño del cuerpo, que pueden estar asociadas con la habilidad cognitiva individual (Kotrschal *et al.* 2013). La habilidad cognitiva individual ha sido observada en procesos de innovación y de flexibilidad conductual (Lefebvre *et al.* 2013), donde los individuos con un cerebro más grande poseen una mayor capacidad de modificar o crear nuevas conductas (Sol *et al.* 2005). Por su parte, la flexibilidad conductual parece ser un factor determinante de las diferencias entre los fenotipos proactivo y reactivo (Coppens *et al.* 2010), por lo que el tamaño del cerebro puede servir como una herramienta para identificar los tipos de estrategias conductuales en una población.

Para que una estrategia conductual pueda categorizarse como tal, las respuestas individuales deben ser consistentes y tal consistencia no solo indica que los valores de

cada rasgo conductual se mantengan a lo largo de la ontogenia (Herde y Eccard 2013) y de los contextos (Wilson y Stevens 2005), sino que las diferencias entre los individuos también deben ser constantes. Por ejemplo, algunos individuos son más agresivos que otros a lo largo de distintas situaciones, aunque es posible que cambien sus niveles de agresividad dependiendo de la situación; sin embargo, algunos individuos permanecerán más agresivos que otros (Sih *et al.* 2004). Por consiguiente, es prudente sugerir la existencia de diferencias conductuales entre hembras y machos dentro de una población, en especial si ambos sexos experimentan diferentes presiones de selección. A pesar de esto, existe muy poca evidencia enfocada a explicar las causas y consecuencias de las diferencias en la conducta individual entre sexos.

La variabilidad ambiental también juega un papel importante en la expresión y mantenimiento de las estrategias conductuales. Actualmente, distintos estudios indican que el incremento en las temperaturas ambientales a nivel global es una de las principales adversidades a las que se enfrentan las especies del mundo, teniendo un mayor impacto sobre los organismos ectotermos por su necesidad inherente de obtención de temperatura por medios externos (Huey y Tewsbury 2009; Kearney *et al.* 2009; Sinervo *et al.* 2010). Bajo el escenario del calentamiento global, los lacertilios presentan dos alternativas para evitar una posible extinción: migrar hacia áreas con condiciones térmicas más aceptables o adaptarse a las nuevas condiciones térmicas a las cuales se enfrentan (Berg *et al.* 2010). A este respecto, la flexibilidad conductual es considerada una de las respuestas primarias que emplean los organismos para hacer frente a las fluctuaciones ambientales (Rymer *et al.* 2013), por lo que la flexibilidad conductual durante la termorregulación puede ser clave para amortiguar los efectos del calentamiento global en estos organismos (Huey y Tewsbury 2009; Kearney *et al.* 2009). El proceso de termorregulación en lacertilios se lleva a cabo mediante distintas estrategias conductuales como la expresión de posturas corporales, el uso de distintos microhábitats térmicos, cambios entre sol y sombra y la regulación en los tiempos de actividad (Angilletta 2009). Por lo tanto, la modificación y ajuste de estas estrategias en ambientes térmicos críticos pueden evitar la disminución o extinción de las poblaciones silvestres de lacertilios.

Distintos estudios han abordado las posibles causas y consecuencias de las diferencias entre los dos tipos de estrategias conductuales (Wolf y Weissing 2010), no

obstante, todavía se desconocen los factores que causan las diferencias en las estrategias conductuales entre sexos en poblaciones silvestres y más aún en lacertilios. Se ha propuesto que las distintas presiones de selección dentro de una población pueden promover las diferencias conductuales entre sexos (Schuett *et al.* 2010). La temporada de reproducción representa una de las etapas más críticas en las que se puede ver comprometida la adecuación de los individuos, por lo que puede ser un factor que module la conducta de las especies. Con base a lo anterior, se formuló la siguiente pregunta de investigación: ¿existen diferencias en las estrategias conductuales entre hembras y machos dentro de la temporada de reproducción? Esta interrogante es abordada en el capítulo II al evaluar las estrategias conductuales de cada sexo en la lagartija *Sceloporus aeneus* dentro de la temporada de reproducción. Por otro lado, como se mencionó previamente, el incremento de las temperaturas ambientales es una amenaza para las especies de ectotermos por lo que los individuos deberán desarrollar distintas estrategias para contrarrestar sus efectos. Dado que la fisiología de los organismos parece limitar la habilidad de los individuos de sobrevivir en temperaturas extremas (Gunderson y Stillman 2015), se ha sugerido la conducta de termorregulación como la estrategia más viable. En consecuencia, se establecieron las siguientes preguntas de investigación las cuales son discutidas en el capítulo III: ¿la conducta de termorregulación se puede ajustar dependiendo de la temperatura ambiental a la cuál son expuestos los individuos? ¿La conducta de termorregulación puede ser un mecanismo que permita a los lacertilios mitigar los efectos del calentamiento global?

Por último, en el capítulo IV se realizó una revisión bibliográfica con la finalidad de responder a las siguientes cuestiones: ¿existe una relación entre las estrategias conductuales y la conducta de termorregulación con la actividad de los sistemas dopaminérgicos y serotoninérgicos así como de la testosterona de los individuos de *Sceloporus aeneus*? ¿El tamaño del cerebro está asociado con una mayor capacidad cognitiva y con el fenotipo reactivo de las estrategias conductuales?

Sceloporus aeneus es una lagartija de actividad diurna, con un tamaño máximo de 78mm de longitud hocico-cloaca, es endémica al centro de México y su distribución se encuentra dentro del intervalo altitudinal de los 2250 hasta los 3100 metros (Benabib *et al.* 1997). Habita en lugares con vegetación de tipo zacatonal alpino con pinos y pastos amacollados de los géneros *Festuca*, *Calamagrostis* y *Eringium*. Es una especie

ovípara con una máxima actividad reproductiva de marzo a julio (Manríquez-Morán et al., 2013). La especie presenta un forrajeo de tipo pasivo y una estrategia termorreguladora de tipo heliotherma, adquiriendo calor directamente de la radiación solar o a través del aire (convección) (Lara-Reséndiz 2014). Su temperatura corporal óptima es de 32°C (Andrews *et al.* 1999). Asimismo, la especie presenta un marcado dimorfismo sexual en la coloración (Figura 1), donde los machos presentan parches ventrales de color azul y tres tipos de coloración lateral: gris, amarillo y naranja.



Figura 1. Individuos de *Sceloporus aeneus* de la localidad de Calimaya Estado de México. Se observa a la hembra de la especie (izquierda) sin coloración lateral, mientras que el macho (derecha) presenta coloración naranja en esta región.

1.1. HIPÓTESIS Y PREDICCIONES

En distintas especies de lacertilios se ha observado a los machos como individuos territoriales. Esta territorialidad puede ser más evidente durante la temporada de reproducción con la finalidad de monopolizar la mayor cantidad de recursos que permitan un mayor éxito reproductivo, es por ello que se esperan altos niveles de actividad, intrepidez y agresividad en machos de *Sceloporus aeneus*. Por otra parte, debido a sus características, los machos presentarían una conducta de termorregulación flexible que les permita ajustar el uso de posturas corporales, microhábitats térmicos y cambios entre sol y sombra a las distintas temperaturas ambientales a las que sean expuestos. Lo anterior, permitiría a los individuos mantener una temperatura corporal alejada de sus críticos máximos, mitigando los efectos del calentamiento global. Finalmente, se planteó la hipótesis de que la actividad del sistema dopaminérgico, serotoninérgico y de la testosterona modulan la expresión de la conducta de los individuos. De manera particular, el fenotipo proactivo tenderá a mostrar una mayor

actividad del sistema dopaminérgico y de la testosterona, mientras que la actividad del sistema serotoninérgico será menor; lo opuesto será cierto para los individuos reactivos. Asimismo, dado que el tamaño del cerebro está asociado con una mayor capacidad cognitiva, la cual puede ser observada a través de una flexibilidad conductual, se sugirió que los individuos reactivos presentarían un tamaño de cerebro más grande que los proactivos.

1.2. OBJETIVOS

Objetivo general

- Evaluar las estrategias conductuales de machos y hembras, la conducta de termorregulación de los machos y los mecanismos neurofisiológicos que subyacen estas conductas en *Sceloporus aeneus*.

Objetivos particulares

- Determinar las estrategias conductuales de machos y hembras de *Sceloporus aeneus* durante la temporada de reproducción.
- Evaluar la flexibilidad de la conducta de termorregulación en machos de *Sceloporus aeneus* bajo tres temperaturas ambientales.
- Realizar una revisión bibliográfica de la actividad del sistema dopaminérgico, serotoninérgico, testosterona y tamaño del cerebro como mecanismos neurofisiológicos que subyacen las respuestas conductuales y su asociación con las respuestas conductuales observadas en *Sceloporus aeneus*.

1.3. METODOLOGÍA GENERAL

Durante los meses de Marzo a Junio de 2016 se colectaron veinte hembras y treinta y cinco machos adultos (LHC>40mm) de *Sceloporus aeneus* en Calimaya Estado de México (19°, 08', 44.3''N, 99°, 34', 56.6''). La localidad presenta un clima templado subhúmedo con lluvias en verano, su temperatura promedio anual es de 12°C con un intervalo de 4°C a 14°C (INEGI 2005). La zona es un área abierta con pastos rasos y pastos amacollados del género *Festuca*. El uso de suelo está destinado primordialmente para actividades agrícolas (INEGI 2005). Los individuos fueron colectados a mano, capturándolos directamente al estar posados en el sustrato y fueron buscados también

extensivamente dentro de los macollos, con la finalidad de obtener una muestra representativa y evitar un sesgo muestral. Los organismos capturados fueron colocados individualmente en bolsas de tela para su transporte a cautiverio en el laboratorio de Ecología y Conducta de la Facultad de Ciencias de la Universidad Autónoma del Estado de México. En el laboratorio se mantuvieron en terrarios de plástico (47cm L x 30cm An x 30cm Al), provistos por una lámpara de calor y una de luz natural. El terrario se dividió en cuatro secciones (23.5cm L x 15 An x 30cm Al) cada una con un macollo como refugio/sitio de termorregulación y peat moss como sustrato. Se colocó un individuo de *Sceloporus aeneus* en cada sección y fueron alimentados con larvas de tenebrio (*Tenebrio molitor*) y grillos (*Acheta domesticus*). El agua fue suministrada con un aspersor así como en un pequeño contenedor de plástico.

1.4. LITERATURA CITADA

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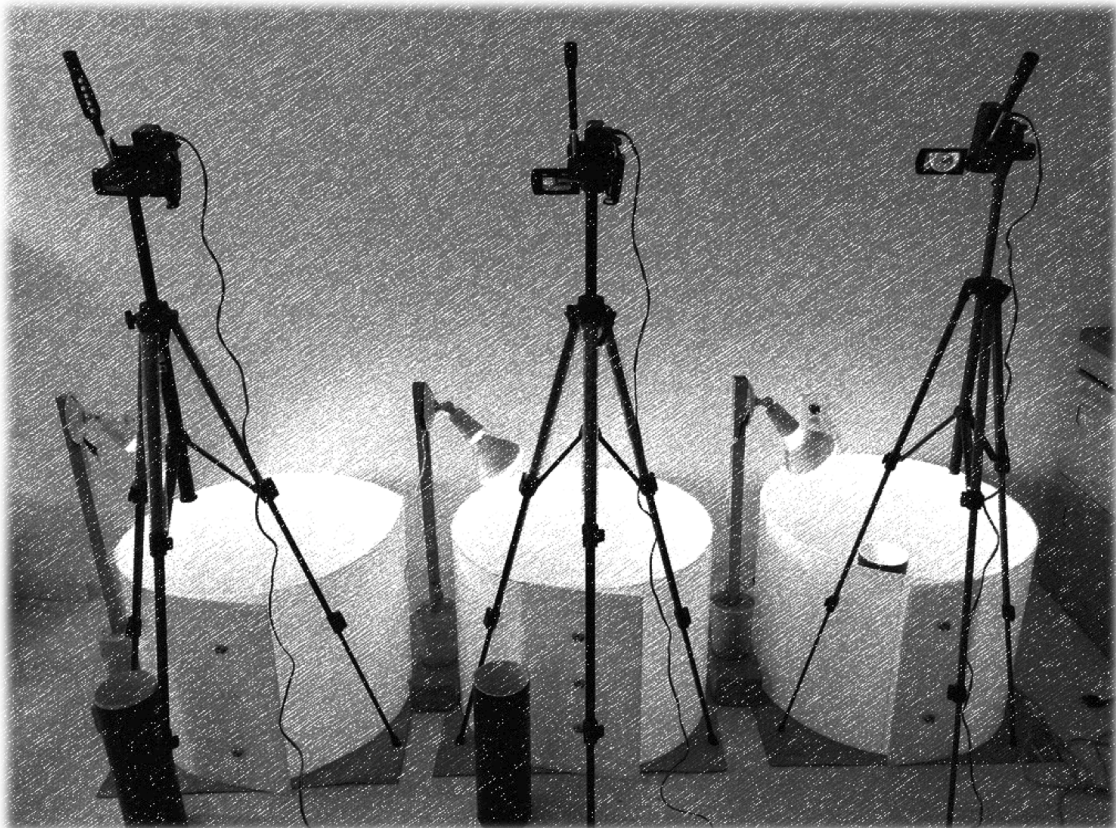
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Capítulo 2

Diferencias en las estrategias conductuales entre hembras y machos de *Sceloporus aeneus*



La temporada de reproducción es considerada un evento medular para la adecuación de los organismos, por lo que puede representar un factor que promueva variaciones en las estrategias conductuales entre hembras y machos de una población. Es por ello que en el presente capítulo se determinaron las estrategias conductuales de machos y hembras de *Sceloporus aeneus* durante la temporada reproductiva. Para ello, se estudió la conducta intrépida, de actividad y agresividad entre sexos durante los meses de Marzo a Junio de 2016, periodo que abarca la mayor actividad reproductiva para la especie. Los resultados de este estudio derivaron en un artículo publicado en la revista *Ethology*, donde se reporta que los machos presentan una estrategia conductual caracterizada por altos niveles de intrepidez, actividad y agresividad. La conducta expresada por los machos puede estar relacionada a la necesidad de establecer territorios y con la búsqueda de un incremento en su éxito reproductivo. Sin embargo, también conlleva un alto costo ya que pueden estar sujetos a una mayor tasa de depredación. En el caso de las hembras, se registraron altos niveles de agresividad, los cuales les pueden permitir competir con otras hembras por el acceso a recursos como sitios de anidación, alimento y machos para el apareamiento. Del mismo modo, las hembras se caracterizaron por presentar bajos niveles de actividad e intrepidez, lo cual puede favorecer su supervivencia y la de sus crías. En conjunto, los resultados sugieren que la temporada de reproducción puede favorecer la presencia de diferencias individuales en la conducta entre sexos, donde sus estrategias conductuales parecen permitir a los individuos de ambos sexos un mejor desempeño durante la temporada de reproducción. No obstante, es prudente mencionar la necesidad de evaluar la relación entre el éxito reproductivo de cada uno de los sexos y el tipo de estrategias conductuales, lo cual permitirá elaborar un panorama más completo de los efectos que tiene la temporada reproducción y la conducta de las especies.

Personality and its variation between sexes in the black-bellied bunchgrass lizard *Sceloporus aeneus* during the breeding season.

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Personality and its variation between sexes in the black-bellied bunchgrass lizard *Sceloporus aeneus* during the breeding season

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Abstract

Personality defined as individual differences in behavioural traits, which are consistent through time and across situations, has been observed among individuals of the same population in several animal groups. However, it is well known that as selective pressures may act upon behaviour, they can potentially drive differences in personality; in this sense, the breeding season may function as a promotor of differences between males and females that allow them to maximize their fitness. Nevertheless, results from studies comparing differences in personality between males and females are still non-conclusive. Therefore, we aimed to test the presence of differences in personality between males and females during the breeding season by evaluating the consistency over time and across situations of three behavioural traits in the black-bellied bunch grass lizard *Sceloporus aeneus*. We found that males were more risk-prone and active than females, whereas aggression was similar between sexes. Personality traits were observed in both sexes throughout the breeding season; however, they were more consistent in females than in males. Specifically, personality in males is characterized by higher levels of activity, boldness and aggressiveness; whereas females behave more cautiously, although aggressively when confronted with other females. Our results suggest that the personality differences between males and females observed in *Sceloporus aeneus* may be expressed to secure individual current reproductive value, and to enhance their fitness success.

KEYWORDS

aggressiveness, boldness, individual behaviour, lizards, sex differences

1 | INTRODUCTION

Growing evidence shows that suites of behavioural traits tend to vary between individuals of the same sex within a population in a broad number of vertebrate and invertebrate species (Dall & Griffith, 2014). Such differences have been referred to as animal personality (Gosling, 2001), temperament (Réale, Reader, Sol, McDougall, & Dingemanse, 2007) or coping styles (Koolhaas et al., 1999). For a behavioural trait to be considered part of personality it must show consistency across time, measurements or contexts (Bell, Hankinson, & Laskowski, 2009; Wuerz & Krüger, 2015); and this has been the case

for boldness (Wilson & Stevens, 2005), aggressiveness (Kralj-Fiser & Schneider, 2012), activity and exploration (Urzsán, Török, Hettyey, Garamszegi & Herczeg, 2015). Likewise, consistency has been observed not only throughout life stages (Herde & Eccard, 2013; Schuster, Carl, & Foerster, 2017), but also after an abrupt change such as metamorphosis (Hedrick & Kortet, 2012; Wexler, Subach, Pruitt, & Scharf, 2016), or even after a change of sex (Sprenger, Dingemanse, Dotchtermann, Theobald, & Walker, 2012).

Although several models have aimed to explain the evolution and maintenance of individual variation in behaviour (Réale et al., 2010; Wolf & Weissing, 2010; Wolf, Doorn, & Weissing, 2008), only

a few reports have addressed whether males and females differ in personality and the potential causes and consequences of such variation. Since males and females experience different selection pressures, life-history trade-offs and sex-specific strategies have been proposed as a possible explanation of behavioural variation between sexes (Schuett, Tregenza, & Dall, 2010). In this case, the breeding season is a critical stage that can define the fitness outcome on an individual; therefore, one could expect differences in behaviour between males and females that allow them to maximize their fitness, although some costs may incur. For instance, bolder and more aggressive individuals show increased mating success at the expense of a decreased survival rate (Reaney & Backwell, 2007); an example of this has been found in the fish *Poecilia reticulata*, for which males increase their reproductive success by being more explorative, while females invest more in their offspring (Croft et al., 2003). Furthermore, it is well accepted that physiological mechanisms underlie and modulate behaviour (Coopens, Boer, & Koolhaas, 2010); thus, hormonal shifts during the breeding season might be a plausible explanation for the differences in behaviour expressed by males and females.

While interest in the study of animal personality has rapidly grown, there is little evidence regarding differences in personality between sexes. Therefore, this study aimed to determine the presence of personality in the black-bellied bunchgrass lizard *Sceloporus aeneus* by evaluating the consistency over time and across situations of three different behavioural traits between adult males and females during the breeding season. *Sceloporus aeneus* is a small terrestrial, oviparous lizard endemic to México; its maximum reproductive activity ranges from March to July (Manríquez-Morán, Villagrán Santa Cruz, & Méndez-de la Cruz, 2013) during which they present sexual dimorphism in coloration. Since it has been shown that males are more active during mate acquisition increasing the risk of predation (Magnhagen, 1991), our predictions were twofold. First, we expected for males to be bolder and more active than females in risky situations (Novel Environment and High-Risk tests); and second, we suggest no differences in activity between sexes in less risky scenarios (Low-Risk test), as this behaviour may promote resource acquisition. On the other hand, we also expect higher levels of aggression in males since they tend to defend more resources related to breeding. Finally, we put to the test the hypothesis proposed by Bell, Hankinson & Laskowski (2009), which states an increased behavioural consistency in males compared to females, due to the physiological variations between sexes during the breeding season, which may underlie such differences in behaviour.

2 | MATERIALS AND METHODS

2.1 | Animal collection and husbandry

We conducted three samplings during the breeding season (March to June 2016) in Calimaya, State of México, México (19° 08' 44.3"N, 99° 34' 56.6"W), each group of lizards collected was evaluated

after arrival; hence, all individuals spent the same time in captivity (6 weeks). We captured 55 adult (Snout-Vent Length > 45 mm) females ($n = 20$) and males ($n = 35$) of *Sceloporus aeneus*. Lizards were searched for thoroughly on the substratum and inside the bunches of grass they use as a refuge, in order to have a representative sample and to avoid collection bias. Organisms were individually placed in cloth bags and transported to the Ecology and Behaviour Lab at the Autonomous University of the State of México where they were kept individually in opaque-plastic terraria (23.5 cm L × 15 cm W × 30 cm H). Each lizard was provided with a bunchgrass for shelter, a thermoregulation site, and peat moss was used as substrate. They were fed daily with mealworms and crickets, and water was delivered by misting the terrarium walls everyday. Each terrarium was fitted with a heat lamp (100 W) placed 35 cm above and a Vita-Lite® lamp provided natural lighting indoors, the lamps were turned on and off automatically from 08:00 to 18:00 hr.

Four assays were designed to determine individual behaviour in the following order: Novel Environment test (NE), Low-Risk test (LR), High-Risk test (HR) and Mirror Test (MT). The first set of assays (NE, LR and HR tests) was performed a week after capture, whereas the MT was performed the following week. To evaluate the consistency of behaviour, a second set of assays was repeated in the same order one week after the first round was accomplished; the order in which lizards were evaluated was randomized. Only one set of assays (NE, LR and HR Tests) was performed by an individual on a given day. From 11 to 13 days elapsed between assays for each individual and in total, lizards spent in average 42 days in captivity (including the settling and the resting between assay's periods). At the start of each test, individual's body temperature was recorded with an infrared thermometer (Fluke 62®) to ensure that lizards had reached their optimal body temperature (32°C) (Andrews, Méndez-de la Cruz, Villagrán-Santa Cruz, & Rodríguez-Romero, 1999). All tests were carried out during the activity period reported for the species (09:00–16:00 hr) (Jiménez-Arcos, 2013). Behavioural assays were recorded with a camcorder (Sony HDR-XR150) and one observer analysed all films (R-P). The research was carried in agreement with international (*Anim. Behav.* 2003. 65, 249–255) and local (NOM-062-ZOO-1999) ethical principles of animal maintenance and welfare. Once the study was concluded, all individuals were marked by toe-clipping to avoid recapture and released at their original sampling site.

NE, LR and HR tests were performed in a round-shaped white plastic arena (60 cm diameter × 45 cm high), which featured a heat lamp (150 W) placed 70 cm above, and the base was evenly lined with cork. A small bunch of grass from the study site (15 cm high) was placed at the centre of the terraria to serve as a refuge, at the beginning of NE test the bunch of grass was covered with a removable black plastic cylinder (10 cm diameter × 25 cm High), which was used as a settling chamber.

MT was used to quantify individual levels of aggression. For this, a terrarium was built with three opaque-plastic walls (50 cm L × 30 cm W × 30 cm H) and one plexiglass wall (50 cm L × 30 cm H) to allow video recording. The terrarium was divided into two sections, separated by a removable white plastic wall (30 cm L × 30 cm H), and featured

a thermoregulation area which had a heat lamp (150 W) placed 70 cm above the terrarium, and an interaction area which included a mirror on the opposite end of the thermoregulation area. At the end of each individual test, all terraria were cleaned with 15% bleach and aerated to avoid scent cues from interfering with the lizard's response during the tests.

2.2 | Behavioural tests

2.2.1 | Novel Environment (NE)

Individuals were gently placed in the settling chamber for 10 min to prevent altered responses due to handling. After this, the cylinder was carefully removed, and the lizard was allowed to freely move around the terrarium for 10 min. The following data were retrieved from the recordings: (a) time to leave the refuge, considered when an individual moved one body length away from the bunchgrass. If an individual did not leave the refuge at the end of the experiment, it was given a maximum score of 600 s; and (b) time active, measured as the time the individual spent moving in the terrarium.

2.2.2 | Low-Risk Environment (LR)

Following the NE test, individuals were let to explore the terrarium for 30 min. After this, their behaviour was recorded for further 10 min. For each individual, the time active (time moving) was recorded.

2.2.3 | High-Risk Environment (HR)

At the end of the LR test, individuals were exposed to a simulated predator attack with a model that resembled a bird made with black EVA foam attached to a wooden stick with a paintbrush at the far end, which was used to gently touch the lizard in the dorsum. The model was moved vigorously above the lizard three times to simulate the attack of an avian predator. After the attack, the time to resume activity and the time active were recorded for 10 min.

2.3 | Mirror Test (MT)

Individuals were placed in the thermoregulation area of the terrarium for 10 min to avoid altered responses due to handling. Afterwards, the plastic division was removed allowing the individual to interact with its reflection for 15 min. The agonistic behaviours recorded were defined in pilot tests using information available for the genus (Bastiaans, Morinaga, Castañeda, Marshall, & Sinervo, 2013), and through personal observations. The agonistic behaviours observed were defined as push-ups, lateral compressions, bite attempts, tail movements, throat expansions and lunges.

2.4 | Data analysis

The latency to emerge from the refuge in the NE test and the latency to resume activity after the simulation of a predatory attack in the HR test were used as a measurement of boldness. Activity was

determined as the total time spent moving during each behavioural test. Since all the behaviours observed in the MT are associated to some level of aggression in other closely related species of the genus (Bastiaans, Morinaga, Castañeda, Marshall, & Sinervo, 2013; Smith & John-Alder, 1999), we added up their frequencies to obtain a single value of aggressiveness per individual. All statistical analyses were carried out in the software SPSS v21.0. Overall, data did not meet the assumptions of a normal distribution (Shapiro-Wilk test <0.05) therefore, non-parametric tests were used. Differences between sexes in personality traits were assessed using Mann-Whitney *U* tests. The consistency of behaviour by sex was evaluated by comparing the values from the first set of assays with the second set using a Spearman's rank correlation test, as previously reported (Bell, et al., 2009; Chapman, Hegg, & Ljunberg, 2013; Herde & Eccard, 2013). To evaluate consistency over time, we compared the values of each behaviour measured in the first set of assays with the behaviours from the second set. Consistency across situations was evaluated by comparing each behaviour in each context (i.e., boldness in NE vs. boldness in HR). Statistical significance was set at $p < 0.05$. Results are expressed as median \pm standard deviation (SD) unless otherwise is stated.

3 | RESULTS

All 55 lizards collected (20 females and 35 males) completed all tests, no signs of distress or sickness were observed in any of the individuals.

3.1 | Comparisons between sexes

In the NE test, males were more active than females during the first set of assays, whereas the levels of boldness were similar in both sets of experiments (Table 1). In the LR test, there were no differences in activity between sexes, but in the HR test males were bolder than females during the first and second assays although activity did not differ between males and females. Finally, females and males were equally aggressive in both sets of assays (Table 1).

3.2 | Consistency of behaviour

Consistency over time: when data for males and females were pooled together, the behavioural traits evaluated showed consistency throughout time in NE (boldness: $r_s = 0.28$, $p = 0.03$; activity: $r_s = 0.29$, $p = 0.02$), LR (activity: $r_s = 0.36$, $p = 0.001$), HR (boldness: $r_s = 0.67$, $p = 0.001$; activity: $r_s = 0.50$, $p = 0.001$) and the MT assays (aggressiveness: $r_s = 0.48$, $p = 0.001$). When tested separately, differences in consistency were observed between sexes, females being more consistent than males (Figure 1). In females, none of the behavioural traits evaluated in the NE test was consistent (boldness: $r_s = 0.42$, $p = 0.06$; activity: $r_s = 0.30$, $p = 0.19$); however, activity was consistent across time in the LR assays ($r_s = 0.54$, $p = 0.01$), as well as boldness ($r_s = 0.66$, $p = 0.001$), and activity ($r_s = 0.55$, $p = 0.01$) in

TABLE 1 Comparison of personality traits in males and females of the black-bellied bunchgrass lizard *Sceloporus aeneus* for each context evaluated in both, the first and second set of assays

Context	Sex	Boldness (s)		Activity (s)		Aggressiveness	
		$\bar{x} \pm SD$	Statistics	$\bar{x} \pm SD$	Statistics	$\bar{x} \pm SD$	Statistics
First set of assays							
Novel Environment	Males	314 ± 229	$U = 257$ $p = 0.09$	205 ± 151	$U = 234$ $p = 0.03^a$	—	
	Females	600 ± 222		0 ± 124			
Low Risk	Males	—	$U = 170$ $p = 0.001^a$	222 ± 139	$U = 307$ $p = 0.45$	—	
	Females	—		152 ± 145			
High Risk	Males	58 ± 161	$U = 170$ $p = 0.001^a$	172 ± 142	$U = 267$ $p = 0.14$	—	
	Females	162 ± 235		151 ± 138			
Mirror Test	Males	—	$U = 310$ $p = 0.48$	—	$U = 310$ $p = 0.48$	31 ± 61	
	Females	—		—		31 ± 34	
Second set of assays							
Novel Environment	Males	220 ± 215	$U = 298$ $p = 0.36$	222 ± 155	$U = 331$ $p = 0.73$	—	
	Females	243 ± 181		185 ± 146			
Low Risk	Males	—	$U = 150$ $p = 0.001^a$	159 ± 115	$U = 331$ $p = 0.73$	—	
	Females	—		189 ± 164			
High Risk	Males	43 ± 136	$U = 150$ $p = 0.001^a$	148 ± 111	$U = 286$ $p = 0.26$	—	
	Females	136 ± 252		53 ± 155			
Mirror Test	Males	—	$U = 299$ $p = 0.36$	—	$U = 299$ $p = 0.36$	9 ± 53	
	Females	—		—		31 ± 39	

Note. The median and standard deviation are shown, as well as the value for the Mann-Whitney U test.

^aSignificant differences.

the HR tests. Additionally, aggressiveness was also consistent only in females between both tests ($r_s = 0.86$, $p = 0.001$). On the other hand, consistency over time in males was only observed for activity in the NE assay ($r_s = 0.32$, $p = 0.03$), and boldness ($r_s = 0.54$, $p = 0.001$) and activity in the HR test ($r_s = 0.36$, $p = 0.03$).

Consistency across situations (contexts): In the first set of assays, females showed consistency across situations as boldness (NE-HR: $r_s = 0.56$, $p = 0.001$) and activity (NE-HR: $r_s = 0.64$, $p = 0.001$; LR-HR: $r_s = 0.63$, $p = 0.001$) were positively correlated with the different contexts evaluated. On the other hand, consistency across situations in males was only observed for activity (LR-HR: $r_s = 0.58$, $p = 0.001$).

Additionally, for the second set of assays females were similarly consistent in both contexts in boldness (NE-HR: $r_s = 0.69$, $p = 0.001$) and activity (LR-HR: $r_s = 0.62$, $p = 0.001$); whereas in males, only activity was consistent across contexts (NE-HR: $r_s = 0.38$, $p = 0.02$; LR-HR: $r_s = 0.44$, $p = 0.001$).

4 | DISCUSSION

Our study shows that males and females of the black-bellied bunchgrass lizard differ in personality during the breeding season. In line with our predictions, males of *S. aeneus* were more active and bolder than females under risky situations (Table 1). These behavioural patterns have also been observed

in other species, in which males are more willing to take risks and increase their activity levels during the breeding season to enhance their reproductive success (Cooper, 1999; Salvador, Díaz, Veiga, Bloor, & Brown, 2007). Furthermore, exploration and activity in new habitats have been related to information gathering where bolder and more exploring individuals perform better in spatial learning tasks (Carazo, Noble, Chandrasoma, & Whiting, 2014), which could be advantageous to find resources during the breeding season (e.g., refuges, females, food). Nevertheless, boldness and activity can also compromise survival due to an increased risk of predation (Carter, Goldizen, & Tromp, 2010). On the other hand, we found that females tend to be more cautious, presenting longer latencies to explore and to keep immobile when compared to males, which in hazardous situations could improve their survival by being able to readily evaluate possible threats (Quinn & Cresswell, 2005). Moreover, the low levels of activity expressed by females could also be related to anti-predator behaviours such as crypsis, where individuals remain motionless to deceive potential predators, as it has been observed in other species of the genus *Sceloporus* (Vitt & Congdon, 1978). Males and females presented similar levels of activity in situations where risk is low or absent, which possibly helps them to increase foraging to compensate the energy spent, especially during critical events such as breeding. For instance, males actively perform courtship behaviours and

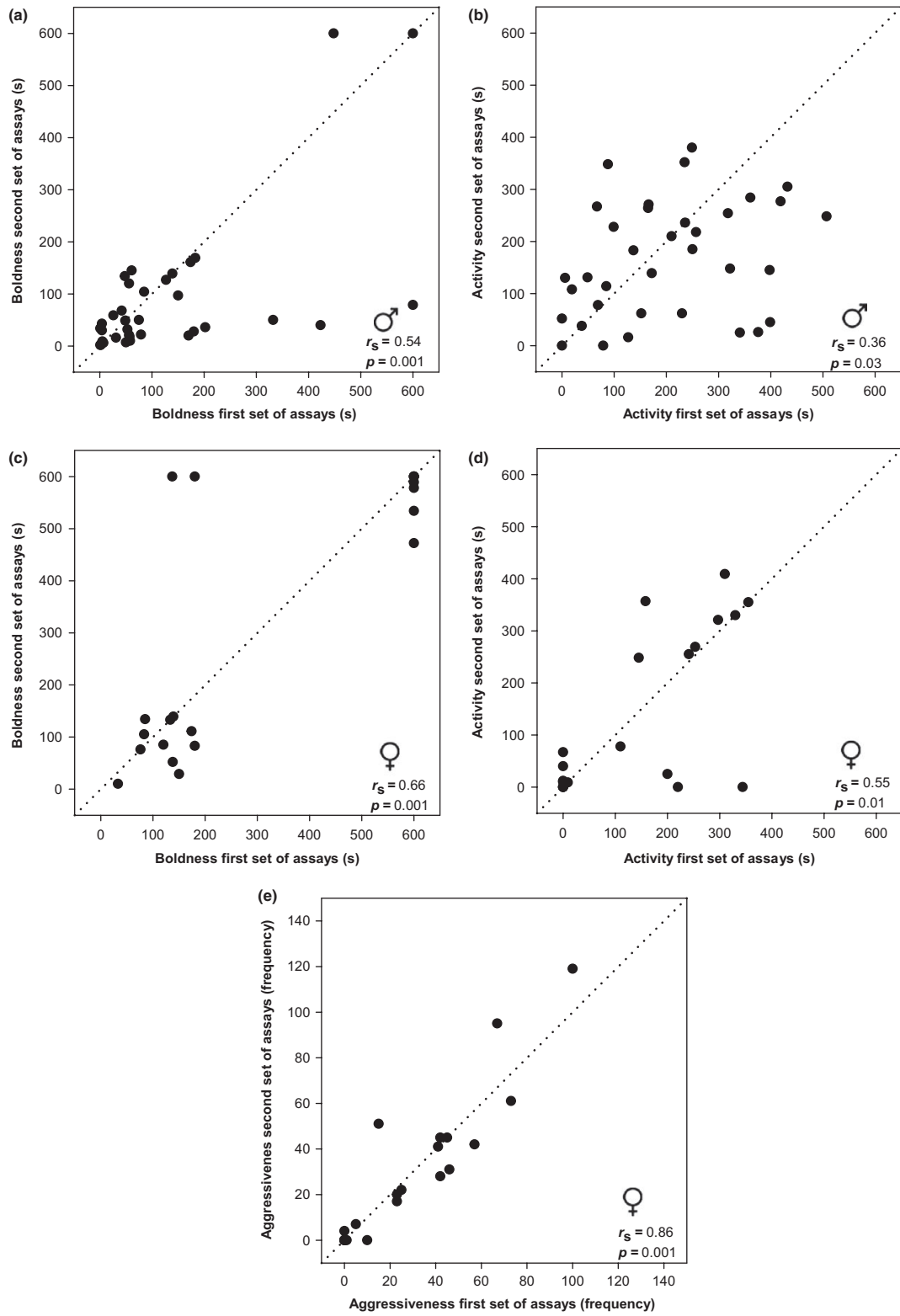


FIGURE 1 Consistency over time of personality traits in the High-Risk test, and aggressiveness in the Mirror Test for males (a, b) and females (c, d, e) of the black-bellied bunchgrass lizard *Sceloporus aeneus*. The value and significance of the relationship between traits, as well as the line of best fit are shown for each panel

usually defend a territory from other males, whereas females invest energy mainly in the production of eggs, foraging, and in some cases competition for nesting sites (Kunz & Orrell, 2004). During the breeding season, aggressiveness is expected to be more frequent in males due to higher competition during resource defence (Scordato, 2017); however, we found that the levels of aggression were similar in males and females. We suggest that in this species, high levels of aggression in females could be the outcome of intrasexual competition for resources as previously reported in other species (Clutton-Brock, 2009; Rosvall, 2011). In our case, females were the most common sex in the population, showing a sex ratio of three females to one male (3:1), which has also been found in other populations of this species (Jiménez-Arcos, 2013); thus, high levels of aggression in females could be the outcome of intrasexual competition.

Contrary to our predictions, we found that females were more consistent in their behaviour than males (Figure 1). Overall, females expressed more consistent behaviours measured in the LR, HR and MT tests. In males, consistency was found in a single behaviour during the NE and all behaviours measured in the HR test. Similar results have been found in other species (Hedrick & Kortet, 2012; Wuerz & Krüger, 2015), where consistency is mainly driven by females, perhaps because of differences in ecological and reproductive pressures between sexes. Furthermore, the consistency of behaviours observed over time and across situations also suggests that individuals could adopt different strategies through the breeding season to improve their reproductive success; such as males being more active and bolder whereas females behaving generally more cautiously, but aggressively in the presence other females. However, in situations of low risk, males and females present similar activity patterns. These behavioural strategies could have a direct impact on their fitness, since bolder and more aggressive individuals tend to have higher reproductive success; however at the expenses of their survival (Smith & Blumstein, 2008). For example, in the Nambian rock agamas (*Agama planiceps*) males with greater flight initiation distance (FID) during the breeding season tend to lose resources such as mates and territories, whereas those with lower FID are in higher risk of predation (Highcock & Carter, 2014). In the case of *S. aeneus*, it seems that adult males survive less (59%) than adult females (81.5%) (Carmen-Cristóbal unpublished data). Therefore, it is possible that males are more active and bolder during the breeding season to gain resources despite the cost for survival being high. Nevertheless, further studies on reproductive success and predation rates across the breeding season will clarify this assumption. Our results also show a decrease in the frequency of agonistic behaviours in males between the first and second set of assays, whereas the levels of aggression in females remained similar between assays. A decrease in the

levels of aggression in males seems to be a strategy to reduce energy expenditure in contests with other males (Sheldahl & Martins, 2000); whereas females may take advantage from their consistently high levels of aggression by gaining access to direct (nesting sites, food resources, territories) and indirect (genetic) benefits (Rosvall, 2011).

The differences in personality observed between males and females of *S. aeneus* could also be associated with a life-history strategy related to current and future reproductive value. From this perspective, in the wild passerine bird (*Cyanistes caeruleus*) males and females differ in their tendency to take risks (nest defence and handling aggression), in which females enhance their current reproductive value by expressing high nestling defence against a possible treat (Fresneau, Klun, & Brommer, 2014). Regarding the females of *S. aeneus*, risk aversion seems to be an important feature that may help individuals to protect their future reproductive value by lowering their predation risk. Although life-history traits are similar between males and females, it has been observed that females are able to produce up to two clutches in one reproductive season (Manríquez-Morán, Villagrán Santa Cruz, & Méndez-de la Cruz, 2013; Ramírez-Bautista, Hernández-Salinas, Cruz-Elizalde, Lozano, & Rodríguez-Romero, 2016), therefore caution could secure future reproductive events.

In summary, here we report differences in personality between sexes of *S. aeneus*, where males are more active and bolder than females in situations that represent possible risks, while activity in low-risk situations and aggressiveness are similar. Consistency of personality traits suggests that the behaviours expressed by males and females could reflect a particular strategy during the breeding season to enhance reproductive success and future reproductive value in the species. In addition, life-history traits could be a driving force modulating intersexual differences in personality, since males and females are under different selective pressures during the breeding season. Further studies on the differences in sexual selection, reproductive success, and physiology between sexes are needed to construct a comprehensive perspective of the roles of personality and life-history traits during the breeding season.


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CONFLICT OF INTEREST

None declared.

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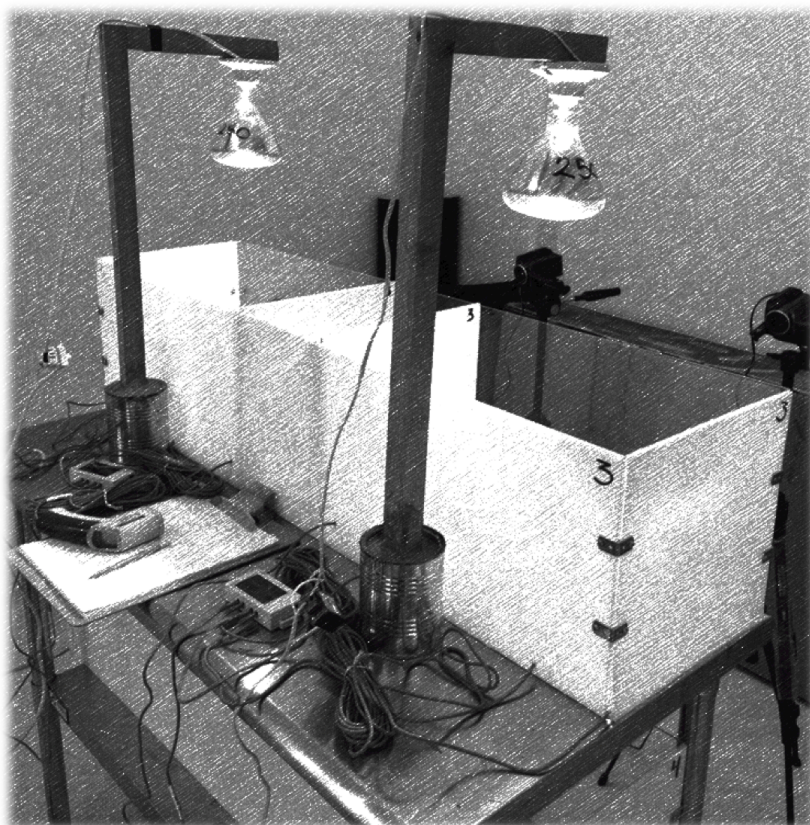
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Capítulo 3

Evaluación de la conducta de termorregulación en machos de *Sceloporus aeneus* en diferentes escenarios térmicos



Recientemente hay un reconocimiento amplio del calentamiento global como una de las principales causas de la pérdida de biodiversidad, motivo por el cuál se han evaluado los mecanismos que las especies adoptan para hacer frente a las temperaturas hostiles a las que se ven expuestas. De forma particular, en lacertilios se ha propuesto que una conducta de termorregulación flexible puede ser una estrategia que permita a los organismos mitigar el efecto del incremento en la temperatura ambiental. Por consiguiente, en esta sección se evaluó la flexibilidad de la conducta de termorregulación en machos de *Sceloporus aeneus* bajo distintos escenarios térmicos. Para ello, se midieron las frecuencias de las posturas corporales de los individuos, la utilización de microhábitats térmicos y los cambios entre sitios cálidos y sitios fríos. Los individuos fueron expuestos a tres temperaturas ambientales (25, 35 y 45°C) y bajo dos escenarios: con la presencia de un refugio térmico y sin el refugio. Los resultados indican que los machos presentan una conducta de termorregulación flexible, caracterizada por un ajuste de sus posturas corporales, el uso de microhábitats térmicos y el cambio entre zonas cálidas-frías dependiendo de la temperatura ambiental a la que se expusieron. Esta flexibilidad conductual permitió a los individuos mantener temperaturas corporales por debajo de los 40°C aún cuando estaban sujetos a una temperatura ambiental hasta de 45°C y en ausencia de un refugio térmico. Lo anterior sugiere que los individuos pueden hacer frente al incremento adverso en las temperaturas ambientales a través de un ajuste de sus conductas de termorregulación lo que permite elaborar modelos de predicción de vulnerabilidad de las especies más precisos bajo escenarios de calentamiento global. Los resultados obtenidos en este capítulo fueron enviados a la revista *Behavioral Ecology* para su publicación.

When things get hot: Thermoregulation behavior in *Sceloporus aeneus* at different thermal conditions.

Submission Confirmation

 Print

Thank you for your submission

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Keywords:	Thermoregulation behavior, ectotherm, global warming, lizard, environmental temperature, flexibility

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1 **Lay summary**

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3 As environmental temperatures continue rising, species must adopt strategies to cope
4 with adverse thermal conditions, and cold-blooded animals are the most susceptible to
5 these variations. Despite, behavioral thermoregulation can be a plausible mechanism to
6 counteract the negative effects of high temperatures. Here, we found under controlled
7 conditions that lizards can deal with the effects of extreme temperatures by adjusting
8 their thermoregulatory behavior, which allows them to maintain a body temperature
9 below their critical threshold.

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11 **When things get hot: thermoregulation behavior in *Sceloporus aeneus* at different
12 thermal conditions**

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14 **Running header:** Thermoregulation behavior in *Sceloporus aeneus*.

15

16 **Abstract**

17 Rising environmental temperatures have become a global threat for ectotherms,
18 increasing overheating risk and promoting population decline. Flexible
19 thermoregulatory behavior has been proposed as a plausible mechanism to mitigate the
20 effects of extreme hostile temperatures. Here we evaluated thermoregulatory behavior
21 in the bunchgrass lizard *Sceloporus aeneus* at three different environmental
22 temperatures (25, 35 and 45°C) under two different scenarios: with a thermal refuge or
23 without a thermal refuge. We found that behavioral thermoregulation in *Sceloporus*
24 *aeneus* is characterized by the expression of various body postures, adjusting their
25 frequencies depending on the environmental temperature, coupled with a selection of

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3 26 appropriate thermal conditions by expressing shuttling behaviors between hot and cold
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5 27 patches. The interaction of these behavioral responses allows individuals to maintain a
6
7 28 mean body temperature below 40°C, the critical thermal maximum of a temperate
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9 29 species, even at extreme environmental temperatures (45°C). These results demonstrate
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11 30 that the thermoregulation behavior in *Sceloporus aeneus* is a feasible mechanism to
12
13 31 cope with extreme temperatures, which can aid to formulate accurate predictions on
14
15 32 future species vulnerability related to increasing global environmental temperatures.
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21 34 **Keywords:** Thermoregulation behavior, ectotherm, global warming, lizard,
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23 environmental temperature, flexibility.
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51 **Introduction**

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53 Environmental temperature is an important factor directly affecting numerous biological
54 processes, and extreme variation in temperature can represent an acute stressor with
55 lethal consequences for those individuals that are unable to cope with such variations
56 (Wingfield et al. 2011). Various studies have established that increasing environmental
57 temperatures, as well as the frequencies of heat waves, are becoming more common as a
58 response to anthropogenic accelerated climate change (Alexander et al. 2005; Fischer
59 and Knutti 2015); consequently, scientists have addressed the potential impact that this
60 could have on biodiversity (Pacifci et al. 2015; Pearce-Higgins et al. 2015). Among all
61 vertebrate groups ectotherm species, because of their dependence of environmental
62 temperature, have received more attention as they may be more vulnerable to suffer
63 population decreases and extinction if temperatures continue rising (Sinervo et al. 2010;
64 Medina et al. 2016). However, ectotherms have an array of thermal responses for
65 dealing with variations in environmental temperatures; the most common is
66 thermoregulation, defined as the ability of an individual to maintain a particular mean or
67 variance of body temperature (T_b) despite fluctuations in environmental temperatures
68 (Angilletta 2009). Organisms use different strategies to thermoregulate such as
69 physiological (Seebacher and Franklin 2005), morphological (Zamora-Camacho et al.
70 2014) and behavioral mechanisms (Ortega et al. 2016). Among them, behavioral
71 thermoregulation has been described as the most efficient thermoregulatory response
72 because its energetic demand is lower and can be sustained over long time scales,
73 compared to the physiological responses (Rey et al. 2015). In lizards, behavioral
74 thermoregulation can be achieved through different strategies: shuttling between sun
75 and shade (Kearney et al. 2009), using different thermal microhabitats (Goller et al.

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3 76 2014), regulating activity times (Gvoždík 2002), and adjusting body postures (Aguado
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5 77 and Braña 2014).
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10 79 Behavioral thermoregulation has been suggested as a plausible mechanism to lessen the
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12 80 adverse effects of increasing environmental temperatures on ectotherms (Huey et al.
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14 81 2012; Abram et al. 2016; Ortega et al. 2016), and studies agree that behavior must be
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16 82 sufficiently flexible to allow an adjustment to extreme thermal variations therefore,
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18 83 avoiding extinction. Studies focused on evaluating behavioral thermoregulation in the
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20 84 field using artificial models that resemble the organisms' body characteristics, have
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22 85 provided valuable information about heat exchange between the environment and the
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24 86 model (Ortega et al. 2016; Domínguez-Guerrero et al. 2019). However, as individuals
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26 87 do not remain in the same postures and at the same places for extended periods of time,
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28 88 temperature recordings can be biased because an individual can achieve different body
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30 89 temperatures depending on whether it is in full contact with the surface or if it sits with
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32 90 two legs raising the anterior region of the body. Therefore, it is important to perform
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34 91 studies in which flexible thermal behavior and body temperature (T_b) recordings are
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36 92 obtained directly from live organisms under controlled scenarios, where behavior is
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38 93 observed as a response of environmental temperature and not from other stimuli. Hence,
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40 94 the present study aimed to evaluate individual thermoregulation behaviors such as
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42 95 shuttling, the use of thermal microhabitats, the expression of body postures and the
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44 96 flexibility of behavioral strategies under three environmental temperatures (25, 35 and
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46 97 45°C) in the presence and in the absence of a thermal refuge in males of the bunchgrass
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48 98 lizard *Sceloporus aeneus*. *Sceloporus aeneus* is a diurnal, small, oviparous lizard
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50 99 endemic to Mexico. The species is characterized by a sit and wait foraging mode and a
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52 100 heliotherm strategy that allows them to acquire heat directly from solar radiation or
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3 101 through the air (convection) (Lara-Reséndiz et al. 2014). Furthermore, the species has
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5 102 been identified as an efficient thermoregulator (Lara-Reséndiz 2008) with an optimal
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7 103 body temperature of 32°C (Andrews et al. 1999). We predicted that regardless of the
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10 104 presence of a thermal refuge, individuals would adjust to the thermal environment
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12 105 through the expression of behaviors that allow them to approximate their optimal Tb.
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14 106 Particularly, at higher temperatures individuals will show higher frequencies of body
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16 107 postures changes, and shuttling activity will increase as individuals will be actively
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18 108 searching for patches with temperatures closer to their preferred Tb to avoid
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20 109 overheating. Despite this, Tb will be higher in the absence of a refuge due to the thermal
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22 110 homogeneity of the environment and the lack of a cooling area; however, we suggest
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24 111 that individuals can rely on their behavioral plasticity by showing a wide range of
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26 112 thermoregulatory behaviors that under any scenario (in the presence or in the absence of
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28 113 a thermal refuge), will prevent them to reach critical body temperatures.
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35 115 **Material and methods**

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38 117 **Animal collection and husbandry**

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44 119 Fieldwork was conducted from March to June 2016 in Calimaya State of Mexico,
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46 120 Mexico (19°, 08', 44.3''N, 99°, 34', 56.6''W). The landscape of the site is an open area
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48 121 covered with grasses and bunchgrasses of the genus *Festuca*, no rocks or trees are
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50 122 observed nearby. We collected 15 individuals per month, giving a total of 60 adult
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52 123 males (Snout-Vent Length > 45mm) of *Sceloporus aeneus*. Lizards were hand captured
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54 124 and individually placed in cloth-bags and transported to the Ecology and Behavior Lab
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57 125 at the Universidad Autónoma del Estado de México where they were housed
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3 126 individually in opaque-plastic terraria (23.5 cm L x 15 cm W x 30 cm H). Individuals
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5 127 were fed daily with mealworms and small crickets, and water was provided by misting
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7 128 the terrarium walls every day. Each terrarium had peat moss as substrate, a small bunch
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10 129 of grass from the study site as a refuge and it was fitted with a heat lamp (100 W)
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12 130 placed 35 cm above, and a Vita-Lite® lamp provided natural lighting indoors. The
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14 131 lamps were turned on and off automatically from 08:00 to 18:00 h respectively.
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19 133 In the field, individuals of *Sceloporus aeneus* can frequently be observed on the ground
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21 134 near a bunchgrass or on the bunchgrass while basking; hence, we recorded the actual
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23 135 environmental temperature at the study site using a digital temperature data-logger
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25 136 (HOBO® U23-003, range= -40°C to 100°C, precision ± 0.21°C). The data-logger was
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27 137 programed to record the temperature every hour with two sensors, one of which was
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29 138 placed inside the bunchgrass and the other on the ground, 20 cm away from the refuge
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31 139 in the open. Additionally, in April 2016 we recorded field Tb of 52 adult males
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33 140 (Min=21.8°C, Mean=30.92°C, Max=37.8°C; SE=0.653) with an infrared thermometer
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35 141 (Fluke® 62). The protocol to record the Tb was to aim (at distance ~ 15 cm) the infrared
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37 142 beam of the thermometer in the dorsum of each individual between the shoulders. This
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39 143 protocol was followed in the field and in the laboratory using the same infrared
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41 144 thermometer. The infrared thermometer was used to record Tb from a distance to avoid
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43 145 changes in body temperature due to handling and altered behaviors while performing
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45 146 the tests.
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54 **Experimental set-up**

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3 150 Our records of field thermal conditions during the lizard's activity period (9:00-16:00 h)
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5 151 (Jiménez-Arcos 2013) indicated that individuals are exposed to different environmental
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7 152 temperatures inside (min=2.05, mean=12.97 ± 3.56, max=29.14) and outside
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10 153 (min=6.10, mean= 17.13 ± 5.34, max=49.65) the bunchgrass. Consequently, we decided
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12 154 to experimentally expose the lizards to three temperatures that include the temperature
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14 155 variation at their collection site: 25, 35 and 45°C. The experiments began one week after
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16 156 capture, and were divided into two treatments: with a thermal refuge (WTR) and
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19 157 without a thermal refuge (WOTR), the thermal refuge consisted on a bunch of grass
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21 158 placed at one end of the experimental arena. Each treatment included the evaluation of
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23 159 lizards under the three environmental temperatures (25, 35 and 45°C). All individuals
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25 160 collected in a given month (15) were exposed once to each of the three temperatures for
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27 161 both treatments (WTR and WOTR), starting from the lowest temperature (25°C),
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29 162 followed by the tests at 35°C and finishing with the highest temperature (45°C). It took
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31 163 five days to tests all individuals in each temperature trial, and two days with no tests
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33 164 were given before the next temperature trial started, the order in which lizards were
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35 165 evaluated in each treatment was randomized. The experimental arena had a cork floor,
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37 166 three opaque-plastic walls (50 cm L x 30 cm W x 30 cm H) and one plexiglass wall (50
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39 167 cm L x 30 cm H) that allowed video recording. The temperature was adjusted using a
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41 168 heat lamp placed at 70 cm above the terrarium whose intensity was controlled with a
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43 169 dimmer switch (Simon® 25 plus, 25313). To achieve the desired temperatures, different
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45 170 wattage heat lamps were used: a 75W heat lamp for the 25°C test, whereas 150W and
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47 171 250W lamps were used for the 35°C and 45°C assays respectively. To monitor the
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49 172 temperature inside the arena, a four-channel digital thermometer (HOBO® UX120-
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51 173 006M) with four sensors TMC6-HD was used (range= -40°C a 100°C, precision ±
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53 174 0.15°C). The sensors were equally distributed along the surface of the terrarium in the
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3 175 WOTR experiments. For the WTR tests, two sensors were placed on the arena floor and
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5 176 the other two sensors were placed one inside the refuge and the other at the top surface
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7 177 of the refuge (above it). Additionally, during the experiments individuals were
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10 178 monitored for the onset of spasms as an indicator of maximum thermal tolerance
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12 179 (Lutterschmidt and Hutchinson 1997) and examined for any other signals of distress.
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14 180 All individuals remained in the lab for 30 days and concluded successfully all the tests;
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16 181 period after which, they were individually marked by toe-clipping and released at their
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19 182 original collecting site. All tests were performed during the activity period of the
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21 183 species and in agreement with international (*Anim. Behav.* 2003. 65, 249-255) and local
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23 184 (NOM-062-ZOO-1999) ethical guidances for animal maintenance and welfare.
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28 186 **Behavioral assays and video analysis**
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33 188 At the beginning of the trial each individual was gently placed in the center of the
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35 189 experimental arena and its behavior was recorded for 60 minutes with a camcorder
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37 190 (Sony HDR-XR150). Tb was measured every 10 minutes for the duration of the test
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39 191 with an infrared thermometer. To extract the data from the videos, all behaviors were
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42 192 recorded for the five minutes prior to each Tb measurement, in order to associate the
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44 193 behaviors to a Tb. Therefore, for each trial we obtained 6 Tb records and 30 minutes of
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47 194 behavioral observations per individual. Five basking behaviors were identified in a pilot
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49 195 test and in the field (Table 1) and one thermoregulatory behavior was assigned every
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51 196 time the individual assumed a posture for longer than 30 s, as previously reported
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53 197 (Martín et al. 1995). When the posture was sustained longer, the same behavior was
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56 198 recorded every 30 s for the time the posture lasted. Additionally, during the video
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58 199 analysis, the surface of the terrarium was digitally divided into 60 quadrants (5 x 5 cm)
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3 200 to document the spatial location of the focal individual on the arena during the test and
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5 201 to aid in the Emerging Hot Spot Analysis (see below). The spatial location in which the
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7 202 lizard was found at every behavioral evaluation (each 5 minutes) was recorded; this
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10 203 allowed us to determine the individual preference for microthermal regions in each test.
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14 205 **Data Analysis**
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19 207 Since behavioral data did not meet the assumptions of a normal distribution (Shapiro-
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21 208 Wilk test, $p < 0.05$), we performed non-parametric statistics tests. An exploratory
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23 209 analysis was used to compare behaviors between months, since lizards could previously
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25 210 be acclimated to different temperatures at different months, however no significant
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27 211 differences were observed (Kruskall-Wallis test, $p > 0.05$). Therefore, we combined the
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29 212 frequencies of thermoregulation behaviors from all months and compared them between
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31 213 treatments (WTR and WOTR) for all temperatures with a Friedman test for repeated
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33 214 measurements. Furthermore, a Wilcoxon test was used to assess differences between
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35 215 temperatures within each treatment. AR, IR and PR behaviors were not observed in the
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37 216 WOTR, since such behaviors require a bunchgrass as basking site. We also compared
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39 217 HA, and BA between treatments to determine differences in their frequencies in the
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41 218 presence or absence of a refuge. To evaluate possible differences between treatments in
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43 219 the mean T_b at the same environmental temperature, a t -test for paired samples was
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45 220 conducted. Furthermore, since the experimental temperature was collected with only
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47 221 four sensors evenly distributed along the terrarium, to assign a temperature value for
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49 222 any given area, we used the nearest neighbor method to interpolate the temperature data
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51 223 recorded during the whole experiment using SigmaPlot (v11.00). In addition, to
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53 224 determine the tendencies in the frequency of thermal microhabitat use with time, an
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3 225 Emerging Hot Spot Analysis in ArcMap (v10.4.1) was performed. This analysis
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5 226 identifies trends in the clustering of points densities (frequencies) of parameter data
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7 227 such as neighborhood distance and neighborhood time step values. As input we created
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9 228 a space-time cube (60 quadrants (5cm X 5cm) x 12 measurements of 5min = 720bins)
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11 229 (Getis-Ord Gi) (Mitchell 2005), each quadrant represents a relationship between the
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13 230 frequency of all lizards' visits during the time evaluated which was then associated with
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15 231 its temperature. Using a Mann-Kendall trend test (Hamed 2009), the analysis clusters
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17 232 neighbouring (adjacent) bins to identify tendencies of visits in a given time, generating
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19 233 significant patterns of lizard's presence or absence in a specific area (quadrant). A
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21 234 positive hot spot pattern represents a pattern in the increment of the tendency of lizards
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23 235 to use a given area (quadrant) over time; whereas a negative tendency, or a cold spot,
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25 236 represents a pattern of decreased use of a given area over time. When no pattern is
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27 237 identified (null hypothesis), the analysis supposes a random distribution of individuals
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29 238 which is independent of temperature and time. Statistical significance was set at $p < 0.05$
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31 239 for all analysis. Behavioral and Tb data were analysed with SPSS v21.0. All graphs
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33 240 were plotted using SIGMAPLOT (v11.00).
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42 **Results**

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46 244 Individuals showed variable Tb throughout time and at different environmental
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48 245 temperatures WTR (Fig. 1a) and in WOTR (Fig. 2a) of a thermal refuge. Mean Tb was
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50 246 higher in the presence of a thermal refuge at 25°C (WTR: min=11.4, mean= 25 ± 1.5 ,
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52 247 max=28.8 and WOTR: min=21.8, mean= 24.7 ± 0.7 , max=26.6, $t=4.56$, $p=0.00$);
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54 248 however, at 45°C the Tb was lower when a thermal refuge was present (WTR:
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56 249 min=25.3, mean= 36.4 ± 3.1 , max=42.2 and WOTR: min=29.5, mean= 37.4 ± 1.7 ,
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3 250 max=41.8, $t=-6.3$, $p=0.00$). Additionally, Tb was similar at 35°C independent of the
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5 251 presence of a refuge (WTR: min=23.6, mean= 33 ± 2.2 , max=39 and WOTR: min=22.4,
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7 252 mean= 32.9 ± 2 , max=37, $t=0.49$, $p=0.62$).
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12 254 **Thermoregulation behavior with a thermal refuge**

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17 256 The frequency of body postures varied across environmental temperatures in the
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19 257 presence of a thermal refuge (Fig. 1a). Individuals tended to express HA more
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21 258 frequently at 35°C followed by the 25°C condition; while BA, AR and PR were more
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23 259 frequent at 45°C whereas IR was also more frequent at 45°C and 25°C (Table 2). In
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25 260 addition, the results from the Emerging Hot Spot Analysis indicated that lizard's
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27 261 preference for different thermal microhabitats varied at each environmental
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29 262 temperature, using more the open area at 35°C while at 25° and 45°C they showed a
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31 263 tendency to be above, inside, and near the thermal refuge (Fig. 1b).
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37 265 **Thermoregulation behavior without a thermal refuge**

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42 267 When individuals did not have access to a thermal refuge, the frequency of body
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44 268 postures also varied depending on the environmental temperature (Fig. 2a). HA
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46 269 behavior was more frequently observed at 35° and 25°C and less common at 45°C. In
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48 270 the case of BA, this posture was expressed more frequently at 45°C, scarcely used at
49
50 271 35°C and not observed at 25°C (Table 2). Furthermore, thermal microhabitat use also
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52 272 depended on environmental temperature; in this case, at 25 and 45°C individuals had a
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54 273 tendency to be close to the edges of the terrarium, whereas at 35°C individuals tended to
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56 274 be at the center (Fig. 2b).
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276 **Comparison of thermoregulation behavior with and without a thermal refuge**

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278 When comparing the expression of body postures (HA and BA) in the presence and
279 absence of a thermal refuge, we found that HA was more frequent in the WOTR
280 treatment at 25, 35 and 45°C; however, the expression of BA did not depend on the
281 presence of a thermal refuge ($p>0.05$) (Table 2). Regarding thermal microhabitat use
282 (fig. 1b), at 25° and 45°C in the WTR there is a tendency for individuals to use more
283 frequently the thermal refuge; whereas at 35°C they more frequently visited the center
284 of the terraria. However, without a thermal refuge (fig. 2b), individuals tend to visit the
285 edges of the arena at 25° and 45°C, which coincides with the cooler temperatures (fig.
286 2c); whereas at 35°C, individuals tend to visit more frequently the middle of the
287 terrarium.

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289 **Discussion**

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291 We found that males of the lizard *Sceloporus aeneus* modify their thermoregulation
292 behaviors according to the thermal environment they are exposed to, allowing them to
293 mitigate the effects of adverse environmental temperatures by maintaining a T_b close to
294 their preferred temperature. Overall, in the presence of a thermal refuge we observed
295 that individuals initially expressed postures that maximize heat acquisition (HA), and
296 once their optimal T_b is reached, individuals start to use thermoregulation postures that
297 evade further heat gain (BA, AR, IR, PR), being able to maintain an optimal T_b and
298 preventing them from reaching critical temperatures that could compromise their
299 survival. Although HA and AR are behaviors that can increase heat absorption through

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3 300 radiation, AR also helps to regulate heat gain, as wind currents in the upper region of a
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5 301 bunchgrass are higher than on the substratum's surface. Additionally, in the 25 and
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7 302 35°C tests, behaviors such as HA and AR were the most common although not as
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9 303 frequent in the 45°C tests. In a scenario of high environmental temperature (in this case
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11 304 45°C), HA was expressed only during the first minutes of exposure, and was
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13 305 subsequently changed for thermoregulation postures in which heat gain was minimized
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15 306 (Fig. 1a). This behavioral thermoregulation strategy has previously been observed in
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17 307 other lizard species for which it was found that in cooler environments, individuals
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19 308 assume body positions that maximize heat gain from solar radiation, whereas in hot
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21 309 environments postures that favor heat loss are more common (Muth 1977; Asbury and
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23 310 Adolph 2007; McConnachie et al. 2009). Furthermore, the increase in the frequency of
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25 311 postures that involve the use of a thermal refuge, and BA postures at 45°C might be
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27 312 explained as a response to minimize the effects of increasing environmental
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29 313 temperatures as previously proposed (Kearney et al. 2009), where individuals need to
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31 314 adjust their temperature by shuttling between shady and sunny patches. On the other
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33 315 hand, in the absence of a thermal refuge similar results were observed, where HA was
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35 316 more frequent at 25 and 35°C, but decreased after a few minutes in the 45°C test. In this
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37 317 case, BA was the only thermoregulation behavior that could help individuals to prevent
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39 318 surpassing their thermal limits, and therefore it was more recurrent in the 45°C tests. In
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41 319 *S. aeneus*, postural adjustments can also be related to the fact that lizards with small
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43 320 body sizes need small fractions of time to reach an optimal T_b (Garrick 2008); thus,
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45 321 individuals must frequently change postures to maintain an optimal body temperature
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47 322 and to avoid reaching the limits of thermal tolerance. Furthermore, a rapid increase of
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49 323 T_b can be beneficial as energy and time expenditure are minimized while attaining an
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51 324 optimal T_b ; however, they are also more susceptible to reaching critical internal
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3 325 temperatures, specially when environmental temperatures increase. Consequently, and
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5 326 in accordance with our first prediction, males of *S. aeneus* present an active adjustment
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7 327 of thermoregulation behaviors at 45°C compared to lower environmental temperatures.
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10 328 In addition, we observed that the tendency in the use and selection of a thermal
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12 329 microhabitat in *S. aeneus* was based on the suitability of the available thermal patches in
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14 330 each condition. In the presence of a thermal refuge, at the lower and higher
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16 331 temperatures (25 and 45°C), individuals tended to visit more frequently the refuge;
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18 332 whereas at 35°C, which represents a closer value to their optimal T_b (32°C), individuals
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20 333 tended to visit the middle of the arena. Similarly, when a thermal refuge was absent,
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22 334 individuals were more frequently observed at the middle of the terraria when they were
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24 335 exposed to 35°C; however, they tended to visit the edges of the terrarium at 25°C, which
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26 336 may not be related to the environmental temperature, but to seek protection due to an
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28 337 increased vulnerability in the open when they have not reached an optimal T_b . At 45°C
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30 338 they also spent most of the time around the edges of the terrarium, which corresponds to
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32 339 the coldest temperatures in the arena (fig. 2c), perhaps as a strategy to maintain a T_b
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34 340 closer to their optimal. The overall tendency of microhabitat use observed in males of *S.*
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36 341 *aeneus* could be based on the selection of areas with temperature values closer to the
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38 342 preferred temperature of the species (33.8-35.3°C) (Lara-Reséndiz et al. 2014). In the
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40 343 field, individuals are commonly observed basking closer to bunchgrasses or above
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42 344 them, possibly using them as a buffer area especially in hotter conditions, since the
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44 345 temperature inside the bunchgrass is always lower than outside. Thus, the species may
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46 346 be well adapted to exploit the thermal conditions it inhabits by moving from open areas
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48 347 to their refuge depending on their thermal necessities. Models of the costs and benefits
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50 348 of thermal heterogeneity suggest that greater availability of microhabitats with preferred
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52 349 temperatures leads to enhanced thermoregulation performance and decreased energetic
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3 350 expenditure (Sears and Angilletta 2015). In our study, the costs and benefits of
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5 351 thermoregulation could be associated with such environmental complexity, for which
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7 352 the presence of bunches of grass (thermal refuges) represent a thermally structured
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10 353 environment that could lower the energetic costs of thermoregulation by allowing
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12 354 individuals to move less, since their preferred microclimates are easier to locate (Sears
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14 355 et al. 2011), diminishing also the risk of predation and other associated costs.
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17 356 Accordingly, in the small lizard *Zootoca vivipara*, greater heating rates are achieved by
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19 357 selecting more suitable microhabitats for basking and through body postures (Gvoždík
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21 358 2002). Thus, males of *Sceloporus aeneus* employ a thermoregulation strategy that
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23 359 benefits from both, the selection of suitable thermal microhabitats and the adoption of a
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25 360 set of thermoregulation behaviors, which allows them to keep a T_b far from thermal
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27 361 limits but closer to their preferred temperature. Furthermore, our study offers a novel
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29 362 method to evaluate microhabitat preference that encompasses both, individual
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31 363 behavioral observations and spatial-time analysis based on a thermal distribution in an
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33 364 environment. Here, we provide a finer approach to the thermal environmental factors
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35 365 experienced by organisms in natural conditions, which most studies fall behind
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38 366 (Deutsch et al. 2008), as they use broader scales biasing the effects that thermal
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40 367 heterogeneity has on ectotherms (Sears et al. 2011).
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46 369 Selection of behavioral postures and preferred thermal microhabitats, mutually enable
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48 370 individuals of the lizard *S. aeneus* to regulate their body temperature within a particular
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50 371 range. We found that at 35°C as individuals are closer to their preferred temperature, no
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52 372 differences in T_b were observed in the presence or absence of a thermal refuge. In
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54 373 contrast, the differences observed in T_b between WTR and WOTR tests at 25 and 45°C
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56 374 can be related to the degree of the thermal distribution in each treatment. Greater
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3 375 thermal heterogeneity is observed in the presence of a thermal refuge as more suitable
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5 376 thermal microhabitats were available, and individuals could express shuttling behaviors
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7 377 and variable body postures. A refuge, apart from its thermal benefits, also offers
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10 378 individuals easy escape from predators when needed maximizing, in different ways,
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12 379 individual survival. This could also favor enhanced thermoregulation performance by
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14 380 maintaining body temperatures closer to their preferences, contrasting to environments
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16 381 without refuges, where thermal distribution is more homogeneous and options to
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18 382 thermoregulate, and even escape from predators seem scarce. In this regard, it is
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21 383 important to note that changes in land use, in which replacing extensive areas of forest
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23 384 and grasslands for concrete a common practice in the area, have a direct effect on
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25 385 environmental heterogeneity, imposing severe challenges for ectotherms, not only
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27 386 regarding to food and refuge availability but also enforcing further compromises in
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29 387 relation with thermoregulation. In the study area, lizard refuges frequently disappear
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31 388 due to controlled fires; furthermore, in recent years grasslands are being removed to
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33 389 give way to urbanized areas. Therefore, understanding how ectotherms cope with
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35 390 human-made changes will aid to promote conservation alternatives for species that are
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37 391 showing a dramatic decline in their populations and that require a well-structured
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39 392 environment for their survival. Additionally, body temperatures especially at high
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41 393 temperatures, were not as pronounced as expected; this is remarkable for the species,
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43 394 especially because individuals were able to sustain a mean body temperature under 40°C
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45 395 principally in the absence of a thermal refuge. Hence, evaluating the physiology behind
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47 396 those responses will help us to understand how body temperature is maintained around
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49 397 the preferred mean in species that depend on environmental temperature to survive. In
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51 398 other *Sceloporus* species, critical thermal maximum (CT_{Max}) values range from 43 to
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53 399 45°C (Larson 1967; Crowley 1985). In the case of *S. aeneus*, CT_{Max} has not been
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3 400 reported; however, we believe that in our study the temperature threshold was not
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5 401 reached as no signs of spasms or distress were observed during the trials thus,
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7 402 behavioral thermoregulation probably helps to buffer the effects of rising environmental
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9 403 temperatures. Our observations help to better understand the proposed ectotherm
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11 404 extinctions due to environmental temperatures rising above critical thermal maximum
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13 405 (Sinervo et al. 2010), especially when physiological plasticity has little potential to
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15 406 mitigate the effects of extreme temperatures (Gunderson and Stillman 2015).
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547 **Figure Legends**

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549 **Figure 1.** Behavioral thermoregulation expressed by males of *Sceloporus aeneus* at
550 three environmental temperatures with a thermal refuge (WTR). a) Frequencies of body
551 postures and Tb of all individuals during the tests. b) Trends in the frequencies of all
552 lizards' visits during the experiment associated to the environmental temperature. A
553 positive hot spot pattern (spotted squares) represents the tendency of lizards to
554 frequently use a given quadrant overtime, the color of the squares intensifies to black
555 for the most visited areas. A negative tendency (solid color squares) or cold spot,
556 represents the movement of the lizards from such quadrants, the color of the squares
557 intensifies to black as lizards move from those areas. Blank squares (no pattern)
558 represent a random distribution of individuals which is independent of temperature and
559 time, or areas not used by the lizards during the test. c) Thermal distribution of the
560 experimental arena during the assays. The spaces inside and above the thermal refuge
561 are enclosed at the inferior end of the graph.

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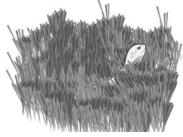
563 **Figure 2.** Behavioral thermoregulation expressed by males of *Sceloporus aeneus* in
564 three environmental temperatures without of a thermal refuge (WOTR). a) Frequencies
565 of body postures and Tb of all individuals during the tests. b) Trends in the frequencies
566 of all lizards' visits during the experiment associated to the environmental temperature.
567 A positive hot spot pattern (spotted squares) represents the tendency of lizards to
568 frequently use a given quadrant overtime, the color of the squares intensifies to black
569 for the most visited areas. A negative tendency (solid color squares) or cold spot,
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597 **Table 1.** Thermoregulatory body postures observed in males of the lizard *Sceloporus*
598 *aeneus* both, in the field and in captivity.
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Posture	Description	Example
Heat Acquisition (HA)	The ventral region of the body, limbs and tail rest on the substrate's surface while the head is raised or on the ground.	
Body Arched (BA)	The anterior region of the body is elevated by full extensions of the anterior limbs, whereas the forelimbs and tail rest on the ground. This behavior can be accompanied with an open snout.	
Above Refuge (AR)	The ventral region of the body, head, limbs and tail rest on the surface of a refuge (bunchgrass).	
Inside Refuge (IR)	The individual remains completely inside the bunchgrass.	
Partially in the Refuge (PR)	The individual maintains the anterior region of the body (particularly the head) on the surface of the bunchgrass, while the posterior region of the body remains inside.	

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601 **Table 2.** Comparison of the frequencies of thermoregulatory body postures in males of
602 *Sceloporus aeneus* at different environmental with (WTR) or without (WOTR) a
603 thermal refuge. Median values were obtained from the combined frequencies of all
604 individuals evaluated in each treatment.
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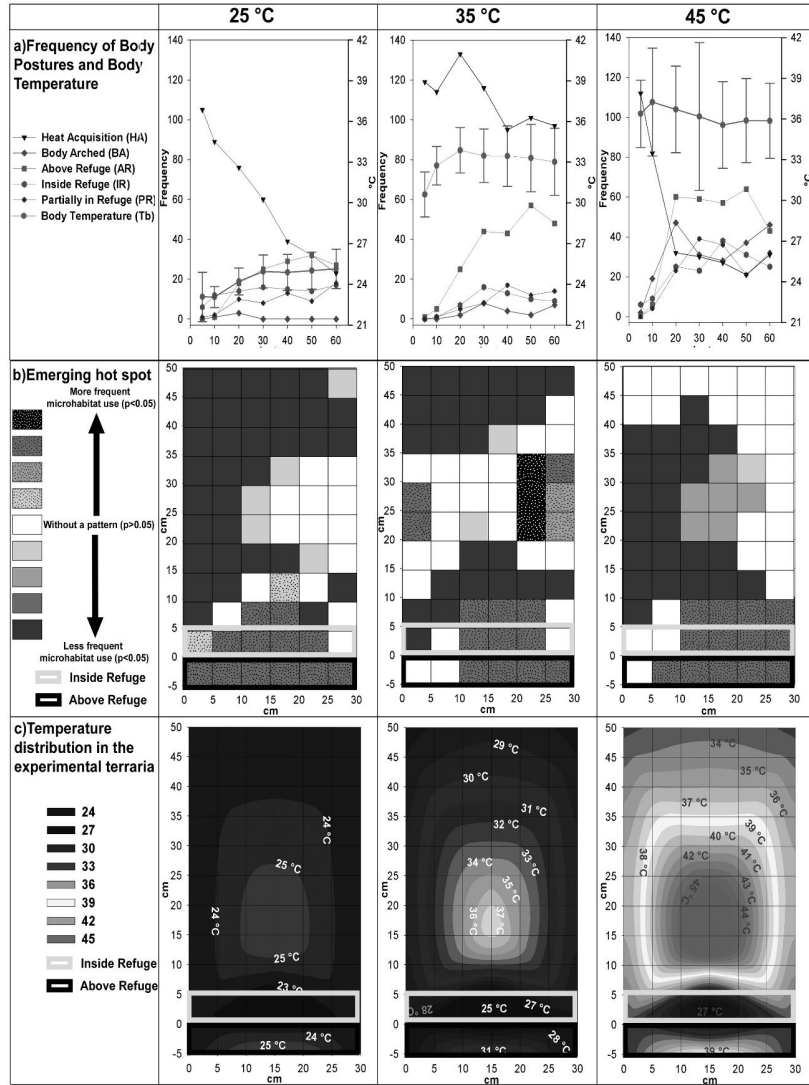
Trials without a thermal refuge (WOTR)				
Body Posture/Test	Median \pm SD	Friedman's Test Statistics	Between Group Comparison	Wilcoxon's tests Statistics
Heat Acquisition (HA)				
25°C	118 \pm 15.9	$\chi^2=8.96$, p=0.01	25°C vs 35°C	Z=-1.85, p=0.06
35°C	154 \pm 52.8		25°C vs 45°C	Z=-2.20, p=0.02
45°C	66 \pm 25.3		35°C vs 45°C	Z=-2.20, p=0.02
Body Arched (BA)				
25°C	0 \pm 0	$\chi^2=11.56$, p=0.01	25°C vs 35°C	Z=-2.06, p=0.03
35°C	8 \pm 5.3		25°C vs 45°C	Z=-2.20, p=0.02
45°C	114 \pm 50.9		35°C vs 45°C	Z=-2.20, p=0.02
Trials with a thermal refuge (WTR)				
Body Posture/Test	Median \pm SD	Friedman's test Statistics	Between Group Comparison	Wilcoxon's tests Statistics
Heat Acquisition (HA)				
25°C	60 \pm 30.8	$\chi^2=11.14$, p=0.01	25°C vs 35°C	Z=-2.37, p=0.01*
35°C	114 \pm 13.7		25°C vs 45°C	Z=-1.60, p=0.10
45°C	31 \pm 34.8		35°C vs 45°C	Z=-2.36, p=0.01*
Body Arched (BA)				
25°C	0 \pm 1.1	$\chi^2=11.18$, p=0.01	25°C vs 35°C	Z=-1.57, p=0.11
35°C	2 \pm 3.1		25°C vs 45°C	Z=-2.36, p=0.01*
45°C	31 \pm 15.8		35°C vs 45°C	Z=-2.36, p=0.01*
Above Refuge (AR)				
25°C	25 \pm 13.2	$\chi^2=9.85$, p=0.01	25°C vs 35°C	Z=-2.36, p=0.01*

35°C	43 ± 21.9		25°C vs 45°C	Z=-2.20, p=0.02
45°C	57 ± 27.0		35°C vs 45°C	Z=-1.60, p=0.10
Inside Refuge (IR)				
25°C	28 ± 6.6	$\chi^2=11.14,$ p=0.01	25°C vs 35°C	Z=-2.37, p=0.01*
35°C	9 ± 5.8		25°C vs 45°C	Z=-1.35, p=0.17
45°C	25 ± 11.3		35°C vs 45°C	Z=-2.36, p=0.01*
Partially in the Refuge (PR)				
25°C	9 ± 5.9	$\chi^2=7.46,$ p=0.02	25°C vs 35°C	Z=-0.63, p=0.52
35°C	8 ± 6.5		25°C vs 45°C	Z=-2.19, p=0.02
45°C	23 ± 15.2		35°C vs 45°C	Z=-2.20, p=0.02
Comparison Between Treatments				
Body Posture/Test	Median ± SD		Wilcoxon's tests Statistics	
Heat Acquisition (HA)				
25°C	WOTR=118 ± 15.9, WTR=60 ± 30.8		Z=-2.36, p=0.01*	
35°C	WOTR=154 ± 52.8, WTR=114 ± 13.7		Z=-2.36, p=0.01*	
45°C	WOTR=66 ± 25.3, WTR=31 ± 34.8		Z=-2.36, p=0.01*	
Body Arched (BA)				
25°C	WOTR=0 ± 0, WTR=0 ± 1.1		Z=-1.34, p=0.18	
35°C	WOTR=8 ± 5.3, WTR=2 ± 3.1		Z=-2.03, p=0.04	
45°C	WOTR=114 ± 50.9, WTR=31 ± 15.8		Z=-2.19, p=0.02	

*Denotes statistical significance of Wilcoxon signed rank *post hoc* analysis with a Bonferroni adjustment set at p=0.01.

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613 **Figure 1.**



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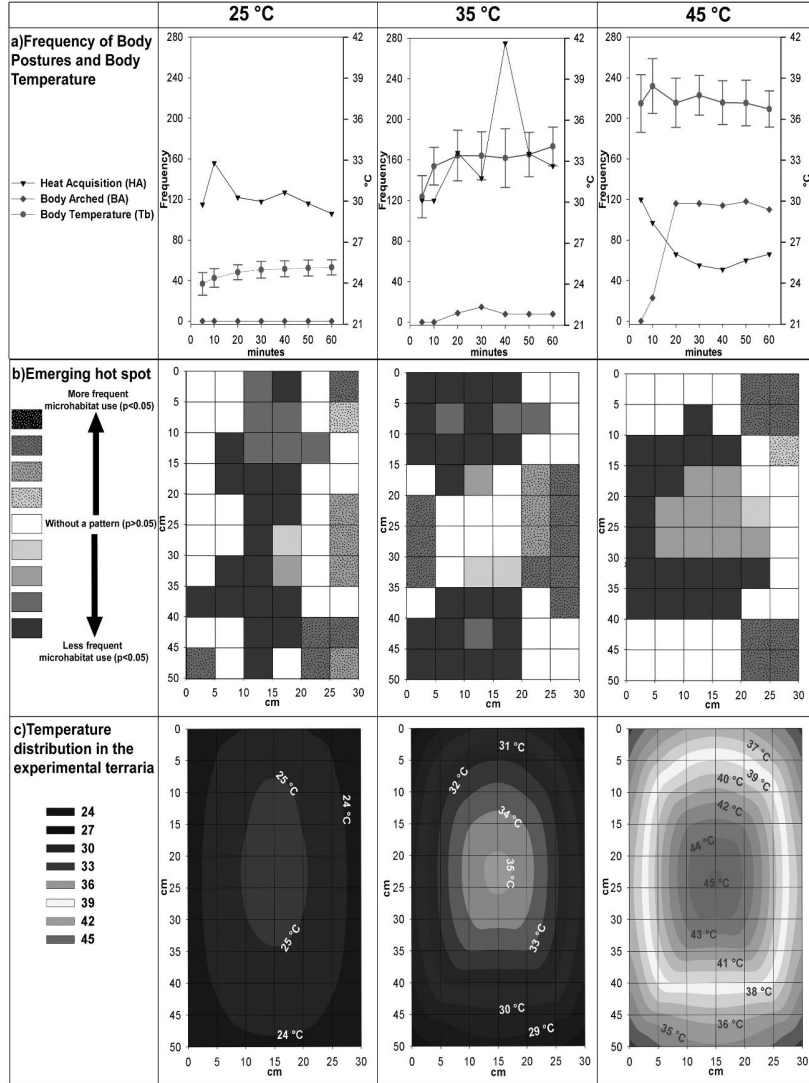
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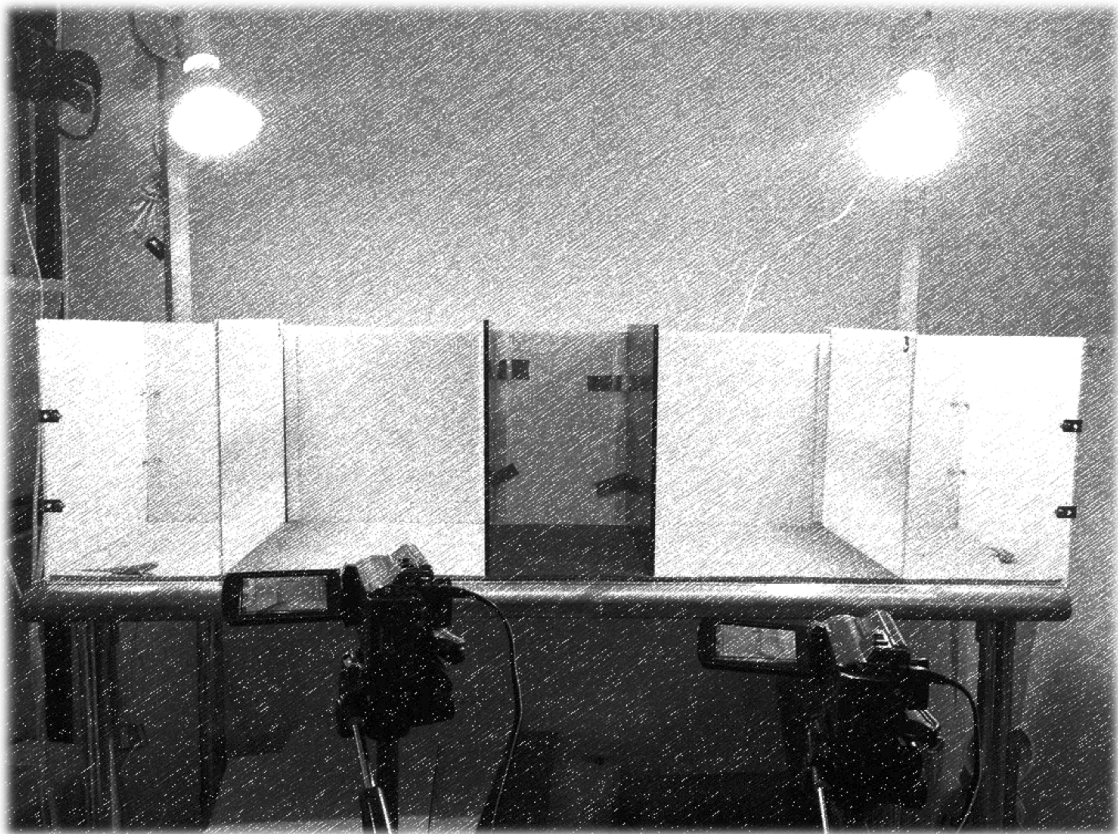
618 **Figure 2.**



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Capítulo 4

Bases neurofisiológicas de la conducta



La conducta es la expresión de una compleja organización de mecanismos neuronales y fisiológicos que actúan de forma conjunta para modular la respuesta de los individuos ante un estímulo ambiental. De acuerdo con las estrategias conductuales, se pueden observar dos fenotipos (proactivo y reactivo) los cuales difieren en sus respuestas conductuales, posicionando un fenotipo al extremo opuesto del otro (Koolhaas *et al.* 1999). Se ha propuesto que los niveles de agresividad (Koolhaas *et al.* 2010), así como la flexibilidad conductual (Coppens *et al.* 2010), son parámetros que permiten diferenciar un fenotipo de otro. En el caso de la agresividad, esta diferenciación entre fenotipos puede estar asociada principalmente por la actividad del sistema serotoninérgico y el eje hipotalámico-pituitario-gonadal (HPG). Referente a la serotonina (5-HT), su actividad como inhibidor de la agresividad está bien fundamentada en distintos grupos de vertebrados (Perreault *et al.* 2003; Larson y Summers 2001; Sperry *et al.* 2003). Sin embargo, una interpretación más acertada del papel que tiene la serotonina sobre la agresividad es determinar su sitio de acción en el cerebro ya que este neurotransmisor se encuentra involucrado en distintos procesos fisiológicos. Se ha establecido que el núcleo dorsal del rafe es la fuente principal de la innervación de la serotonina hacia el núcleo accumbens, amígdala y córtex prefrontal (Puglisi-Allegra y Andolina 2014), regiones que son activadas durante enfrentamientos agonistas en ratones seleccionados por sus bajos niveles de agresividad (Haller *et al.* 2006). En el caso de la lagartija *Anolis carolinensis*, se reporta que las diferencias en la agresividad también están asociadas a la actividad de la serotonina en distintas regiones del cerebro como el hipotálamo anterior, el núcleo accumbens, la amígdala media, el septum y el rafe (Summers *et al.* 2005). Resultados similares se han encontrado en el pez espinoso *Gasterosteus aculeatus* al presentarse una relación negativa entre la conducta agresiva y la concentración de serotonina en distintas regiones del cerebro (Bell *et al.* 2007). Basado en lo anterior, se puede sugerir que la actividad de la serotonina en regiones específicas del cerebro es responsable de modular la agresividad y que puede ser un mecanismo evolutivamente conservado en vertebrados.

Por otra parte, distintos reportes señalan una relación entre la actividad del eje HPG y la agresividad, donde los niveles de testosterona actúan principalmente sobre el hipotálamo y la amígdala incrementando los niveles de agresividad de los individuos (Bernhardt 1997). Esta alta actividad de la testosterona en el hipotálamo y la amígdala actúa de forma conjunta con los bajos niveles de serotonina en el córtex prefrontal

promoviendo la impulsividad, disminuyendo el miedo y predisponiendo impulsos agresivos en los individuos (Montoya *et al.* 2012). Al evaluar la actividad de la testosterona en plasma y el número de receptores de andrógeno en dos especies del género *Sceloporus* que difieren en sus niveles de agresividad, se observó que los machos de la especie agresiva presentaban mayores concentraciones de testosterona en el plasma, así como un mayor número de receptores de andrógenos en regiones del hipotálamo (Hews *et al.* 2012), confirmando la relación entre los niveles de agresividad y la actividad del eje HPG. Sin embargo, es importante resaltar que la mayoría de los estudios en los que se ha evaluado esta relación entre la secreción de testosterona y la agresividad se ha llevado a cabo dentro de la temporada de reproducción por lo que los resultados deben ser abordados con cautela. Por ejemplo, en la lagartija *Egernia whitii* la agresividad en hembras y machos mantuvo una relación con los niveles de testosterona a lo largo de la temporada de reproducción; no obstante, esta relación fue negativa al finalizar la temporada (While *et al.* 2010) por lo que la agresividad puede ser contexto-dependiente como lo sugieren otros autores (Adkins-Regan 2005).

Como se indicó previamente, la flexibilidad conductual puede ser otro parámetro que permita diferenciar entre un fenotipo reactivo y un proactivo, ya que las acciones de este último suelen basarse en predicciones rígidas del ambiente confiando en experiencias previas y formando rutinas; mientras que los individuos reactivos se basan en la información disponible en el ambiente, es decir, existe una relación directa estímulo-respuesta. Estas diferencias en la flexibilidad conductual y formación de rutinas están relacionadas con el funcionamiento del córtex prefrontal y el sistema dopaminérgico (Coppens *et al.* 2010). El sistema dopaminérgico es el responsable del proceso de recompensa y el desarrollo de la adicción (Kelley y Berridge 2002), el cual presenta sus cuerpos celulares en el área ventral tegmental del cerebro inervando el núcleo accumbens y el córtex prefrontal (Coppens *et al.* 2010). Lo anterior sugiere que aquellos individuos que presenten una mayor expresión de receptores de dopamina en estas regiones del cerebro presentarán una mayor dificultad en la inhibición de las conductas debido a un proceso de reforzamiento de la conducta a través de la recompensa. Giorgi y colaboradores (2007) observaron que, en ratones seleccionados por su estrategia conductual, los individuos identificados como reactivos presentaban una menor densidad de receptores de dopamina en el núcleo accumbens a diferencia de los individuos proactivos. Asimismo, en líneas de trucha arcoíris (*Oncorhynchus mykiss*)

seleccionadas por sus características conductuales y fisiológicas, se observó que los individuos proactivos presentaban una mayor actividad de dopamina en regiones límbicas del telencéfalo, indicando que basan su conducta en rutinas previamente establecidas impidiendo ajustes conductuales a nuevas situaciones (Höglund *et al.* 2017). Alternativamente, se ha observado que el córtex prefrontal desempeña un papel importante en el control de la conducta impulsiva y la flexibilidad conductual (Johnston *et al.* 2006), el cuál puede estar asociado a la inervación que recibe del sistema serotoninérgico (Andolina *et al.* 2013) y dopaminérgico (Coppens *et al.* 2010). En efecto, lesiones en el córtex prefrontal han permitido identificar su importancia en la flexibilidad de los individuos. Por ejemplo, lesiones en el córtex orbito-frontal han resultado en déficits en la inhibición de conductas previamente aprendidas por otras nuevas (aprendizaje regresivo o inverso) (Boulougouris *et al.* 2007).

Por otro lado, la eficiencia de la conducta de termorregulación también depende de la capacidad de los individuos de percibir el ambiente térmico en el que se encuentran. En el caso de los reptiles, el complejo pineal puede actuar como un sensor térmico (Seebacher y Franklin 2005); sin embargo, sus sensores neuronales específicos aún son inciertos. De forma general, se conoce que la glándula pineal influye en la conducta de termorregulación a través de los centros termorreguladores del hipotálamo, y, por lo tanto, podría afectar la vía fisiológica de termorregulación (Ralph *et al.* 1979). En el hipotálamo, el área pre-óptica (POA) es la encargada de integrar información acerca de la temperatura del cerebro y de otras regiones del cuerpo, así como de dirigir las repuestas termorreguladoras que permitan una temperatura corporal apropiada (Boulant 1998). Por ejemplo, lesiones en la POA en la lagartija *Dipsosaurus dorsalis* causaron efectos pronunciados en la temperatura corporal de los individuos al afectar la conducta de cambio de lugares calientes a fríos (Berk y Heath 1975). La actividad de la POA parece estar asociada al aporte que puede recibir de los neurotransmisores serotonina y dopamina, los cuales actúan sobre segundos mensajeros como APMc y GMPc aumentando la sensibilidad térmica de los individuos (Bicego *et al.* 2007). En referencia a la dopamina, su actividad parece estar allegada al hipotálamo y a la sustancia negra, mediando la pérdida de calor en los organismos (Lee *et al.* 1985). Por el contrario, la actividad de la serotonina en el hipotálamo está relacionada con la regulación de la producción de calor y su disipación (Tsai y Wang 1997). Aunado a ello, la actividad de la serotonina parece estar involucrada en el comportamiento de la

selección de temperaturas favorables (Gryer y Ogilvie 1978). La selección de temperaturas ideales para los individuos está posiblemente relacionada con la búsqueda de incrementar la temperatura en el tronco del encéfalo, lo cual permitirá un aumento en la ventilación y el ritmo cardiaco de los individuos (Crawshaw *et al.* 1973). El incremento y decremento del ritmo cardiaco conllevan a un calentamiento más rápido y a un enfriamiento más lento respectivamente (Grigg *et al.* 1979); lo anterior, puede favorecer a los reptiles al disminuir los costos de termorregulación manteniendo la temperatura corporal por periodos de tiempo más largos.

Finalmente, se ha determinado que el tamaño del cerebro puede relacionarse con las diferencias individuales en la conducta, ya que los individuos con cerebros más grandes (en proporción al tamaño corporal) pueden procesar, integrar y almacenar más información acerca del ambiente físico y social, incrementando la capacidad de los individuos de modificar o crear nuevas conductas (Sol *et al.* 2005). Bajo este planteamiento, se esperaría que la flexibilidad conductual asociada con individuos de cerebros más grandes (Sol 2009) también pueda estar relacionada con el fenotipo reactivo, ya que estos individuos presentan la capacidad de ajustar sus conductas a nuevas situaciones (Coppens *et al.* 2010), desarrollando nuevas respuestas ante un estímulo novedoso o alterando respuestas existentes ante un estímulo familiar (Leal y Powell 2011). Ciertamente, en el pez guppy (*Poecilia reticulata*), los individuos que presentan cerebros más grandes fueron asociados a una mayor flexibilidad cognitiva que los individuos con cerebros más pequeños, al ser expuestos a una prueba de aprendizaje regresivo (Buechel *et al.* 2017). Aunado a ello, se ha observado en distintas especies de peces que los individuos con cerebros más grandes presentan una mayor habilidad para evaluar los riesgos potenciales, característica del fenotipo reactivo, favoreciendo una mayor sobrevivencia (Kotrschal *et al.* 2015; Van der Bijl *et al.* 2015; Walsh *et al.* 2016). No obstante, Kotrschal y colaboradores (2013a) reportan que individuos con mayores niveles de exploración, habituación y formación de rutinas, así como bajos niveles de estrés, características de un fenotipo proactivo, presentaban cerebros más grandes. Una posible explicación para este contraste entre la relación del tamaño del cerebro y el tipo de estrategia conductual, puede ser abordada desde el planteamiento en el que los individuos con cerebros más grandes pueden intercambiar la flexibilidad conductual por otro tipo de habilidades cognitivas que sean favorables en el ambiente en el que se encuentren. Por ejemplo, el hecho de que una situación se repita de forma

constante requiere poca capacidad cognitiva una vez que la solución se ha encontrado, por lo que la decisión de formar rutinas puede liberar cierta capacidad cognitiva para otras tareas (Sih y Del Giudice 2012; Kotschal *et al.* 2013a). Siguiendo esta línea, los altos niveles de actividad, exploración e intrepidez de los individuos proactivos pueden conducir a un mayor consumo de alimento lo cual, de acuerdo a la hipótesis del tejido costoso (Aiello y Wheeler 1995), conlleva a una reducción de los intestinos para dirigir el gasto de energía en la producción de un cerebro más grande como se ha observado en otras especies (Kotschal *et al.* 2013b). En consecuencia, se puede concluir que el tamaño del cerebro y su asociación con el tipo de estrategia conductual parece depender de las condiciones ambientales en las cuales estén sujetas las especies, ya que en ambientes desafiantes o cambiantes la flexibilidad conductual confiere una ventaja sobre la formación de rutinas resultando en el desarrollo de un cerebro más grande (Sol 2009).

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Capítulo 5

Discusión general y conclusiones



En el presente trabajo se evaluaron las estrategias conductuales en machos y hembras de *Sceloporus aeneus* durante la temporada de reproducción, así como la habilidad de los machos de esta especie para modificar su conducta de termorregulación en distintas temperaturas ambientales y en presencia-ausencia de un refugio para la termorregulación. Se observó que hembras y machos difieren en sus estrategias conductuales durante la temporada de reproducción, lo cuál puede estar asociado con sus estrategias de historia de vida y para asegurar su éxito reproductivo. En el caso de los machos, estos presentan altos niveles de agresividad siendo intrépidos y activos en condiciones de alto riesgo, lo cual puede incrementar su éxito de reproducción, pero a su vez incurrir en un alto costo al presentar un mayor riesgo de depredación, como se ha reportado en otras especies (Reaney y Blackwell 2007). Por el contrario, las hembras presentan bajos niveles de intrepidez y actividad mientras que sus niveles de agresividad fueron similares a los de los machos. Los altos niveles de agresividad pueden estar asociados a un alto grado de competencia entre hembras, ya que en la población, al ser el sexo más abundante (en proporción), puede existir un mayor número de enfrentamientos entre hembras por diversos recursos (Rosvall 2011). Asimismo, altos niveles de agresividad pueden estar asociados en machos y hembras por la alta actividad hormonal durante la temporada de reproducción (Woodley y Moore 1999; Weiss y Moore 2004). Es bien sabido que la cantidad de testosterona que se produce puede variar durante la temporada de reproducción (Eikenaar *et al.* 2012) y aunque estos parámetros no fueron evaluados en el presente estudio, se esperaría que las hembras presenten niveles altos y constantes de testosterona durante dicha temporada, así como su actividad en distintas regiones del cerebro a diferencia de los machos, derivando en niveles de agresividad equiparables entre sexos. De acuerdo con lo anterior, se ha reportado una similitud en la agresividad en machos y hembras de la especie *Sceloporus jarrovi* asociada a niveles similares entre sexos de testosterona en la sangre y de receptores de andrógeno en ciertas regiones del cerebro (Hews *et al.* 2012). Aunado a ello, al parecer la producción de testosterona en las hembras parece ser más constante que en los machos ya que su conducta agresiva fue mas consistente, lo cual puede incurrir en costos reproductivos como la infertilidad (Stockley y Campbell 2013), por lo que requieren dirigir la actividad de la testosterona a regiones del cerebro donde no se vea comprometido su éxito reproductivo.

Por otra parte, las características conductuales de machos y hembras en *Sceloporus aeneus* se aproximan a las estrategias conductuales sugeridas por Koolhaas y colaboradores (1999) en la cual los machos presentan semejanzas con el fenotipo proactivo (altos niveles de agresividad, actividad, intrepidez, exploración), mientras que las hembras con el fenotipo reactivo (bajos niveles de actividad, timidez y agresividad). Sin embargo, se observó que las hembras presentan una mayor consistencia en sus rasgos conductuales, lo cual puede ser explicado por los mecanismos neurofisiológicos que subyacen su conducta. La actividad de la serotonina y dopamina en el córtex prefrontal puede ser uno de los principales factores neurológicos que moldean la conducta en las hembras, donde una alta actividad de dopamina puede resultar en una deficiente inhibición de conductas, formando rutinas y por lo tanto propiciando repetitividad en la conducta (Klanker *et al.* 2013), mientras que una baja actividad de la serotonina puede estimular la expresión de conductas agonistas (Puglisi-Allegra y Andolina 2014). En contraste, los machos presentaron una menor consistencia en sus rasgos conductuales, lo cual puede reflejar un grado mayor de flexibilidad conductual al poder responder directamente a los estímulos del ambiente, pudiéndose desempeñar mejor en ambientes cambiantes e impredecibles. En este sentido, en años recientes los organismos ectotermos han experimentado cambios en sus regímenes térmicos a consecuencia del calentamiento global (Deutsch *et al.* 2008), por lo que es indispensable para los organismos presentar conductas de termorregulación lo suficientemente flexibles para hacer frente a estos cambios (Abram *et al.* 2016; Ortega *et al.* 2016). En el presente estudio se observó que los machos de *Sceloporus aeneus* muestran una conducta de termorregulación flexible, ajustando el número de posturas corporales, el uso de microhábitats térmicos, así como los movimientos entre sol y sombra dependiendo de la temperatura ambiental en la que se encuentren. Esta conducta de termorregulación flexible favorece a los individuos al poder mantener sus temperaturas corporales lejos de las temperaturas críticas máximas, incrementando su sobrevivencia en condiciones donde las temperaturas ambientales son hostiles. Aunado a ello, podemos sugerir que la serotonina y dopamina, entre otros parámetros neurofisiológicos, desempeñan un papel importante en la conducta de termorregulación de los machos, ya que su actividad en regiones del cerebro asociadas con la termorregulación como la POA, el bulbo olfatorio, el hipotálamo, tálamo y el córtex prefrontal (Ishiwata 2014), pueden permitir un mejor control de la temperatura corporal de los individuos. Por lo tanto, la regulación de la temperatura corporal a través de la

actividad serotoninérgica, dopaminérgica y de la conducta en machos de *Sceloporus aeneus* posiblemente ha permitido que los individuos puedan amortiguar los efectos de posibles escenarios del calentamiento global. Bajo condiciones del calentamiento global, se reporta que en México el incremento de la temperatura ambiental máxima conducirá a una extinción del 66% y 61% de las especies de lagartijas vivíparas y ovíparas respectivamente para el año 2080 (Sinervo *et al.* 2010); empero, los resultados derivados de la presente investigación ofrecen una alternativa más alentadora ante esta perspectiva de la pérdida de diversidad a consecuencia de los estragos del cambio climático global, ya que los individuos biológicamente disponen de una estrategia de termorregulación que les ayuda a contrarrestar los efectos de temperaturas ambientales adversas. En el caso de las hembras, se esperaría una respuesta conductual aún más acertada que la de los machos, ya que se ha reportado en otras especies del género *Sceloporus* que las hembras, especialmente aquellas que están preñadas, llevan a cabo un proceso de termorregulación más preciso que el de los machos disminuyendo sus temperaturas corporales (Beuchat 1986), a través de un cambio en sus periodos de actividad y de alternancia entre sitios calientes y fríos (López-Alcaide *et al.* 2014). Por último, es importante resaltar la necesidad de llevar a cabo estudios donde se evalúe la relación que existe entre la actividad de la hormona testosterona, el sistema dopaminérgico y serotoninérgico y el tamaño del cerebro con las estrategias conductuales, lo que permitirá obtener un panorama más claro acerca de los mecanismos neurofisiológicos que modulan la conducta individual de los organismos.

En conclusión, hembras y machos de la lagartija *Sceloporus aeneus* presentan estrategias conductuales diferentes, las cuales pueden estar asociadas a distintas bases neurofisiológicas como la actividad de la serotonina, dopamina y testosterona. Las hembras presentan una conducta consistente caracterizada por bajos niveles de actividad e intrepidez y altos niveles de agresividad. En el caso de los machos, su conducta se caracteriza por altos niveles de exploración, intrepidez y agresividad, presentando una mayor flexibilidad conductual. Estas diferencias en las estrategias conductuales entre sexos parecen estar asociadas con las distintas presiones de selección a las que están expuestos los individuos durante la temporada de reproducción. La conducta flexible de los machos también se expresa en otros contextos como el de termorregulación, donde los individuos pueden ajustar sus posturas corporales, la selección de microhábitats

térmicos, así como los cambios entre sol y sombra, amortiguando los efectos del calentamiento global.

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