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Preferred body temperatures are increasing in 3 anguimorph lizards with passive thermoregulation

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Synopsis Rising environmental temperatures and extreme climatic events are negatively affecting ectothermic animals, especially those with limited opportunities for behavioral thermoregulation (i.e., passive thermoregulators). Rather than rely on behavioral buffering, thermally passive ectotherms may instead adjust their thermal preferences (either lowering or increasing them) to perform their biological activities at warmer temperatures. Nevertheless, temporal comparisons of preferred temperatures in wild populations of passive thermoregulators remain scant, limiting our capacity to broadly anticipate their responses to rising temperatures. Here, we compared laboratory thermal preferences across years (2003–2004 vs. 2016–2018) in 3 thermally passive lizard species from Central Mexico: the anguimorphs *Gerrhonotus liocephalus*, *Xenosaurus rectocollaris*, and *X. tzacualtipantecus*. These species exhibit different habitat use and live in places where heat wave events have increased over time, allowing temporal comparisons of thermal preferences in warming habitats. We discovered that the 3 species increased their thermal preferences by $\sim 1^\circ\text{C}$ in 12–15 years. Our results indicate that these, and likely other passive thermoregulators must adjust their thermal preferences in response to global warming, rising a profound concern about their long-term viability as they approach intrinsic limits in their thermal physiology.

Spanish: El incremento de la temperatura ambiental y eventos climáticos extremos están afectando negativamente a los animales ectotermos, especialmente a aquellos con oportunidades limitadas para termorregulación conductual (i.e., termorreguladores pasivos). En lugar de amortiguación conductual, los termorreguladores pasivos podrían ajustar sus preferencias térmicas (ya sea reduciéndolas o incrementándolas) para desempeñar sus actividades biológicas a temperaturas mayores. Sin embargo, las comparaciones temporales de temperaturas preferidas en poblaciones naturales de termorreguladores pasivos son escasas, limitando nuestra capacidad para anticipar sus respuestas a temperaturas altas. Aquí, comparamos las temperaturas preferidas de laboratorio entre años (2003–2004 vs. 2016–2018) en 3 especies de lagartijas con termorregulación pasiva del centro de México: *Gerrhonotus liocephalus*, *Xenosaurus rectocollaris*, y *Xenosaurus tzacualtipantecus* (Anguimorpha). Esas especies con diferente uso de hábitat viven en sitios donde las olas de calor han incrementado a través del tiempo, permitiendo comparaciones temporales de preferencias térmicas en ambientes que se calientan. Descubrimos que las 3 especies han incrementado sus preferencias térmicas $\sim 1^\circ\text{C}$ en 12–15 años. Nuestros resultados indican que esas lagartijas, y quizás otros termorreguladores pasivos deberán ajustar sus preferencias térmicas en respuesta al calentamiento global, con riesgo de reducir su viabilidad a largo plazo conforme se acercan a sus límites intrínsecos de fisiología térmica.

Introduction

Environmental temperatures and heat wave events are rapidly increasing, posing a growing existential threat to animals, especially those that depend on the

environment to regulate their core body temperature (i.e., ectothermic animals, such as amphibians, insects, and reptiles) (Deutsch et al. 2008; Jørgensen et al. 2022; Harvey et al. 2023). When ectothermic animals main-

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tain their field body temperature within their preferred range, their biological processes, such as digestion, growth, and locomotion, are usually optimized (Huey and Kingsolver 1989; Martin and Huey 2008). During contemporary climate warming, however, the field body temperature of ectothermic animals may exceed their preferred thermal ranges, leading to reduced performance, lower survivorship, and decreased reproductive success (Angilletta 2009; Sinervo et al. 2010; Huey et al. 2012). Mobile ectotherms from heterogeneous thermal habitats (e.g., forest edges) may respond to climate warming through buffering behavior, such as by shuttling between warm and cold microhabitats to maintain their field body temperatures within their preferred range with high effectiveness (i.e., active thermoregulation) (Kearney et al. 2009; Huey et al. 2012; Sears et al. 2016; Domínguez-Guerrero et al. 2019, 2022). In addition, active thermoregulators may maintain similar thermal preferences over decades (Angilletta 2009; Díaz et al. 2022) or even prefer lower temperatures to avoid “metabolic meltdown,” particularly when food is scarce or activity time is limited (Gilbert and Miles 2016; Huey and Kingsolver 2019; Wild et al. 2025).

However, ectotherms with limited mobility or from homogeneous thermal habitats (e.g., closed-canopy rainforests), are limited in their capacity to thermoregulate and, therefore, they are usually passive in their thermoregulatory behavior and conform their temperature to the local thermal habitat (Huey 1974; Huey and Slatkin 1976). Thus, rising environmental temperatures and an increased frequency of heat waves may cause thermally passive ectotherms to operate at suboptimal body temperatures, potentially threatening their survival in a warming world (Huey et al. 2009; Cicchino et al. 2023). Because the negative consequences of rising temperatures are projected to be steepest for tropical passive thermoregulators—which represent most ectothermic diversity worldwide—(Tewksbury et al. 2008; Huey et al. 2009), it is a priority to anticipate their potential responses to global warming. As a compensatory response to global warming, these passive thermoregulators may lower their thermal preferences—like their actively thermoregulating counterparts—or alternatively they may prefer warmer temperatures to adjust their biological functions to the prevailing thermal environment (Huey et al. 2012). For example, individuals of the thermally passive Desert Night Lizard (*Xantusia vigilis*) maintained at laboratory temperatures of 30°C prefer warmer temperatures and run faster (at higher body temperatures) than individuals maintained at 20°C (Kaufmann and Bennett 1989). Testing behavioral responses could be accomplished through interannual comparisons of thermal preferences in wild populations of passive thermoregulators to evaluate

their potential adjustments to contemporary climate warming, yet such data are still scarce.

Here, we leveraged thermal preference data collected 12–15 years apart from populations of 3 anguimorph lizard species to evaluate potential adjustments to recent environmental warming. These lizard species are the Texas Alligator Lizard *Gerrhonotus liocephalus* (Fig. 1A), the Pallid Knob-scaled Lizard *Xenosaurus rectocollaris* (Fig. 1F), and the Zacualtipan Knob-scaled Lizard *X. tzacualtipantecus* (Fig. 1K). Anguimorph lizards, including the species examined in this study, usually exhibit passive thermoregulation (Kingsbury 1994; Woolrich-Piña et al. 2012; García-Bastida 2013; García-Rico et al. 2015; Fierro-Estrada et al. 2019, 2023; Lazcano et al. 2022; Muñoz-Nolasco et al. 2022). This thermal passivity means that individuals do not allocate much energy or time to maintaining their core temperature within a narrow range; as a result, their field body temperature tracks microenvironmental temperatures (Hertz 1974; Huey 1974). Furthermore, the studied species differ in their natural history traits. *Gerrhonotus liocephalus* is an oviparous, ground-dwelling species broadly distributed across Central and Southern Mexico, including Ciudad de México, Chiapas, Estado de México, Guerrero, Michoacán, Morelos, Oaxaca, Puebla, and Veracruz (García-Vázquez et al. 2018). In contrast, *X. rectocollaris* and *X. tzacualtipantecus* are viviparous, crevice-dwelling species with restricted distributions. Whereas the Pallid Knob-scaled lizard inhabits the xeric forests from Southeast Puebla and Northwest Oaxaca, the Zacualtipan Knob-scaled Lizard occurs in a small montane cloud forest along the Sierra Madre Oriental between Hidalgo and Veracruz (Woolrich-Piña and Smith 2012; Woolrich-Piña et al. 2012; Nieto-Montes de Oca et al. 2017). Taken together, the anguimorph species studied here represent 3 empirical case studies to assess how passive thermoregulators with varying ecological requirements may respond to climate change.

We initially collected baseline data (2003–2004) on microenvironmental temperatures (substrate and operative temperatures), field body temperature of active individuals, and preferred body temperatures of lizards from a population of each species. From these data, we estimated the thermoregulatory effectiveness (E) of the populations to more quantitatively assess the notion that they are passive thermoregulators. More than a decade later (2016–2018), we revisited the same localities (in the same month) to repeat the measurements and estimation of E , allowing for temporal comparisons. Finally, we compiled information of maximum air temperatures for each locality over the last 3 decades (1990–2020) to estimate climatic trends. We anticipate that environmental temperatures and/or heat wave events

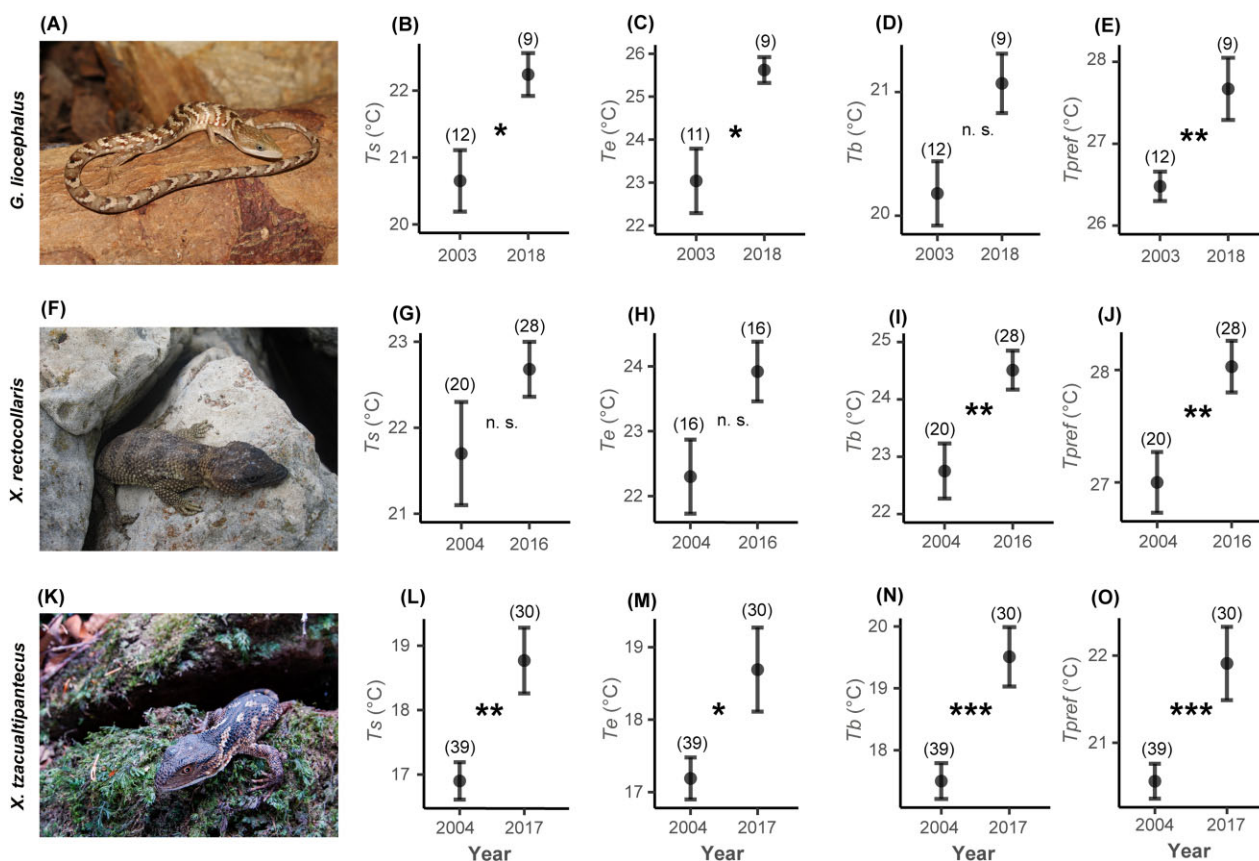


Fig. 1 Three anguimorph lizard species included in this study; the Texas Alligator Lizard *G. liocephalus* (A), the Texas Knob-scaled Lizard *X. rectocollaris* (F), and the Zacualtipan Knob-scaled Lizard *X. tzacualtipantecus* (K). Substrate (B, G, L) and operative (C, H, M) temperatures of 3 anguimorph lizard species tend to rise across years. Tracking these thermal trends, field body temperatures (D, I, N) and/or preferred body temperatures (E, J, O) of *G. liocephalus*, *X. rectocollaris*, and *X. tzacualtipantecus* have increased over the same time interval. Substrate temperature (T_s) indicates the temperature of the substratum where we captured active individuals. Operative temperatures (T_e) were recorded each hour during activity time (daytime) of lizards using pipe models. Field body temperatures (T_b) were measured during the activity time (diurnal) of the lizards. Preferred body temperatures (T_{pref}) were estimated in a laboratory thermal gradient. Asterisks denote significant shifts (***) indicates $P \leq 0.001$, ** indicates $P \leq 0.01$, and * indicates $P < 0.05$). n.s. indicates non-significant differences. Sample sizes are indicated in parentheses. Pictures of *G. liocephalus* (photo by Anibal H. Díaz de la Vega Pérez) and *X. tzacualtipantecus* (photo by Cristian R. Olvera Olvera) were downloaded from iNaturalist and used with permission of the photographers. Picture of *X. rectocollaris* by G.A.W.-P.

should increase over the years, consistent with global trends. In parallel with temperature trends, we predict that anguimorph lizards should increase their field body temperatures and adjust thermal preferences over the years. If our prediction is correct, then *G. liocephalus*, *X. rectocollaris*, *X. tzacualtipantecus*, and likely other passive thermoregulators could buffer, at least partially, the negative effect of climate warming by adjusting their preferred body temperatures.

Methods

Ethics statement

Field work and thermal preference measurements were conducted in accordance with the collecting permits (SGPA/DGVS/01196/03, SGPA/DGVS/01629/16,

SGPA/DGVS/01205/17, and SGPA/DGVS/002491/18) approved by Dirección General de Vida Silvestre, SEMARNAT, México.

Field work

We conducted field work during 2003 (November 20–23) and 2018 (November 15–19) in the xeric forest from Zapotitlán Salinas Puebla México (18.395N, -97.491W; 2120 meters in elevation) to capture individuals of *G. liocephalus* (Fig. 1A). In the same locality, we captured individuals of *X. rectocollaris* (Fig. 1F) during 2004 (May 06) and 2016 (May 26–29). Lastly, we conducted field work during 2004 (May 27–30) and 2017 (May 29–June 1) in the cloud forest from Zacualtipán de Ángeles Hidalgo México (20.641N, -98.602W; 1958 m. elev.) to capture individuals of *X. tzacualtipantecus* (Fig. 1K).

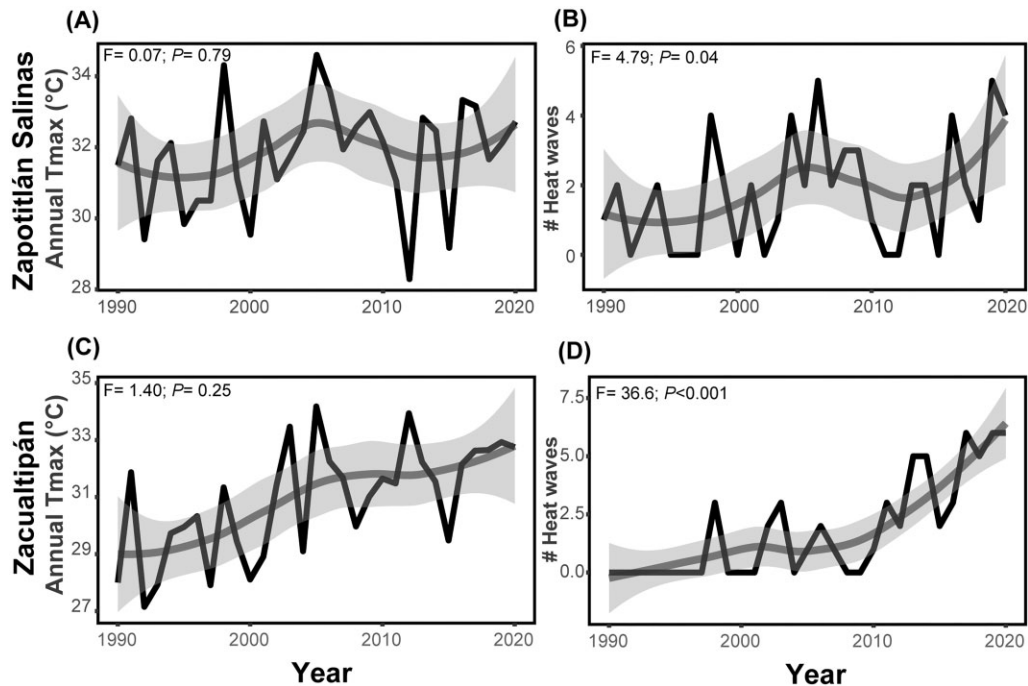


Fig. 2 Annual maximum air temperature has remained stable over the last 3 decades (from 1990 to 2020) in the Zapotitlán Salinas (A) and Zacualtipán (C), but heat waves have significantly increased in both localities (B, D) over the same interval of time. Zapotitlán Salinas is the locality where we collected individuals of *G. liocephalus* and *X. rectocollaris*, and Zacualtipán is the locality where we collected *X. tzacualtipantecus* lizards.

Sampling years correspond to periods of opportunistic fieldwork conducted at the study sites by one of us (G.A.W.-P). Notably, the frequency of heat wave events increased significantly after 2003–2004 (Fig. 2B, D), offering an opportunity to test for potential shifts in thermal preferences among anguimorph lizards in the context of global warming. In each locality and during each visit, 3 researchers performed field work during the activity period of the individuals (09:00 and 18:00 h) to capture adult lizards manually or by a lasso attached to an extendable fishing pole. For *G. liocephalus*, we captured individuals on the ground below small chaparral shrubs or perched on branches of these bushes. For *Xenosaurus* species, we captured lizards from inside small crevices. Within 20s of capture, we measured the field body (cloacal) temperature (T_b), and substrate temperature (T_s) of each lizard by using a thermocouple (Type K) connected to a digital thermometer (Fluke 51-II⁺ $\pm 0.1^\circ\text{C}$). Then, we placed each lizard within an individual muslin bag, and we transported all lizards to laboratory conditions to estimate their thermal preferences (described below).

Operative temperatures

During the days of field work, we also recorded operative temperatures (T_e), which represent the equilibrium temperature of an ectotherm in absence of behavioral

thermoregulation (Bakken 1992). Records of operative temperatures were used to compare available microenvironmental temperatures and thermoregulatory effectiveness (described below) of anguimorph lizards across years. Following our previous work with lizards, we used field-calibrated pipe models (polyvinylchloride; PVC) to record operative temperatures (Domínguez-Guerrero et al. 2019; Cardona-Botero et al. 2023). Field calibration for each species consisted of simultaneously measuring the temperature of an adult lizard and a pipe model (100 mm length, 20 mm diameter, and painted with gray spray) every 10 min for 1–2 h under different thermal conditions (“shade,” “Sun,” and “mosaic”). Although PVC have a lower conductivity than copper (Taylor et al. 2021), our pipe models still offered a good representation of the studied organisms. Temperatures of the lizard (T_b) and pipe model (T_e) were correlated in the 3 species (Pearson’s correlation, $r = 0.97$, $P < 0.001$ for *G. liocephalus*, $r = 0.96$, $P < 0.001$ for *X. rectocollaris*, and $r = 0.97$, $P < 0.001$ for *X. tzacualtipantecus*). Further, temperatures of the lizard and pipe model were not statistically different in *G. liocephalus* ($t = 0.23$, $P = 0.82$; mean $T_b = 22.15 \pm 0.69\text{SE}$, mean $T_e = 22.38 \pm 0.71$, $n = 13$ measurements), *X. rectocollaris* ($t = 0.97$, $P = 0.34$; mean $T_b = 23.3 \pm 0.35$, mean $T_e = 22.9 \pm 0.27$, $n = 10$ measurements), or *X. tzacualtipantecus* ($t = 0.17$, $P = 0.85$; mean $T_b = 19.11 \pm 0.55$, mean $T_e = 18.39 \pm 0.53$, $n = 10$ measurements).

During our days of field work (when we measured field body temperatures of active individuals), we placed pipe models in microhabitats where we observed active lizards. We placed 11 pipe models in 2003 and 9 in 2018 in microhabitats used by *G. liocephalus*, 16 in 2004 and 16 in 2016 in microhabitats used by *X. rectocollaris*, and 39 in 2004 and 30 in 2017 in microhabitats used by *X. tzacualtipantecus*. For one day, we manually recorded temperature of each pipe model at each hour from 9:00 to 18:00 h (activity time of the studied species) with the same thermocouple and thermometer used in the field work. We inserted the thermocouple into a small hole in each pipe model and recorded the temperature once it stabilized (~ 15 s). We chose this manual methodology to remain consistent with the 2003–2004 measurements, when we did not have access to automatic data-loggers.

Thermal preferences

Preferred body temperatures (T_{pref}) refer to the body temperatures that lizards experience in absence of abiotic and biotic restrictions, and are often correlated with temperatures at which individuals optimize their performance and fitness (Huey and Kingsolver 1989; Martin and Huey 2008; Huey et al. 2012). After field work, we transported individuals of *G. liocephalus*, *X. rectocollaris*, and *X. tzacualtipantecus* to the “Laboratorio de ecofisiología” located in Tecnológico Nacional de México campus Zacapoaxtla, Puebla, Mexico. This laboratory consisted of a room with stable ambient temperature of $\sim 15^\circ\text{C}$. Lizards were maintained in laboratory conditions between 24 and 48 h before thermal preference experiments. During that period, lizards were maintained in individual cages, and we offered them food (waxworms) and water *ad libitum*. In the same laboratory and following our previous work (Cardona-Botero et al. 2023), we built a thermal gradient, which consisted of a horizontal wooden box (150 cm long, 100 cm wide, and 40 cm high) divided into 10 tracks and filled with 2 cm of rocky/sandy sediment from the study site to simulate the microhabitat where lizards were captured. For *Xenosaurus* lizards, we also included some flagstones (uniformly distributed through each track) to avoid stress in these crevice-dwelling lizards (Cardona-Botero et al. 2023). Above each track (at one extreme of the thermal gradient), we suspended one 100 w bulb at ~ 30 cm above the ground. This thermal gradient afforded temperatures ranging $\sim 15^\circ\text{C}$ on the colder extreme to $\sim 40^\circ\text{C}$ at the hotter extreme. After 1 day in laboratory conditions, we placed lizards individually into a lane from 9:00 to 18:00 h. At each 3 h (12:00, 15:00, and 18:00 h) during the experiment, we manually captured each lizard and measured their body temperature with

the same thermocouple and thermometer used in the field work. We estimated T_{pref} as the average of body temperatures measured during this experiment. After experiments, we sexed, measured (snout-vent length; SVL), fed, and hydrated *ad libitum*, marked with toe clips (to identify potential recaptures during posterior field work), and released each lizard back to their original capture site.

Thermoregulatory behavior

We estimated the thermoregulatory effectiveness (E) of the lizards following the equation ($E = 1 - \frac{\overline{db}}{\overline{de}}$) proposed by Hertz et al. (1993). In this equation, \overline{db} and \overline{de} indicate the average deviation of field body temperatures and operative temperatures, respectively, from a set-point temperature range (T_{set}). This T_{set} refer to the interquartile range of laboratory preferred body temperatures (25% and 75%; $T_{set_{25}}$ and $T_{set_{75}}$, respectively). If each $T_b < T_{set_{25}}$, then each $db = T_{set_{25}} - T_b$, and if each $T_b > T_{set_{75}}$, then each $db = T_b - T_{set_{75}}$. If each T_b is within $T_{set_{25}} - T_{set_{75}}$, then each $db = 0$. Likewise, if each $T_e < T_{set_{25}}$, then each $de = T_{set_{25}} - T_e$, and if each $T_e > T_{set_{75}}$, then each $de = T_e - T_{set_{75}}$. If each T_e is within $T_{set_{25}} - T_{set_{75}}$, then each $de = 0$. Values of \overline{db} or \overline{de} close to 0, indicate high accuracy of field body temperatures (within T_{set}) and high quality of the thermal habitat, respectively. Lastly, E values close to 1 indicate active thermoregulation, values near 0 suggest thermoconformism, and negative values reflect avoidance of suitable thermal microhabitats. In other words, lizards with E values close to 1 thermoregulate carefully, whereas lower or negative values suggest passive thermoregulation.

Environmental temperature and heat waves

As microenvironmental temperatures represent a snapshot of thermal conditions to which lizards were exposed during our field work, we were also interested in evaluating macroclimatic trends over the years. To this end, we download data of estimated daily maximum air temperature (T_{max}) from 1990 to 2020 in Zapotitlán Salinas Puebla (locality of *G. liocephalus* and *X. rectocollaris*) and Zacualtipán de Ángeles Hidalgo (locality of *X. tzacualtipantecus*) using the Daymet V4 (1 km² grid) (Thornton et al. 2021); <https://daymet.ornl.gov/>. Then, we calculated the 95th percentile of T_{max} estimated in each locality during these years (1990–2020). A heat wave represents an event of at least 3 consecutive days during which T_{max} exceeds the estimated 95th percentile, and heat wave events were considered independent from each other if they were separated by more than 3 consecutive days (Tripathy et al. 2023).

Statistical analyses

We compared substrate and operative temperatures between years for each species using *t* tests (for normally distributed data) or Mann–Whitney *U* tests (for non-normally distributed data), and adjusted *P*-values using a Bonferroni correction to control the family wise error rate across multiple comparisons. Of the individuals captured and marked during 2003–2004, none were recaptured during 2016–2018. We then performed a generalized linear model (GLM) to compare population means of field body temperatures of each species over time. Field body temperature was the dependent variable, log transformed SVL was a continuous predictor, and sex and year were categorical predictors. Because we recorded multiple temperature measurements for each lizard within the laboratory thermal gradient, we used a linear mixed model (LMM) for each species to evaluate potential shifts in thermal preferences across years. In these analyses, lizard ID was included as a random effect. Laboratory body temperature was the dependent variable, log transformed SVL was included as a continuous predictor, and sex and year were treated as categorical predictors. Lastly, we performed Generalized Additive Mixed Model (GAMM) analyses with Poisson error term to evaluate potential increases of annual maximum air temperature or heat wave events in each locality.

Results

Microenvironmental temperatures

We found that substrate and operative temperatures increased significantly over years for 2 anguimorph species included in this study. From 2003 to 2018, substrate temperatures increased 1.6°C ($t = 2.65$, $P = 0.03$, mean $T_s = 20.65^\circ\text{C} \pm 0.46\text{SE}$ ($n = 12$) in 2003, and 22.24 ± 0.32 ($n = 9$) in 2018) and operative temperatures increased 2.6°C ($t = 2.95$, $P = 0.02$, mean $T_e = 23.04^\circ\text{C} \pm 0.75$ ($n = 11$) in 2003, and 25.62 ± 0.3 ($n = 9$) in 2018) for *G. liocephalus* (Fig. 1B, C). From 2004 to 2017, substrate temperatures increased 1.9°C ($U = 229.5$, $P = 0.002$, mean $T_s = 16.90^\circ\text{C} \pm 0.29$ ($n = 39$) in 2004, and 18.77 ± 0.51 ($n = 30$) in 2017) and operative temperatures increased 1.5°C ($U = 359.5$, $P = 0.04$, mean $T_e = 17.19^\circ\text{C} \pm 0.29$ ($n = 39$) in 2004, and 18.69 ± 0.58 ($n = 30$) in 2017) for *X. tzacualtipantecus* (Fig. 1L, M). However, from 2004 to 2016, substrate temperatures ($t = 1.57$, $P = 0.24$, mean $T_s = 21.68^\circ\text{C} \pm 0.6$ ($n = 20$) in 2004, and 22.68 ± 0.33 ($n = 28$) in 2016) and operative temperatures ($t = 2.20$, $P = 0.07$, mean $T_e = 22.30^\circ\text{C} \pm 0.57$ ($n = 16$) in 2004, and 23.91 ± 0.46 ($n = 16$) in 2016) did not increase significantly for *X. rectocollaris* (Fig. 1G, H).

Field body and preferred temperatures

We found that field body temperatures of *G. liocephalus* remained similar between 2003 and 2018, but their thermal preferences increased by 1.2°C over the same interval of time (Fig. 1D, E; Table 1). Although body size (SVL females = $98.1 \text{ mm} \pm 1.1\text{SE}$ ($n = 12$), and SVL males = 94.3 ± 1.4 ($n = 9$)) did not affect T_b or T_{pref} , we found a significant effect of sex on thermal preferences (Table 1). Then, we compared thermal preferences across years by sex, and we did not find significant differences in thermal preferences of females ($t = 1.92$, $P = 0.07$, mean T_{pref} 2003 = $26.2^\circ\text{C} \pm 0.2$, $n = 7$, mean T_{pref} 2018 = $27.2^\circ\text{C} \pm 0.5$, $n = 5$; Fig. 3). Yet, males have significantly increased by 1.5°C their T_{pref} over the years ($t = 2.85$, $P = 0.04$, mean T_{pref} 2003 = $26.8^\circ\text{C} \pm 0.2$, $n = 5$, mean T_{pref} 2018 = $28.3^\circ\text{C} \pm 0.5$, $n = 4$; Fig. 3). In *X. rectocollaris*, we discovered that field body temperatures increased by 1.8°C and thermal preferences by 1°C between 2004 and 2016 (Fig. 1I, J), and these changes were not influenced by body size (SVL females = 91.2 ± 2.5 ($n = 29$), and SVL males = 81.4 ± 3.2 ($n = 19$)) or sex (Table 1). Lastly, we found that field body temperatures increased by 2.0°C and thermal preferences by 1.3°C between 2004 and 2017 in *X. tzacualtipantecus* (Fig. 1N, O), with no effect of body size (SVL females = 81.0 ± 2.5 [$n = 40$], and SVL males = 102.8 ± 2.3 [$n = 29$]) or sex on the observed shifts (Table 1).

Thermoregulatory effectiveness

We found that *G. liocephalus* behaviorally avoids suitable thermal habitats, as indicated by the thermoregulatory effectiveness estimated in 2003 ($E = -1.1$) and 2018 ($E = -3.7$) (Fig. 4A, B) for this species. Knob-scaled lizard species approach the thermoconformer extreme on the continuum of thermoregulatory effectiveness. *Xenosaurus rectocollaris* maintained their thermoregulatory effectiveness close to 0 in 2004 ($E = 0.05$) and 2016 ($E = 0.03$) (Fig. 4C, D), and *X. tzacualtipantecus* maintained their thermoregulatory effectiveness close to 0 in 2004 ($E = -0.16$) and 2017 ($E = 0.20$) (Fig. 4E, F). All 3 anguimorph lizard species show a consistent pattern of passive thermoregulation, as they do not actively thermoregulate to maintain their field body temperatures within their T_{set} .

Environmental temperatures and heat waves

Annual maximum air temperatures have not significantly changed in Zapotitlán Salinas (locality of *G. liocephalus* and *X. rectocollaris*; $F = 0.07$, $P = 0.79$, $n = 31$; Fig. 2A) or Zacualtipán de Ángeles (locality of *X. tzacualtipantecus*; $F = 1.40$, $P = 0.25$, $n = 31$;

Table 1 GLM and LMMs used to evaluate potential interannual shifts in field body temperature (T_b) and laboratory preferred body temperatures (T_{pref}), respectively, in 3 anguimorph lizard species.

Species	Trait \pm SE (n)	Effect	Statistic	P-value
<i>Gerrhonotus liocephalus</i>	T_b ($^{\circ}$ C)	Year	$t = 1.98$	0.06
	Mean 2003 = 20.18 ± 0.26 (12)	SVL	$t = -0.28$	0.79
	Mean 2018 = 21.07 ± 0.24 (9)	Sex	$t = -0.57$	0.58
	T_{pref} ($^{\circ}$ C)	Year	$t = 3.1$	0.007
	Mean 2003 = 26.48 ± 0.18 (12)	SVL	$t = 0.30$	0.76
	Mean 2018 = 27.67 ± 0.38 (9)	Sex	$t = 2.2$	0.04
<i>Xenosaurus rectocollaris</i>	T_b ($^{\circ}$ C)	Year	$t = 2.82$	0.01
	Mean 2004 = 22.75 ± 0.48 (20)	SVL	$t = 0.36$	0.72
	Mean 2016 = 24.51 ± 0.34 (28)	Sex	$t = 1.66$	0.11
	T_{pref} ($^{\circ}$ C)	Year	$t = 3.1$	0.004
	Mean 2004 = 26.95 ± 0.26 (20)	SVL	$t = 0.95$	0.35
	Mean 2016 = 28.03 ± 0.23 (28)	Sex	$t = 1.33$	0.19
<i>Xenosaurus tzacualtipantecus</i>	T_b ($^{\circ}$ C)	Year	$t = 3.78$	<0.001
	Mean 2004 = 17.5 ± 0.29 (39)	SVL	$t = -0.66$	0.51
	Mean 2017 = 19.51 ± 0.48 (30)	Sex	$t = -0.12$	0.91
	T_{pref} ($^{\circ}$ C)	Year	$t = 3.62$	<0.001
	Mean 2004 = 20.56 ± 0.2 (39)	SVL	$t = -0.05$	0.96
	Mean 2017 = 21.88 ± 0.42 (30)	Sex	$t = -1.46$	0.15

T_b and T_{pref} were the dependent variables, log transformed SVL was a continuous predictor, and sex and year were categorical predictors. Lizard ID was included as a random effect for the LMM analyses.

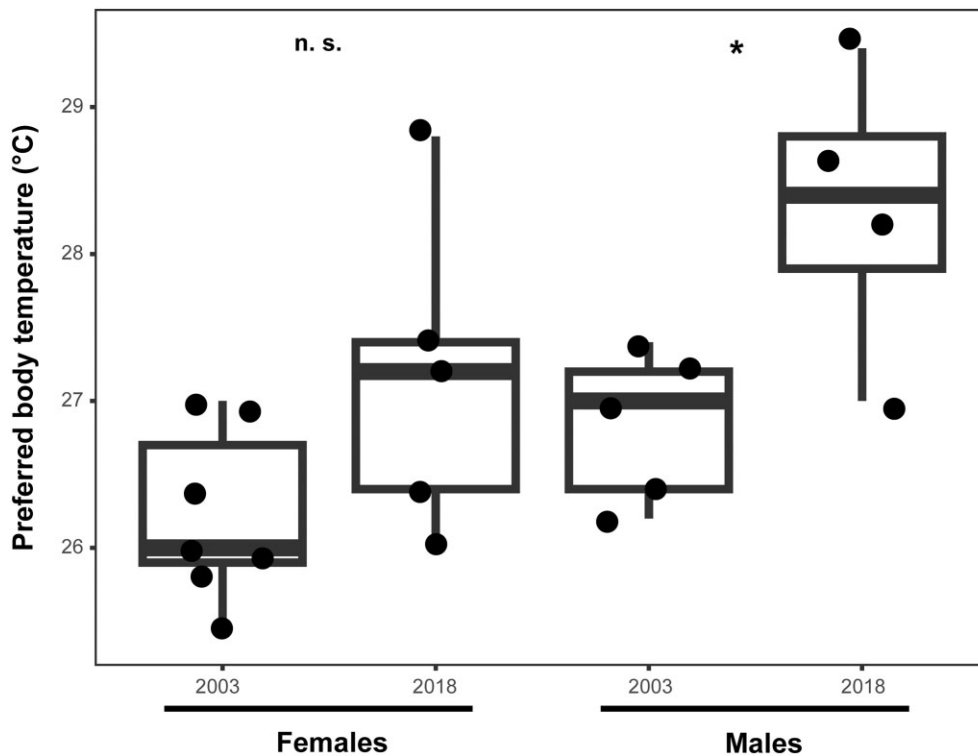


Fig. 3 Whereas females of *G. liocephalus* did not significantly shift their thermal preferences ($t = 1.92$, $P = 0.07$, mean T_{pref} 2003 = 26.2° C \pm 0.2, $n = 7$, mean T_{pref} 2018 = 27.2° C \pm 0.5, $n = 5$), males did ($t = 2.85$, $P = 0.04$, mean T_{pref} 2003 = 26.8° C \pm 0.2, $n = 5$, mean T_{pref} 2018 = 28.3° C \pm 0.5, $n = 4$). n.s. indicates non-significant differences and * indicates $P < 0.05$.

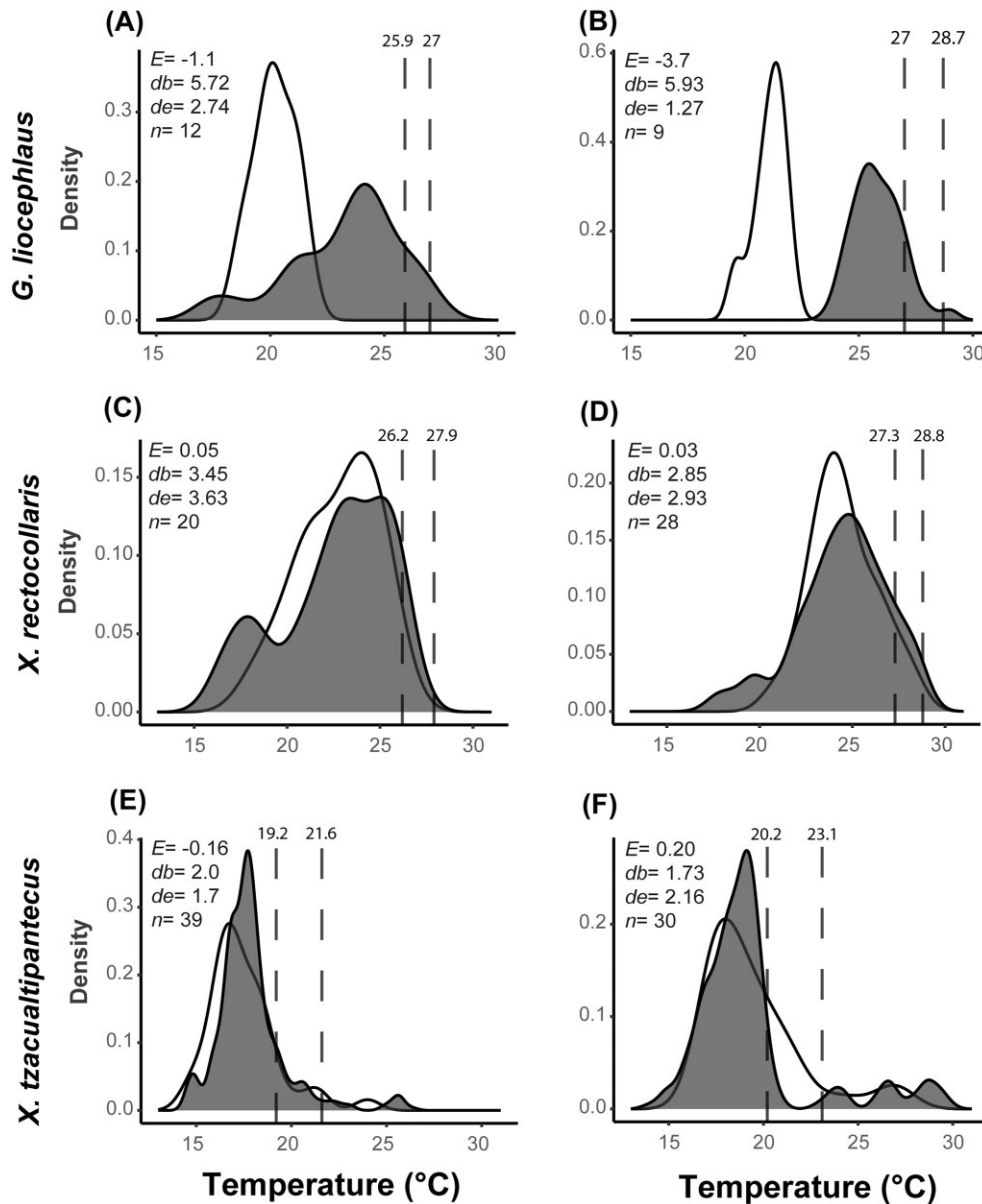


Fig. 4 Thermoregulatory effectiveness (E) of 3 anguimorph lizard species across the years. Data for *G. liocephalus* were estimated in 2003 (A) and 2018 (B), data for *X. rectocollaris* were estimated in 2004 (C) and 2016 (D), and data for *X. tzacualtipantecus* were estimated in 2004 (E) and 2017 (F). White color represents field body temperatures of active lizards and gray color represents the operative temperatures. Dashed lines represent the set-point preferred temperature range ($T_{set_{25}}-T_{set_{75}}$) of the lizards. db = accuracy of body temperature, de = quality of the thermal habitat.

Fig. 2C). Over the same years, however, heat waves have significantly increased in Zapotitlán Salinas ($F = 4.79$, $P = 0.04$, $n = 31$; Fig. 2B), and Zacualtipán de Ángeles ($F = 36.6$, $P < 0.001$, $n = 31$; Fig. 2D).

Discussion

We found that annual maximum air temperatures have remained relatively stable from 1990 to 2020 in both localities where we conducted field work (Fig. 2A, C). Yet, the frequency of heat wave events has significantly

increased over the same interval of time (Fig. 2B, D). Likewise, microenvironmental temperatures (substrate and operative temperatures) for *G. liocephalus*, *X. rectocollaris*, and *X. tzacualtipantecus* tended to increase from 2003–2004 to 2016–2018 in their respective localities (Fig. 1). A mismatch between macro- and microenvironmental temperature trends can be related with anthropic factors at the local scale (Kearney et al. 2014). In both localities where we conducted field work, we observed a progressive habitat transformation over the last decade. Whereas in Zapotitlán Salinas (locality of

G. liocephalus and *X. rectocollaris*) vegetation cover has been reduced by goat grazing (Reséndiz-Melgar et al. 2005), in Zacualtipán de Ángeles (locality of *X. tzacualtipantecus*) vegetation cover has been decreased by transformation from forest to human land-fill (Woolrich-Piña and Smith 2012). Therefore, loss of canopy, which affords shade, could be responsible for the observed warming trend in substrate and operative temperatures for anguimorph lizards in the studied localities. Both rising microenvironmental temperatures and increasing heat wave events, which have intensified in the current century, pose an existential threat for passive thermoregulators, those with limited mobility or from homogeneous thermal habitats (Tewksbury et al. 2008; Huey et al. 2009; Coumou et al. 2013; Stillman 2019; Clusella-Trullas 2022). Under the contemporary scenario of climate warming, it has been projected that anguimorph lizards are highly susceptible to extinction, especially because they prefer lower temperatures than species from several other lizard families (Sinervo et al. 2010; Berriozabal-Islas et al. 2018; Lara-Reséndiz et al. 2021; Fierro-Estrada et al. 2022).

In this study, we evaluated the hypothesis that *G. liocephalus*, *X. rectocollaris*, and *X. tzacualtipantecus*—anguimorph lizards with a passive thermoregulatory behavior (Woolrich-Piña et al. 2012; García-Bastida 2013; García-Rico et al. 2015)—should adjust their thermal preferences in response to climate warming. We began by evaluating the thermoregulatory effectiveness of anguimorph populations across years to quantitatively assess whether they are, indeed, passive thermoregulators. We found that field body temperature of *G. liocephalus* lizards is lower than their set-point and even lower than operative temperatures, which resulted in negative values of their thermoregulatory effectiveness (Fig. 4A, B). Negative values of E indicate that individuals actively avoid suitable operative temperatures for thermoregulation, likely in response to some abiotic and biotic restrictions (Hertz et al. 1993; Taylor et al. 2021). As documented in other populations of alligator lizards, we observed that individuals of *G. liocephalus* forage mainly in shaded microhabitats, likely because these areas offer lower temperatures and higher humidity compared to open microhabitats (García-Bastida 2013; Lazcano et al. 2022). Therefore, we infer that behavioral avoidance of suitable temperatures for thermoregulation in *G. liocephalus* could be related to water availability in the xeric forest from Zapotitlán Salinas. Another possible explanation for the behavioral avoidance of suitable temperatures is that lizards may follow the spatial dynamics of prey availability or be avoiding predators (Hertz et al. 1993; Fierro-Estrada et al. 2019; Lazcano et al. 2022). In any case, shaded substrates where individuals perform their biological

activities have warmed 1.6°C from 2003 to 2018 (Fig. 1B), imposing a potential thermal hazard.

For *Xenosaurus* species, we discovered that their field body temperatures track operative temperatures, even when these rarely fall within their thermal preference range (Fig. 4C–F). This match between field body and operative temperatures outside of a set-point supports the notion that knob-scaled lizards are passive thermoregulators with a tendency toward perfect thermoregulation (Lemos-Espinal et al. 1998; Woolrich-Piña et al. 2012; García-Rico et al. 2015; Cardona-Botero et al. 2019, 2023), but see (Muñoz-Nolasco et al. 2022). Passive thermoregulation of knob-scaled lizards is related to their peculiar microhabitat use (Woolrich-Piña et al. 2012; García-Rico et al. 2015; Cardona-Botero et al. 2019, 2023). These lizards spend a major part of their entire life within crevices where they perform their biological activities, including courtship, reproduction, and foraging (Herrel et al. 2001; Lemos-Espinal et al. 2003; Woolrich-Piña et al. 2012). For example, we observed that individuals of *X. rectocollaris* ($n = 4$) can use the same crevice during the course of 5 years, which represents 75–100% of their life expectancy (unpubl. data). Certainly, the choice of crevices in *Xenosaurus* is not random (Lemos-Espinal et al. 1998). Knob-scaled lizards and other rock-dwelling ectotherms usually take refuge where the risk from overheating is low (Huey et al. 1989; Lemos-Espinal et al. 1998; Rojas-González et al. 2022). When knob-scaled lizards choose a crevice, they rarely emerge from it (Maciel-Mata et al. 2020). Therefore, choice of crevices where operative temperatures are lower than set-point (Fig. 4C–F) can be a strategy to avoid suboptimal performance. Nevertheless, we discovered that crevices (places where we measured substrate and operative temperatures of lizards) tend to warm across the years (Fig. 1G, H, L, M). In short, passive thermoregulation and/or rising microenvironmental temperatures have caused field body temperatures tend to increase in *G. liocephalus* (Fig. 1D) and have increased by 2°C in *Xenosaurus* lizards (Fig. 1I, N). As a potential compensatory response to more common heat wave events, and rising microenvironmental and/or field body temperatures, anguimorph lizards increased their preferred body temperature over a period of 12–15 years (Fig. 1E, J, O).

We discovered that *G. liocephalus*, *X. rectocollaris*, and *X. tzacualtipantecus* increased their thermal preferences by $\sim 1^\circ\text{C}$ from 2003–2004 to 2016–2018 (Fig. 1E, J, O). This shift in thermal preferences correspond with a $0.5\times$ shift in comparison with the observed shift ($\sim 2^\circ\text{C}$) in microenvironmental temperatures for *G. liocephalus* and *X. tzacualtipantecus* (Fig. 1). Although we observed shifts of thermal preferences in both females and males of knob-scaled lizards (Table 1) significant

shifts were found only in males of *G. liocephalus* (Fig. 3). This result may be related to greater avoidance of warming substrate temperatures by females compared to males, which might be more exposed to elevated temperatures during territory defense. The observed increase of thermal preferences in *Xenosaurus* lizards could be product of phenotypic plasticity. For example, *X. fractus* (a species not included in this study) can adjust their thermal preferences across seasons to track environmental temperatures (Cardona-Botero et al. 2023). When ectothermic animals maintain their field body temperature below or within their preferred range, their biological processes and fitness are usually maximized (Martin and Huey 2008). Therefore, thermal preferences are a good proxy of temperatures where individuals exhibit a maximal survivorship and reproductive success (Martin and Huey 2008). We infer that warmer preferred body temperatures in anguimorph lizards afford an advantage to perform biological activities and maximize their physiological functions at higher microenvironmental and/or core temperatures. For example, neonates of *X. platyceps* grew faster at warmer temperatures (Rojas-González et al. 2022). As a caveat, we still need to estimate performance of different biological functions (such as digestion, growth, reproductive success, and survivorship) at different body temperatures to evaluate the potential matching between thermal preferences and optimal temperatures. G.A.W.-P. previously estimated bite force of some anguimorph lizards (including *Xenosaurus*) at different temperatures and discovered that the temperature at which bite force is maximized matches observed field body temperatures and is usually below the preferred thermal range of the lizards (Woolrich-Piña et al. 2021). As bite force influences survivorship and reproductive success of knob-scaled lizards (Herrel et al. 2001), we hypothesize that the thermal performance curve of bite force should be increased in parallel with higher field and preferred body temperatures. Nevertheless, we do not have historical data of thermal performance for the species included in this study to test that hypothesis.

Although higher thermal preferences have been associated with higher fitness of ectothermic animals (Gilbert and Miles 2017), it is not a linear and permanent strategy to survive in warming conditions because core temperatures cannot exceed some biological limits, such as the critical thermal maximum (Angilletta 2009; Jørgensen et al. 2022). Furthermore, higher preferred body temperatures may induce some negative effects on survivorship and reproduction of the individuals (Huey and Kingsolver 2019). Preferring higher temperatures in a warming world can be detrimental when food is scarce because it can drive a metabolic meltdown

and therefore individuals can die or stop their reproduction (Sinervo et al. 2010; Gilbert and Miles 2016; Huey and Kingsolver 2019; Wild et al. 2025). Higher preferred body temperatures can also negatively affect pregnancy of viviparous species, such as knob-scaled lizards. For example, when pregnant females of the Yarrow's spiny lizard are experimentally maintained at temperatures higher than their thermal preferences, the developing embryos die, or the neonates born with deleterious abnormalities (Beuchat 1986, 1988). Taken together, it is important to understand the potential benefits and consequences of behavioral adjustments of ectothermic animals to rising temperatures. Simultaneously, it is a priority to improve conservation strategies because fragmentation and loss of habitat (such as the observed in localities where we performed field work) are also causing negative impacts on populations of ectothermic animals (Halsch et al. 2021). Although some habitats are expected to serve as thermal refugia for ectothermic animals, we found that substrate temperatures and the frequency of heat waves are increasing in the cloud forest at rates similar to those in the xeric forest. In a warming world, ectothermic animals can potentially adjust to some stressors, but not to all of them (Huey et al. 2012; Moritz and Agudo 2013).

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Supplementary data

Supplementary data available at *ICB* online.

Data availability

Raw data are included as Supplementary data.

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