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Interactions between thermoregulatory behavior and physiological acclimatization in a wild lizard population

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ARTICLE INFO

Abreviations:
Ct_{max}Critical thermal maximum
Ct_{min}Critical thermal minimum
db¯Accuracy of body temperatures
de¯Thermal quality of the habitat
*E*Effectiveness of temperature regulation
*ET*Environmental air temperature
ET_{act}Environmental temperature of the activity period
ET_{ina}Environmental temperature of the inactivity period
T_bBody temperature
T_eOperative temperatures
T_{pref}Preferred body temperature

Keywords:
Behavioral thermoregulation
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Critical temperatures
Plasticity
Preferred body temperature

ABSTRACT

Although the importance of thermoregulation and plasticity as compensatory mechanisms for climate change has long been recognized, they have largely been studied independently. Thus, we know comparatively little about how they interact to shape physiological variation in natural populations. Here, we test the hypothesis that behavioral thermoregulation and thermal acclimatization interact to shape physiological phenotypes in a natural population of the diurnal lizard, *Sceloporus torquatus*. Every month for one year we examined thermoregulatory effectiveness and changes in the population mean in three physiological parameters: cold tolerance (Ct_{min}), heat tolerance (Ct_{max}), and the preferred body temperature (T_{pref}), to indirectly assess thermal acclimatization in population means. We discovered that *S. torquatus* is an active thermoregulator throughout the year, with body temperature varying little despite strong seasonal temperature shifts. Although we did not observe a strong signal of acclimatization in Ct_{max}, we did find that Ct_{min} shifts in parallel with nighttime temperatures throughout the year. This likely occurs, at least in part, because thermoregulation is substantially less effective at buffering organisms from selection on lower physiological limits than upper physiological limits. Active thermoregulation is effective at limiting exposure to extreme temperatures during the day, but is less effective at night, potentially contributing to greater plasticity in Ct_{min} than Ct_{max}. Importantly, however, T_{pref} tracked seasonal changes in temperature, which is one the factors contributing to highly effective thermoregulation throughout the year. Thus, behavior and physiological plasticity do not always operate independently, which could impact how organisms can respond to rising temperatures.

1. Introduction

The contemporary rate of environmental warming presents an unprecedented challenge to organisms worldwide (Barnosky et al., 2011). Understanding how climate warming will impact natural populations is a central imperative for scientists and conservation managers alike (Bellard et al., 2012; Thomas et al., 2004). This goal is especially relevant for ectotherms because their physiology and life history are highly sensitive to temperature change (Deutsch et al., 2008; Huey and Tewksbury, 2009; Huey et al., 2009). Some forecasts, for example, predict massive global declines in lizard populations over the next century, largely due to the tight connection between environmental temperature, physiological performance, and activity times in these organisms (Sinervo et al., 2010). Yet, some biological impacts of climate warming can be mitigated by the organisms themselves through short-time responses, namely through behavioral adjustments and physiological plasticity (Huey et al., 2012; Kearney et al., 2009; Seebacher et al., 2015; Sunday et al., 2014).

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Ectotherms may use behavioral tactics to compensate for the effects of thermal variation and, thus, maintain body temperatures (T_b) within their preferred ranges, even in the face of rising temperatures (Kearney et al., 2009; Sunday et al., 2014). For example, individuals may preferentially select thermally suitable microhabitats, shuttle between sun and shade, or retreat to thermal refuges when environmental conditions become too hostile (Cowles and Bogert, 1944; Kearney et al., 2009; Kirchhof et al., 2017; van den Berg et al., 2015). In addition to behavioral adjustments, ectotherms may physiologically respond to environmental warming through plastic shifts in their thermal requirements or their thermal tolerances (Seebacher et al., 2015). In response to changes in thermal environment, for example, reptiles can often produce both short- and long-term acclimation responses to better match their physiological performance to the local thermal conditions (Gunderson and Stillman, 2015; Pintor et al., 2016; Seebacher, 2005).

Importantly, the ability for organisms to plastically remodel their physiology or to alter their behavioral strategies are unlikely to operate in isolation. Rather, behavioral thermoregulation and physiological plasticity are likely to interact (Huey et al., 2012; Williams et al., 2008). Specifically, regulatory behaviors (e.g., thermoregulation) effectively buffer organisms from environmental variation, thus precluding the need to shift their physiology (and physiological plasticity) even in the face of environmental change, a phenomenon known as the Bogert effect (Huey et al., 2003). As such, physiological traits that may be behaviorally buffered should exhibit less plasticity than traits that behavior cannot as effectively shield from thermal variation (Marais and Chown, 2008). For example, lizards can behaviorally mitigate high temperatures in the daytime (when thermal heterogeneity is high, allowing for behavior to be effective), thus buffering their upper physiological limits from selection (Huey et al., 2003; Muñoz et al., 2014; Muñoz and Bodensteiner, In press). In contrast, lizards cannot as effectively behaviorally buffer the thermal environment at night because temperatures are more stable, resulting in stronger selection on lower physiological limits (Ghalambor et al., 2006; Muñoz et al., 2014). As such, physiological plasticity on upper limits should be limited by behavioral thermoregulation in the daytime, whereas the ineffectiveness of behavioral thermoregulation during the night should result in greater plasticity in lower physiological limits. In some cases, however, behavioral thermoregulation and physiological compensation can work synergistically: for example, some reptiles behaviorally select lower body temperatures in cold months, even when environmental conditions do not constrain thermoregulation (Firth and Belan, 1998). Thus, the potential interactions between behavioral flexibility and physiological compensation are likely complex, and illuminating these interactions can greatly improve our knowledge of how vulnerable organisms will be to environmental warming (Kearney et al., 2009; Seebacher et al., 2015). In general, examinations of behavioral flexibility have been conducted in field settings, whereas physiological plasticity has largely been examined in the laboratory through acclimation experiments in which plastic shifts are induced in response to set temperature change in a controlled thermal environment (Franklin et al., 2007; Kaufmann and Bennett, 1989; Kolbe et al., 2012; Pintor et al., 2016). However, studies simultaneously examining both behavior and plasticity in a natural setting are currently lacking (Nielsen and Papaj, 2017).

The goal of our study was to simultaneously examine the connections between behavioral thermoregulation and physiological plasticity induced by seasonal environmental fluctuations in natural populations of animals (thermal acclimatization). We focused our study on a population of the spiny lizard, *Sceloporus torquatus*, that inhabits xerophytic scrub in Central Mexico, where air temperatures fluctuate both daily and seasonally (Castillo Argüero et al., 2007; Página PEMBU, 2017). We note that "seasonal" is a relative term, and that seasonality at this site, though present, does not occur at the scale or magnitude of more temperate latitudes. *Sceloporus torquatus* is a boulder- and rock-dwelling lizard, which tends to bask during daytime hours and retreat to crevices at night (Jiménez Arcos, 2008). *Sceloporus* lizards are well-recognized thermoregulators (Lara-Reséndiz et al., 2014), which (in addition to the fluctuating thermal conditions of its habitat) make them an ideal organism for studying the interactions between behavioral buffering and physiological plasticity in a natural setting.

We address two specific hypotheses in this study. First, we predicted that thermoregulation allows diurnal lizards to behaviorally buffer extreme temperatures during daytime hours, thus maintaining a relatively constant body temperature throughout the year. Second, we predicted that the behavioral thermoregulation limits physiological plasticity for upper thermal limits, but not lower thermal limits. Specifically, we predicted that diurnal thermoregulatory efficiency should remain constant (or nearly so) throughout the year, resulting in limited physiological plasticity in heat tolerance and the preferred temperature. In contrast, cold tolerance should shift throughout the year in parallel with local temperatures, such that lizards should be more cold tolerant during winter than during summer.

2. Material and methods

2.1. Field sites and measurement of environmental temperatures

Field work was conducted from May 2016 to April 2017 in "Reserva Ecológica del Pedregal de San Ángel" (REPSA; 19° 19′ 8.8″ N, 99° 11′ 36.4″ W, elevation 2320 m), Mexico City, Mexico. The vegetation of study site is characterized by xerophytic scrub and the climate is subhumid temperate with a mean annual temperature of 15.6 °C (Castillo Argüero et al., 2007). The soil of the study site is covered with solidified lava (Xitle volcano) and crevices in the volcanic rocks provide refuges for the lizards (Feria Ortiz et al., 2001). Our study focused on adults of *Sceloporus torquatus* (> 73 mm snout-vent-length [SVL] in females and > 70 mm SVL in males; Feria Ortiz et al., 2001). During two consecutive days of each month for one year, four people did field work from 9:00–18:00 (activity period of lizards) and captured active (perching) lizards by noose. The field body temperature (T_b) was measured within 10 s of capture by inserting a thermocouple (Type K) connected to digital thermometer (Fluke 51-II ®) approximately 5 mm into the lizard's cloaca. Concurrent with the two days of behavioral observations per month, we also recorded operative temperatures (T_e, which represents the equilibrium temperature of an animal in the absence of physiological temperature regulation) (Bakken, 1992). By creating a null distribution of operative temperatures, we could determine the effectiveness of thermoregulation during the same period (Hertz et al., 1993). T_e´s were recorded using ten previously field-calibrated pipe models (polyvinylchloride; PVC) painted with gray spray paint. Into each model we inserted one temperature data logger (Thermochron iButton®; DS1921G), which recorded temperature every 10 min during the activity period of lizards. The models were similar in shape and size (10 cm of length and 20 mm of diameter) with respect to *S. torquatus*. The temperatures of the pipe model are strongly correlated with body temperatures of the lizards (Pearson´s correlation, $r = 0.94$, $P < 0.001$). The pipe models were placed randomly in ten semi-lit microsites occupied by lizards following Lara-Reséndiz et al. (2015). Concurrent with the two days of behavioral observations per month, we recorded the operative temperatures during the inactivity period of lizards (T_e night).

For the experimental physiological procedures (see Section 2.2 for details) the individuals were transported to the laboratory (Laboratorio de Herpetología2, Instituto de Biología-UNAM, located ~300 m from the study site).

To know the environmental air temperature (*ET*) of the xerophytic scrub throughout the year (i.e., not just on T_e sampling days), we downloaded weather station data (April 2016-April 2017). This database registered air temperature every 30 min from a weather station "CCH S" located ~ 1 km away from the study site (Página PEMBU, 2017). The downloaded environmental temperatures were separated by time of day, with the 'activity period' represented by 9:00–18:00 (ET_{act})

and the 'inactivity period' represented by 18:00–9:00 (ET_{ina}). We averaged data of *ET* for the whole year. To test for differences in *ET* among the months of year we performed Kruskal-Wallis one-way tests. We also averaged *ET* for each month (the mean of previous ~30 days for field work period). Thus, whereas operative temperature (T_e) data were collected during the same days as field sampling with the purpose of calculating the effectiveness of thermoregulation, environmental temperatures (*ET*) were collected throughout the year for the purpose of correlating with physiological traits. Our motivation for collecting both T_e and *ET* is that behavioral traits tend to vary with local weather conditions (discussed in Angilletta, 2009), whereas physiological traits tend to shift in parallel with weekly and seasonal trends (Phillips et al., 2016).

2.2. Estimates of preferred body temperatures and critical temperatures

Within a day of field collection, we estimated the preferred body temperature (T_{pref}) of lizards (Hertz et al., 1993) by placing them within a laboratory thermal gradient during their activity period (9:00–18:00). This trait is used to calculate the effectiveness of thermoregulation (described in Section 2.3). The preferred temperature was estimated every hour during this experiment, and we measured the T_b using the same digital thermometer used in the field work. The laboratory thermal gradient consisted of a wooden shuttle box (dimensions: 100 cm long, 100 cm wide, and 30 cm tall) divided into ten tracks with insulation barriers to prevent behavioral interactions among lizards (Lara-Reséndiz et al., 2015) and filled with 1–2 cm of Peat Moss. The wooden shuttle box was housed in the laboratory at an ambient temperature of ~20 °C. We placed one bulb of 90 W into each track at a height of 25 cm to generate a thermal gradient ranging from ~20 °C to ~50 °C. During the first two months of the study (May and June) we measured snout-vent length (SVL) and weight of every individuals to determine whether body size or mass affected their physiological traits. We performed Pearson´s correlation analysis and did not find any correlation between SVL and T_{pref} ($r = -0.06$, $P > 0.05$) or between weight and T_{pref} ($r = -0.07$, $P > 0.05$). Thus, for the remaining ten months of the experiment, we did not measure body size and mass.

After the laboratory thermal gradient experiment, we estimated the critical thermal maximum (Ct_{max}) once per individual and, on the following day, the critical thermal minimum (Ct_{min}) once. The Ct_{max} and Ct_{min} are the upper and lower temperatures, respectively, at which organisms loses locomotion, thus representing the viable thermal range for motion (Huey, 1982). Following established methods (Muñoz et al., 2014; Spellerberg, 1972), we estimated heat and cold tolerance, as described below.

So as to avoid inducing detrimental effects on embryos (Beuchat, 1986), we did not include gravid females in the thermal limits experiments. To estimate Ct_{max} we placed each lizard into a circular plastic container (25 cm diameter and 30 cm height) and increased their T_b at a rate of 1 °C/min by exposing them to a 100 W bulb suspended 30 cm above the container. We began flipping lizards onto their back when we observed panting behavior (Moreno Azócar et al., 2013). To estimate Ct_{min} we placed each lizard into a small plastic container (dimensions: 15 cm long, 15 cm wide, and 5 cm tall). The plastic container was placed into an ice box filled with 10 cm of crushed ice and each 30 s we flipped the lizard until failed to right itself in the next 15 s (Muñoz et al., 2014; Spellerberg, 1972). In both experiments we registered the lizard´s body temperature by inserting ~1 cm of a thermocouple into the lizard´s cloaca when the lizard could not right itself when is flipped onto its back. Finally, after these experiments all lizards were fed and hydrated ad libitum and released back at their capture sites. To test whether sex impacts T_{pref}, Ct_{max}, or Ct_{min} we performed *t*-tests with data from May and June. We did not find any significant effects of sex for T_{pref} ($t = 0.2$, $P > 0.05$), for Ct_{max} ($t = 0.4$, $P > 0.05$) or for Ct_{min} ($t = 1.9$, $P > 0.05$). Thus, we combined male and female data for our analyses.

During the first three months of the study we marked lizards using non-toxic paint. We never re-captured any of these individuals in subsequent months, although the shedding period meant some of the lizards could have lost their marking. Given the large sampling site (several hundred square meters) and the large population densities *Sceloporus* lizards achieve (Degenhardt et al., 1996), we suspect that most if not all individuals were not resampled during the study. In the unlikely case that we did resample an individual, the transient impacts of thermal tolerance trials (i.e., hardening) are unlikely to impact our results, especially given the long spacing between experimental days.

2.3. Effectiveness of behavioral thermoregulation

Thermoregulation occurs when organisms use behavior to maintain a certain mean body temperature (Cowles and Bogert, 1944; Huey, 1982). The effectiveness (*E*) of thermoregulation estimates how well organisms maintain their body temperature (T_b) within their preferred thermal range (T_{pref}), given the operative temperatures (T_e) available in their habitat. We estimated the effectiveness (*E*) of temperature regulation for each month of the experiment following Hertz et al. (1993), via the following equation: $E = 1\text{-}(\bar{db}/\bar{de})$. $\bar{db}$ is the average of the accuracy of body temperatures and $\bar{de}$ is the average thermal quality of the habitat. $\bar{db}$ indicates the deviation of T_b from T_{pref}, with values close to zero 0 indicating that lizards accurately maintain temperatures within their preferred range. $\bar{de}$ indicates the deviation of T_e from T_{pref}, with values close to 0 indicating high thermal quality of the habitat (i.e., habitat naturally falls within the preferred range, or close to it). Highly efficient thermoregulators will have a low $\bar{db}$ even in habitats where operative temperatures deviate from the preferred range (high $\bar{de}$), resulting in *E* values close to 1. As thermoregulatory efficiency decreases, in contrast, *E* will approach 0.

Monthly data for field body temperature (T_b), monthly interquartile range of T_{pref} (25% and 75%; T_{pref25} and T_{pref75}, respectively) and all monthly data of operative temperatures (T_e) of the ten models were used each month to calculate the indices (Hertz et al., 1993). If T_b for each individual $< T_{pref25}$, then *db* for each individual $= T_{pref25}\text{-}T_b$, and if T_b for each individual $> T_{pref75}$, then *db* for each individual $= T_b\text{-}T_{pref75}$. If T_b for each individual is within interquartile range of T_{pref} then *db* for each individual $= 0$. If each $T_e < T_{pref25}$, then $de = T_{pref25}\text{-}T_e$., and if each $T_e > T_{pref75}$, then $de = T_e\text{-}T_{pref75}$. If each T_e is within interquartile range of T_{pref} then $de = 0$.

2.4. Statistical analysis

Due to differences in the distribution of the data, we tested for differences in T_b, T_{pref} and Ct_{max} through the months of year using a Kruskal-Wallis one-way tests and to tested for differences in Ct_{min} through the months of year using a one-way Analysis of Variance (ANOVA). We examined differences among months using post hoc tests. To test the influence of environmental temperature on thermal physiology (acclimatization) of *S. torquatus* we performed Pearson´s correlation analysis between environmental traits (ET_{act} and ET_{ina}) and all physiological traits (T_{pref}, Ct_{min} and Ct_{max}).

3. Results

3.1. Environmental temperatures

The mean of *ET* in the xerophytic scrub was 16.3 ± 4.6 °C s.d. We did find significant differences in mean monthly of *ET* ($H_{11,\ 17514} = 1599.2$, $P < 0.001$; Fig. 1A). Monthly mean of *ET* ranged from 14.2 °C to 19 °C, with the monthly mean of ET_{act} ranging from 18.5 °C to 23.5 °C and the monthly mean of ET_{ina} ranging from 11.2 °C to 16 °C (Table 1). Thus, the monthly means ranged roughly 5 °C across seasons both during the day and at night, and nights were substantially colder than daytime temperatures. Nonetheless, the mean temperature of

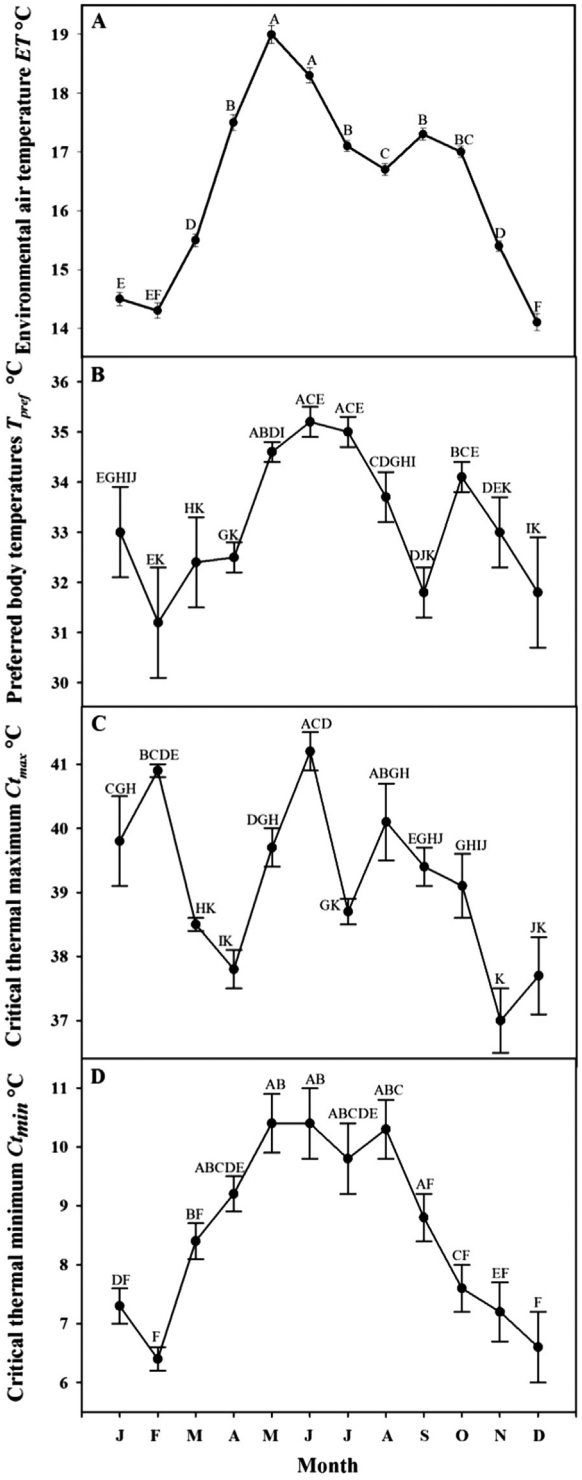

Fig. 1. A. Monthly environmental air temperature (*ET*) at Reserva Ecológica del Pedregal del San Ángel. B. Monthly preferred body temperatures (T_{pref}) of *Sceloporus torquatus*. C. Monthly critical thermal maximum (Ct_{max}) of *Sceloporus torquatus*. D. Monthly critical thermal minimum (Ct_{min}) of *Sceloporus torquatus*. Letters represent significant differences and bars represent ± 1 s.e.m.

activity periods were substantially cooler than observed body temperatures, indicating that, throughout the year, lizards were targeting a warmer subset of environmental temperatures. The monthly mean of operative temperatures in the day (T_e) registered at xerophytic scrub ranged from 15 °C to 28.2 °C and was highly variable compared with the monthly mean of operative temperatures registered at night (T_e night), which ranged from 6.6 °C to 14.7 °C (Table 1). Overall, T_e ranged from − 0.5–63 °C throughout the year (Fig. 2).

3.2. Summary of body temperatures and physiological traits

We collected body temperatures from 5 to 19 *S. torquatus* individuals every month for a year. The monthly mean of T_b ranged less than 4 °C across the year, ranging from 31.1 °C in June to 34.9 °C in May (Table 1). Individual T_b ranged from 27.1 °C to 38.5 °C throughout the year (Fig. 2). The monthly mean of preferred body temperatures (T_{pref}) of *S. torquatus* ranged from 31.2° to 34.6°C (Table 1). The monthly mean of Ct_{min} ranged from 6.4° to 10.4°C and the mean of Ct_{max} ranged from 37° to 41.2°C (Table 1).

3.3. Effectiveness of behavioral thermoregulation

The monthly effectiveness of temperature regulation (*E*) of *S. torquatus* remained high throughout the year, ranging from 0.71 to 1. This occurred through high behavioral accuracy, as ($\bar{db}$) remained low throughout the year, ranging from 0 to 3.2 despite relatively poor thermal habitat quality ($\bar{de}$ ranged from 5.4 to 18.1) (Table 2). The T_{pref25} ranged from 25.8° to 34.2°C and the T_{pref75} ranged from 34.3° to 36.8°C (Table 2).

3.4. Statistical analyses comparing environment to physiology

We did not find any significant differences in mean monthly T_b throughout the year ($H_{11,\ 118}$ = 13.8, P = 0.25). However, we did find significant differences in mean monthly T_{pref} ($H_{11,\ 118}$ = 31.6, P < 0.001; Fig. 1B), Ct_{max} ($H_{11,\ 99}$ = 44.8, P < 0.001; Fig. 1C) and Ct_{min} ($F_{11,\ 99}$ = 8.25, P < 0.001; Fig. 1D). Thus, in addition to the linear correlations with *ET* described below, there were month-to-month differences in mean population variables.

We found positive correlations between ET_{ina} and T_{pref} (r = 0.7, P = 0.01; Fig. 3a) and between ET_{ina} and Ct_{min} (r = 0.84, P < 0.001; Fig. 3b), but we did not find a correlation between ET_{ina} and Ct_{max} (r = 0.18, P = 0.6; Fig. 3c) or between ET_{act} and Ct_{max} (r = 0.27, P = 0.4; Fig. 3d).

4. Discussion

In the face of rising temperatures, ectotherms such as lizards may respond through behavioral changes, physiological plasticity, or through a combination of these two features (Huey et al., 2012; Kearney et al., 2009; Sunday et al., 2014). The goal of our study was to determine whether and how behavioral thermoregulation and physiological plasticity interact in a natural population of *Sceloporus torquatus*, and consider how these interactions might shape their vulnerability to climate change. Our results suggest that thermoregulatory behavior is highly effective at buffering *S. torquatus* from thermal variation. Over the course of the year of this study, we found dramatic differences in thermal environment (observed daily range in operative temperatures exceeding 40 °C), and mean environmental temperatures ranging from 11.2 °C (at night in winter) to 23.5 °C (during the day in spring). Despite living in both seasonally and diurnally variable habitats, lizards were remarkably efficient at actively targeting a relatively narrow range of body temperatures (~31.1–34.9 °C) during the day, resulting in near-perfect thermoregulatory effectiveness (*E* close 1) during their active period throughout the year.

Due to behavioral thermoregulation *S. torquatus* maintained relatively constant T_b, throughout the year. This result supports our first hypothesis that behavioral thermoregulation allows diurnally active lizards to avoid environmental extremes in the daytime. The maintenance of T_b is relevant because of the tight relationships between body temperature, whole-organism performance and fitness of ectotherms (Angilletta et al., 2002). The ability to effectively

Table 1
Monthly mean of field body temperatures (T_b), preferred body temperature (T_{pref}), critical temperatures (Ct_{min} and Ct_{max}), operative temperatures in the day (T_e) and at night (T_e night) and environmental temperatures (ET) in the activity and the inactivity period (ET_{act} and ET_{ina}) of *Sceloporus torquatus* in a xerophytic scrub in Mexico City, Mexico. Within parenthesis we show ± standard deviation. N indicates the sample size and N_c indicates the sample size used for critical temperatures.

Month	N	N_c	T_b	T_{pref}	Ct_{min}	Ct_{max}	T_e	T_e night	ET	ET_{act}	ET_{ina}
J	7 (2♀,5♂)	6	34.3(1.5)	33(6)	7.3(0.9)	39.8(1.8)	18.3 (7.9)	6.6 (3.7)	14.5(4.6)	18.7(3.6)	11.8(2.8)
F	5 (2♀,3♂)	3	34(2.1)	31.2(6.2)	6.4(0.5)	40.9(0.2)	23.3 (8.9)	9.4 (4.3)	14.3(5.1)	18.9(3.5)	11.2(3.3)
M	7 (4♀,3♂)	3	33.6(2)	32.4(5.4)	8.4(0.6)	38.5(0.1)	28.2 (11.9)	11.2 (5.4)	15.5(4.8)	19.9(3.4)	12.6(3.2)
A	19 (13♀,6♂)	10	34(2)	32.5(4.1)	9.2(1.1)	37.8(0.9)	27.8 (8.3)	14.7 (4)	17.5(5.1)	22.5(3.2)	14.3(3.2)
M	11 (6♀,5♂)	10	34.9(2.4)	34.2(2.8)	10.4(1.7)	39.7(0.9)	27.3 (7.2)	13.2 (2.8)	19(5.1)	23.5(3.8)	16(3.5)
J	10 (5♀,5♂)	10	31.1(3.7)	34.6(2.8)	10.4(1.8)	41.2(1.1)	23.4 (5.8)	12.9 (2.9)	18.3(4.4)	22.2(3.5)	15.7(2.6)
J	10 (5♀,5♂)	10	34.2(3.2)	34.5(2.4)	9.8(1.7)	38.7(0.8)	21.5 (4.7)	13.7 (2.2)	17.1(3.7)	20.7(2.6)	14.7(2)
A	11 (4♀,7♂)	10	31.9(3)	33.4(4.6)	10.3(1.8)	40.1(1.9)	20.3 (3.6)	14.6 (2.1)	16.7(3.6)	20.7(2.6)	14.4(1.9)
S	9 (4♀,5♂)	9	33.7(2.8)	31.7(4.1)	8.8(1.2)	39.4(0.7)	21.1 (5.6)	13.8 (2.4)	17.3(3.6)	20.8(2.7)	15(2)
O	11 (3♀,8♂)	11	33.1(2)	34.4(2.5)	7.6(1.3)	39.1(1.6)	21.3 (5.2)	13.6 (2.2)	17(3.6)	20.5(2.8)	14.8(1.9)
N	9 (5♀,4♂)	8	32.9(3.9)	33.1(3.3)	7.2(1.3)	37 (1)	15 (2.1)	12.6 (1.2)	15.4(3.8)	18.5(3.4)	13.4(2.3)
D	9 (2♀,7♂)	9	32.8(2.6)	31.8(6.2)	6.6(1.9)	37.7(1.4)	18 (4.9)	14.6 (1.7)	14.2(4.8)	18.5(3.8)	11.3(2.8)

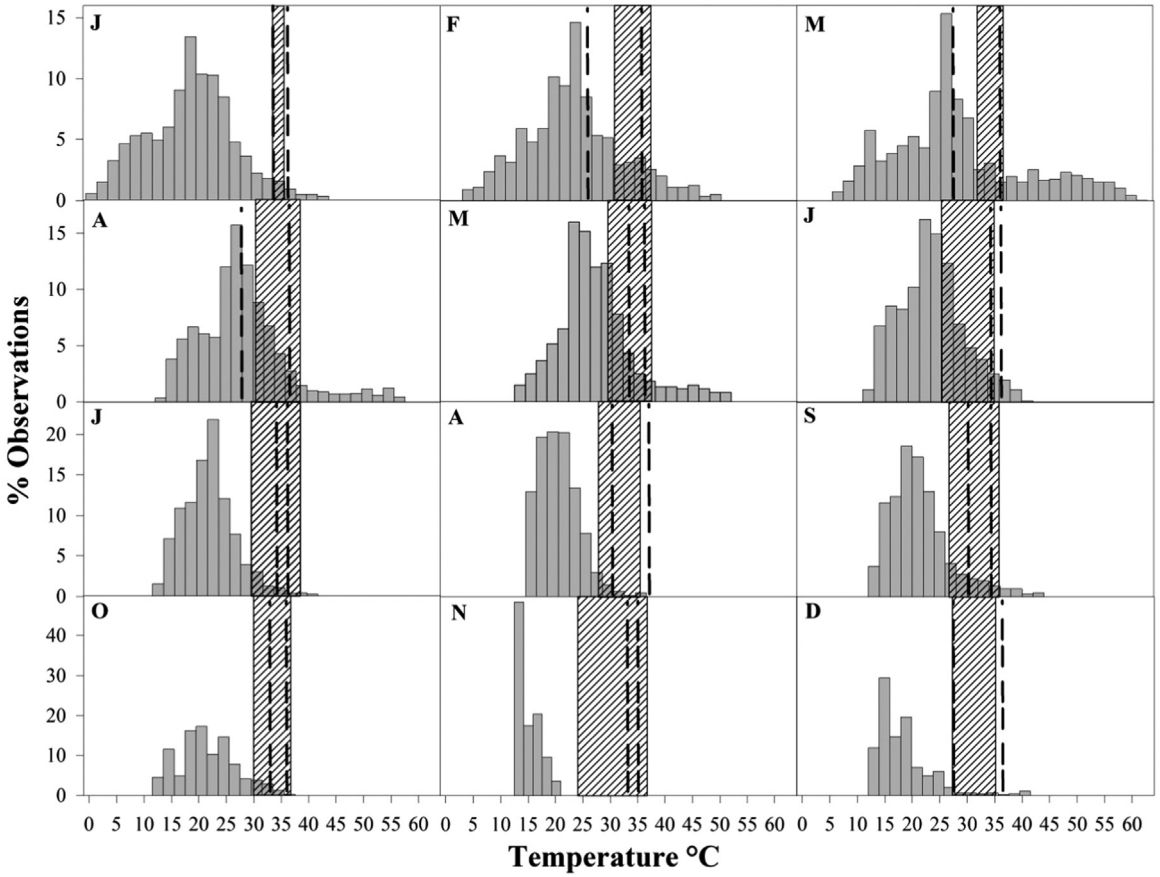

Fig. 2. Monthly body temperatures (T_b) and preferred body temperatures (T_{pref}) of *Sceloporus torquatus* and operative temperatures (T_e) at Reserva Ecológica del Pedregal del San Ángel. The diagonal shading represents the monthly range of T_b, the dashed lines represent the monthly interquartile range of T_{pref} and vertical bars represent the observations of T_e.

thermoregulate is certainly not limited to *S. torquatus*. Indeed, active thermoregulation is typical of many other lizards (including other phrynosomatids) (Artacho et al., 2017; Díaz de la Vega-Pérez et al., 2013; Hertz et al., 1993; Kirchhof et al., 2017; Lara-Resendiz et al., 2013, 2014, 2015; Muñoz et al., 2016; Muñoz and Losos, 2018; Ortega et al., 2016; Sartorius et al., 2002), amphibians (Balogová and Gvoždík, 2015; Gvoždík and Kristín, 2017; Strickland et al., 2016) and insects (Kearney et al., 2009; Kingsolver, 1983; Sunday et al., 2014), to give a few examples. The stability in thermoregulatory efficiency that we observe in *S. torquatus* may be a relatively widespread ectotherm mechanism for buffering environmental variation.

In the face of rising environmental temperatures, active thermoregulation has a relevant role for the ectotherms avoiding detrimental temperatures (Kearney et al., 2009; Sunday et al., 2014). For example, when the environmental temperature is high, *Sceloporus* lizards may retreat to cool thermal refuges to avoid encountering lethal temperatures (Sinervo et al., 2010). We do not address the proximate mechanisms facilitating thermoregulation in this study (i.e., relative sun/shade use, structural microhabitat use), but note that if the availability of preferred microsites is eroded due to warming, so too will the ability to thermoregulate. Nonetheless, behavioral efficiency is likely constrained by fundamental limits: below a minimum amount of activity, organisms cannot grow or maintain their body condition. If constraints on activity persist, population size may decrease over time

Table 2
Monthly interquartile range of preferred body temperature (T_{pref}) (25% and 75%; T_{pref25} and T_{pref75}), accuracy of body temperatures ($\bar{db}$), quality thermal of the habitat ($\bar{de}$) and effectiveness of temperature regulation (E) of *Sceloporus torquatus* in a xerophytic scrub in Mexico City, Mexico.

Month	T_{pref25}	T_{pref75}	$\bar{db}$	$\bar{de}$	E
J	33.2	36	0	15.1	1
F	25.8	35.7	0.3	7.2	0.96
M	27.6	36.3	0.03	6.4	0.99
A	29.9	35.6	0.2	5.4	0.97
M	33.3	36	0.7	7.8	0.91
J	34.2	36	3.2	10.9	0.71
J	33.9	35.9	1.7	12.4	0.86
A	30.1	36.8	0.7	9.8	0.93
S	30.1	34.3	0.8	9.5	0.91
O	33.1	35.9	0.9	11.9	0.92
N	33.1	34.9	1.8	18.1	0.9
D	27.2	36.4	0.01	9.3	1

and, eventually, go extinct (Sinervo et al., 2010, 2011). Thus, while behavioral efficiency may be effective in the short run – and it is a clear tack employed by *S. torquatus* over the course of a year – other mechanisms such physiological plasticity are also important for ensuring that lizards are able to maintain activity as environmental constraints continue to mount.

Consistent with our hypotheses, we found that Ct_{min} is positively correlated with nocturnal environmental temperatures in *S. torquatus* (ET_{ina}; Fig. 3b), such that in the wintertime cold tolerance was ~4 °C lower than in the summer. The changes in the population mean of Ct_{min} across months correlated with changes in the monthly mean of ET_{ina} suggesting thermal acclimatization (phenotypic plasticity induced by thermal changes; Pörtner et al., 2009). We observed significant differences in Ct_{min} among seasons, such that means in this trait were similar across spring and summer, and autumn means were similar to winter means (Fig. 1D). This seasonal shift in thermal acclimatization within a single population is quite dramatic; such differences are usually observed over substantially greater environmental scales and among species (Huey and Tewksbury, 2009). This result indicates that cold tolerance is labile within *S. torquatus*, and shifts in parallel with environmental conditions throughout the year.

In contrast to cold tolerance, we found no relationship between Ct_{max} and nocturnal environmental temperatures (Et_{ina}; Fig. 3c) or daytime environmental temperature (Et_{act}; Fig. 3d) in *S. torquatus*. Ct_{max} was also variable (~4 °C, similar to Ct_{min}), but we did not find a pattern with seasonal thermal variation (Fig. 1C). The variation in Ct_{max} was somewhat surprising given that this trait is often relatively inert within populations, among populations, or even among closely related species (e.g., Cruz et al., 2005; Kellermann et al., 2012; Muñoz et al., 2014, 2016). Although Ct_{max} was uncorrelated with ET_{act} or ET_{ina}, it is possible that shifts in heat tolerance were induced by other environmental changes or physiological traits, such as precipitation regimes (Clusella-Trullas et al., 2011), evaporative water loss (Tracy et al., 2008) or to dehydration (Rezende et al., 2011).

Our results are consistent with the idea that thermoregulation is remarkably effective at buffering organisms from variation during the

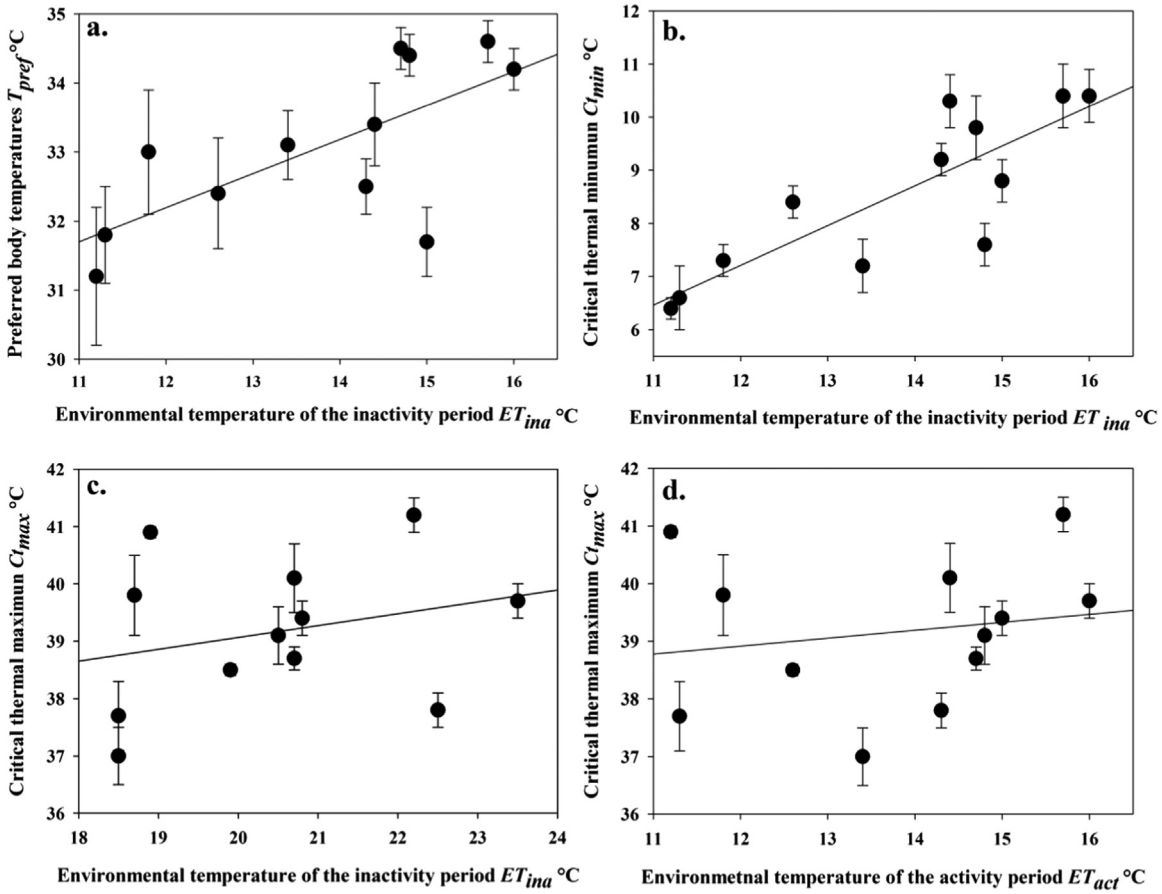

Fig. 3. a. Correlation between environmental temperature in the inactivity period of *Sceloporus torquatus* (ET_{ina}) and preferred body temperatures (T_{pref}) (r = 0.7, P = 0.01) of the lizards. b. Correlation between environmental temperature in the inactivity period of *S. torquatus* (ET_{ina}) and critical thermal minimum (Ct_{min}) (r = 0.84, P < 0.001) of the lizards. c. Weak, non-significant correlation between environmental temperature in the inactivity period of *Sceloporus torquatus* (ET_{ina}) and critical thermal maximum (Ct_{max}) (r = 0.18, P = 0.6). d. Weak, non-significant correlation between environmental temperature in the activity period of *Sceloporus torquatus* (ET_{act}) and critical thermal maximum (Ct_{max}) (r = 0.27, P = 0.4). Bars represent ± 1 se.m.

day, but not at night. Indeed, nighttime temperatures were both cooler and more stable than daytime temperatures, supporting the idea that the Bogert effect – and the behavioral regulation that underlies it – hinge on the thermal heterogeneity of the habitat (Ghalambor et al., 2006; Huey et al., 2003; Muñoz and Bodensteiner, in press). The role of behavioral thermoregulation in limiting exposure to selection on physiology has been demonstrated to dampen rates of evolution in Ct_{max} relative to Ct_{min} (Kellermann et al., 2012; Muñoz et al., 2014), and to impact geographic patterns of tolerance ranges across latitude (Araújo et al., 2013; Sunday et al., 2014; Gunderson and Stillman, 2015). Our study extends this interspecific framework to also incorporate the distinct intraspecific footprints of behavioral thermoregulation on plasticity in physiological traits within a single species.

Our findings that T_{pref} varies among months (Fig. 1B) and shifts in parallel with thermal conditions throughout the year (Fig. 3a) indicate that behavioral thermoregulation, though highly effective, is not sufficient for compensating for seasonal changes in thermal environment. During the winter *S. torquatus* targets a slightly lower temperature (~31 °C), whereas in summer it tracks higher temperatures (~34 °C). Because thermoregulatory effectiveness is contingent on the ability for organisms to maintain body temperatures within their preferred ranges, a seasonal shift in T_{pref} likely contributed to the often near-perfect estimates of effectiveness that we observed. Thus, while *S. torquatus* behaviorally thermoregulates, seasonal acclimation in the target core temperature range appears to assist in the effectiveness of this mechanism.

Our observation that physiological plasticity of T_{pref} of *S. torquatus* is correlated with ET_{ina} (Fig. 3a) is also consistent with laboratory acclimation experiments. For example, Kaufmann and Bennett (1989) experimentally treated two groups of the desert night lizard *Xantusia vigilis* at two acclimation temperatures (20 °C and 30 °C) during 50 days and they found differences in T_{pref} between groups (with the group acclimated to 30 °C have high T_{pref} than the group acclimated to 20 °C). As a caveat, however, we note that our assessments of physiological plasticity were indirect, as we did not measure the same individuals or genotypes across seasons. Without enclosures, it is challenging to track the same individuals over time, but doing so would be a fruitful future study as it would illustrate whether population-level patterns that we detected also occur within individuals across seasons.

In the face of ongoing environmental warming (IPCC, 2014), behavioral buffering and physiological plasticity are the key mechanisms that can help individuals compensate for the increase in environmental temperature (Farrell and Franklin, 2016; Franklin et al., 2007; Muñoz and Moritz 2016; Palumbi et al., 2014). Rather than working synergistically, however, behavioral thermoregulation and physiological plasticity appear to function in a complementary fashion, which should actually limit the ability for organisms to respond to rising temperatures. If thermoregulatory behavior does, indeed, contribute to limited acclimatization in upper physiological traits, then this might limit additive responses in behavior and physiological plasticity that organisms could mount. In light of this, if behavioral thermoregulation is not successful at buffering organisms from rising temperatures (discussed in Sinervo et al., 2010; Sinervo et al., 2011), we suggest that its limiting influence over thermal acclimatization in Ct_{max} could further limit the ability for ectotherms to mount sufficient responses through plasticity (Seebacher et al., 2015). In contrast, behavioral thermoregulation and plasticity in the preferred temperature do appear to interact additively, resulting in near-perfect thermoregulation throughout the year. Thus, the effects of behavioral thermoregulation on plasticity might vary between traits.

Interactions between behavioral buffering and physiological plasticity may be generally widespread. For example, color change and thermal refuge seeking behavior in butterfly larvae appear to also function non-independently, with total adaptive responses limited by their interactions (Nielsen and Papaj, 2017). We argue that disentangling whether and how behavior and plasticity interact to shape physiological variation can provide a more holistic view of the mechanisms by which ectothermic organisms will be impacted by rising environmental temperatures.

In conclusion, we propose that behavioral thermoregulation and plasticity do not operate in isolation, rather these two features interact to shape physiological phenotypes. *Sceloporus torquatus* is a near-perfect thermoregulator that maintains its body temperature within a narrow range during their activity period throughout the year. Consequently, behavioral thermoregulation allows individuals to avoid high temperatures during the day. In contrast, behavioral thermoregulation is not efficient at night, which is correlated with greater plasticity in cold tolerance. Finally, effective behavioral thermoregulation is, aided in large part by marked plastic shifts in the preferred temperature, indicating that behavior and plasticity interact to shape temporal patterns of physiological variation.

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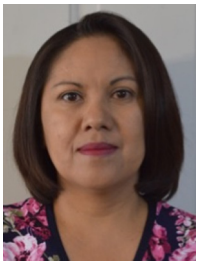

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