Original paper

Intra-population variation of body temperature of the lizard *Sceloporus anahuacus* (Squamata: Phrynosomatidae) in Sierra del Ajusco, Mexico

Variación intrapoblacional de la temperatura corporal de la lagartija *Sceloporus anahuacus* (Squamata: Phrynosomatidae) en la Sierra del Ajusco, México

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Responsible editor: Eduardo Pineda

ABSTRACT. We evaluated intra-population variation of body temperature of the Mexican lizard *Sceloporus anahuacus* (Phrynosomatidae) in Sierra del Ajusco, Mexico. The geographic distribution of this lizard is restricted to the higher parts of the mountains bordering the south of the Mexican Valley in Mexico City. The study of the body temperature of *S. anahuacus* and its relationship with the environment is important because high elevation taxa are seriously threatened by climate change. For that reason, and compared body temperature between sex, age class, reproductive condition and activity state. Overall, mean body temperature was 26.2 ± 5.5 °C with a range between 9–39 °C. We did not find differences between body temperatures of males and females. However, we found significant differences

depending on activity state in both sexes. In females, body temperature did not vary as a function of age class or reproductive status. Instead, we found differences in body temperature between males of different age classes. Juveniles had the highest body temperature, probably due to differential temperature requirements associated with development. On the other hand, body temperature of active and inactive *S. anahuacus* was strongly associated with environmental temperature, perhaps due to sedentary habits and territorial behavior. Exploring why such variation exists on body temperature regulation may provide information on factors influencing the survivorship of this endemic Mexican lizard.

Key words: thermal ecology; ectotherms; reptiles; pine forest; *Sceloporus anahuacus*; Mexico

RESUMEN. Evaluamos la variación intrapoblacional de la temperatura corporal de la lagartija mexicana S*celoporus anahuacus* (Phrynosomatidae) en la Sierra del Ajusco, México. La distribución geográfica de esta lagartija se limita a las partes más altas de las montañas que bordean el sur del valle mexicano en la Ciudad de México. El estudio de la temperatura corporal de *S. anahuacus* y su relación con el medio ambiente es importante debido a que los taxones de alta elevación están seriamente amenazados por el cambio climático. Por esa razón, exploramos la relación de la temperatura corporal de *S. anahuacus* con la temperatura del aire y del sustrato, y comparamos la temperatura corporal entre sexos, clase de edad, condición reproductiva y el estado de actividad. En general, la temperatura corporal promedio fue de 26.2 ± 5.5 °C con un rango entre 9–39 °C. No encontramos diferencias entre las temperaturas corporales de machos y hembras. Sin embargo, encontramos diferencias significativas según el estado de actividad de ambos sexos. En las hembras, la temperatura corporal no varió en función de la edad o el estado reproductivo. En cambio, encontramos diferencias en la temperatura corporal entre machos de diferentes clases de edad. Los juveniles tuvieron la temperatura corporal más alta, probablemente debido a los requisitos de temperatura diferencial asociados con el desarrollo. Por otro lado, la temperatura corporal de *S. anahuacus* activos e inactivos estuvo fuertemente asociada con la temperatura ambiental, tal vez debido a hábitos sedentarios y comportamiento territorial. Explorar por qué existe esta variación en la regulación de la temperatura corporal puede proporcionar información sobre los factores que influyen en la supervivencia de esta lagartija endémica mexicana.

Palabras clave: ecología térmica; ectotermos; reptiles; bosque de pino; *Sceloporus anahuacus*; México

INTRODUCTION

In squamate reptiles, body temperature exerts a significant influence on a variety of physiological and behavioral mechanisms, which have effects on survivorship, growth rate and reproductive success (Sinervo & Adolph, 1989). For example, body temperature affects locomotion (Chen *et al.*, 2003), immune infection (Mondal & Rai, 2001), sensory input (Stevenson *et al.*, 1985), foraging ability (Pianka, 1973; Ayers & Shine, 1997), predation risk (Herczeg et al., 2008), food assimilation and growth (Angilletta, 2001; Chen *et al.*, 2003; Tattersall *et al.*, 2004; Brown & Griffin, 2005), courtship (Stapley, 2006), offspring fitness (Mathies & Andrews, 1997), sex determination (Janzen, 1994; Juliana *et al.*, 2004), activity period (Llewelyn *et al.*, 2005; López-Alcaide *et al.*, 2014) and

microhabitat selection (Pianka, 1973; Angert *et al.*, 2002; Amat *et al.*, 2003; Lara-Reséndiz *et al.*, 2014).

Importantly, reptile body temperature is constrained by phylogeny (Casas-Andreu & Gurrola-Hidalgo, 1993; Andrews, 1998), environment (Gillis, 1991; Angilletta, 2001) and life history characteristics like sex (Lee, 1980), reproductive status (Mathies & Andrews, 1997) and age class (Lemos-Espinal *et al.*, 1998). Therefore, reptiles mainly use behavioral mechanisms to regulate body temperature for optimal function of cellular and organismal processes (Bartholomew, 1982). Behavioral thermoregulation includes changes in posture (Kearney, 2001), activity periods (Grant & Dunham, 1988) and microhabitat selection (Adolph, 1990). Consequently, they tend to explore the temporal and spatial variability of the thermal environment, which promotes a close relationship between the organism's body temperature and the environment (Mathies & Andrews, 1995).

Genus *Sceloporus* is composed by 111 species (Uetz *et al.*, 2022) and has a wide latitudinal and altitudinal distribution from western Panama in Central America to Washington in the United States (Andrews, 1998). Field body temperatures measured during normal activity periods range from 14.2–40 °C with an average of 33.9 °C (Bogert, 1949; Sinervo, 1990; Smith & Ballinger, 1994; Clusella-Trullas & Chown, 2014). Species for which body temperatures have been measured on thermal gradients in the laboratory exhibit preferred temperatures from 28.6–38.8 °C, with an average of 33.96 °C (Brattstrom, 1965; McGinnis, 1966; Sinervo & Adolph, 1989; Mathies & Andrews, 1997; Andrews *et al.*, 1999). For that reason, genus *Sceloporus* has long been considered to be thermally conservative (Andrews, 1998). However, there is not a consistent pattern between field body temperature and preferred temperature in *Sceloporus* species with respect to latitude and altitude (Clusella-Trullas & Chown, 2014).

Sceloporus anahuacus Lara-Góngora, 1983, is a small viviparous phrynosomatid lizard inhabiting open pine forest. They are indicators of forest disturbance since they proliferate in areas of intense commercial clearing, recovering burns, or any other kind of disturbance that creates a more open forest structure (Lara-Góngora, 1983). Until now, the ecology of *S. anahuacus* is relatively unstudied, although there are some contributions concerning thermal ecology (Ávila-Bocanegra *et al.*, 2012), selected body temperature under laboratory conditions (Lara-Reséndiz & García-Vázquez, 2013) and thermal habitat quality (Lara-Reséndiz *et al.*, 2014). However, what is usually overlooked in these efforts is that species can be composed of different populations or geographical groups across their ranges, which are under different selective pressures deriving in an independently potential response to climate (Araújo *et al.*, 2006; Güizado-Rodríguez *et al.*, 2012). Therefore, the more information we can gather on the temperature relationships of lizards across all its distribution ranges, the better we might be able to predict the thermoregulatory profiles and propose appropriate conservation strategies. For that reason, in this paper, we analyzed the relationship with air and substrate temperatures, and compared body temperature between sex, age class, reproductive condition and activity state.

MATERIALS AND METHODS

Study site. This study was carried out in the Ejido Magdalena Petlatalco, Delegación Magdalena Contreras, Sierra del Ajusco, Ciudad de México, México, (19° 13′ 15.5″ N, 99° 17′ 8.2″ W) from 3,500 to 3,930 meters above sea level. The climate of the study area is temperate semihumid with a mean annual temperature of 7.5–13.5 °C and mean annual rainfall of 1,340 mm with less than 5 % of this occurring in the winter (García, 1973). Vegetation includes pine forest (*Pinus hartwegii*) and grasslands (Álvarez del Castillo, 1987).

Field work. We collected 539 lizards (active and inactive lizards) during the period from 1,000 to 1,600 h, from August 2007 through April 2009. This work was part of a project including demographic and ecological aspects of *S. anahuacus*. Each lizard was permanently marked by clipping toes, and only one observation per individual was used in statistical analyses. If more than one observation was available for an individual, a single observation was chosen at random for inclusion in statistical analyses.

Activity state was determined as follows: active lizards were basking on rocks or fallen trees, foraging, pursuing mates, whereas inactive lizards were beneath rocks or hidden under vegetation and debris in crevices or depressions (Güizado-Rodríguez *et al*., 2011). Active lizards were captured by noosing and returned to their habitat after collecting data. We measured body temperature from lizards' cloaca (T_b) and obtained substrate (T_s on the site where the lizard was first observed) and air (T_a 5 cm off the ground) temperatures with a quick-reading thermometer (model 4D2672, Miller and Weber, Inc., New York; $0–50 \pm 0.2$ °C). Care was taken to prevent the temperature from being influenced by handling, therefore all data from lizards requiring extensive capture effort was excluded for temperature records. To avoid errors, we only analyzed data collected within 10 s after capture (Lee, 1980; Gillis, 1991). In addition to T_b, we recorded snout-vent length (SVL) with a digital caliper to 0.1 mm and body mass was measured with a Pesola scale (Pesola AG, Baar, Switzerland) to the nearest 0.2 g. Sex was determined by examining the sexually dimorphic scales and color pattern (Lemos-Espinal *et al*., 1997a). Female reproductive state (pregnant *vs.* non-pregnant) was determined by palpation (Lemos-Espinal *et al*., 1997b).

Statistics. The assumptions of normality and homogeneity of variances were tested and met with Shapiro-Wilk and Bartlett tests, respectively. We performed an Analysis of Covariance by sex to evaluate the effect of factors such as age class (offspring, juvenile, adult), activity state (active and inactive) and in the case of females, the reproductive condition (reproductive and no reproductive) on lizard's T_b including T_a, T_s and SLV of lizards as covariates. Hypotheses were tested with ANOVA (such as F tests). Data are presented as mean ± standard deviation (SD). Statistical analyses were performed with XLSTAT (Addinsoft, 2014). Data analysis and statistical software for Microsoft Excel, Paris, France; http:// www.xlstat.com) software implementing an α of 0.05 to indicate significance.

RESULTS

Mean T_b for active lizards was 28.31 ± 3.6 °C (17–39 °C, n = 365). On the other hand, mean T_b for inactive lizards was 22.01 ± 6.4 (9–33 °C, n = 174). Mean SVL in males was 38.5 ± 9.9 mm (n = 213) and in females was 37.6 ± 7.8 mm (n = 326). Mean body mass of males was 2.4 ± 1.8 g (n = 213)

and for females was 2.0 ± 1.1 g (n = 326). Tb of individuals with different sex, age class and activity state are shown in Table 1. Mean Ta was 17.63 ± 3.11 °C and mean Ts was 19.31 ± 6.46 °C. In females, according to the goodness of fit and ANOVA test performed in global factorial ANCOVA model, the set of independent variables (age, SVL, reproductive state, activity state, Ta and Ts) analyzed significantly explain the variation in lizards' Tb (R2 = 0.52; $F7,283$ = 43.857; P <0.0001). Furthermore, the Type I sum of squares indicates that the independent variables that provide the greatest amount of information on lizards' Tb were Ts ($F1,289$ = 201.131; P < 0.0001), Ta ($F1,289$ = 66.567; P < 0.0001) and the activity state ($F1,289$ = 32.947; P < 0.0001) whereas SVL ($F1,289$ = 0.303; P = 0.583), age class ($F1,289$ = 1.508; P = 0.223) and reproductive state ($F1,289$ = 3.035; P = 0.223) did not have an effect on Tb.

Table 1. Field body temperature of different sex, age class and activity state in *Sceloporus anahuacus*. Mean (± SD). Abbreviations: M= Male; F= Female; n= number; Mx= Maximum; Mn= Minimum; Off= Offspring; Juv= Juvenile; Adu= Adult; Act= Active; Ina= Inactive.

Sex	Tb				Age Class					Activity State				
	x±SD	n	Mx	Mn		x±SD (°C)	n	Mx	Mn		x±SD (°C)	n	Mx	Mn
M	26.7±5.4	213	36	9	Off	25.4±4.8	49	32	15	Act	28.58±3.45	149	36	18
					Juv	27.6±4.3	55	34	14	Ina	22.46±6.67	63	33	9
					Adu	26.8±6.0	110	36	9					
F	25.9±5.6	326	39	12	Off	26.1±4.3	52	32	16	Act	28.12±3.76	216	39	17
					Juv	27.0±5.6	87	39	12	Ina	21.76±6.27	110	33	12
					Adu	25.5±5.8	186	34	12					

In the case of males, the independent variables (age class, SVL, activity state Ta and Ts) analyzed also significantly explain the variation in lizards' Tb (R2 = 0.57; $F6,193$ = 43.218; P <0.0001). The Type I sum of squares indicates that the independent variables that provide the greatest amount of information on lizards' Tb were Ts ($F1,198$ = 197.164; P < 0.0001), Ta ($F1,198$ = 16.389; P < 0.0001) and the activity state ($F1,198$ = 38.097; P < 0.0001) whereas SVL ($F1,198$ = 1.444; P = 0.238) and age class ($F1,198$ = 4.769; P = 0.301) did not have an effect on Tb.

On the one hand, the post hoc analysis (Tukey HSD) with a confidence interval of 95 % did not detect any significant difference in females Tb between age classes and reproductive condition, but a difference was found between females with different activity state (P < 0.0001). In the other hand, with respect to males the post hoc analysis identified significant differences between individuals with different activity state (P < 0.0001) and age classes (juvenile vs. adult, P = 0.025).

DISCUSSION

Our study provides an examination of field body temperature variability of *Sceloporus anahuacus* at intraspecific level. Although found at a wide range of latitudes and altitudes and in a variety of habitats, all *Sceloporus* species studied maintain similar Tb during activity in nature and in thermal gradients in laboratory (Bogert, 1949; Wilhoft & Anderson, 1960; Brattstrom, 1965; Mayhew, 1968;

McGinnis, 1966; Mueller, 1970; Avery, 1982; Crowley, 1985). This study showed that active *S. anahuacus* had one of the lowest T*b* (28.3 °C) registered for members of genus *Sceloporus* (Vial, 1984; Andrews, 1998; Andrews *et al.*, 1999). However, Ávila-Bocanegra *et al.* (2012) reported a significantly warmer T*b* (30.88 ± 0.14 °C) for another *S. anahuacus* population. This may be due to the fact that population studied by these authors is located at a lower altitude site (3,200 m) with a higher ambient temperature (T*a* = 20.88 ± 0.24 °C; T*s* = 20.47 ± 0.24 °C) than the registered in our study (T*a* = 17.63 ± 3.11 °C; T*s* = 19.31 ± 6.46 °C).

Such as *S. anahuacus*, there are other *Sceloporus* species that show a low T*b* like *S. malachiticus* (T*b* = 28.6 °C; Vial, 1984), *S. mucronatus mucronatus* (T*b* = 29.4 ± 0.7 °C; Lemos-Espinal *et al.*, 1997a), *S. bicanthalis* (T*b* = 28.8 ± 0.69 °C; Andrews *et al.*, 1999) and *S. palaciosi* (T*b* = 27.82 ± 5.31 °C; Güizado-Rodríguez *et al.*, 2011). This low T*b* is presumably due to thermal constraints imposed by the spatial and temporal distribution of environmental temperatures that determine daily and seasonal activity because usually at high elevations, thermal quality is low (Lymburner & Blouin-Demers, 2020). Lara-Reséndiz *et al.*, (2014) evaluated the thermal habitat quality of a lizard community along an altitude gradient, in order to determine if thermal environment has an effect on distribution and thermal ecology. Authors suggest that altitude and vegetation have an influence on thermal quality, therefore thermal ecology studies should be carried out at different spatial scales to understand the factors involved in thermal niche and thermoregulation. According to the results showed by the authors, the operative temperatures where *S. anahuacus* lives, had the lowest values compared to other studied sites. This means that landscape characteristics, have a influence on the thermal properties of the habitat and therefore thermoregulatory opportunities for *S. anahuacus*.

In thermally challenging habitats, ectotherms may passively reach body temperature in the field and not match preferred temperatures. In that situation, ectotherms should thermoregulate, frequently being exposed to predators, or otherwise maintain suboptimal temperatures, with the concomitant physiological costs (Zamora-Camacho *et al.*, 2016). According to Lara-Reséndiz *et al.* (2014), *S. anahuacus* habitat has a low thermal quality, therefore, when lizards are under laboratory thermal gradients they select a higher body temperature (32.64 ± 2.73 °C, range = 26.0–36.5 °C) (Lara-Reséndiz & García-Vázquez, 2013) than in the field (T*b* = 28.31 ± 3.6 °C).

Another thermal constrain for *S. anahuacus* could be the availability of suitable microhabitats for thermoregulation due to deforestation, since this activity promotes openness patches and reduce habitat heterogeneity and sites available for thermoregulation. Sierra del Ajusco is located within the Transverse Volcanic Belt, which has a long history of human disturbance that has increased in recent decades due to its boundary with one of the world's largest cities, the metropolitan area of Mexico City. These disturbances are the result of increasing population density, land use change, forest and wildlife resources exploitation, and the effects of contamination (Granados Sánchez *et al.*, 2004). However, as a descriptive study, there were not enough data to elucidate the ultimate and proximate causes of the low T*b* found in *S. anahuacus*. To further clarify this, we need to address the influence of the spatial distribution of operative temperatures on activity and microhabitat use using biophysical models that can provide

information to some extent about how this species thermoregulates and will lend insight into the observed patterns for these lizards (Heath, 1964).

On the other side, body temperature of *S. anahuacus* did not differ between sexes; this can be due to similar use of microhabitats, activity periods and feeding habits by males and females such as in other diurnal lizards (Güizado-Rodríguez *et al.*, 2011). Unlike some sympatric species like *S. mucronatus*, shows a difference in Tb between males and females due to different activity periods (e.g., females emerge later than males) or because females may be forced to use sub-optimal basking sites by males (Lemos-Espinal *et al.*, 1997a).

In addition, we did not find evidence for variation in Tb as a function of reproductive condition in females. This may be the result of females being unable to alter their Tb due to phylogenetic constraints (Lemos-Espinal *et al.*, 1997b), or because differences between early pregnancy-stage and non-pregnant females may be difficult to detect. Another reason could be that *S. anahuacus* females have not had the opportunity to choose microhabitats with better thermal conditions; therefore, it is probable that pregnant females do not reach unfavorable body temperatures for embryos. Females of some *Sceloporus* species exhibit lower Tb when gravid or pregnant because normal activity temperatures are detrimental to embryos (Van Damme *et al.*, 1986; Andrews & Rose, 1994). However, Ávila-Bocanegra *et al.* (2012) found that *S. anahuacus* pregnant females had a higher Tb than non-pregnant females. This is due to the altitude of the studied site where *S. anahuacus* was observed by Ávila-Bocanega *et al.* (2012). Isidro Fabela at the northeastern Estado de México has a lower altitude than the Ajusco where *S. anahuacus* was collected during this study. According to work carried out by Lara-Reséndiz *et al.* (2014), El Ajusco, Ciudad de México is a site with low thermal quality and a highly variable operating temperature (To) (-8.5–68.4 °C), therefore, *S. anahuacus* tends to show a narrow selected body temperature (Tsel) with intervals (≤ 2.1 °C), which means that cost of thermoregulation is high for this species mainly because conifer forests have greater coverage and the availability of perching sites such as rocks, trees or sunny patches on the ground for this high mountain phrynosomatid are scarce.

We also did not find a difference between Tb among different female age classes. This may be because the environment lacks a wide range of temperatures, and all age classes are constrained to select similar thermal microclimates. However, there are no data about age class specific behavior in *S. anahuacus*; therefore, we need to concentrate our efforts to answer these kinds of questions in future studies. In the case of males, we found differences between Tb among different age classes. Juveniles had the highest Tb and the offsprings presented the lowest Tb. In some diurnal reptiles, juveniles select higher body temperatures than adults (Pérez-Quintero, 1994), presumably due to differential temperature requirements associated with development (Hitchcock & McBrayer, 2006).

Sceloporus lizards are sit-and-wait insectivores that spend much of their time perched conspicuously on rocks and fallen trees. For this reason, they maintain a strong relationship with the microhabitat temperature. We found a significant relationship between Tb and Ta and Ts in both sexes of *S. anahuacus*. This strong relationship may be due to sedentary habits and territorial behavior of *Sceloporus* (Pianka & Vitt, 2003). Although, Ávila-Bocanegra *et al.* (2012) found slight

variation in body temperature explained by environmental temperatures, which suggest that these lizards may be able to regulate their body temperatures to some extent.

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