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Thermoregulation in the Andean lizard *Anolis heterodermus* (Squamata: Dactyloidae) at high elevation in the Eastern Cordillera of Colombia

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ABSTRACT. Low thermal quality environments, such extreme latitudes or high elevation regions, are highly expensive for reptiles in terms of thermoregulation. Thus, physiological adaptations or behavioral adjustments to live in these habitats have evolved in some species. *Anolis heterodermus* (Duméril, 1851) is an anole lizard that lives at high elevations in the Andes region. In this paper, we attempted to elucidate the thermoregulation strategy of a population of this species from the eastern cordillera of Colombia during wet and dry seasons. We measured body temperatures (T_b), operative temperatures (T_e) and preferred temperatures (T_{pref}). Based on these data, we obtained accuracy ($\bar{d}_b$), environmental thermal quality ($\bar{d}_e$) and efficiency of thermoregulation (E) indexes. There were no significant differences of T_b or $\bar{d}_b$ between seasons, sexes, ages, and for T_{pref} between sexes or ages, but we found differences in T_e and $\bar{d}_e$ between seasons. The indexes suggested high thermoregulatory accuracy, low thermal environment quality and indicated that *A. heterodermus* was an active thermoregulator in both seasons. Broad ranges of T_b and the species association with microhabitats with high solar radiation suggest eurythermy and heliothermy. *Anolis heterodermus* lives in a low thermal quality habitat, using exposed perches, which seems the most efficient thermal microhabitats. We concluded that *A. heterodermus* performed behavioral adjustment for compensating seasonal variation in the environmental thermal costs.

KEYWORDS. Thermal quality, thermoregulatory accuracy, seasonal variation, heliothermy.

RESUMEN. Termorregulación en el lagarto andino *Anolis heterodermus* (Squamata: Dactyloidae) a una alta elevación en la Cordillera Oriental de Colombia. Ambientes con baja calidad térmica, tales como las latitudes extremas o regiones en altas elevaciones, son altamente costosos para los reptiles en términos de termorregulación, por lo cual algunas especies han adquirido adaptaciones fisiológicas o ajustes conductuales para habitar estos ambientes. *Anolis heterodermus* (Duméril, 1851) es un lagarto que habita a altas elevaciones en la región andina. En el presente trabajo se evaluó la termorregulación de una población de esta especie en la cordillera oriental de Colombia durante las épocas húmeda y seca. Se midieron temperaturas corporales (T_b), operativas (T_e) y de preferencia (T_{pref}). Con base en estas variables, se obtuvieron los índices de calidad térmica ambiental ($\bar{d}_e$), exactitud ($\bar{d}_b$) y eficiencia (E) de la termorregulación. No hubo diferencias significativas entre la T_b o $\bar{d}_b$ entre épocas, sexos o edades y tampoco de la T_{pref} entre sexos o edades, pero encontramos diferencias de T_e y $\bar{d}_e$ entre épocas. Los índices sugieren alta exactitud termorreguladora y baja calidad térmica del ambiente, por lo tanto indican que *A. heterodermus* es un termorregulador activo para ambas épocas. El amplio intervalo de T_b y la asociación de la especie a microhábitats con alta radiación solar sugieren euritérmia y heliotermia. *Anolis heterodermus* habita en un ambiente de baja calidad térmica, usando perchas expuestas, las cuales parecen ser los microhábitats más eficientes para termorregular. Concluimos que *A. heterodermus* realiza ajustes conductuales para compensar la variación estacional en los costos térmicos del ambiente.

PALABRAS-CLAVE. Calidad térmica, exactitud termorreguladora, variación estacional, heliotérmia.

Thermoregulation in lizards and other reptiles comprises a set of physiological and behavioral phenomena closely related to the environment and to any several aspects of the biology of these ectotherms (Huey & Stevenson, 1979; Huey, 1982). Active thermoregulation imply the selection of microhabitats that provide optimal or nearly optimal temperature required by individuals for performing their biological activities in an effective way (Pianka, 1986; Pianka & Vitt, 2003). This strategy involves a series of physiological (reproductive state, body size, sex, and in general their physical condition) and ecological (predation or competence by thermal resources) constraints (Adolph, 1990; Smith & Ballinger, 2001). Thus, when costs associated to active thermoregulation are too high, organisms adopt a thermoconformer strategy, which consists in following environmental temperature, which could be far from the optimal temperature required for their optimal performance (Huey, 1974, 1982; Huey & Slatkin, 1976).

High altitude and extreme latitude environments impose important challenges for thermoregulatory activities, due to the extreme low temperature and/or high thermal variance that is typical in these environments (Huey & Webster, 1976; Hertz & Huey, 1981; Hertz, 1981; Ibargüengoytía *et al.*, 2010). Very low environmental temperature, relative to the preferred and/or critical temperature of individuals would decrease the available time needed for organisms to effectively basking and thermoregulate. Thus, lizards from highland environments could face the effects of low temperatures using two strategies as extremes of a continuum: by behavioral adjustments, such as searching more exposed and sunny microsites and reducing activity time (Hertz & Huey, 1981; Hertz, 1981; Gvoždík & Castilla, 2001; Gvoždík, 2002) or by physiological adaptation, such as decreased in the critical temperature minimum values to hold out cold environments (Muñoz *et al.*, 2014). Besides, based on data about thermal biology, Sinervo *et al.* (2010) hypothesized that high elevation reptile species are particularly threatened by climate change, due to their restricted distribution, which would decrease progressively as temperature increase, and as these environments are colonized by competitors or predators from lowlands, pushing up highland species toward an "endless road", at higher elevations.

Both thermoregulatory strategies have been reported in *Anolis* lizards, which is a Neotropical and highly diversified genus that has successfully colonized many different environments (Losos, 2009). Species of this genus has been used as model organisms to design a methodology to characterize thermoregulatory strategy in reptiles (Hertz *et al.,* 1993); a protocol widely used since then (Díaz & Cabezas-Díaz, 2004; Blouin-Demers & Nadeau, 2005; Hitchcock & McBrayer, 2006; Row & Blouin-Demers, 2006; Herczeg *et al.*, 2008). Studies on *Anolis* have showed that thermoregulatory strategy varies among species, elevations and seasons, revealing high behavioral and physiological plasticity for dealing with the challenges imposed by the environment (Huey & Webster, 1975; Hertz & Huey, 1981; Hertz, 1981; Hertz *et al.*, 1993; Muñoz *et al.*, 2014).

Anolis heterodermus (Duméril, 1851) is part of a lineage previously known as *Phenacosaurus* that occupy high elevation environments in the Andes system (above 1,800 m AMSL; Dunn, 1944; Lazell, 1969; Rangel-Ch & Aguilar-P, 1995). *Anolis heterodermus* is a large arboreal lizard (Maximum snout-vent-length [SVL]: males = 85.4 mm, females = 85 mm; Moreno-Arias & Urbina-Cardona, 2013), that inhabits shrubs and trees of Andean and high Andean forests (Dunn, 1944; Osorno-Mesa & Osorno-Mesa, 1946; Lazell, 1969; Miyata, 1983; Moreno-Arias & Urbina-Cardona, 2013; Vargas-Ramírez & Moreno-Arias, 2014). Despite its particularly interesting highland distribution, thermoregulatory strategy has not been studied in this species. Thus, the aim of this paper is to describe the thermoregulation strategy of individuals of *A. heterodermus* from a population at 2,650 AMSL. in the eastern Cordillera of Colombia during both dry and wet seasons.

MATERIALS AND METHODS

We studied a population of *Anolis heterodermus* at north area of Majuy mountains, Tabio municipality, in Cundinamarca, Colombia. This locality was visited at two sites: El Recodo farm (4°55'19.86"N, 74°4'13.96"W) and Tygua Magüe Ecopark (4°55'9.79"N, 74°4'39.11"W, WGS84). This region has two wet seasons, from April to May and from October to November, with annual rainfalls around 850 mm (Cortés, 2003). The vegetation in this region is usually Andean scrubland, or Andean forests at the highest elevations (Cortés, 2003; Moreno-Arias & Urbina-Cardona, 2013).

We carried out this study from April to March 2014, from September to November 2014, and in February 2015. Body temperature data were collected from 9:00 - 16:00 h. Body temperature (T_b) was recorded 30 s after each individual was captured by inserting a K thermocouple connected to a digital thermometer (SE ± 0.6 °C) in the lizard's cloaca. In addition, we recorded their snout-vent length (SVL), and the sex of adults, considering as adults individuals with SVL > 55 mm (Miyata, 1983).

In order to obtain operative temperatures (T_e), we used six empty artificial models (green polyvinylchloride [PVC] pipes, 100 mm length, 127 mm diameter) connected to an external temperature data-loggers (Adolph, 1990; Sinervo *et al.*, 2010). Data-loggers recorded T_e each minute for one week during wet season in 2014, one week during dry season in 2014, and four weeks during the dry season in 2015; only data from 9:00 to 17:00 h were used for the analyses, considering the period of activity previously recorded and literature (Moreno-Arias & Urbina-Cardona, 2013). Models were distributed in potential lizard microhabitats (branches randomly selected between 0 and 2 m), three under direct sun exposition and three under shaded conditions.

Models were previously validated with an adult male lizard (SVL=68.4 mm, 6.5 g). In order to achieve the calibration, lizard, PVC pipe, copper pipe, syringe with water and empty syringe models were kept in a glass terrarium (200 x 400 x 400 mm). Then, we changed the temperature in the terrarium using one 200 W bulb and cooling packs, which were alternated each 10 min during temperature recording. Lizard and models temperatures were recorded for 2.5 h using an USB data-logger, with ultrafine thermocouples adapted to the cloaca of the lizard and inside the models with a micropore tape. PVC model was selected based on the best correlation with lizard body temperature ($R^2 = 0.903$, $n = 300$, $p < 0.05$).

For laboratory phase, we used a subsample of 33 individuals (10 adult males, 11 adult females and 12 juveniles) from the field capture. Lizards were housed in separated terraria (450 x 450 x 450 mm) with natural light conditions. All lizards we provided water and two adult flour beetles (*Tribolium castaneum*) *ad libitum.* In order to estimate the preferred temperature (T_{pref}) interval, we exposed lizards to a vertical thermal gradient (1000 x 500 x 500 mm) divided in four tracks (one track per individual) of 1000 x 250 x 250 mm (Fig. 1). We used a vertical thermal gradient because our study model is a tree lizard that commonly use vertical branches as perches (Moreno-Arias *et al.*, 2010; Moreno-Arias & Urbina-Cardona, 2013). The thermal gradient (18-32°C) was created with 200 W bulbs in the upper extreme and cooling gels at the base. We provided tree upright branches of 1 m height and perch diameter, according to species perch use (16 ± 2.8 mm; 13.4-20 mm diameter) inside each vertical sections of the gradient. This perch device allowed lizards to move up and down (Fig. 1).

Additionally, since tree branches provided to record T_{pref} in these populations might include perches with different diameters, we posteriorly evaluated possible influence of perch characteristics (diameter, slope and surface texture) on lizard T_{pref}. For this we recorded data of adult individuals from two localities: Chicaque Natural Park, municipality of San Antonio del Tequendama (4°36’55.18”N, 74°18’44.14”W, 2,200 AMSL, n = 17) and Ecological Park Matarredonda, municipality of Choachi (4°33’36.07”N, 73°59’58.92”W, 3,350 AMSL, n = 16), in Cundinamarca, Colombia, in April and May 2016. We compared T_{pref} of lizards exposed to thermal gradient and using different perch diameters (10 mm, 20 mm diameter and tree branch or heterogeneus diameter), perch surfaces (tree twig branches *vs.* balsa wood branches covered with angeo surface), and perch slope (vertical *vs.* horizontal gradient). These comparisons were performed among perches within same locality, and since we did not observe any differences of T_{pref} recorded under these different perch characteristics (see results), we pooled data per locality and compared T_{pref} among Chicaque and Matarredonda localities and the three localities: Chicaque, Tabio and Matarredonda. Kruskal-Wallis and *t* tests were used in these comparisons.

Ultrafine thermocouples, connected to an USB data-logger, were adapted to the cloaca of each lizard with the help of micropore tape. Preferred temperature was recorded each minute during two hours. Each lizard remained in the gradient for 30 minutes before to temperature recording for acclimation to experimental conditions. Lizards were ventrally marked with a temporal number using a permanent marker pen and released in the field after preferred body temperature estimation. Preferred temperature range was estimated for each individual including 25-75% interquartile data (Hertz *et al.*, 1993).

We estimated three biophysical indexes based on T_b, T_e and T_{pref} according to Hertz *et al.* (1993): index of thermoregulation accuracy ($\bar{d}_b$), environmental thermal quality ($\bar{d}_e$), and thermoregulatory efficiency (E). Differences between T_b or T_e and T_{pref} (d_b and d_e, respectively) were estimated with the 25-75% quartiles of all T_{pref} data as follows: if T_b and T_e are lower than T_{pref}, d_b and d_e are the deviations between T_b or T_e and 25% T_{pref} quartile value; if T_b and T_e are higher than T_{pref}, d_b or d_e are the deviations between T_b or T_e and 75% T_{pref} quartile value; finally, if T_b or T_e are inside 25-75% quartile T_{pref} values, d_b or d_e are equal to zero. Average values of individual´s d_b and model’s d_e were considered as indexes for the population; values of $\bar{d}_b$ and $\bar{d}_e$ closer to zero would correspond to a high accuracy of thermoregulation and environment thermal quality, respectively. Thermoregulatory efficiency index E was estimated using the formula ($E = 1 - [\bar{d}_b/\bar{d}_e]$); values closer to 1 would correspond to active thermoregulation, those closer to zero would correspond to thermoconformism, while negative values would be interpreted as individuals avoiding good quality thermic microsites due to high costs imposed by other ecological pressures (Hertz *et al.*, 1993; Blouin-Demers & Nadeau, 2005).

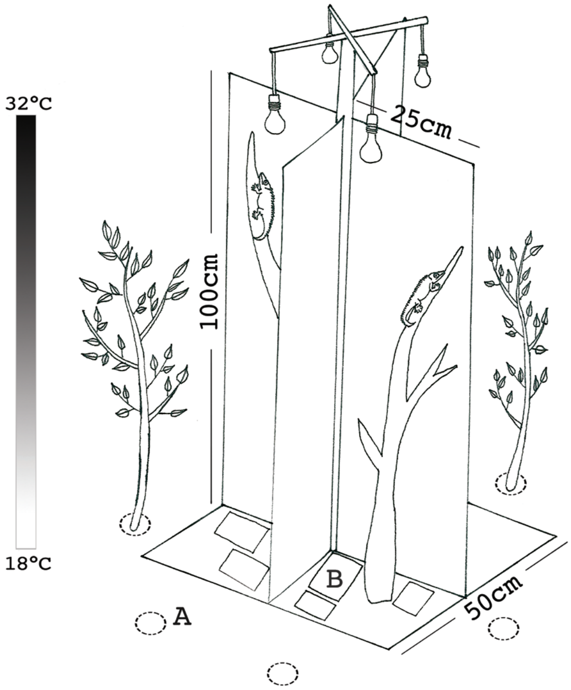

Fig. 1. Thermal gradient scheme: (A) shrubs to create a suitable habitat for lizards in the gradient; (B) cooling packs.

Variation of body temperature (T_b) and accuracy of thermoregulation ($\bar{d}_b$) was evaluated between sexes in adults, age stage (adults *vs*. juveniles), and seasons (wet *vs*. dry). Additionally, we compared T_{pref} between sexes in adults and seasons. We previously analyzed if T_b and T_{pref} were related to body size (SVL), through linear regression. If significantly regressed, residuals of the regression were used to compare these variables between adults and juveniles. Data from all individuals were included in indexes estimation, since values for juveniles and adults were not statistically different (see results). A single averaged value of T_{pref} per individual was used in all tests. Operative temperatures (T_e) and environmental thermal quality ($\bar{d}_e$) were compared between seasons. In addition, operative temperatures were compared between microhabitat types (sunny vs. shaded microhabitats). Mann-Whitney and Student’s *t* test were used in these comparisons. Some data that could not meet parametric assumptions were normalized using square root transformation allowing the use of parametric tests. When the transformation was not sufficient to normalize data non-parametric tests were performed. Statistical analyses were performed using StatSoft, Inc. (2007) STATISTICA, version 8.0 and graphics were made using SigmaPlot (Systat Software, San Jose, CA).

RESULTS

Body temperature in the field was similar between seasons ($t = 0.293$, $n = 96$, $p = 0.77$, Tab. I.), sex ($U = 417$, $z = 0.459$, $n = 60$, $p = 0.645$) and age ($t = 1.398$, $n = 98$, $p = 0.165$). Similarly, T_{pref} did not vary between the sexes ($t = -0.859$, $n = 21$, $p > 0.401$) and seasons ($U = 65$, $z = -1.718$, $n = 33$, $p = 0.086$). Unlike T_b ($R^2 = 0.026$, $n = 84$, $p = 0.144$), T_{pref} was related to individual size ($R^2 = 0.197$, $n = 21$, $p = 0.0435$). However, residuals of the regression concerning to T_{pref} and SVL did not differ between juvenile and adult individuals ($t = -0.144$, $n = 21$, $p = 0.887$).

Perch characteristics did not influence T_{pref} within both, Chicaque and Matarredonda localities: a) perch diameter (Chicaque: $H = 4.132$, $n = 13$, $p = 0.127$; Matarredonda: $H = 0.609$, $n = 13$, $p = 0.737$), b) perch surfaces (Chicaque: $t = -0.555$, $n = 17$, $p = 0.587$; Matarredonda: $t = -0.81$, $n = 16$, $n = 0.732$) and c) perch slope (Chicaque: $t = 1.679$, $n = 10$, $p = 0.131$; Matarredonda: $t = -1.021$, $n = 10$, $p = 0.337$). Also, pooled data of T_{pref} did not vary between these two localities ($t = 1.291$, $n = 33$, $p = 0.206$). Finally, T_{pref} did not vary between Chicaque, Tabio and Matarredonda localities ($H = 2.442$, $n = 54$, $p = 0.295$).

Operative temperatures (T_e) were different between seasons ($U = 2.79 \times 10^9$, $z = -112.3$, $n = 125500$, $p < 0.05$) and between sunny and shaded microhabitats ($U = 5.28 \times 10^9$, $z = -795.1$, $p < 0.05$). In both seasons, operative temperatures were usually below T_{pref}, particularly during the wet season (Fig. 2). Besides, dry season and sunny microhabitats exhibited the highest operative temperatures (Tab. I., Fig. 2), especially around 11:00 to 13:00 h, corresponding with the activity peak of the species, around 10:00 to 12:00 h (Fig. 3). Additionally, T_b during the day, especially between 10:00 and 13:00, was within or close to T_{pref} interval (Fig. 3).

As well as T_b, thermoregulatory accuracy ($\bar{d}_b$) was similar between seasons ($U = 504.5$, $z = -1.623$, $n = 84$, $p > 0.104$, Tab. II.) sexes ($U = 329$, $z = 0.128$, $n = 52$, $p > 0.898$) and ages ($t = 0.427$, $n = 84$, $p = 0.67$). In contrast, thermal quality index ($\bar{d}_e$) was different between seasons ($U = 7.235 \times 10^9$, $z = -19.16$, $n = 125500$, $p < 0.05$, Tab. II.), being the thermal environmental quality slightly better for *A. heterodermus* in the dry season. These values suggest low thermal quality for *A. heterodermus*, since T_e's were different of T_{pref} (Tab. I; Fig. 2). Nevertheless, thermoregulatory efficiency indexes (E) were relatively high, especially in wet season (Tab. II).

DISCUSSION

Anolis heterodermus exhibited an average T_b lower than other anole species distributed under 1,130 m AMSL (Sinervo *et al.*, 2010, supplementary material), and very similar to the T_b recorded for species distributed at higher elevations (1,130-2,200 m) in Puerto Rico and La Hispaniola, such as *A. cristatellus*, *A. gundlachi*, *A. roquet* and *A. cybotes* group (Hertz & Huey, 1981; Hertz, 1981; Hertz *et al.*,

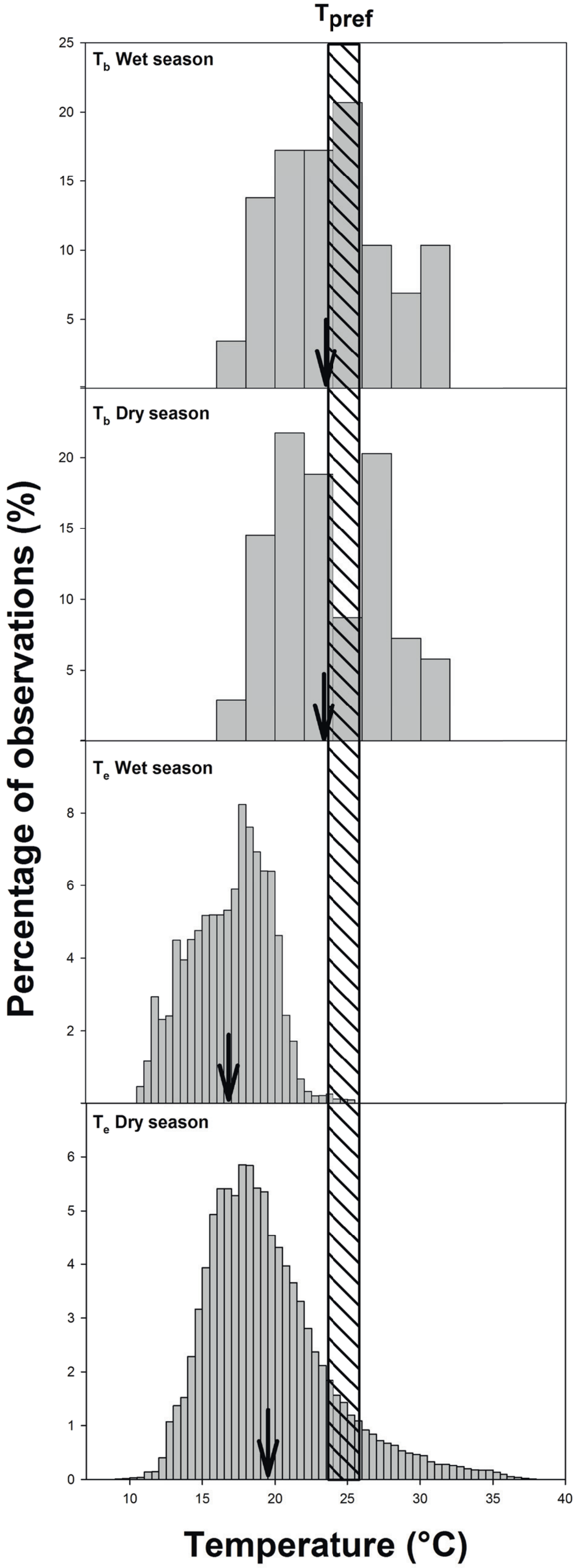

Fig. 2. Frequency of body (T_b) and operative (T_e) temperatures during wet and dry season in *Anolis heterodermus* (Duméril, 1851). Average values are shown by black arrows. Striped area corresponds to averaged preferred temperature (T_{pref}) interval for both seasons.

1993). Similarly, T_{pref} for this species is lower than that recorded in other anole species (*A. cooki*: 29.6-31.6°C; *A. cristatellus*: 28.1-30.9°C; *A. unifilis*: 28.9-30.9°C; *A. nebulosus*: 34.4°C; Hertz *et al.*, 1993; Lara-Resendiz *et al.*, 2013b; Woolrich-Piña *et al.*, 2015), but it is very similar to T_{pref} recorded in *A. gundlachi* (24.3-26.1°C) at 1,130 m AMSL in Puerto Rico (Hertz *et al.*, 1993). This can be explained since *A. gundlachi* is a thermoconformer species that has low operative temperature and is distributed in a high quality habitat. It suggested that it has physiological adaptations to high altitude (Hertz, 1981; Hertz *et al.*, 1993).

Apparently, highland *Anolis* species has low T_b's contrast to lowland species (Sinervo *et al.*, 2010, supplementary material; Muñoz *et al.*, 2014). Similarly, *Sceloporus graciosus*, at 2,580 m AMSL has a lower T_b than its conspecific *S. occidentalis*, at 1,250 ASML. and both species at 2,230 m ASML have similar T_b (Adolph, 1990). In contrast, Marquet *et al.* (1989), observed similar T_b among four species of *Liolaemus* lizards distributed through an altitudinal gradient. However, at intraspecific level, T_b is similar or slightly low despite altitudinal changes in several *Anolis* lizards studies (Hertz & Huey, 1981; Hertz, 1981, 1992; Hertz *et al.*, 1993; Muñoz *et al.*, 2014). Other lizards like *Podarcis tiliguerta*, *Psammodromus algirus*, *Sceloporus jarrovi* and *Zootoca vivipara* also exhibit the former trend (Van Damme *et al.*, 1989; Van Damme *et al.*, 1990; Díaz, 1997; Gvoždík, 2002). Similarly, at high latitudes *Phrynosoma douglassi* populations have low T_b with respect to other populations (Christian, 1998).

In the other hand, inter- and intraspecific T_{pref} in lizards is highly conservative (Huey & Bennet, 1987; Van Damme *et al.*, 1990; Hertz *et al.*, 1993; Díaz, 1997; Labra, 1998; Gvoždík & Castilla, 2001; Gvoždík, 2002; Medina *et al.*, 2009). However, interspecific variation in T_{pref} has been observed in Australian geckos and some Chilean *Liolaemus* lizards (Angilletta & Werner, 1998; Labra, 1998), as well as variation in *Takydromus septentrionalis* over a latitudinal gradient (Du, 2006). In *A. heterodermus* T_{pref} seems highly conserved between localities, sexes, ages and seasons; however, we found that individuals from Tabio exhibited wide range of T_{pref} (19.1-30.2°C, = 24.6 ± 3.2°C). High individual variation in T_{pref} is not related to heterogeneity in perch characteristics (diameter, slope or surface) in the thermal gradient. It has been observed that variation in perch selection occurs in *Anolis* species, and that use of perch with different characteristics affects individual performance in escape behavior (Scott *et al.*, 1976; Losos & Irschick, 1996); however, it seems that individuals of *A. heterodermus* in laboratory conditions choose temperature rather than

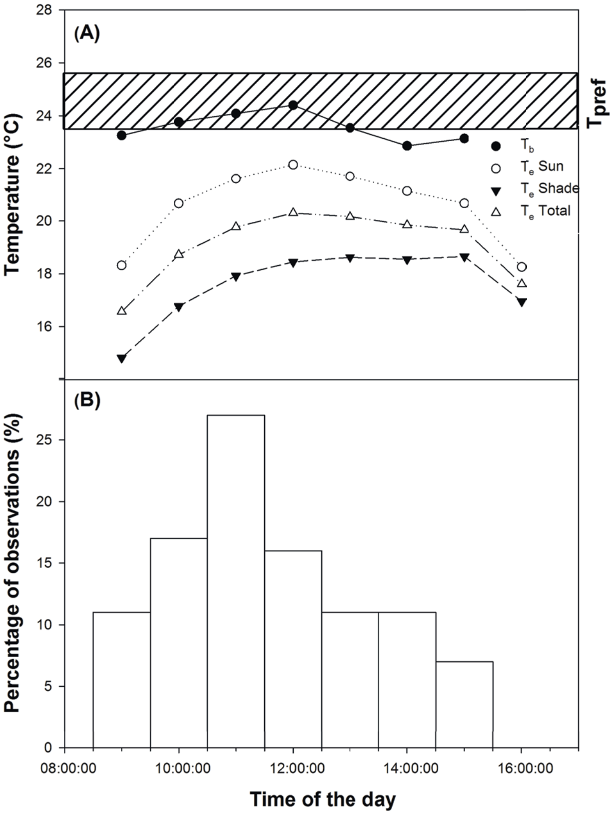

Fig. 3. (A) Average hourly variation of body temperature (T_b) and operative temperatures (T_e) of light exposed, shaded and all models in function of time of the day. Striped area corresponds to preferred temperature interval. (B) Daily activity pattern of *Anolis heterodermus* (Duméril, 1851).

Tab. I. Body (T_b), operative (T_e) and preferred (T_{pref}) temperatures at wet and dry season, and pooled data of both seasons. Sunny and shaded microhabitat data for operative temperatures are shown.

Season	T_b (°C)		T_e (°C)					T_{pref} (°C)	
	Mean ± SD	n	Sunny	Shaded		Total		Mean ± SD	n
			Mean ± SD	Mean ± SD	n	Mean ± SD	n		
Dry season	23.7 ± 3.6 16.6-31.9	69	21.2 ± 4.6 9.2-38.4	17.9 ± 3.0 8.7-37.8	52220	19.5 ± 4.2 8.7-38.4	104440	25.3 ± 3.1 19.5-30.2	24
Wet season	23.9 ± 3.9 17.9-31.7	29	17.6 ± 2.8 10.5-26.5	16.1 ± 2.4 10.6-25.1	10532	16.8 ± 2.7 10.5-26.5	21064	22.7 ± 2.9 19.1-27.1	8
Both seasons	23.8 ± 3.7 16.6-31.9	98	20.6 ± 4.6 9.2-38.4	17.6 ± 3.0 8.7-37.8	62752	19.1 ± 4.1 8.7-38.4	125504	24.6 ± 3.2 19.1-30.2	33

Tab. II. Preferred temperature (T_{pref}) range, index of thermoregulation accuracy ($\bar{d}_b$), environmental thermal quality ($\bar{d}_e$), and thermoregulatory efficiency (E) at each season and pooled data of both seasons.

Season	T_{pref} range (25-75%) (°C)	$\bar{d}_b$ (°C) ± SD	$\bar{d}_e$ (°C) ± SD	E
Dry season	24.1-26.4	2.2 ± 1.6	4.83 ± 2.9	0.54
Wet season	21.6-23.8	2.25 ± 2.1	6.66 ± 2.7	0.66
Both seasons	23.5-25.7	2.21 ± 1.8	5.14 ± 2.9	0.57

perch characteristics. However, we do not know if perch selection occurs in the field, and if this selection is driven by temperature or other perch characteristics. Then, we cannot explain what determines this wide plasticity in T_{pref} between individuals of this population.

Thus, lizard thermoregulation at high altitudes could be explained by two non-mutually exclusive hypotheses: (1) by behavioral responses to the variation in environmental temperature to compensate the effects of elevation on the thermal environment (HERTZ & HUEY, 1981; HERTZ, 1981, 1992; HERTZ *et al*., 1993; SMITH & BALLINGER, 1994; GVOŽDÍK, 2002) and (2) by physiological adaptation to low temperatures at high elevations (HERTZ, 1981; VIDAL *et al.*, 2008; IBARGÜENGOYTÍA *et al.*, 2010; MUÑOZ *et al*., 2014). Both hypotheses are supported by intraspecific evaluation of T_b and T_{pref} in populations at different altitudinal distribution in *Anolis* (HERTZ & HUEY, 1981; HERTZ, 1981,1992; HERTZ *et al*., 1993; MUÑOZ *et al*., 2014). However, we did not evaluate if *Anolis heterodermus* thermal strategy varies through its elevational range, but given that this species occupies localities above 1,600 m ASML, it would be interesting to examine the hypothesis of locally adaptive thermal strategies (behavioral or physiological) over an altitudinal gradient.

In contrast to other lizard species (HERTZ *et al.*, 1993; CHRISTIAN & BEDFORD, 1995, 1996; DÍAZ & CABEZAS-DÍAZ, 2004), T_b in *Anolis heterodermus* did not vary between seasons, probably due to the high within variation observed among individuals, and consequent wide T_b range (16.6-31.9°C). This observation suggests that *A. heterodermus* behaves like a eurythermic organism, with a broad range of optimal temperature. However, this hypothesis requires further research through evaluation of performance and temperature relationship (VAN BERKUM, 1986; HUEY & BENNET, 1987). Alternatively, the explanation might be related to behavioral adjustments in wet season to compensate ecological costs for low quality thermal environment (CHRISTIAN & BEDFORD, 1995, 1996; DÍAZ & CABEZAS-DÍAZ, 2004), which is consistent with our findings.

Seasonal variation of operative temperature of *Anolis heterodermus* is similar to the results reported in previous other studies, where lowest T_e were observed during the winter periods or wet seasons (HERTZ *et al.*, 1993; CHRISTIAN & BEDFORD, 1995, 1996; DÍAZ & CABEZAS-DÍAZ, 2004). Operative temperatures were usually below T_b, revealing the poor thermal quality of the environment ($\bar{d}_e$) for this species, particularly during the wet season. However, the variable T_b observed within each season was always inside the T_{pref} range, even during the wet season. Thus, accurate thermoregulation ($\bar{d}_b$) seems to have occurred in this species in spite of the low thermal quality of the environment. This suggests that anole lizards from this population exhibit behavioral adjustment to maintain T_b close to its T_{pref} range, particularly during the wet season. A similar strategy was described in *Podarcis melisellensis*, *P. murallis* and *Phyllodactylus bordai* (GRBAC & BAUWENS, 2001; LARA-RESENDIZ *et al*., 2013a). These results reveal that in contrast with the cost-benefit model for thermoregulation proposed by HUEY & SLATKIN (1976), *A. heterodermus* exhibit active thermoregulatory behavior even when the cost are higher (low quality environment). These results agree with those of BLOUIN-DEMERS & NADEAU (2005), which included several squamates; these authors suggest that if lizards do not behaviorally adjust in these high cost environments; their survival probabilities would be reduced.

Despite this low thermal quality, values of T_e closer to T_{pref} were observed in models exposed to sunlight, especially in midday hours, in agreement with the thermoregulatory strategy and activity pattern found in this species, and showing a heliothermic behavior for it. This also suggests that appropriate thermal microhabitats for *A. heterodermus*, consist of exposed perches at bordering vegetation and high stratum in the inner of each patch (1-2 m) (MORENO-ARIAS *et al.*, 2010; MORENO-ARIAS & URBINA-CARDONA, 2013).

High elevation species exhibit higher extinction risk under climate change scenarios, and such vulnerability is usually assesed when observing T_e values over T_{pref} during most of the day (SINERVO *et al.*, 2010). However, in this studied population of *A. heterodermus*, operative temperatures (T_e) were mostly below T_{pref} through the day, suggesting that at least in this population, an increase in air temperature (which would affect T_e temperatures), would not exceed their thermal physiological threshold. Thus, it would not be immediately affected by climate change. However, this result must be taken with caution. This species should be evaluated using ecophysiological models of extinction risk, as proposed by SINERVO *et al.* (2010) for a more reliable conclusion about threatening.

In conclusion, *Anolis heterodermus* can be considered as a heliotermic, potentially eurythermic lizard. It inhabits a low thermal quality environment and exhibits active thermoregulation. Thus, it had to adjust behaviorally to compensate seasonally variation in environmental thermal costs. Evaluation of thermal ecology of this species through an altitudinal gradient and the description of its performance vs. temperature relationship would provide a clearer panorama to estimate the potential impact of environmental temperature increasing on *Anolis heterodermus* populations, as expected in the coming years due to global warming.

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