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<sub>b</sub>), operative temperatures (T<sub>e</sub>) and preferred temperatures (T<sub>pref</sub>). Based on these data, we obtained accuracy (d̄), environmental thermal quality (d̄) and efficiency of thermoregulation (E) indexes. There were no significant differences of T<sub>pref</sub> between seasons, sexes, ages, and for T<sub>pref</sub> between sexes or ages, but we found differences in T<sub>b</sub> and T<sub>e</sub> between seasons. The indexes suggested high thermoregulatory accuracy, low environmental quality and indicated that *A. heterodermus* was an active thermoregulator in both seasons. Broad ranges of T<sub>b</sub> and the species association with microhabitats with high solar radiation suggest eurythermy and heliotermia. *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, heliotermia.

**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<sub>b</sub>), operativas (T<sub>e</sub>) y de preferencia (T<sub>pref</sub>). Con base en estas variables, se obtuvieron los índices de calidad térmica ambiental (d̄), exactitud (d̄) y eficiencia (E) de la termorregulación. No hubo diferencias significativas entre la T<sub>b</sub> o T<sub>e</sub> entre épocas, sexos o edades y tampoco de la T<sub>pref</sub> entre sexos o edades, pero encontramos diferencias de T<sub>b</sub> y T<sub>e</sub> 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<sub>b</sub> y la asociación de la especie a microhabitats con alta radiación solar sugieren eurístermia y heliotermia. *Anolis heterodermus* habita en un ambiente de baja calidad térmica, usando perchas expuestas, las cuales parecen ser los microhabitats 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, heliotermia.

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...
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Thermoregulation in the Andean lizard *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 Ancestral 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 m 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 (Tb) 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 (Te), 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 Te 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 microprobe tape. PVC model was selected based on the best correlation with lizard body temperature (R² = 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 (Tmax) 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)

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was estimated using the formula 

$$E = 1 - \left[ \bar{d}_b / \bar{d}_e \right];$$

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).

Variation of body temperature ($T_b$) and accuracy of thermoregulation ($d_b$) was evaluated between sexes in adults, age stage (adults vs. juveniles), and seasons (wet vs. dry). Additionally, we compared $T_{perf}$ between sexes in adults and seasons. We previously analyzed if $T_b$ and $T_{perf}$ 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 $T_{perf}$ per individual was used in all tests. Operative temperatures ($T_i$) and environmental thermal quality ($d_i$) were compared between seasons. In addition, operative temperatures were compared between microhabitats (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 x 10^9, z = -112.3, n = 125500, p < 0.05) and between sunny and shaded microhabitats (U = 5.28 x 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_e, thermoregulatory accuracy (d_{\bar{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 (d_{\bar{e}}) was different between seasons (U = 7.235 x 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_prev 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.,...
Similarly, T\textsubscript{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-Rezendê et al., 2013b; Woolrich-Piña et al., 2015), but it is very similar to T\textsubscript{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\textsubscript{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\textsubscript{b} than its conspecific S. occidentalis, at 1,250 ASML and both species at 2,230 m ASML have similar T\textsubscript{b} (Adolph, 1990). In contrast, Marquet et al. (1989), observed similar T\textsubscript{b} among four species of Liolaemus lizards distributed through an altitudinal gradient. However, at intraspecific level, T\textsubscript{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, Psammomodromus 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\textsubscript{b} with respect to other populations (Christian, 1998).

In the other hand, inter- and intraspecific T\textsubscript{pref} in lizards is highly conservative (Huey & Bennett, 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\textsubscript{pref} has been observed in Australian geckos and some Chilean Liolaemus lizards (Angilletta & Werner, 1998; Labra, 1998; Gvoždík & Castilla, 2001; Gvoždík, 2002; Medina et al., 2009). This can be explained as variation in T\textsubscript{pref} seems highly conserved among localities, sexes, ages and seasons; however, we found that individuals from Tabo exhibited wide range of T\textsubscript{pref} (19.1-30.2°C, = 24.6 ± 3.2°C). High individual variation in T\textsubscript{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 & Irshick, 1996); however, it seems that individuals of A. heterodermus in laboratory conditions choose temperature rather than

![Thermoregulation in the Andean lizard Anolis heterodermus...](image)

Tab. I. Body (T\textsubscript{b}), operative (T\textsubscript{e}) and preferred (T\textsubscript{pref}) temperatures at wet and dry season, and pooled data of both seasons. Sunny and shaded microhabitat data for operative temperatures are shown.

| Season     | Mean ± SD | n |
|------------|-----------|---|
| Dry season | 23.7 ± 3.6 | 69 |
|            | 16.6-31.9 |   |
| Wet season | 23.9 ± 3.9 | 29 |
|            | 17.9-31.7 |   |
| Both seasons | 23.8 ± 3.7 | 98 |
|            | 16.6-31.9 |   |

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

| Season     | T\textsubscript{pref} range (25-75%) | \(d\) (°C) ± SD | \(\overline{d}\) (°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 \( T_{\text{pref}} \) 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 \( T_{\text{pref}} \) 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 & Bennett, 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 \( T_b \) 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 \((\delta_e)\) for this species, particularly during the wet season. However, the variable \( T_b \) observed within each season was always inside the \( T_{\text{pref}} \) range, even during the wet season. Thus, accurate thermoregulation \((\delta_e)\) 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 \( T_{\text{pref}} \) 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 \( T_b \) closer to \( T_{\text{pref}} \) 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 heliothermal 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 assessed when observing \( T_b \) values over \( T_{\text{pref}} \) during most of the day (Sinervo et al., 2010). However, in this studied population of A. heterodermus, operative temperatures \((T)\) were mostly below \( T_{\text{pref}} \) through the day, suggesting that at least in this population, an increase in air temperature (which would affect \( T_b \) 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 heliothermic, 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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REFERENCES

Adolph, S. C. 1990. Influence of behavioral thermoregulation on microhabitat use by two Sceloporus lizards. Ecology 71(1):315-327.

Anigletta, M. J. & Werner, Y. L. 1998. Australian geckos do not display diel variation in thermoregulatory behavior. Copeia 1998(3):736-742.

Blouin-Demers, G. & Nadeau, P. 2005. The cost-benefit model of thermoregulation does not predict lizard thermoregulatory behavior. Ecology 86(3):560-566.
CHRISTIAN, K. A. 1998. Thermoregulation by the short-horned lizard (*Phrynosoma douglassii*) at high elevation. *Journal of Thermal Biology* 23(6):395-399.

CHRISTIAN, K. A. & BEDFORD, G. S. 1995. Seasonal changes in thermoregulation by the frillneck lizard, *Chlamydosaurus kingii*, in tropical Australia. *Ecology* 76(1):124-132.

CHRISTIAN, K. A. & BEDFORD, G. 1996. Thermoregulation by the spotted tree monitor, *Varanus scalaris*, in the seasonal tropics of Australia. *Journal of Thermal Biology* 21(2):67-73.

CORTÉS, S. P. 2003. Estructura de la vegetación arbórea y arbustiva en el costado oriental de la Serranía de Chía (Cundinamarca, Colombia). *Caldasia* 25(1):119-137.

DÍAZ, J. A. 1997. Ecological correlates of the thermal quality of an ectotherm's habitat: a comparison between two temperate lizard populations. *Canadian Journal of Zoology* 75(1):79-89.

DIAZ, J. A. & CABEZAS-DIAZ, S. 2004. Seasonal variation in the contribution of different behavioural mechanisms to lizard thermoregulation. *Functional Ecology* 18(6):867-875.

DU, W. 2006. Preferred body temperature and thermal tolerance of the northern grass lizard *Takydromus septentrionalis* from localities with different longitudes. *Acta Zoológica Sinica* 52(3):478-482.

DUNN, E. R. 1944. The lizard genus *Phacocercus*. *Caldasia* 3(11):57-62.

GEBIACI, I. & BAUCZKIS, D. 2001. Constraints on temperature regulation in two sympatric *Podarcis* lizards during autumn. *Copeia* 2001(1):78-186.

GVOŽDIK, L. 2002. To heat or to save time? Thermoregulation in the lizard *Zootoca vivipara* (Squamata: Lacertidae) in different thermal environments along an altitudinal gradient. *Canadian Journal of Zoology* 80(3):479-492.

GVOŽDIK, L. & CASTILLA, A. M. 2001. A comparative study of preferred body temperatures and critical thermal tolerance limits among populations of *Zootoca vivipara* (Squamata: Lacertidae) along an altitudinal gradient. *Journal of Herpetology* 35(3):486-492.

HERCZEK, G.; HERRERO, A.; SAAREKIVI, J.; GONDA, A.; JÄNTTI, M. & MERILÄ, J. 2008. Experimental support for the cost–benefit model of lizard thermoregulation: the effects of predation risk and food supply. *Ecologia* 155(1):1-10.

HERZ, P. E. 1981. Adaptation to altitude in two West Indian anoles (Reptilia). *Journal of Zoology* 195(1):25-37.

HERZ, P. E. 1992. Temperature regulation in Puerto Rican *Anolis* lizards: a field test using null hypotheses. *Ecology* 73(4):1405-1417.

HERZ, P. E. & HUX, R. B. 1981. Compensation for altitudinal changes in the thermal environment by some *Anolis* lizards on Hispaniola. *Ecology* 62(3):515-521.

HERZ, P. E.; HUX, R. B. & STEVENSON, R. D. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *The American Naturalist* 142(5):796-818.

HITCHCOCK, M. A. & McBRAYER, L. D. 2006. Thermoregulation in nocturnal ectotherms: seasonal and intraspecific variation in the Mediterranean gecko (*Hemidactylus turcicus*). *Journal of Herpetology* 40(2):185-195.

HUX, R. B. 1974. Behavioral thermoregulation in lizards: importance of associated costs. *Science* 184(4140):1001-1003.

HUX, R. B. 1982. Temperature, physiology, and ecology of reptiles. In: GANS, C. & POUGH, F.H. eds. *Biología de la Reptilia*. New York, Academic Press, v. 12, p. 25-74.

HUX, R. B. & BENNETT, A. F. 1987. Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. *Evolution* 41(5):1098-1115.

HUX, R. B. & SLONNEN, M. 1976. Cost and benefits of lizard thermoregulation. *Quarterly Review of Biology* 51(3):363-384.

HUX, R. B. & STEVENSON, R. D. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *American Zoologist* 19(1):357-366.

HUX, R. B. & WEBSTER, T. P. 1975. Thermal biology of a solitary lizard: *Anolis marmoratus* of Guadeloupe, Lesser Antilles. *Ecology* 56(2):445-452.

HUX, R. B. & WEBSTER, T. P. 1976. Thermal biology of *Anolis* lizards in a complex fauna: the *Cristatellus* group on Puerto Rico. *Ecology* 57(5):985-994.

IBARGUENGÜÍTIA, N. R.; MEDINA, S. M.; FERNÁNDEZ, J. B.; GUTIÉRREZ, J. A.; TAPPARI, F. & SCOLARO, A. 2010. Thermal biology of the southernmost lizards in the world: *Liolema sarmientoi* and *Liolema magellanicus* from Patagonia, Argentina. *Journal of Thermal Biology* 35(1):21-27.

LABRA, A. 1998. Selected body temperatures of seven species of Chilean *Liolema* lizards. *Revista Chilena de Historia Natural* 71:349-358.

LARA-RESENDIZ, R. A.; ARENAS-MORENO, D. M. & MÉNDEZ-DE LA CRUZ, F. R. 2013a. Termorregulación diurna y nocturna de la lagartija *Phyllodactylus bordoi* (Gekkota: Phyllodactylidae) in una región semiárida del centro de México. *Revista Chilena de Historia Natural* 86(2):127-135.

LARA-RESENDIZ, R. A.; DÍAZ DE LA VEGA-PÉREZ, A. H. & CHARRUAU, P. 2013b. *Anolis uniformis* (Lesser Scaly Anole). Selected body temperature. *Herpetological Review* 44(4):662.

LAZELL, J. D. 1969. The genus *Phenacosaurus* (Sauria: Iguanidae). *Breviora* (325):1-24.

LOSOS, J. B. 2009. Lizards in an evolutionary tree: ecology and adaptive radiation of anoles. Berkeley, University of California Press. 507p.

LOSOS, J. B. & ISCHICK, D. J. 1996. The effect of perch diameter on escape behaviour of *Anolis* lizards: Laboratory predictions and field tests. *Animal Behaviour* 51(3):593-602.

MARTÍNEZ-MÉNDEZ, N.; CALDERÓN-ESPINOZA, M. L.; MEZA-LÁZARO, R. N.; GAISSEN, H.; AVILA, L. J.; MORANDO, N.; DE LA RIVA, I. J.; SEPÚLVEDA, P. V.; DUARTE ROCHA, C. F.; IBARGUENGÜÍTIA, N.; AGUILAR-PÉREZ, C. & JÍNGEZ, J. M. 2014. Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328(5980):894-899.

SMITH, G. R. & BALLINGER, R. E. 1994. Temperature relationships in the high-altitude viviparous lizard, *Sceloporus jarrovi*. *The American Midland Naturalist* 131(1):181-189.
Thermoregulation in the Andean lizard Anolis heterodermus...

Smith, G. R. & Ballinger, R. E. 2001. The ecological consequences of habitat and microhabitat use in lizards: a review. Contemporary Herpetology 3:1-37.

Van Berkum, F. H. 1986. Evolutionary patterns of the thermal sensitivity of sprint speed in Anolis lizards. Evolution 40(3):594-604.

Van Damme, R.; Bauwens, D.; Castilla, A. M. & Verheyen, R. F. 1989. Altitudinal variation of the thermal biology and running performance in the lizard Podarcis tiliguerta. Oecologia 80(4):516-524.

Van Damme, R.; Bauwens, D. & Verheyen, R. F. 1990. Evolutionary rigidity of thermal physiology: the case of the cool temperate lizard Lacerta vivipara. Oikos 57(1):61-67.

Vargas-Ramírez, M. & Moreno-Arias, R. A. 2014. Unknown Evolutionary Lineages and Population Differentiation in Anolis heterodermus (Squamata: Dactyloidae) from the Eastern and Central Cordilleras of Colombia Revealed by DNA Sequence Data. South American Journal of Herpetology 9(2):131-141.

Vidal, M. A.; Ortiz, J. C. & Labra, A. 2008. Intraspecific variation in a physiological thermoregulatory mechanism: the case of the lizard Liolepis tetra (Liolepidinae). Revista Chilena de Historia Natural 81:171-178.

Woolrich-Piña, G. A.; Smith, G. R.; Lemos-Espinal, J. A. & Ramírez-Silva, J. P. 2015. Do gravid female Anolis nebulosus thermoregulate differently than males and non-gravid females? Journal of Thermal Biology 52:84-89.