



Thermal ecophysiology of *Basiliscus galeritus* (Squamata: Corytophanidae) in two populations at different altitudes: Does the crest participate actively in thermoregulation?

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ABSTRACT

Thermoregulation is a critical process for ectotherms as non-avian reptiles, since their vital physiological processes depend on it. These organisms have a temperature range where their physiological processes are more efficient, this range is usually a requirement set phylogenetically even though they vary in the use of habitats. This research compares the thermal ecophysiology of *Basiliscus galeritus* (western basilisk) in two populations with altitudinal differences in the northwestern of Ecuador. The results suggest that the difference of altitude between the two locations (500 m) influences the thermal ecophysiology of the species since the body temperature (T_b), operative temperature (T_e) and preferred body temperature (T_{set}) showed significative differences. Furthermore, *B. galeritus* obtains its T_b through heliothermy and it behaves as an active thermoregulator. On the other hand, the crest temperatures reach higher values than their T_{set} , the results suggested that the species uses the crest as an alternative to regulate its body temperature when exceeding its T_{set} . Besides, this thermoregulatory behavior has been suggested only in some extinct synapsids.

1. Introduction

Non-avian reptiles, as all ectothermic organisms, depend on an adequate environmental temperature to carry out their vital activities (Huey, 1982; Shine and Kearney, 2001). However, when the body temperature of the organisms is outside the range of their preferred temperatures, their physiological processes may be slower or not take place at all (Prieto and Whitford, 1971).

Thermal conditions and body temperature of species may vary geographically or between habitats (Huey and Stevenson, 1979). This reflects on the differences in the thermoregulation process of tropical forest populations and those that inhabit open areas (Huey, 1974; Ruibal, 1961; Ruibal and Philobosian, 1970). On the other hand, it has been

considered that phylogenetically close species tend to maintain similar thermal preferences, even when they occupy different habitats or regions. This is known as the Bogert hypothesis (Bogert, 1949) and has been addressed directly and indirectly in some reptile families: Eublepharidae (Dial, 1978), Phrynosomatidae (Soulé, 1963; Prieto and Whitford, 1971; Pianka and Parker, 1975; Adolph, 1990; Andrews, 1998; Grover, 1996; Lara-Reséndiz et al., 2015; Woolrich-Piña et al., 2012), Scincidae (Youssef et al., 2008), Teiidae (Schall, 1977; Woolrich-Piña et al., 2011; Díaz de la Vega-Pérez et al., 2013), Xantusiidae: (Arenas-Moreno et al., 2018), and Xenosauridae: (García-Rico et al., 2015). However, few studies compare the thermal ecophysiology from an intraspecific perspective, in populations that inhabit at different altitudes.

Abbreviations: body temperature, (T_b); substrate temperature, (T_s); air temperature, (T_a); operative temperatures, (T_e); preferred body temperature, (T_{set}); crest temperature, (T_{crest}); thermal quality of the environment, (d_e); accuracy of thermoregulation, (d_b); effectiveness of thermoregulation, (E and d_e-d_b).

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Fig. 1. *B. galeritus* microhabitat in Mindo (A) and Alluriquín (B).

Within reptile species, two strategies to thermoregulate are recognized. Both depend on the thermal quality of the habitat and determines the plasticity of the organisms (Soule, 1963; Hertz et al., 1993). When the organisms behave as thermoconformers, the thermal preference is available in the environment, and the preferred temperatures are reached with minimum to no effort. However, when thermal conditions are not favorable for the organism, it must behave as an active thermoregulator through physiological or behavioral mechanisms. Hence, an active thermoregulator could become a thermoconformer when the environmental temperature provides the preferred temperature (Huey et al., 2009; Sinervo et al., 2010). Nevertheless, a thermoconformer cannot behave as a thermoregulator due to their limited preferred ranges in temperature. For thermoregulation, lizards can use more specific strategies, such as changes in their coloration known as metachrosis, to absorb or reflect heat (Velasco and Tattersall, 2008); differences in the number and size of scales to counteract heat loss or gain, between populations of the same species (Soule and Kerfoot, 1972); and in some extinct synapsids (*Dimetrodon* and *Diphosaurus*) the use of dorsal sails as an alternative for thermoregulation (Bennett, 1996; Romer, 1948). Despite this last strategy, the role that some conspicuous structures (spines and crests) may play in the thermoregulation of current lizards has not been studied.

A group of lizards, that present evident morphological structures, is the genus *Basiliscus*, a taxon with a wide geographic and altitudinal range of distribution in a variety of habitats. Particularly, *Basiliscus galeritus*, is the southernmost species present from the south of Panama



Fig. 2. Sexual dimorphism between male (A) and female (B).

to Colombia and Ecuador, and an altitudinal distribution from sea level to up to 1000 m (Köhler, 2008). The study of thermal aspects of *B. galeritus* is of interest, not only due to its abundance, wide distribution, and its occupation of diverse habitats, but also due to the fact that males present an evident head crest, which could be used actively in thermoregulation by withstanding temperatures that exceed its preferred body temperature (T_{set}). Additionally, the presence of this structure may explain how the different populations present a narrow T_{set} , supporting the Bogert hypothesis (1949) at an intraspecific level. The present study evaluated and compared the thermal ecology of the species *B. galeritus* in two populations with altitudinal differences and showed that the head crest participates in thermoregulation.

2. Methodology

2.1. Study areas

The present research was carried out in two locations with differences in altitude. The first locality was Mindo (1281 masl) in the province of Pichincha, located within the Nambillo mountain range to the northwest of Quito. It has a temperature range between 15–24 °C throughout the year with a rainy and foggy climate. The mean relative humidity is 95% and has an annual mean rainfall from 2000 to 4000 mm (Salas, 2014). The second locality was the town of Alluriquín (777 masl) which is located in the west of the Andes mountains, within the province of Santo Domingo de Los Tsáchilas. The temperature range oscillates between 12 and 24 °C and relative humidity of 65–90% and has an annual mean rainfall of over 2000 mm (Benavides, 2015).

2.2. Data collection

The data and samples from both localities (Mindó and Alluriquín) were obtained during April 2018, during the activity hours of the species (9.00–18.00), according to field observations. The organisms were found on rocks and tree branches near rivers, both in disturbed and conserved areas (Fig. 1). The capture of the individuals was done with a fishing rod with a slip knot. After capture, the sex was determined in young and adult individuals through the presence of crest (males) or absence/undeveloped crest (females), since the genus *Basiliscus* presents sexual dimorphism defined by this structure (Lee, 2000), as observed in Fig. 2. In addition, males present bulges in the cloaca, as in many families of lizards (Böhme and Ziegler, 2009). It should be noted that in the

Table 1

Thermal data and of the index of thermoregulation (Hertz et al., 1993 and; Blouin-Demers and Weatherhead, 2002) by population. All thermal data are represented in mean (°C), their standard error (\pm), their minimum and maximum values inside parentheses and the number of organisms in bold type, except for the T_{set} interval (25–75%) and the index of thermoregulation.

| | T_b | T_s | T_a | T_e | T_{set} | 25–75% | T_{crest} | d_b | d_e | E | d_e-d_b |
|------------|---|---------------------------------------|---|--|---|-----------|--|-------|-------|-----|-----------|
| Mindo | 25.6 ± 0.75 (22.4–33.4) | 24.3 ± 0.77 (20.7–32.4) | 23.9 ± 0.60 (20.1–29.4) | 21.7 ± 0.08 (18–33) | 31.2 ± 0.45 (15.9–36.2) | 29.7–33.3 | 34.7 ± 0.37 (33.2–35.2) | 3.9 | 8 | 0.5 | 4 |
| Alluriquín | 17 29.4 ± 0.96 (21.6–34.5) | 16 27 ± 0.74 (22.3–33.5) | 17 24.9 ± 0.41 (23.2–27.4) | 748 24.6 ± 0.11 (19.5–34) | 11 31.9 ± 0.37 (10.4–37.3) | 31.1–34 | 5 34.5 ± 0.24 (33.9–35.3) | 2.2 | 6.5 | 0.7 | 4.3 |
| | 15 | 14 | 15 | 595 | 14 | | 5 | | | | |

hatchlings it is not possible to determine the gender. A total of 32 organisms were captured (17 in Mindo and 15 in Alluriquín), of which 20 were adults (10 males and 10 females), 2 young males, and 10 hatchlings. The information obtained from the organisms was the body temperature (T_b) from the cloaca, measured immediately after their capture with a digital thermometer Fluke 51-II®. In addition, substrate temperature (T_s) and air temperature (T_a) from the captured place of the organism, were recorded (Hertz et al., 1993). The operative temperatures (T_e) were obtained using biophysical models (PVC tubes painted in gray) with measurements of 150 × 25 mm previously calibrated and presented an $r^2 = 0.9144$. This indicates that the model emulates adequately the organism temperature. The models' temperatures were recorded and stored with an electronic device (Ibutton®) programmed to measure the temperature every 15 min, during fieldwork days in every location (7 days). Each model was placed in the different microhabitats where the organisms were observed (Lara-Reséndiz, 2013).

All the captured organisms were taken to laboratory conditions to determine the preferred body temperature (T_{set}) through a controlled thermal gradient, where individuals were able to select temperatures, which are not always reached in natural conditions. The thermal gradient consisted of four polycarbonate sheets measuring 1.70 × 1 m each. In the cold part, ice packs were placed and replaced every 2–3 h. For the hot part, a heating plate on the floor and 100 W incandescent bulbs at 80 cm high were placed. The temperature interval (15–45 °C) was established with the records of body temperatures of *B. galeritus* obtained in the field and the maximum critical temperature of some species of the genus *Basiliscus* suggested by Brusch et al. (2015). Within the gradient, tree branches, rocks and dry leaves as substrate were placed to resemble the natural habitat of the species. The organisms were introduced in the gradient for 1 h to habituate them, prior to recording the T_{set} . During the experiment, the body temperature was recorded every hour for 8 h within their activity period (10:30–17:30 h) (Hertz et al., 1993). Additionally, the crest temperature (T_{crest}) was simultaneously recorded. Finally, all the organisms were released where captured.

With the obtained data in the different experiments (T_b , T_e and T_{set}), the thermoregulation index reported by Hertz et al. (1993) was calculated: environment's thermal quality (d_e), thermoregulation's accuracy (d_b), and thermoregulation effectiveness (E). The d_e and d_b were calculated as the deviation mean between T_b or T_e and the quartile T_{set} range. When the value of T_b or T_e is below the value of 25% of T_{set} , then d_b or $d_e = 25\% - T_b$ or T_e . If the value of T_b or T_e is within the range 25–75% of T_{set} , then d_b or $d_e = 0$. When the value of T_b or T_e is above the value of 75% of T_{set} , d_b or $d_e = T_b$ or $T_e - 75\%$. If the values of d_b and d_e are close to 0, then it is considered close to an ideal thermal environment or with high thermoregulatory precision of the species. Conversely, high values indicate low thermal quality and low thermoregulatory precision of the organisms. The effectiveness of thermoregulation was calculated as $E = 1 - (d_b/d_e)$, E values close to 0 indicate that the species is a thermoconformer and when close to 1 then indicates active thermoregulation. The thermoregulation effectiveness index (d_e-d_b) by Blouin-Demers and Weatherhead (2002), was also calculated. This index indicates in

negative numbers, that the organisms avoid thermally favorable habitats, 0 when organisms behave like thermoconformers, and in positive numbers indicates thermoregulatory organisms.

2.3. Statistical analysis

For the comparison between sexes and T_{crest} , per locality, T-student tests were used. The T_b comparison was done through an ANOVA test. For the comparison between T_e and T_{set} , by locality, Mann-Whitney tests were used. In addition, a linear regression, to determine if the species is an heliotherm or a tigmotherm, was made between T_b and T_s , and T_b and T_a . Furthermore, a bootstrap test (1000 repetitions) was used to resample the data from the Hertz et al. (1993) index (d_e , d_b and E). After obtaining the results, the distribution of E between both populations was compared using the Kolmogorov-Smirnov test. All statistical analysis and graphs were done with Sigmaplot version 11.0 (Systat Software, 2011) and SPSS 15.0.1 (SPSS Inc, 2006) software.

3. Results

The mean body temperature between sexes did not show significant differences ($t_{20} = -1.634$, $P = 0.118$), although males had body temperatures slightly higher than females (26.1 ± 0.96 °C and 28.7 ± 1.2 °C respectively). The mean body temperature of the adult was 26.9 ± 0.83 °C, 32.5 ± 0.85 °C for young males, and 27.4 ± 1.2 °C for hatchlings. On the other hand, the body temperature by population showed statistical differences between the localities of Mindo and Alluriquín ($F_1 = 10.08$, $P = 0.003$). Furthermore, the operative and selected temperatures also presented significant differences between the two populations (T_e : $U = 543558.5$, $P < 0.001$ and T_{set} : $U = 4037.0$, $P = 0.036$). The data of thermoregulation by population are summarized in Table 1. The crest temperature did not show statistical differences ($t_8 = 0.314$, $P = 0.762$). The results suggest that the species obtains its body temperature through heliothermy, since the T_s ($r^2 = 0.59$; $P = 0.001$) and T_a ($r^2 = 0.36$; $P = 0.001$), had statistical differences with T_b . The distributions of E index (Hertz et al., 1993), obtained by bootstrap, presented significant differences between both populations ($LTR = 0.161$; $P = 0.0001$). The data from the Hertz et al. (1993), and Blouin-Demers and Weatherhead (2002) indexes are also shown in Table 1.

4. Discussion

The Bogert hypothesis (1949) can be defined as the conservation of thermal preferences within closely related species. Although there are some studies on its effect in between species, little has been addressed from an intraspecific level. The data obtained in the present investigation indicate that *Basiliscus galeritus* showed differences in T_{set} between both localities, due to the differences in the elevation. This suggests that the T_{set} of *B. galeritus* is a plastic requirement and depends on the thermal offer of the environment (Bogert, 1949; Díaz de la Vega-Pérez et al., 2013). Therefore, the results of the present study define that the Bogert hypothesis (1949) does not apply to *B. galeritus* at an intraspecific level.

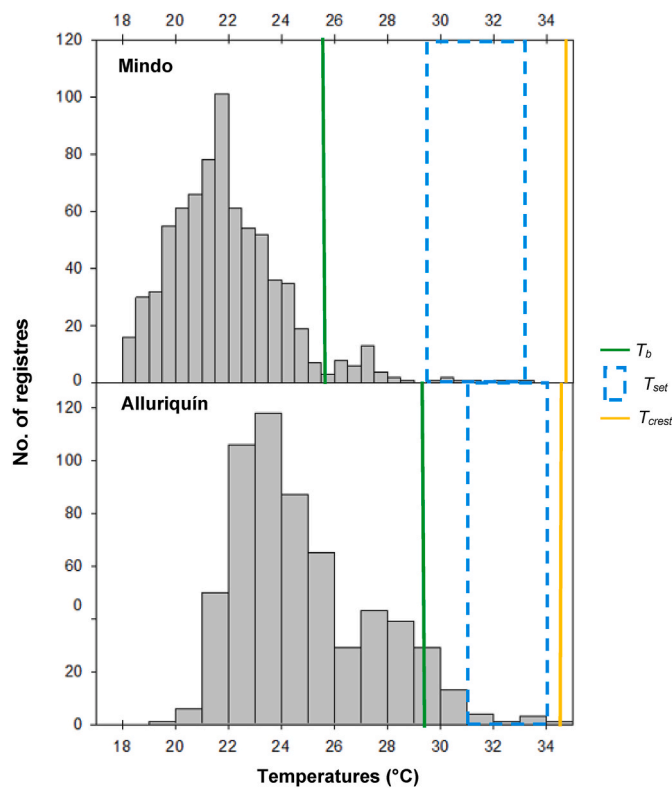


Fig. 3. Thermal data graph of *B. galeritus* by population (°C). The operative temperature (T_e) is represented with bars (histogram), the body temperature (T_b) is represented by the green line, the interval of preferred body temperature (T_{set}) is represented by a blue rectangle and the crest temperature (T_{crest}) is represented by yellow line.

Differences in T_b between populations of the same species have been well documented (Van Damme et al., 1989; Smith and Ballinger, 1994; Gutiérrez et al., 2010; among others). However, for the T_{set} there are few records. Trochet et al. (2018) reported this behavior within an altitudinal gradient in the species *Lacerta (Zootoca) vivipara* (viviparous lizard) and *Podarcis muralis* (common wall lizard). There, it was reported that organisms from lower altitudes have higher thermal preferences than those in areas with colder environmental conditions. This suggests that the plasticity of the species allows them to adapt to local temperatures. This is the case for *B. galeritus*.

The Hertz et al. (1993) index determines that both studied populations have low thermal environmental quality (d_e) and low thermoregulation accuracy (d_b). The effectiveness of thermoregulation (E) showed statistical differences between both populations. This difference is due to the fact that in Alluriquín, the thermal quality and precision are better than in Mindo. Which facilitates to reach a closer T_{set} compared to the other locality. On the other hand, the Blouin-Demers and Weatherhead index (2002) indicates that the species behaves as an active thermoregulator since organisms reach 4 °C in both populations, however, it is not enough to reach their T_{set} . Sinervo et al. (2010) suggests that the Corytophanidae family behaves as a thermoconformer due to its distribution in tropical areas, where the thermal conditions are homogeneous, and the species do not need to strive to reach the preferred temperature (Huey et al., 2009; Sinervo et al., 2010). In fact, our results suggest that *B. galeritus* can behave as an active thermoregulator when thermal conditions are not suitable and change to a thermoconformer when appropriate, as suggested by the index (E). This behavior has been previously reported by Herczeg et al. (2006), under laboratory conditions, on the *Lacerta (Zootoca) vivipara* lizard. In this work, it is concluded that the species can change its thermoregulatory strategy in response to thermal quality, as proposed by the cost-benefit model of

thermoregulation by Huey and Slatkin (1976). This strategy is not only particular, but it also represents an advantage for the species, since it can be used in harsh environmental conditions. Thus, allowing them to inhabit wider environmental conditions.

The Corytophanidae family lack studies on thermal aspects, even though there are only some published data. In comparison with the literature of other species of the genus *Basiliscus*, *B. galeritus* has a T_b close to that reported by Brattstrom (1965) for *B. basiliscus* (common basilisk) (26 °C). However, it shows lower values of T_b , in comparison to *B. plumifrons* (green basilisk) (31.7 °C) reported by Hirth (1965), and *B. vittatus* (brown basilisk) (35 °C and 35.9 °C) recorded by Brattstrom (1965) and Brusch et al. (2015). These differences may be due to the participation of the crest thermoregulation performance in *B. galeritus*, found during laboratory data recording. Throughout the experiments, the temperature of the crest of each adult male individual was also obtained. Their data showed that, in comparison to the T_{set} , the temperatures of the crests presented higher values. In addition, the increase in temperatures was also observed in this structure until reaching a limit, this being the registered data. The evidence suggests that with the crest, the species can endure unfavorable temperatures that exceed the T_{set} . Is important to point out that the value of the crest temperature is close to the limit of operative temperatures in both locations (Fig. 3). Hence, the values are, apparently related to the maximum temperatures that the environment offers to the species. Although there are statistical differences in the T_{set} , the intervals of both locations are close. Additionally, the absence of statistical differences between the T_{crest} may suggest that it is a conserved requirement that intervenes in the selection of preferred temperatures in the field.

Conspicuous structures (spines, crests, and dorsal sails) were very common in extinct tetrapods such as amphibians (*Astreptorachis* and *Platyhystrix*), synapsids (*Dimetrodon*, *Secodontosaurus*, *Lupeosaurus*, and *Edaphosaurus*), and dinosaurs (*Spinosaurus* and *Ouranosaurus*) (Lewis and Vaughn, 1965; Vaughn, 1971). Their function varied from supporting the vertebral column (Romer, 1927), intimidation and sexual exposure (Bakker, 1986), and thermal aspects (Romer, 1948). However, the study of these structures has only been investigated in fossil organisms and has not yet been addressed in extant lizards. The phenomenon of thermoregulation through a conspicuous structure in extinct synapsids (*Edaphosaurus* and *Dimetrodon*) consisted of using the dorsal sails to thermoregulate effectively through the loss and/or gain of heat. Mainly by air convection as suggested by Bennett (1996) and Romer (1948), analogous to what was observed in *B. galeritus*. In conclusion, although more data and histological evidence are needed, the evidence on hand highlights the importance of the crest in thermoregulation. Since this structure would not only have a function on sexual dimorphism in the species but would also help adult males to withstand harsh weather conditions. This also would represent an advantage when facing global warming.

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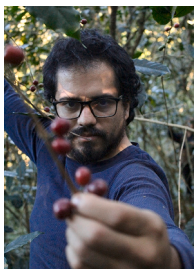
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