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Behavioral and physiological thermoregulation of Atacama desert-dwelling *Liolaemus* lizards¹

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Abstract: The behavioral and physiological thermoregulation of three Atacama desert-dwelling *Liolaemus* lizards was studied and compared with previous data on *Liolaemus* from other ecosystems. The thermoregulatory mechanisms of the desert-dwelling species differed from those of the others, a consequence of differences in the habitat structure of the species. Desert species have higher critical thermal minima and, contrary to expectations, lower selected body temperatures than *Liolaemus* from Mediterranean environments. Results of the rates of thermal time constants suggest mechanisms to cope with the fast decrease of environmental temperature that occurs in the desert during the mid-afternoons. Finally, the manner in which selection of low body temperatures may allow survival in desert conditions is discussed. *Keywords*: thermal time constants, operative temperature, physiological and behavioral thermoregulation.

Résumé : L'étude porte sur la thermorégulation comportementale et physiologique de trois espèces de lézards du genre *Liolaemus* habitant le désert d'Atacama. Les résultats sont comparés à ceux obtenus précédemment pour des *Liolaemus* habitant d'autres écosytèmes. Les espèces désertiques se différencient les unes des autres par les mécanismes de thermorégulation qu'elles utilisent face aux conditions de température du désert. Il s'agirait d'une conséquence des différences existant au niveau de la structure de l'habitat des espèces. Les espèces du désert présentent des valeurs plus élevées de température limite inférieure et, contrairement aux prévisions, sélectionnent des températures corporelles inférieures aux espèces d'environnements méditerranéens. Les résultats concernant les changements des constantes de temps thermiques suggèrent des mécanismes permettant de faire face à une baisse rapide de la température ambiante qui survient pendant le milieu de l'après-midi dans le désert. Pour terminer, une discussion traite de la sélection de faibles températures corporelles pour permettre la survie dans des conditions désertiques.

Mots-clés : constantes de temps thermiques, température opérante, thermorégulation physiologique et comportementale.

Introduction

Some ectotherms are able to maintain relatively constant body temperatures through behavioral and/or physiological thermoregulation (Avery, 1982; Huey 1982; Spotila & Standora, 1985; Lemos-Espinal & Ballinger, 1995; Schwarzkopf, 1998). Many studies of lizard thermoregulation are centered on behavioral mechanisms (Huey, 1982). The most important thermoregulatory behaviors to cope with temporal and spatial variability in the availability of thermal resources are variations in microhabitat use and/or changes in daily and seasonal activity (Van Damme et al., 1987; Adolph, 1990; Muchlinski et al., 1990 and references therein; Gillis, 1991; Andrews, 1994; Bauwens et al., 1996; Schäuble & Grigg, 1998). On the other hand, the most important physiological thermoregulatory mechanism involves changes in the rate of heat transfer through modifications of heart rate and blood flow (Seebacher, 2000). Many authors have reported that lizards from cold/cool habitats are able to increase their body temperature more quickly than lizards from warmer areas, thus achieving longer daily or seasonal activities (Tessini et al., 1995; Díaz et al., 1996; Seebacher, 2000). Other mechanisms to cope with extreme environmental temperatures include variations in thermal tolerance, mainly through variations in the highest (Ct_{max}) and lowest (Ct_{min}) body temperatures at which the lizards lose their ability to right themselves (Brown, 1996). These thermal tolerances are positively correlated with acclimation or acclimatization temperatures (Kour & Hutchison, 1970; Corn, 1971; Pollack, 1971; Brown, 1996). Thus, lizards from cooler habitats have lower Ct_{min} , allowing them to be active at lower temperatures (Wilson & Echternacht, 1987; 1990; Doughty, 1994 and references therein).

Information on the thermal biology of *Liolaemus* lizards (Tropiduridae) is scarce, though the genus comprises more than 160 species (Schulte et al., 2000) distributed through a variety of habitats from dry deserts to humid forests (Donoso-Barros, 1966; Cei, 1986; 1993). Studies of behavioral thermoregulation have reported intra- and interspecific differences in the daily activity patterns and type of substrates used (Pearson & Bradford, 1976; Marquet et al., 1989; Núñez, 1996; Carothers et al., 1998, Verrastro & Bujes, 1998). On the other hand, the field body temperature (T_b) of different *Liolaemus* species shows intra- and interspecific variations associated with climatic conditions (Halloy & Laurent, 1987; Rocha, 1995; Labra, 1998 and references therein; Lobo & Espinoza, 1999; Ibarüengoytía & Cussac, 2001). The selected body temperature (T_{sel}) of different Liolaemus measured in a thermal gradient without constraints for thermoregulation (Pough & Gans, 1982) is around 35°C, ranging from 33 to 37°C, and is positively correlated with the species' field minimal air temperature

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recorded over 24 hours (Labra, 1998). Studies of physiological adaptations of *Liolaemus* from Mediterranean ecosystems indicate that species from high altitude have slower heating rates than lowland species but similar thermal tolerances (Carothers *et al.*, 1997). Therefore, *Liolaemus* lizards exhibit physiological mechanisms to cope with environmental conditions.

Deserts represent extreme biotic and abiotic environments for animal colonization and survival. The Atacama desert of Chile is the driest in the world (Ortlieb et al., 2000), and it receives the highest insolation in South America (Ochsenius, 1982). Nonetheless, approximately nine Liolaemus species reside in the area (Núñez, 1992). The thermoregulatory mechanisms of Atacama desertdwelling Liolaemus have not been studied, with the exception of L. fabiani. This lizard, which is restricted to the lakes of the Atacama Salt Flat (Atacama desert), has a T_{sel} (33°C) significantly lower than those of *Liolaemus* from Mediterranean areas (Labra, 1998). Results on Liolaemus fabiani come in contradiciton with other studies of desert lizards, that have comparatively higher body temperature ascribed as an adaptation to the high air temperature (Avery, 1982; Bradshaw, 1986). Labra (1998) proposed that the T_{sel} values of *L. fabiani* could be the consequence of a thermal history different from that of other Liolaemus species.

To unravel the mechanisms used by *Liolaemus* to cope with extreme desert conditions, we studied the behavioral (daily activity patterns) and physiological thermoregulatory (heating and cooling rates, T_{sel} and Ct_{min}) responses of three *Liolaemus* species from the Atacama desert. Because during the day species must endure mainly high temperatures and low spatial heterogeneity of thermal patches, we predicted, based on most of the data from the literature, that they would show narrower patterns of daily activity (through reduction of activity during midday), slower heating rates, faster cooling rates, and higher values of Ct_{min} and T_{sel} than *Liolaemus* from Mediterranean ecosystems.

Material and methods

Adult individuals of three *Liolaemus* species were collected at or near the Atacama Salt Flat (26° 46' s, 68° 14' w, 2400 m above sea level) between November 1999 and February 2000 during similar, typical sunny days. In this area the thermal conditions are highly similar throughout the year (Di Castri & Hajek, 1976). The species were *L. constanzae*, collected at Tilopozo; *L. nigroroseus*, collected at Vilama; and two populations of *L. fabiani*, associated with and collected at internal lakes of the Salt Flat (Puilar and Punta-Brava populations). The mean snout-vent length (SVL) and body mass of the different species are indicated in Table I, while the location of the capture sites is shown in Figure 1.

During three consecutive days, the number of active lizards found (either basking or moving) and the substrate used were recorded. In the habitats of *L. constanzae* and *L. nigroroseus*, four or five parallel 450 m long transects located approximately 25 m apart were walked throughout each day, while for *L. fabiani* a transect of 200 m was walked every half hour. This procedure minimized the prob-

ability of repeatedly observing the same individual lizard, at least during the same day.

During two consecutive days, the thermal characteristics of the substrates used by the three species were evaluated by recording the operative temperature, T_a (Bakken, 1992; Hertz et al., 1993). Six to 10 hollow copper models of lizards were distributed among the substrates in accordance with their use by the species; the compass direction of the models was random. Although size, morphology, and color contribute very little to temperature change in small, lizard-like models (Vitt & Sartorius, 1999), we used models similar in size and color to the different species. The dimensions of the L. constanzae and L. nigroroseus models were SVL = 60 mm and width (middle of the body) = 17 mm, while those of the L. fabiani models were SVL = 70 mm and width = 20 mm. Each model had a Cu-Constantan thermocouple inserted in its core, and operative temperatures were recorded with a digital thermometer (Digi-Sense[®], \pm 0.1°C) every 30 minutes from the beginning to the end of lizard daily activity. Thereafter, some lizards were captured by noose, and the cloacal temperatures (T_b) were recorded within 20 seconds of capture, using the thermocouple and thermometer described above. Lizards were seized by the head to avoid heat transfer during temperature recording. Body temperatures were not recorded if lizards eluded capture for more than 15 seconds,



FIGURE 1. Location of the four study sites in the Atacama Salt Flat (Chile).

TABLE I. Summary statistics (mean \pm SE) of snout-vent length (SVL, mm), body mass (Mb, g), field body temperature (T_b, °C), selected body temperature (T_{sel}, °C) and critical thermal minimum (Ct_{min}, °C) for three desert *Liolaemus* species. In parentheses the number of animals tested. Sample size for SVL and Mb was the same. P = Puilar and P-B = Punta-Brava *L. fabiani* populations.

Species	SVL	Mb	T _b	T _{sel}	Ct _{min}
L. constanzae	59.5 ± 1.20 (17)	5.72 ± 0.32	30.79 ± 0.81 (17)	34.31 ± 0.22 (11)	11.33 ± 0.47 (10)
L. nigroroseus	58.2 ± 1.83 (8)	6.17 ± 0.48	33.89 ± 0.71 (8)	34.74 ± 0.24 (8)	11.64 ± 0.96 (7)
L. fabiani (P)	73.6 ± 0.84 (20)	9.70 ± 0.39	31.76 ± 0.28 (37)	33.03 ± 0.36 (10)	9.20 ± 0.51 (22)
L. fabiani (P-B)	67.8 ± 1.14 (17)	8.30 ± 0.48	$29.78 \pm 0.49 \ (13)$	30.03 ± 0.61 (11)	$7.90 \pm 0.43 \ (11)$

which frequently occurred. Finally, some lizards were transported to the laboratory for physiological measurements.

In the laboratory, T_{sel} was determined in thermal gardients. Lizards were placed in terraria (91 cm \times 37 cm \times 21 cm) that had in one extreme a 250 W infrared lamp to generate a thermal gradient from 18°C to 40°C. After one day, for three consecutive days the cloacal temperature of each individual was recorded hourly using the thermocouple and thermometer described above. The mean T_{sel} value for each individual was obtained; these values were then used to calculate the mean T_{sel} of the species or population (for more details, see Labra, 1998). Critical thermal minima (Ct_{min}) were obtained by cooling lizards in a freezer to a temperature at which, when turned on their back, they were unable to right themselves. To measure heating and cooling rates, lizards had a thermocouple affixed in the cloaca. To prevent movements during the experiments, the lizards' extremities were affixed with tape to a pasteboard chosen because of its low heat conductivity. For heating experiments, lizards were cooled in a freezer to a body temperature of 14°C, then placed in an incubator at 37 ± 0.5 °C. Lizard body temperatures were recorded every 30 seconds, beginning when they were 15°C and ending when they reached 35°C. For cooling experiments, lizards were heated under a 250 W infrared lamp to a body temperature of 36°C, then placed in an incubator at 13 ± 0.5 °C. Body temperatures were recorded every 30 seconds, beginning when they were 35°C and ending when they reached 15°C. The heating and cooling rates were determined by semi-logarithmically plotting the differences between ambient and body temperature over time. Thermal time constants, or tau (τ) values, were calculated from the thermal change rates, considering that data presented in this way have comparative value (Grigg et al., 1979). These constants can be defined as the time in minutes for core temperature to change by 63% of the differential between core temperature and ambient temperature at any particular time during the exponential approach of core temperature to ambient temperature (Grigg et al., 1979).

Data were analyzed through parametric statistics. T_{sel} data were log transformed. Because the populations of *L. fabiani* showed significant differences in the different variables, they were treated independently during statistical analysis. One- or two-way ANOVA tests and *a posteriori* Tukey multiple comparison tests were performed (Zar, 1996). Student *t*-tests were used to compare T_b and T_{sel} . When necessary, body mass was used as a covariate (Ayres & Shine, 1997; O'Connor, 1999). Comparisons of the use of substrates were made with multiple proportion tests (Zar, 1996). Evaluations of the effectiveness of temperature

regulation were made following the propositions of Hertz *et al.* (1993). No gender distinction was made for any of the physiological variables since few females were captured. The use of comparative methods is recommended for interspecific comparisons (Martins & Hansen, 1996). Since the phylogenetic hypothesis proposed by Schulte *et al.* (2000) does not include any of the species studied here, phylogenetic analyses were not performed.

Results

BEHAVIORAL MEASUREMENTS

The daily activity patterns and T_e of the three species are shown in Figure 2. *Liolaemus constanzae* and *L. nigroroseus* exhibited bimodal activity (Figure 2a,b), while the populations of *L. fabiani* were active throughout the day (Figure 2c,d). At the hour of the highest activity (Figure 2), T_e was similar among the four sites (one-way ANOVA, $F_{(3,88)} = 1.622$; p = 0.19; Figure 2). Nevertheless, a twoway ANOVA considering all T_e values recorded while lizards were active, with sites of species and hour of the day (every two hours, from 8:00 to 20:00) as factors, indicated differences. T_e was higher in the habitats of *L. constanzae* and *L. nigroroseus* ($F_{(3,646)} = 78.50$; p < 0.001). Hour of the day also affected T_e ($F_{(5,646)} = 159.66$; p = < 0.001): the maximal T_e was recorded between noon and 15:00. The interaction between factors was also significant ($F_{(15,646)} = 12.43$; p < 0.001). During the morning the habitats of *L. constanzae* and *L. nigroroseus* had higher T_e values than those of *L. fabiani*. However, after 16:00 all sites had the same T_e (Figure 2).

Liolaemus constanzae and L. nigroroseus were observed using salt plates (irregular formations produced by breaks in the salt layer) and rocks, respectively, as substrates in more than 95% of sightings. Only rarely were individuals of these two species observed on ground. Lizards were not sighted when T_e of the most frequently used substrates were higher than the maximal T_b ; most likely, lizards remained in crevices under these circumstances. In contrast, *L. fabiani* used three different types of substrates during the day: water of the internal lakes (shoreline), salt plates, and beaches. Beaches are smooth salt surfaces two to three meters wide located between salt plates and the shoreline. Usually, individuals of *L. fabiani* remained on the beach while T_e was between 35-37°C; otherwise they were observed in the water or on salt plates (Figure 3).

The populations of L. fabiani differed in their thermoregulatory behavior. Daily activity decreased earlier in Punta-Brava than in Puilar. Additionally, lizards in Puilar remained in the water and on the beach for 6 and



FIGURE 2. Daily activity patterns (bars) and operative temperatures (open circles) of *Liolaemus nigroroseus, Liolaemus constanzae* and both populations of *Liolaemus fabiani*. The continuous line and dashed lines represent the mean and the maximal/minimal body temperatures recorded in the field, respectively.



FIGURE 3. Daily activity patterns (bars) and operative temperatures (open circles) of two populations of *Liolaemus fabiani*, in three different substrates. The continuous and dashed lines represent the mean and the maximal and minimal body temperatures recorded in the field, respectively.

8.5 hours day⁻¹, respectively, while in Punta-Brava they remained on each substrate only 4 hours day⁻¹, and beaches were mainly used during mornings. Using all the observations it was found that both populations used the water in similar proportion (Puilar = 0.30; Punta-Brava = 0.32; Multiple Proportions Test, p = 0.64), while they differed in use of the beach (Puilar = 0.51; Punta-Brava = 0.30; p < 0.001) and salt plates (Puilar = 0.19; Punta-Brava = 0.38; p < 0.001). A two-way ANOVA revealed significant differences in overall T_e between the sites of *L*. *fabiani* populations ($F_{(1,366)} = 6.95$; p = 0.009), being higher in Puilar. In addition, there was a significant effect of substrate on T_e ($F_{(2, 366)} = 57.53$; p < 0.001). Beaches showed higher T_e than water, and the T_e of water was higher than that of salt plates. Finally, a significant interaction between factors (populations and substrates) was observed $(F_{(2, 366)} = 3.47, p = 0.03)$: beach and water had similar T_e in both L. fabiani population sites, but salt plates had higher T_e in Puilar than in Punta-Brava.

PHYSIOLOGICAL MEASUREMENTS

There were differences in field body temperature (T_b) among species ($F_{(3,75)} = 5.64$; p = 0.002): *L. nigroroseus* had a significantly higher T_b than *L. fabiani* from Punta-Brava and a marginally higher value than *L. constanzae* (p = 0.052) (Table I). Species differed in their T_{sel} ($F_{(3,34)} = 24.69$; p < 0.001), with the Punta-Brava population showing the lowest values (Table I). Intraspecific comparisons between T_b and T_{sel} indicated that only *L. constanzae* showed a significantly higher T_{sel} than T_b ($t_{25} = 3.22$; p = 0.004) (Table I). The efficiency (E) of thermoregulation was 0.60 for *L. nigroroseus* (means: $d_b = 0.91$ and $d_e = 2.50$), -0.03 for *L. constanzae* (means: $d_b = 2.62$ and $d_e = 2.54$, 0.56 for *L. fabiani* from Puilar (means: $d_b = 1.34$ and $d_e = 3.03$) and 0.98 for *L. fabiani* from Punta-Brava (means: $d_b = 0.04$ and $d_e = 5.88$).

Significant differences were found in Ct_{min} ($F_{(3,60)} = 9.95$; p < 0.001), with the Punta-Brava population showing the lowest mean value (Table I). Heating rates also differed ($F_{(3,26)} = 5.44$; p = 0.031), with the Puilar population showing the slowest rates. No differences were found in cooling rates ($F_{(3,26)} = 0.71$; p = 0.55). Thermal time constants (Table II) showed the same trends observed in the rates of thermal change. Species differed in their τ heating ($F_{(3,26)} = 3.99$; p = 0.003). The Puilar population showed the highest values, indicating a lower heating rate. No differences were recorded among species in either τ cooling ($F_{(3,26)} = 0.81$; p = 0.51) or the ratio τ heating/ τ cooling ($F_{(3,26)} = 2.88$; p = 0.055).

Discussion

The abiotic environment directly affects the physiological and behavioral control of lizard body temperature (Spotila & Standora, 1985), and different species may adopt different strategies to cope with a similar environmental condition. In the present study, the desert-dwelling Liolaemus species differed both in the behavioral and the physiological thermoregulatory mechanisms used to cope with desert conditions, though they all showed one similar pattern: use of a substrate depended on its T_e When T_e of the most frequently used substrates fell outside the measured T_h range, lizards were inactive or used other substrates. This observed behavioral switch, coupled to the habitat characteristics of the different sites, likely determined two behavioral thermoregulatory strategies. A bimodal activity pattern associated with the predominant use of one type of substrate prevailed in L. constanzae and L. nigroroseus: the main peak of activity occurred during the morning, using salt plates and rocks, respectively. These species became inactive around midday and were not observed using shade. The low availability of shady substrates and the relatively large distances separating shady patches probably precluded shuttling behavior because of the risk of overheating. This fact may also explain the low density of lizards observed. In contrast, L. fabiani showed continuous daily activity associated with the use of different substrates, mainly beaches, but also water and salt plates. The use of water brings multiple benefits: lizards are able to prey on flying insects (M. Soto-Gamboa, pers. observ.) without the risk of overheating, and wet lizards outside the water can quickly lose heat by evaporation and convection (O'Connor, 1999). Therefore, L. fabiani can remain active on the beach, close to a source of food, without overheating.

The physiological distinctions among species resulted largely from the differentiation of the *L. fabiani* Punta-Brava population. A statistical analysis (without consideration of phylogeny; see material and methods) comparing the T_{sel} of desert-dwelling *Liolaemus* and those recorded for other *Liolaemus* species (Labra, 1998) indicated significant differences among species ($F_{(9,127)} = 13.17$; p < 0.001), which arose as a consequence of the low T_{sel} values of the *L. fabiani* Punta-Brava population. Nevertheless, it is noteworthy that *L. constanzae* and the two populations of *L. fabiani* have the lowest reported T_{sel} values (Labra, 1998). If a directional selection pressure due to relatively high environmental temperature were influencing T_{sel} or T_b, as in other species (Avery, 1982), desert-dwelling *Liolaemus*.

It can be postulated that desert-dwelling *Liolaemus* differ from other desert lizards in the strategy that they use to

TABLE II. Summary statistics (mean \pm SE) for body mass (g), thermal time constant (τ , minutes) during heating and cooling, and the ratio τ heating/ τ cooling for three desert *Liolaemus* species. In parentheses the number of animals tested. P = Puilar and P-B = Punta-Brava *L*. *fabiani* populations.

Species	Body mass	Heating	Cooling	Heating/Cooling
L. constanzae	5.52 ± 0.28 (10)	3.34 ± 0.13	4.75 ± 0.28	0.72 ± 0.05
L. nigroroseus	6.17 ± 0.47 (7)	3.50 ± 0.25	5.23 ± 0.22	0.67 ± 0.06
L. fabiani (P)	8.31 ± 0.76 (8)	4.09 ± 0.19	5.54 ± 0.39	0.76 ± 0.05
L. fabiani (P-B)	8.27 ± 0.62 (6)	3.34 ± 0.14	5.49 ± 0.41	0.62 ± 0.04

cope with thermal conditions of the environment. Diurnal desert lizard species have low metabolic rates (Duvdevani & Borut, 1974; Snyder, 1975), which may be tightly associated with low T_{sel} values (Jenssen et al., 1996). This may be the pathway used by Liolaemus to adapt to desert conditions, reducing the risk of overheating when there is low spatial thermal heterogeneity for behavioral thermoregulation. In addition, at T_{sel} the aerobic scope is maximal (Wilson, 1974; Labra & Rosenmann, 1991). Therefore, the comparatively low T_{sel} of desert-dwelling Liolaemus species would not have negative effects upon their performance compared to other Liolaemus. Furthermore, the fact that skeletal muscle has the lowest thermal dependence in comparison to other tissues (Morris, 1980) supports the proposition that desert-dwelling *Liolaemus* would not be impaired by their lower T_{sel}. On the other hand, desert Liolaemus have higher Ct_{min} than Mediterranean species (Carothers et al., 1998), suggesting that desert Liolaemus are not impaired by the low temperature experienced from mid-afternoon to the next morning.

The values of different physiological variables associated with thermoregulation may or may not differ among populations as a function of differences in T_e (Wilson & Echternacht, 1987; Brown, 1996; Labra, 1998). The observed interpopulational differences in T_{e} of L. fabiani may be the cause of the local differentiation in behavioral and physiological thermoregulation. The lower Ct_{min} values of the L. fabiani Punta-Brava population allow these lizards to be active at comparatively low air temperatures. However, it is not clear why individuals from Punta-Brava did not exhibit faster heating rates. Moreover, why did the Puilar population show the slowest heating rates? We postulate that L. fabiani selects salt plates at night. Since this substrate showed higher Te values in Puilar than in Punta-Brava, the slow heating rates in the Puilar population may reduce the possibility of overheating during the morning. At present, it remains unclear whether the observed local differentiation in L. fabiani is a consequence of genetic differentiation between populations or physiological plasticity enabling the lizards to tolerate different environmental conditions. In L. bellii, populational differences in T_{sel} were attributed to a low genetic flow among populations (Labra, 1998). In desert environments, the relatively low dispersal capacity of lizards (Pough et al., 1998). coupled to a relatively low availability of shade, should constrain genetic flow among populations, promoting local genetic differentiation. Data from allozyme variation indicate that the Punta-Brava and Puilar populations of L. fabiani showed higher genetic distances (A. Veloso, pers. comm.) than those reported for L. lemniscatus populations, which are separated by greater distances but inhabit low valleys (Espejo, 1989). Thus, the populational differences in thermoregulation of L. fabiani might have genetic bases.

In spite of the fact that *L. constanzae* and *L. nigroroseus* live under higher T_e than *L. fabiani* from Puilar, they did not show the slower heating rates that we had expected. It is not known how plastic the rates of thermal change are in *Liolaemus*. However, Carothers *et al.* (1997) found that *Liolaemus* species from high altitude have slower heating rates than species from lowlands; they claimed that this may reduce the effects of high radiation at high altitude. Due to differences in experimental conditions, our results cannot be compared with those of Carothers *et al.* (1997). Nevertheless, it is remarkable that there are still differences among *Liolaemus* species which correlate with environmental thermal characteristics. Therefore, the proposition that changes in thermal conductance are not an important thermoregulatory mechanism in lizards weighing less than 20 g (Fraser & Grigg, 1984) would not apply to *Liolaemus* since most of the species, including those studied herein and by Carothers *et al.* (1997), weigh less than 20 g.

In all the desert-dwelling *Liolaemus* species and populations studied, the ratio of thermal time constants revealed a comparatively slow cooling rate in relation to heating rate (Table II). This would represent a mechanism to endure the fast decrease of environmental temperature during the mid-afternoon. During daytime, behavioral thermoregulatory mechanisms are probably more important in coping with thermal restrictions, but they are inefficient to endure the fast thermal change following the mid-afternoon. In this case, a physiological thermoregulatory mechanism, a comparatively slow cooling rate, would be more efficient.

Despite the existence of behavioral and physiological thermoregulatory mechanisms to cope with environmental conditions, T_b seems to be affected by T_e. The highest and lowest T_e values were recorded for L. nigroroseus and the L. fabiani Punta-Brava population, which had the highest and the lowest $T_{\rm h}$, respectively. However, and with the exception of L. constanzae, species did not show differences between T_{sel} and T_b. This is also clear from the values of the effectiveness of thermoregulation: L. constanzae showed a negative value, which may be because the animals actively avoid the use of substrates with Te in the Tsel range (possibly due to factors such as predator presence; Hertz et al., 1993) or because of the low availability of spatial heterogeneity of substrates for behavioral thermoregulation. Contrarily, L. fabiani from Punta-Brava showed the highest effectiveness of thermoregulation. It had a high accuracy of thermoregulation since most of the T_b were in the range of T_{sel}. Therefore, this population seems to be well adapted to the comparatively low thermal environmental conditions to which it is exposed.

Considering the wider range of substrates used by *L. fabiani* and the behavioral and physiological interpopulational differences, this species exhibited the most complex thermoregulatory repertory among the desert-dwelling *Liolaemus* so far studied. Nevertheless, further comparative interpopulational studies will be needed to determine whether other species might be as complex as *L. fabiani* in thermoregulatory mechanisms.

Finally, the data on T_{sel} deserve some comments. Labra (1998) proposed that T_{sel} would be a conservative character in *Liolaemus*, but our results do not support this proposition. However, considering that important evolutionary shifts have been proposed inside the *Liolaemus* genus (Schulte *et al.*, 2000), it is possible that the species studied to date represent different thermal histories, which would mean that the genus cannot be characterized by a unique T_{sel} . Studies that include more species from different *Liolaemus* subgenera are needed.

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