THERMAL BIOLOGY OF *Liolaemus occipitalis* (SQUAMATA, TROPIDURIDAE) IN THE COASTAL SAND DUNES OF RIO GRANDE DO SUL, BRAZIL

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Received February 2, 2005 – Accepted March 28, 2005 – Distributed August 31, 2006

(With 5 figures)

ABSTRACT

The thermal biology of the small sand lizard, *Liolaemus occipitalis*, was studied in the coastal sand dunes at Quintão Beach (Palmares do Sul, Rio Grande do Sul, Brazil; 30° 24' S and 50° 17' W), between September, 1998 and August, 1999. *Liolaemus occipitalis* presented a mean body temperature of 30.89 °C (SD = 4.43 °C; min = 16.4 °C; max = 40.2 °C; N = 270), that varied on a daily and seasonal basis according to microhabitat thermal alterations. The substrate temperature was the main heat source for thermoregulation of *L. occipitalis* as in all seasons of the year it was responsible for the animals´ temperature variation (82% of the collected lizards in the spring; 60% in the summer; 84% in the fall and 68% in the winter). The results indicate that *L. occipitalis* is a saxicolous, thigmothermic and heliothermic species that regulates its body temperature through behavioral mechanisms.

Keywords: Tropiduridae, *Liolaemus*, thermal biology, body temperature, restingas.

RESUMO

Biologia termal de *Liolaemus occipitalis* (Squamata, Tropiduridae) nas dunas costeiras do Rio Grande do Sul, Brasil

A biologia termal da lagartixa da areia, *Liolaemus occipitalis*, foi estudada nas dunas costeiras da Praia de Quintão (Palmares do Sul, Rio Grande do Sul, Brasil; 30° 24' S e 50° 17' W), entre setembro de 1998 e agosto de 1999. *Liolaemus occipitalis* apresentou temperatura corpórea média de 30,89 °C (SD = 4,43 °C; min = 16,4 °C; max = 40,2 °C; N = 270), a qual variou diária e sazonalmente relacionando-se às mudanças termais do microhábitat. A temperatura do substrato foi a fonte de calor de maior importância na termorregulação de *L. occipitalis* e, em todas as estações, foi responsável pela variação da temperatura dos animais (82% dos lagartos coletados na primavera; 60% no verão; 84% no outono; e 68% no inverno). Os resultados indicaram que *L. occipitalis* é uma espécie saxícola, tigmotérmica e heliotérmica, que regula sua temperatura corporal por meio de mecanismos comportamentais.

Palavras-chave: Tropiduridae, *Liolaemus*, biologia termal, temperatura corporal, restingas.

INTRODUCTION

Lizards often have a narrow range of body temperatures in which the performance of basic physiological functions (*e.g.* metabolism, digestion and water balance) is maximized (Cloudsley-Thompson, 1965; Waldschmidt *et al.*, 1986; Grant, 1990; Grover, 1996). Although habitat temperatures are considerably variable, many lizards keep their body temperature approximately within this range, which is known as optimal body temperature (Avery, 1982).

The maintenance of metabolic functions in lizards and other ectothermic organisms is dependent on environmental heat sources. The temperature of such organisms is determined by the different environmental heat sources to which they are exposed, by body size (which influences how fast the heat is gained or lost), by the level of thermal insolation of the body, color pattern and evaporation rate (Pough *et al.*, 1993). In order to maintain their body temperature within a narrow but favorable range, lizards thermoregulate, *i.e.*; they regulate the gain or loss of body heat (Pough *et al.*, 1993).

Thermal conditions change seasonally in subtropical areas. Consequently, it is expected that lizards will try to regulate their body temperature by means of behavioral mechanisms, modifying their activity pattern during periods of low environmental temperature (Heatwole *et al.*, 1969).

Thermoregulation may play an important role in several aspects of the ecology of ectotherm species and can be particularly important to ectotherms in high altitudes, for which the thermal environment potentially limits the activity period (Marquet *et al.,* 1989; Grant & Dunham 1990). The capacity of thermoregulation (*i.e.*, of using behavioral mechanisms for keeping body temperature levels separate from air temperature) can extend the activity period, there by increasing the growth rates (Sinervo & Adolph 1989; Sinervo 1990), and represents an interaction between physical and biological environments (Smith *et al.,* 1993).

The tropidurid lizards are extremely diverse ecologically. They inhabit humid and dry forests, deserts and savannas and even high mountains in the Andes, extending to elevations above 5,000 m. The Tropiduridae family includes oviparous and viviparous species with herbivorous (*e.g.*, some *Liolaemus* species) and insectivorous habits. The variability in tropidurids is a consequence of the great number of species still being described. Yet, it is not clear if they represent a monophyletic group. All members of the Tropiduridae occur in South America (Frost & Etheridge, 1989).

The genus *Liolaemus*, subfamily Liolaeminae (Frost & Etheridge, 1989), contains more than 150 species occurring from Bolivia to Tierra del Fuego. In Brazil, there is a tropical species endemic to the State of Rio de Janeiro (*L. lutzae*) and two temperate species in the States of Santa Catarina and Rio Grande do Sul (*L. occipitalis* and *L. arambarensis*).

The aim of the present study is to examine the thermal biology of the small sand lizard (*Liolaemus occipitalis*) by determining the optimal body temperature of this species, and its relations with microhabitat and heat sources. The investigation took place in the coastal sand dunes of the State of Rio Grande do Sul, Brazil encompassing a whole seasonal cycle.

Liolaemus occipitalis Boulenger 1885, is a small lizard from the Tropiduridae family. Males and females have mean snout-vent lengths of 60.2 mm and 53.2 mm, respectively (Verrastro & Bujes, 1998). Its geographical distribution is restricted to the sand dunes of the South Atlantic coast of the States of Santa Catarina and Rio Grande do Sul, Brazil. It has a cryptic color pattern, which makes it inconspicuous in its background environment. The minimum reproductive size is 50 mm for males, and 45 mm for females (Verrastro & Krause, 1994). Reproduction takes place between September and March. The species is mainly insectivorous and it is active during the day (Verrastro & Krause, 1994). Its main defense strategy against predators is burrowing superficially in the sand or escaping into refuges. The most commonly observed thermoregulating behavior of *L. occipitalis* is moving between sunlight exposed sites to shaded sites amidst dense vegetation (Verrastro & Bujes, 1998).

MATERIALS AND METHODS

The study took place in the sand dunes of the beach of Quintão, in Palmares do Sul, Rio Grande do Sul, Brazil (30° 24' S and 50° 17' W). This area was chosen because it had a higher population density. It is situated 4 km from Lagoa do Quintão and 3 km from the Atlantic Ocean in the Coastal Plain. It is flat landscape with walking sand dunes on Holocenic geological substrate (Delaney, 1965). The soil is formed by non-fixed sand-quartz deposits of eolic accumulation and quaternary origin (Porto & Cortazzi, 1982). The climate is of the Cfa type, according to the Köppen classification (Eidt, 1968), with a mean annual rainfall of around 1,323 mm and no characteristic dry season. The mean annual air temperature is 20 °C. Northeastern winds predominate throughout most of the year (Hasenack *et al.*, 1987).

The coastal vegetation in the vicinity of the study site is described in Pfadenhauer & Ramos (1979), Pfadenhauer (1980), and Waechter (1985, 1990). The vegetation in the study area is sparse, with plants covering less than 5%, and consists exclusively of herbaceous, psammophilous species, mainly Poaceae. The habitat includes small hummocks and dunes of sand 20 to 50 cm high, many of which are situated next to clumps of herbaceous plants. In depressed areas among the dunes, temporary flooding may occur due to heavy rainfall. When these depressed areas accumulate organic matter for a long time, they become covered by dense, perennial plant species, such as *Juncus cf. maritimus* (which forms dense, but sparsely distributed clumps), *Lycopodium alopecuroides* (Pterydophyta), *Drosera cf. brevifolia* (Droseraceae) and *Urticularia* spp. (Urticulariaceae). The most abundant species is *Panicum racemosum*, which forms almost homogeneous clusters in wide extensions on top of small elevations. In the lower elevations, other Gramineae occur, *e.g.*, *Panicum sabularum*, *Andropogon arenarium*, *Spartina cf. ciliata*, but also *Hydrocotyle umbellata* (Umbelliferae) and *Senecio crassifolius* (Asteraceae).

A study area of approximately 40,000 m^2 was established. Observations were made monthly from September, 1998 to August, 1999 and the whole area was visited within two days, between 8 h and 18 h. When an individual *L. occipitalis* was spotted, the exact time and the animal's activity were recorded (such as basking, eating, foraging, etc.). Afterwards, the specimen was captured by hand. Immediately after being collected, the following parameters were measured: (1) body temperature (Tb), with a fast reading Schultheis cloacal quick reading thermometer (0.2 °C precision); (2) Microhabitat temperatures (same thermometer), including (a) substrate temperature (Ts) in the initial specimen location, and (b) air temperature (Ta), 1 cm above soil in the same point as Ts; (3) Sex; (4) SVL, snout-vent length (with a 0.1 mm precision caliper); and (5) BM, body mass (with a manual Pesola® balance with precision of 0.25 g).

The average temperature of all active individuals was considered as the optimal body temperature for *L. occipitalis*. The differences among seasons of the year, between sexes and among age classes were tested using a single factor ANOVA (Zar, 1984) and the HSD Tukey test for *a posteriori* multiple comparisons. Age classes are (1) young specimens (undetermined sex); (2) immature (SVL up to 45 mm for females and up to 50 mm for males); and, (3) adults (SVL higher than 45.1 mm, for females and higher than 50.1 mm for males). Regression and correlation analyses were performed for each season considering Tb x Ts and Tb x Ta, and the seasonal relative importance of each heat source was assessed. The relation between Tb and specimen size was also investigated using a regression analysis.

The curve of body temperature throughout the day was obtained by calculating the average of the temperatures measured in each time interval (hour) during the activity period of the animals. A temperature curve was obtained for each season of the year.

RESULTS

The observed mean SVL was 50.31 SD ± 9.83 mm (N = 270: 126 males, 142 females, and 2 young specimens), and the mean BM was 4.92 SD ± 2.62 g.

The mean body temperature of *L. occipitalis* was 30.89 °C (SD = 4.43; ranging from 16.4 to 40.2 °C; N = 270). The frequency of body temperatures is shown in Fig. 1.

There was a seasonal variation in individual body temperature (ANOVA, $F_{2.639} = 92.78$; $P < 0.001$), however, the Tb registered in fall and winter were not significantly different ($\text{Tukey}_{\alpha = 0.05}$; $P = 0.936$).

The mean temperatures for spring, summer, fall and winter were, respectively, 30.62 °C (SD = 3.74; N = 95); 33.87 °C, (SD = 1.97; N = 115); 25.76 °C (SD = 4.19; N = 44) and, 25.22 °C (SD = 2.15; N = 16). Mean Ta and Ts in spring were 25.02 °C (SD = 4.45; N = 95) and 29.82 °C (SD = 5.15; N = 95) respectively; 28,10 °C (SD = 1.87; N = 122) and 31.91 °C (SD = 3.36; N = 122), in summer; 21.67 °C (SD = 4.14; N = 66) and 23.27 °C (SD = 4.65; N = 66) in fall; 20.87 °C (SD = 0.84; N = 18) and 24.51 °C (SD = 2.43; N =18) in winter (see Fig. 2).

No differences of body temperature were observed between the sexes (ANOVA, $F_{3.877}=1.43$;

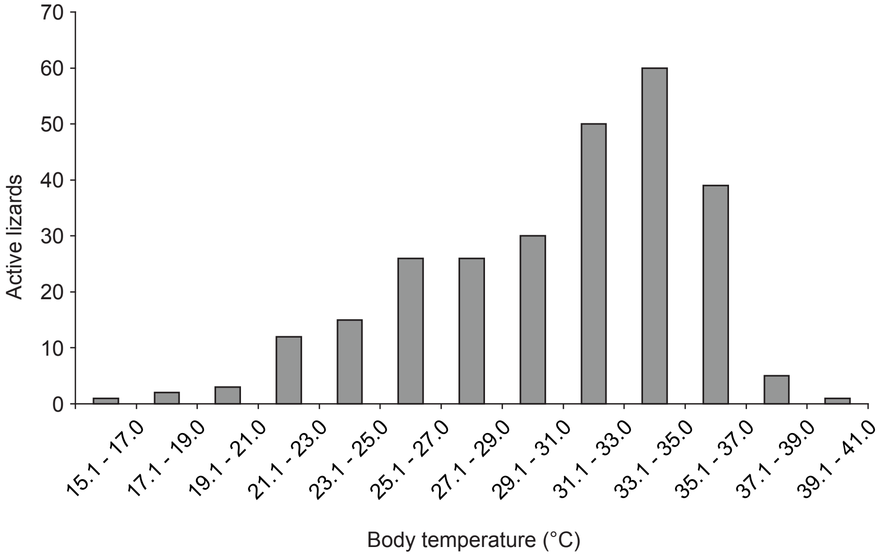

Fig. 1 — Frequency distributions of body temperatures of *Liolaemus occipitalis*, in the sand dunes of Quintão beach, Palmares do Sul-RS, recorded between September 1998 and August 1999. (N = 270).

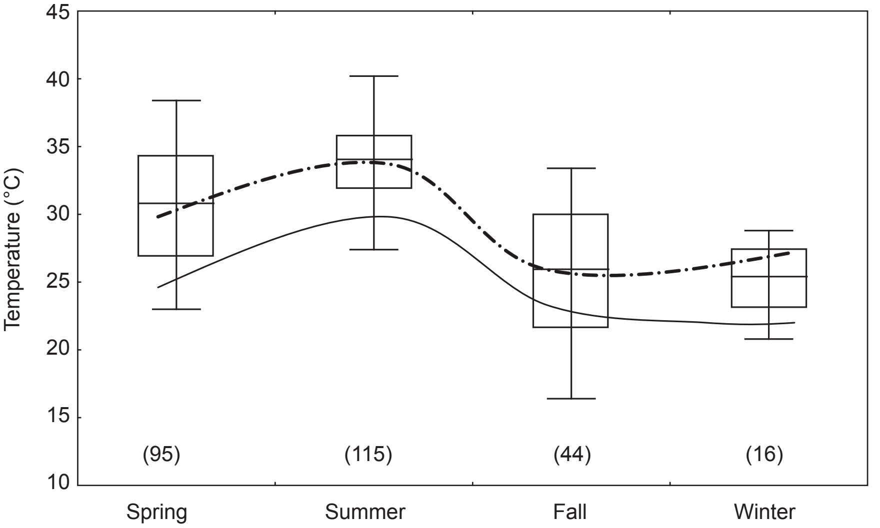

Fig. 2 — Seasonal changes in mean body temperature of *Liolaemus occipitalis* (horizontal line, mean body temperature; vertical line, range; vertical bar, standard deviation; numbers in parenthesis, sample size), and mean microhabitat temperatures (broken lines, mean substrate temperature, and solid lines, mean air temperature).

P = 0.233): mean body temperature for males was 30.63 °C (SD = 4.75; N = 126, range 16.4 to 40.2 °C) and 31.27 °C for females, (SD = 4.00; N = 142; range 18.2 to 38.2 °C).

Age class comparisons showed significant variations in Tb (ANOVA, $F_{2.406}$ = 107.25; P < 0.001): the mean body temperature for young specimens was 21.1 °C (SD = 0.85; N = 2); for the immature, it was 26.83 °C, (SD = 3.92; N = 86); and for adults was 32.92 °C (SD = 2.99; N = 182).

Body temperatures varied according to the time of day in all seasons and was closely related to thermal variations of the microhabitat (Fig. 3).

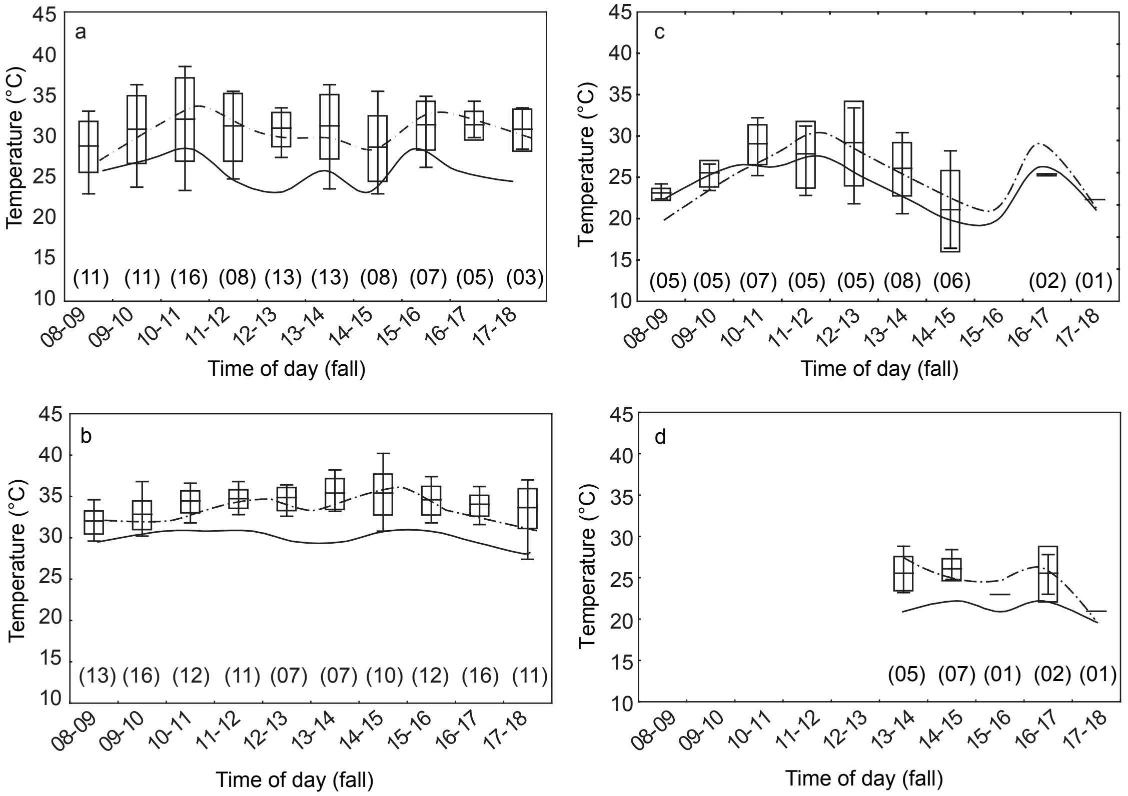

Fig. 3 — Diel changes in mean body temperature of *Liolaemus occipitalis* (horizontal line, mean body temperature; vertical line, range; vertical bar, standard deviation; numbers in parenthesis, sample size), and mean microhabitat temperatures (broken lines, mean substrate temperature, and solid lines, mean air temperature) on four seasons: a) Spring; b) Summer; c) Fall; and d) Winter.

The mean microhabitat temperatures (air and substrate temperatures) were significantly different (ANOVA, $F_{3.857} = 81.64$; $P < 0.001$): mean Ta was 25.74 °C (SD = 4.11; range 13.8 to 36.4 °C; N = 270), and mean Ts was 29.59 °C (SD = 5.20; range 15.2 °C to 40.8 °C; N = 270).

The analysis showed that microhabitat temperatures were significantly different among seasons (ANOVA, $F_{2.638} = 92.78$; $P<0.001$), although there were no significant differences specifically in fall and winter (Ta and Ts; $\text{Tukey}_{\alpha = 0.05}$; P=0.695).

The correlation between Tb and Ta (r = 0.828; $P < 0.001$; N = 270) and Tb on Ts (r = 0.855; $P < 0.001$; N = 270) were statistically significant (Fig. 4).

Body and microhabitat temperatures were positively correlated in spring ($r_{TbXTa} = 0.780$ and $r_{TbXTs} = 0.815$; $P < 0.001$; N = 95), summer ($r_{TbXTa} = 0.413$ and $r_{TbXTs} = 0.599$; $P < 0.001$; N = 115), fall ($r_{TbXTa} = 0.848$ and $r_{TbXTs} = 0.840$; $P < 0.001$; N = 44) and winter ($r_{TbXTs} = 0.679$; $P < 0.001$; N = 16). Only in winter was the correlation between Tb and Ta not significant ($r_{TbXTa} = 0.378$; P = 0.148; N = 16); Fig. 5.

DISCUSSION

Liolaemus occipitalis from the coastal dunes of Quintão presented a relatively low field body temperature (30.89 °C ± 4.43), when compared to other species of the genus from coastal areas of Chile: *L. fuscus* (34.2 °C), *L. leminiscatus* (34.7 °C), *L. nigromaculatus* (34.8 °C), *L. nitidus* (35.4 °C) and *L. platei* (35.5 °C) (Fuentes & Jaksic, 1979).

The differences in mean body temperatures among species of *Liolaemus* are probably not a

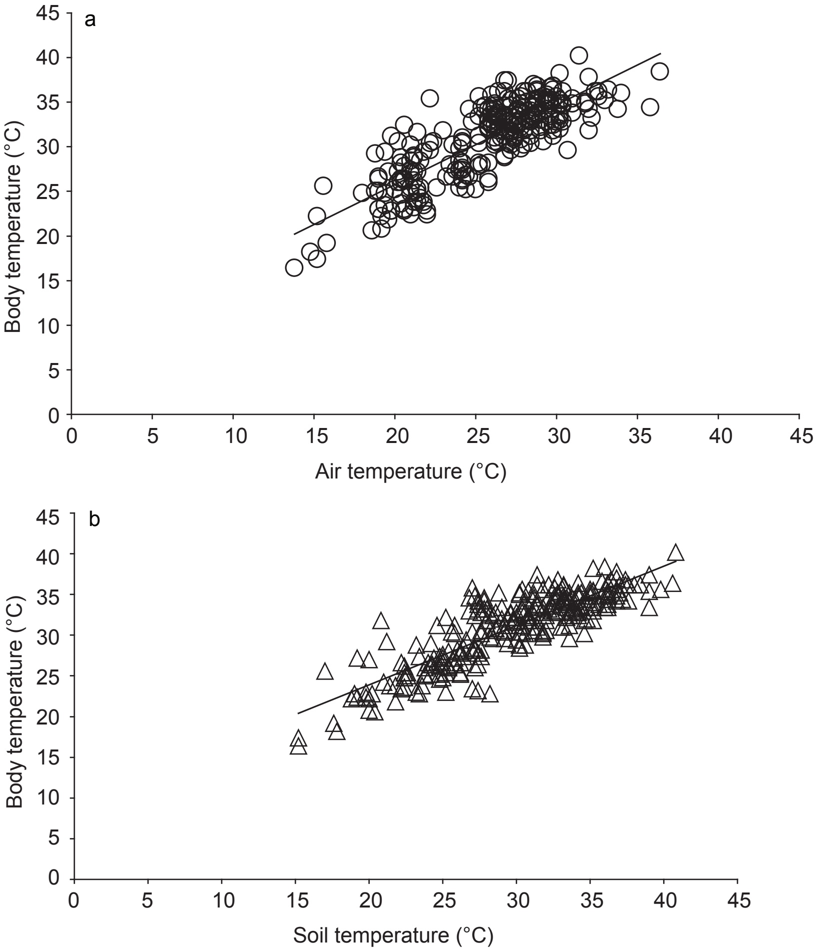

Fig. 4 — Relationship between air and body temperature (a), and soil and body temperature (b) of *Liolaemus occipitalis* in the sand dunes of Quintão beach, Palmares do Sul-RS, on four season. ($r_{TaxTb} = 0.828$; $r_{TsxTb} = 0.855$; $P < 0.001$; $N = 270$).

result of elevation differences alone, but may reflect differences in vegetation structure or wind exposure in the different habitats. They can also result from metabolic and physiological differences among populations, as observed in *Sceloporus merriami* by Beaupre *et al.* (1993).

Bogert (1949, 1959) established that related species of lizards usually have similar body temperatures and this has been observed by many authors who studied species of *Liolaemus* from central Chile (Fuentes & Jaksic, 1979; Valencia & Jaksic, 1981, and others) and southeastern Brazil (Rocha, 1995).

Liolaemus magellanicus, from Tierra del Fuego, in the southernmost tip of South America, presented a lower body temperature (27 °C) than *L. occipitalis* (Jaksic & Schwenk, 1983). These authors postulate that the lower optimal body temperature can be adaptive, meaning longer daily and seasonal activity periods in cold environments. Alternatively, it is possible that in the high latitude of Tierra del Fuego, insolation is insufficient to allow the body temperature to be increased by basking behavior. This confirms that certain ecological factors are dominant over phylogenetic ones (Bowker, 1984; Huey & Webster, 1975; Labra, 1992; Núnez, 1996).

Pianka (1977) and Magnusson (1993) postulated that the type of habitat used by a lizard species is an important factor for its body

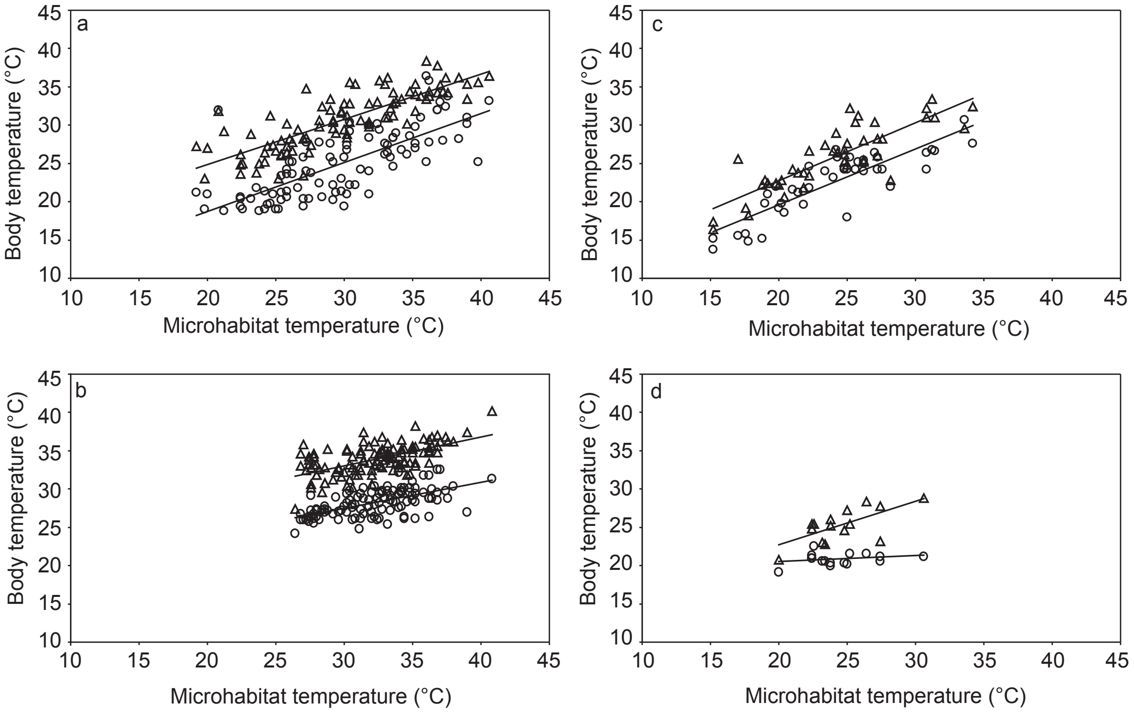

Fig. 5 — Relationship between microhabitat and body temperature of *Liolaemus occipitalis* in the sand dunes of Quintão beach, Palmares do Sul-RS. Diel variation on Spring (a) ($r_{TaxTb} = 0.780$; $r_{TsxTb} = 0.815$; $p < 0.001$; N = 95); on Summer (b) ($r_{TaxTb} = 0.413$; $r_{TsxTb} = 0.599$; $p < 0.001$; N = 115); on Fall (c) ($r_{TaxTc} = 0.848$; $r_{TsxTc} = 0.840$; $p < 0.001$; N = 44), and, on Winter (d) ($r_{TaxTb} = 0.378$; $p = 0.148$; $r_{TsxTb} = 0.679$; $p < 0.001$; N = 16).

temperature. Possibly, high body temperatures (between 33 and 37 °C) could be achieved by many Andean species because they live in dark rocky substrates, which can retain heat for longer periods.

Rocha (1995) argues that not only phylogenetic proximity influences the body temperature and its regulating range in lizards, but other life-history factors such as, foraging pattern, time and extension of activity in the habitat, and type of habitat are also important. Therefore, the low body temperature of *L. occipitalis* could be attributed either to its habitat – clear sand dunes, with scarce vegetation exposed to regular winds all year, and that retains heat for only a short period – or to intrinsic life-history factors. Or even to an interaction between these factors.

When the body temperature of *L. occipitalis* is compared to that of other lizards from arid environments (or strongly homogeneous habitats), and particularly of active foraging lizards (see Pianka, 1977; Pianka, 1986; Magnusson *et al.*, 1985), it will again be considered relatively low and variable. Recent studies (Bowker, 1984; Bowker *et al.*, 1986; Magnusson *et al.*, 1985; Bergallo & Rocha, 1993, Rocha, 1995) show that the average body temperature of active foraging lizards tends to be higher than the temperature of sympatric sedentary foraging lizards.

Pianka (1977) and Pianka *et al.* (1979) argue that species that emerge early in a habitat and that stay active for longer periods, tend to have lower and more variable body temperatures than sympatric species that start their activity later on, and consequently keep active for shorter periods. This can be true for *L. occipitalis* which, in spite of not being sympatric with other lizard species, is an exclusively diurnal species with a long activity period from 6 h to 18 h (Verrastro & Bujes, 1998).

Consequently, although the thermal patterns of *L. occipitalis* reflect phylogenetic affinities within the genus *Liolaemus*, the considerable variation in its body temperature and the relatively low optimal body temperature seem to result from the interaction among the thermal patterns of the local environment, the species activity pattern and its foraging mode, as observed by Rocha (1995).

The clustering of the body temperatures in the frequency histogram (Fig. 1) is typical of ectotherm vertebrates (Spellerberg, 1976; Werner & Whitaker, 1978; DeWitt & Friedman, 1979), which means that such field data represent a complex balance of energetic and ecological costs of thermoregulation and physiological requirements (Powell & Russell, 1985).

The results show an active shift in the thermoregulatory responses of lizards to the physical environment throughout the year. Although globally there is seasonal variation in the observed body temperatures, those registered in fall and winter were not statistically different when analyzed separately. During fall and winter, the temperatures registered in the dunes of Quintão were almost stable, demonstrating that the optimal body temperature of *L. occipitalis* can change seasonally according to alterations in the environmental heat sources (Mayhew, 1963; Pianka, 1971; Huey *et al.*, 1977; Rocha, 1995).

Similarly to what was observed by Rocha & Bergallo (1990), Rocha (1995) and Teixeira-Filho *et al.* (1995), there are three heat sources in the habitat of *L. occipitalis* that may influence its body temperature: direct solar radiation, air heat and substrate heat. The relative importance of these sources varies according to the period of the day and also seasonally. In the present study, direct solar radiation was not considered. Nevertheless, indirect field evidence showed its importance to *L. occipitalis*. The behavior of this species is similar to that observed for *L. lutzae* (Rocha, 1995), *Teius oculatus* (Bujes, 1998), and for a population of *L. occipitalis* studied by Verrastro & Bujes (1998). Early in the morning, while the rest of the body is still burrowed in the sand, it exposes its head to the sun until its body temperature increases enough to allow the onset of daily activities (Bogert, 1968). According to Rocha (1995), the main importance of direct solar radiation as a heat source in the early morning, is that it promotes fast heating of the body when it is still cold (and has low metabolic activity) and lizards are more susceptible to predators.

In Rio Grande do Sul, the four seasons of the year are well defined by temperatures and photoperiod, and our results showed that the relative importance of heat sources changes seasonally. In fact, the body temperatures of *L. occipitalis* were significantly correlated with microhabitat temperatures (air and substrate temperatures) throughout the year. The substrate temperature was more important in explaining the seasonal variations in body temperature (82% of the collected lizards in the spring; 60% in the summer; 84% in the fall and 68% in the winter) than air temperature (78% in spring, 41% in summer, 85% in fall and 38% in winter). The results show that substrate temperature is the most important heat source for thermoregulation in *L. occipitalis*, with the air temperature being of secondary importance. In spite of daily thermal variations, the mean Ts were always higher than Ta (Fig. 5) in all seasons of the year. This suggests that the difference between body and air temperatures is considerably higher than that between body temperature and substrate temperature. The main thermoregulating and escapement behavior of *L. occipitalis* is burrowing itself in the sand (Verrastro & Bujes, 1998). Therefore, in most of its activity period, this species keeps temperatures relatively lower than that of the superficial sand directly exposed to solar radiation. Besides keeping its Tb higher than Ta, *L. occipitalis* avoids the risk of predation related to exposure to the sun in open areas, as well as the constant heat loss caused by prolonged exposure to lower air temperatures. Similar findings were obtained by Rocha (1995) for *L. lutzae*.

The mean body temperature and the range of temperature regulation of *L. occipitalis* reflect the seasonal shifts in temperatures of microhabitat heat sources for this species. In spite of a vast literature on reptile thermoregulation, not much has been demonstrated about seasonal variations of thermal patterns (Christian *et al.*, 1983, Rocha, 1995). Some field studies have shown that optimal body temperature of lizards can change seasonally and that this change can be influenced by variations in the environmental heat sources (Mayhew, 1963; McGinnis, 1966; Mayhew & Weintraub, 1971; Pianka, 1971; Huey *et al.*, 1977; Rocha, 1995).

CONCLUSION

Our results indicate that *Liolaemus occipitalis* is a saxicolous, tigmothermic and heliothermic species that regulates its body temperature through behavioral mechanisms. Its optimal body temperature varies on a daily and seasonal basis, according to thermal variation in the microhabitat. The substrate temperature is the most important heat source for the thermoregulation of *L. occipitalis*. The body temperature of *L. occipitalis*, in spite of being lower, is relatively similar to that of other species of *Liolaemus*.

Acknowledgments — Technical and administrative support were provided by the Post-Graduation Program in Zoology, Pontifícia Universidade Católica do Rio Grande do Sul and by the Herpetology Sector, Department of Zoology, Universidade Federal do Rio Grande do Sul. We are grateful to Dr. Thales de Lema, first author advisor during this work, to Rodrigo Caruccio, Carolina Castilhos, Marina Picolli and Janaína Bujes, for helping in the fieldwork. Financial support was provided by CAPES.

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