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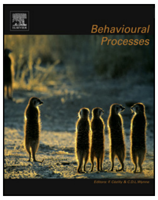

Seasonal variations in behaviour of thermoregulation in juveniles and adults *Liolaemus lutzae* (Squamata, Liolaemidae) in a remnant of Brazilian restinga

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Adaptations of lizards inhabiting hot arid environments should include mechanisms of behavioural thermoregulation. In contrast, in environments with lower temperatures lizards tend to behave as thermoconformers. Herein we aim to infer thermoregulatory behaviours exhibited by *Liolaemus lutzae* (a lizard species endemic to restingas in the coast of the state of Rio de Janeiro, Brazil) in two different seasonal thermal environments. In the dry season, the body temperatures (T_b) of the lizards were higher than air temperature (T_a) and similar to substrate temperature (T_s), suggesting thermoconformer thermoregulatory behaviour using T_s. During the rainy season, the higher percentage of negative values of ΔT_s ($=T_b - T_s$) and ΔT_a ($=T_b - T_a$) and the tendency for lower T_b compared to T_s suggest a more active behavioural thermoregulation in that season. The ΔT_s was higher for juveniles in the rainy season, suggesting that youngest lizards tended to thermoregulate more actively regarding to T_s than adults. *L. lutzae* probably survives under high T_s due to the behaviour of the individuals sheltering inside burrows or under detritus and burying themselves into the sand. This behavioural flexibility may potentially reduce variations in T_b of active lizards in changing thermal environments both during the daily cycle and between seasons.

1. Introduction

Active behavioural adjustments are the main mechanism for proper accomplishment of thermoregulation by lizards (Cowles and Bogert, 1944; Bogert, 1949, 1959; Castilla et al., 1999; Rocha et al., 2009a). This is of relevance considering that body temperature affects overall fitness and performance of different processes of these animals (Adolph and Porter, 1993; Autumn et al., 1994; Brown et al., 2004). Nevertheless, lizards of some species might exhibit thermoconformer behaviour, i.e., their variation in activity body temperatures tend to be similar to that of the surrounding thermal environment (Pough et al., 1998; Kohlsdorf and Navas, 2006). Lizards in the genus *Liolaemus* from different climatic conditions appear to have some level of flexibility regarding their thermal biology, because they are capable of modifications in thermal physiology and behavioural thermoregulation, and have temperature preferences adapted to local thermal environments where they occur (Labra et al., 2009; Rodríguez-Serrano et al., 2009).

Liolaemus lutzae (Liolaemidae) is a lizard species restricted to restinga (sandy coastal plain) habitats along the coast of the state of Rio de Janeiro, in southeast Brazil. The small geographic distribution of these lizards is confined to a narrow coastal strip of beach habitat between the Restinga da Marambaia in the municipality of Rio de Janeiro, and the Restinga of Peró beach in the municipality of Cabo Frio (Vanzolini and Ab'Saber, 1968; Rocha et al., 2009b). This species has a relatively restricted spatial niche, living mainly in the beach habitat covered by halophilous-psammophilous-reptant vegetation (plants adapted to well-drained sandy soils, intense wind regimes, and salt stress) near the sea, which is exposed to high temperatures and intense solar radiation (Rocha, 1988, 1995; Maia-Carneiro et al., 2012; Maia-Carneiro and Rocha, 2013a,b). Lizards of this species dig burrows in the sand, which they use as refuge from predators (Rocha, 1996a; Maia-Carneiro and Rocha, 2013b), and possibly also to avoid the high environmental temperatures of restinga habitats (Rocha, 1988; Maia-Carneiro and Rocha, 2013b).

The availability of thermally suitable microhabitats is potentially the main factor limiting lizard diversity in hot arid environments (Melville and Schulte, 2001). The beach habitat of restingas where *L. lutzae* lives are open environments in which the substrate temperatures can achieve values around 50 °C (Rocha, 1988; Maia-Carneiro et al., 2012; Maia-Carneiro and Rocha, 2013a), besides offering limited shaded refuges to protect lizards from

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sunlight. These environmental characteristics may lead to overheating of lizards, which can be fatal (Mosauer, 1936). Adaptations of lizards inhabiting such hostile environments should include mechanisms of behavioural thermoregulation (Huey and Pianka, 1977; Melville and Schulte, 2001; Kohlsdorf and Navas, 2006; Maia-Carneiro and Rocha, 2013a,b). In contrast, in environments with lower temperatures lizards tend to behave as thermoconformers (Pough et al., 1998; Herczeg et al., 2003; Kohlsdorf and Navas, 2006). Based on these assumptions, herein we compare thermoregulatory behaviours exhibited by juveniles and adults of *L. lutzae* in a restinga beach habitat. Considering the occurrence of seasonal climatic changes in the study area (Scarano, 2002; Maia-Carneiro et al., 2012; Maia-Carneiro and Rocha, 2013a), we attempted to characterize variations in thermoregulatory behaviour displayed by the lizards between seasons with different thermal regimes.

2. Material and methods

2.1. Study area

Field work was conducted in the restinga habitat of Praia Grande (22° 57′ S, 42° 02′ W), municipality of Arraial do Cabo, state of Rio de Janeiro, southeast Brazil. Restingas are habitats originated in the Quaternary that are characterized by sandy soils with high salt concentration and predominance of herbaceous and shrubby vegetation (Suguio and Tessler, 1984). The study area is located near the Área de Proteção Ambiental da Massambaba, an area which is under a higher level of human pressure than other restingas in the same region (Rocha et al., 2009c). The climate in the area is markedly seasonal, with higher precipitation and temperatures concentrated in the summer (rainy season). Mean annual precipitation is approximately 800 mm and mean annual temperature averages 25 °C (Scarano, 2002).

2.2. Data collection

Data were collected in June, July, and September (dry season), and in November and December (rainy season) 2011 using visual encounter surveys (VES) (Crump and Scott, 1994) constrained by time (30 min) to search and capture the lizards. We delimited a study area in the beach habitat parallel to the shore measuring 60 m × 500 m. The VES were performed within the delimited area at each hourly interval between 06:00 h and 18:00 h. Whenever an individual of *L. lutzae* was sighted, an attempt was made to capture it by hand. Sampling effort totalled 4680 min (2880 min in the dry season and 1800 min in the rainy season).

The body temperature (T_b) of each captured lizard was measured using a Schultheis® quick-reading cloacal thermometer (precision of 0.2 °C). We only considered the body temperatures obtained within a maximum interval of 30 s after the first sighting of each lizard. Microhabitat temperatures [substrate temperature (T_s) at the point where the lizard was first sighted, and air temperature (T_a) 1 cm above the substrate at the same point] were also measured. The microhabitat temperatures were considered as measurements of the thermal environment experienced by the lizards.

2.3. Data analyses

We evaluated the degree of behavioural thermoregulation (ΔT) by calculating the difference between T_b in activity and corresponding environmental temperatures, where $\Delta T_s = (T_b - T_s)$ and $\Delta T_a = (T_b - T_a)$ (Vrcibradic and Rocha, 1998; Kiefer et al., 2007; Sousa and Freire, 2011). Active thermoregulatory behaviours imply that a lizard maintains the T_b within ranges suitable for its physiological processes, which does not simply reflect the environmental temperatures experienced by them (Kiefer et al., 2007). Conversely, passive thermoregulation results from a lizard maintaining a T_b similar to those environmental temperatures experienced during activity (Kiefer et al., 2007). Therefore, the degree of active thermoregulation was estimated based on the difference between body temperature and the temperatures of the surrounding thermal environment (Vrcibradic and Rocha, 1998; Kiefer et al., 2007). The larger the absolute value of ΔT_s and ΔT_a, the higher the degree of thermoregulation (active thermoregulation) in relation to the environmental temperatures (substrate and air, respectively) (Vrcibradic and Rocha, 1998; Kiefer et al., 2007). The ΔT_s and ΔT_a were calculated for *L. lutzae* in each season and for each age class using the arithmetic mean ± standard deviation (SD). The degree of behavioural thermoregulation was also estimated by calculating the percentage of negative values of ΔT_s and ΔT_a, which indicates the frequency at which body temperatures were lower than environmental temperatures. High percentages of negative values would therefore indicate a higher degree of active thermoregulation relative to environmental temperatures (Vrcibradic and Rocha, 1998; Kiefer et al., 2007).

In order to evaluate differences between the T_b of both juvenile and adult lizards and the environmental temperatures (air and substrate) which they experienced, we performed either one-way analyses of variance (ANOVA) or Mann–Whitney *U* tests depending on whether the data conformed to the assumptions of normality and homogeneity of variances (Zar, 1999). Additionally, to test for differences between T_a and T_s for lizards in each age class at each season, we performed either ANOVA or Mann–Whitney *U* tests depending on the assumptions (Zar, 1999). To evaluate differences in both ΔT_s and ΔT_a between juveniles and adults in each season we performed Mann–Whitney *U* tests (Zar, 1999). To test for differences in both juveniles and adults regarding ΔT_s and ΔT_a between seasons we performed Mann–Whitney *U* tests (Zar, 1999). Age classes of lizards (juvenile or adult) were assessed on the basis of the minimum size at maturity known for males and females of *L. lutzae* (Rocha, 1992).

3. Results

In the dry season, the T_b of both juvenile and adult lizards and the T_s experienced by them did not differ statistically (juveniles: ANOVA, $F_{1,188} = 0.419$, $P = 0.518$; adults: ANOVA, $F_{1,74} = 1.469$, $P = 0.229$) (Table 1), but there were significant differences between T_b of both juvenile and adult lizards and T_a (juveniles: Mann–Whitney, $U = 2832.5$, $P < 0.0001$; adults: Mann–Whitney, $U = 181.5$, $P < 0.0001$), with higher values for T_b (Table 1). In the rainy season, juveniles had T_b lower than T_s (ANOVA, $R^2 = 0.141$, $F_{1,34} = 5.589$, $P = 0.024$), but the T_b of adult lizards did not differ from T_s (ANOVA, $F_{1,138} = 3.283$, $P = 0.072$) (Table 1). In the rainy season, T_b of juveniles did not differ from T_a (ANOVA, $F_{1,34} = 0.523$, $P = 0.475$), but T_b of adults was significantly higher than T_a (ANOVA, $F_{1,138} = 37.450$, $P < 0.001$) (Table 1). At both dry (juveniles: Mann–Whitney, $U = 2950.0$, $P < 0.0001$; adults: Mann–Whitney, $U = 355.0$, $P < 0.0001$) (Fig. 1) and rainy (juveniles: ANOVA, $F_{1,34} = 9.677$, $P = 0.004$; adults: ANOVA, $F_{1,138} = 34.946$, $P < 0.0001$) (Fig. 2) seasons the T_s experienced by *L. lutzae* was higher than the T_a (Table 1).

The differences between T_b and T_s (ΔT_s) did not differ between age classes in the dry season (Mann–Whitney, $U = 1906.5$, $P = 0.613$), but differed significantly in the rainy season (Mann–Whitney, $U = 441.0$, $P = 0.05$), with higher values for juveniles (Table 2). In the dry season, the differences between T_b and T_a (ΔT_a) were significantly higher for adults than for juveniles (Mann–Whitney, $U = 2653.0$, $P < 0.0001$) (Table 2). In the rainy season, there was no

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