

## THERMOREGULATORY BEHAVIOR OF THE SAXICOLOUS LIZARD, *TROPIDURUS TORQUATUS* (SQUAMATA, TROPIDURIDAE), IN A ROCKY OUTCROP IN MINAS GERAIS, BRAZIL

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**Abstract.**—We studied the body temperature of the Saxicolous Lizard (*Tropidurus torquatus*) in a rocky outcrop of Minas Gerais State, Brazil. The influence of seasonality and the importance of microhabitat temperatures (substrate and air) for *T. torquatus* body temperature regulation were investigated. The mean body temperature of active *T. torquatus* was  $31.2 \pm 3.1^{\circ}\text{C}$  ( $21.0\text{--}37.0^{\circ}\text{C}$ ) and was subject to seasonal variation probably resulting from the adjustment of lizards to changes in the local thermal environment.

**Key Words.**—acclimation process; body temperature; Iguanidae; local adaptation; thermal ecology; thermal regulation; *Tropidurus torquatus*.

### INTRODUCTION

Lizards, like other ectothermic animals, rely on environmental resources to obtain the heat necessary for their body temperature regulation (Bogert 1949, 1959; Huey and Slatkin 1976). Lizards thermoregulate by physiological processes and behavioral mechanisms (Goin et al. 1978). Biochemical reactions in the body proceed optimally within a small range of temperatures, so body temperature is a major factor affecting behavior in ectotherms (Bennett 1980).

Ectotherms attain behavioral thermoregulation by extending or reducing basking time (Cowles and Bogert 1944; Pianka 1986), shifting between sunny and shady areas (Rocha 1988) and/or through regulation of activity periods (Rocha and Bergallo 1990). Lizards usually maintain optimal body temperatures by changing their position in relation to the sun moving to thermoregulation sites to maintain optimal body temperatures (Bogert 1959; Crowley and Pietruszka 1983; Teixeira-Filho et al. 1995).

A lizards' body temperature during active periods varies between the higher values reached during diurnal activities and the lower levels that trigger the end of these activities and the search for shelter. Within this temperature range there is an optimal body temperature for foraging, reproduction, communication, defense, escape from predators, and other social interactions (Bogert 1948, 1959; Brattstrom 1965). However, body

temperature regulation is a complex process, influenced by environmental heat sources and features of the ecology and life history of the species (Huey and Pianka 1983; Pianka 1986; Rocha 1994).

The South American *Tropidurus* of the *torquatus* group (sensu Frost et al. 2001) comprises mainly heliophilous, predominantly insectivorous lizards, living in open habitats such as semiarid caatingas, cerrados, chaco, restingas (coastal sand-dune habitats), savanna enclaves, clearings within mesic lowland forest, and rock outcrop formations (Rodrigues 1987, 1988; Vitt 1993; Vitt et al. 1996). Some species have broad geographic distributions and are mostly microhabitat generalists (e.g., *Tropidurus etheridgei*, *T. hispidus*, *T. itambere*, *T. oreadicus*, and *T. torquatus*; Rodrigues 1988), whereas, other species have more restricted distributions, with more specialized habitat/microhabitat requirements (e.g., *T. cocorobensis*, *T. erythrocephalus*, *T. mucujensis*, *T. psammonastes*, and *T. semitaeniatus*; Rodrigues 1988; Vitt 1995).

The tropidurid lizard *T. torquatus* Wied, 1820 has a wide geographic range and is typical of open areas, occurring from central Brazil to northern Argentina (Rodrigues 1987, 1988). This lizard is a ground dwelling, diurnal species that remains active during the entire photophase of the photoperiod. It lives mainly on rocks, termite nests, and logs, but has also been observed climbing walls and trees with ease (Rodrigues 1987; Van Sluys 1992; Bergallo and Rocha 1993; Rocha 1994). In

Brazil, the species has three distinct groups of populations: an insular group in Abrolhos archipelago (a set of five islands located approximately 70 km off the southern coast of the state of Bahia), an inland group (occurring in cerrado and open areas belonging to the Atlantic Forest Domain), and a coastal group (found in sand-dune habitats in the states of Rio de Janeiro, Espírito Santo and Bahia) (Rodrigues 1987). We report the body temperature during activity of an inland *T. torquatus* population belonging to the Atlantic Forest Domain, in southeastern Minas Gerais state, Brazil. Therefore, we address the following questions: (1) What is the mean body temperature of active *T. torquatus* in different periods of the year?; (2) Which of the microhabitat temperatures (substrate or air) constitutes *T. torquatus* most important heat source for body temperature regulation?; and (3) Do the relative importance of these heat sources vary seasonally?

## MATERIALS AND METHODS

**Study area.**—Our study site was a rocky outcrop (60 x 90 m) near the left bank of the Peixe River (21°48'27.5"S; 43°35'31.7"W, datum: WGS84; altitude 697 m) in the Toledos district, Juiz de Fora municipality, in Zona da Mata Region, southeastern Minas Gerais, Brazil. Herbaceous-shrubby vegetation and under-developed trees growing among quartzitic blocks characterize the study area (locally known as "Funil"). The dominant plant families at the study site included the Apocynaceae (*Mandevilla tenuifolia*), Asteraceae (*Eremanthus erythropappus*), Bromeliaceae (*Dyckia* sp.), Leguminosae (*Clitoria* sp.), Melastomataceae, Myrtaceae, and Velloziaceae (*Vellozia* sp.) (Salimena, unpubl. data). The climate is a Cwa of Köppen (highland tropical climate), with two definite seasons. One that is hot and wet (October through April) and another that is cold and dry (May through September). The annual average precipitation is greater than 150 cm, the mean annual temperatures oscillate around 19.4° C, and the altitude ranges between 700 to 900 m (Plano Diretor, J.F. Print vs. the internet: Clima de Juiz de Fora. 2006. Available from <http://www.pjf.mg.gov.br/cidade/clima.php> [Accessed 22 January 2006]).

**Collecting methods and analyses.**—We conducted fieldwork monthly in three-day trips during portions of the wet (January, February, March, and April 2005) and dry (May, June, August, and September 2005) seasons. A pair of observers conducted diurnal transects at hourly intervals from 08:00 to 17:00 on both sunny and cloudy days along six well-demarcated trails measuring approximately 90 m long and spaced 10 m apart across all rocky outcrop habitat in the focal area. Observers

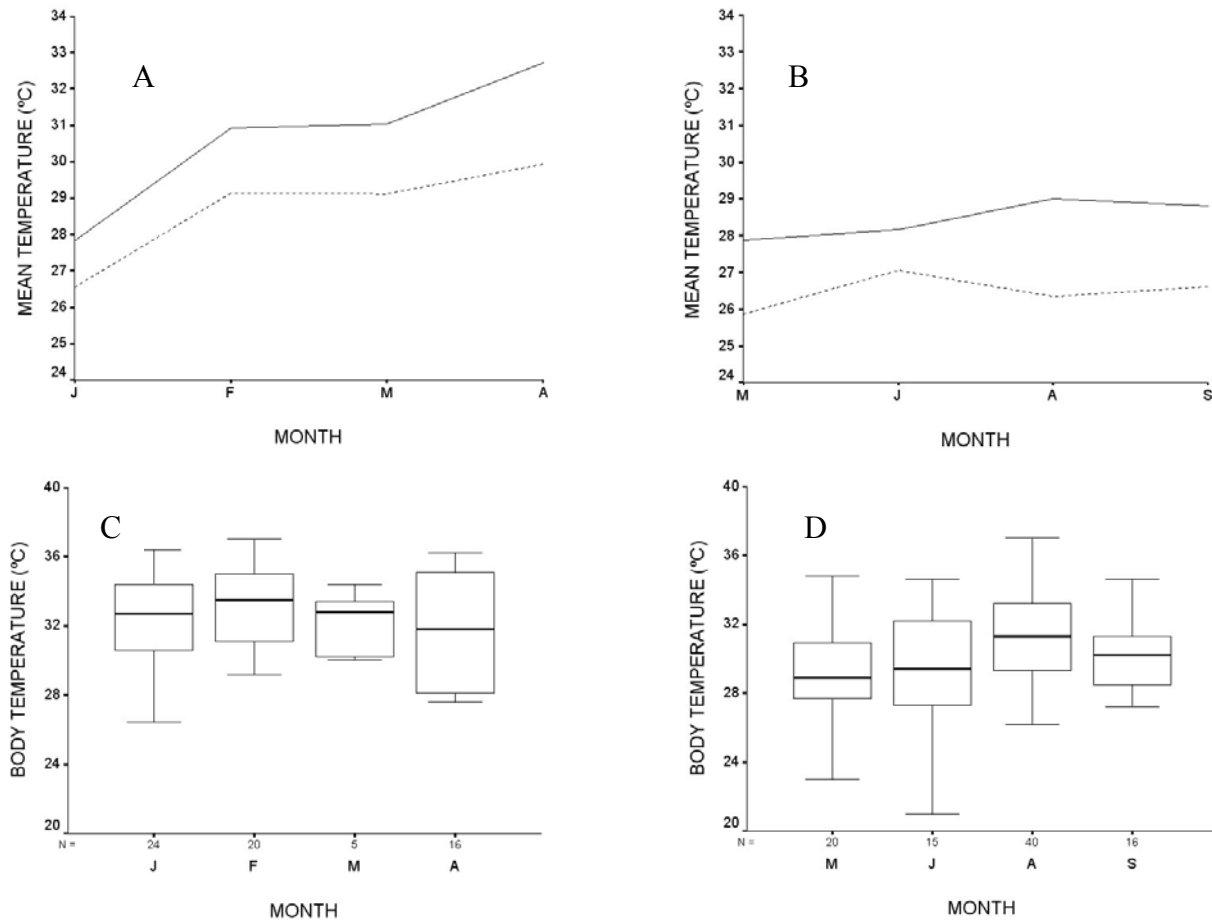
used a nylon noose or hand capture to catch active lizards observed along these paths.

We used a Schulteis quick-reading thermometer (to the nearest 0.2°C) to measure cloacal temperature, and the substrate temperature and the air temperature in the microhabitat 1 cm above the original location of the lizard. We only included body temperatures in our analyses that we obtained within 30s after capture. We positioned the thermometer in surface concavities of irregular substrates such as rocks, to reduce the possible confounding effect of air temperature on the substrate temperature. We recorded the lizards' position with respect to the sun as: sun; filtered sun; or shade. We used elastic hair bands to mark lizards (Ribeiro and Sousa 2006), which can be fitted to a lizard's neck to allow individual identification. Elastic hair bands did not appear to strongly influence lizard movements, and remained intact on lizards for at least three months. We used different colored hair bands to identify individuals, to avoid recaptures during the same month, and for the subsequent study of home range. We determined the sex of lizards and then measured their snout-vent length (SVL, to the nearest 0.1 mm) with manual calipers. We classified individuals as adults according to the minimum maturity size (70 mm for adult males and 65 mm for adult females) established by Wiederhecker et al. (2002).

We identified mean body temperature of *T. torquatus* during activity as the mean cloacal temperature recorded for all active lizards. We used a two-way ANOVA (Zar 1999) to test for seasonal variation and maturity effects on body temperature. We also analyzed seasonal changes in the effects of substrate and air temperatures, and SVL on body temperature using regression analysis. We tested for sexual differences in mean body temperatures during activity using one-way ANOVA (Zar 1999). The significance level adopted for obtaining critical values on all tests was  $\alpha = 0.05$ . Descriptive statistics are represented in the text as mean  $\pm$  SD.

## RESULTS

The mean body temperature of active *T. torquatus* was  $31.2 \pm 3.1^\circ\text{C}$  ( $N = 156$ ), with a range of  $21.0$ – $37.0^\circ\text{C}$ . However, both body and microhabitat temperatures varied during the eight month study period (Fig. 1). Season and maturity did not interact to affect the lizards' body temperatures ( $F_{1,152} = 0.119$ ,  $P = 0.730$ ). It was not affected by the maturity level of the lizard either ( $F = 0.045$ ,  $df = 1$ ,  $P = 0.833$ ). Seasonality affected the body temperature of *T. torquatus*. In the wet season, body temperature ( $32.4 \pm 2.7^\circ\text{C}$ ,  $N = 65$ ) was higher than in the dry season ( $30.4 \pm 3.0^\circ\text{C}$ ,  $N = 91$ ) ( $F_1 = 18.533$ ,  $P < 0.01$ ). Likewise, microhabitat temperatures in the wet season (Air =  $28.3 \pm 3.7^\circ\text{C}$ , Substrate =  $30.2 \pm 4.5^\circ\text{C}$ ,  $N = 65$ ) were higher than microhabitat temperatures during



**FIGURE 1.** Mean substrate (solid lines) and air (dashed lines) temperatures (A, B), and body temperature of active *Tropidurus torquatus* during portions of the wet (C: January, February, March, and April 2005), and dry (D: May, June, August and September 2005) seasons, in the Toledo district, Juiz de Fora, Minas Gerais, Brazil.

the dry season (Air =  $26.4 \pm 3.1^{\circ}\text{C}$ ; Substrate =  $28.5 \pm 4.1^{\circ}\text{C}$ , N = 91) (Air:  $F_1 = 12.473$ ,  $P < 0.01$ ; Substrate:  $F_1 = 5.484$ ,  $P < 0.05$ ).

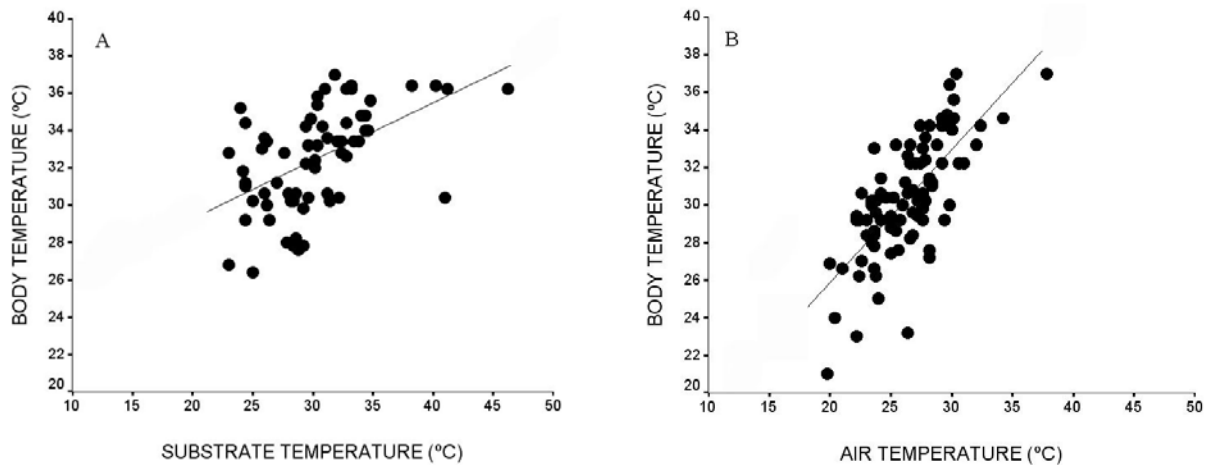
In both seasons body temperatures were related to air (Wet:  $r^2 = 0.25$ ,  $\beta_{\text{standardized}} = 0.50$ ,  $df = 1$ ,  $P = 0.0001$ , N = 65; Dry:  $r^2 = 0.53$ ,  $df = 1$ ,  $\beta_{\text{standardized}} = 0.72$ ,  $P = 0.0001$ , N = 91) and substrate temperatures (Wet:  $R^2 = 0.27$ ,  $\beta_{\text{standardized}} = 0.52$ ,  $df = 1$ ,  $P = 0.0001$ , N = 65; Dry:  $r^2 = 0.47$ ,  $df = 1$ ,  $\beta_{\text{standardized}} = 0.69$ ,  $P = 0.0001$ , N = 91). It must be emphasized that the increase in one unit in each of the microhabitat temperatures (substrate and air) implies a “ $\beta$ ” increase on lizards’ body temperature. Thus, in the wet season the substrate temperature better explained the variation on lizards’ body temperature (larger  $\beta$ -standardized coefficient), whereas in the dry season air temperature accounted for most of the variation in body temperature ( $r^2 = 0.53$ ; Fig. 2). Lizard body temperatures did not differ between males and females ( $F_{1,136} = 1.749$ ,  $P = 0.188$ ), and were not related to SVL ( $r^2 = 0.0001$ ,  $df = 1$ ,  $P = 0.885$ , N = 156).

The number of lizards exposed in sun, shade, filtered sun varied throughout the day (Fig. 3). Lizards

remained in exposed locations and pressed against warm rocks when it was cloudy. When direct sun was available, lizards were active in filtered sun or shade. We seldom encountered lizards in full sun from 11:00-15:00 (Fig. 3). *Tropidurus torquatus* that initiated activities after leaving their burrows usually remained close to burrow openings on the boulders. They kept their dorsum oriented perpendicularly towards the sun and the whole ventral region of the body in contact with the rock surface. Lizards remained in this position for approximately 30 min ( $30.8 \pm 6.4$  min, N = 12), and as the temperature warmed, they retreated to the shade in rock cracks or mixed sunlight and shade areas under vegetation.

## DISCUSSION

In the district of Toledo, the mean body temperature of active *T. torquatus* ( $31.2 \pm 3.1^{\circ}\text{C}$ ) was similar to that recorded by Van Sluys et al. (2004) for congeneric species such as *T. montanus* ( $31.7 \pm 3.5^{\circ}\text{C}$ ) and *T. hispidus* ( $32.2 \pm 3.4^{\circ}\text{C}$ ) in “campos rupestres” (rocky



**FIGURE 2.** Relationship between mean active body temperature and mean substrate temperature (A) in the wet season, and mean air temperature (B) in the dry season for population of *Tropidurus torquatus*, in the Toledos district, Juiz de Fora, Minas Gerais, Brazil.

meadows) habitat of Minas Gerais. Most studies on the thermal ecology of *T. torquatus* populations took place in coastal restingas and oceanic islands of the Abrolhos archipelago (Bergallo and Rocha 1993; Teixeira-Filho et al. 1996; Gandolfi and Rocha 1998; Hatano et al. 2001; Rocha et al. 2002; Kiefer et al. 2005). Their observed mean temperatures (34.0–35.6° C) were relatively higher than the mean body temperature of 31.2°C that we found. *Tropidurus hispidus* from Pernambuco State's caatinga (35.9°C; Vitt 1995), in rock outcrops of the Amazon Forest in the state of Roraima (34.1°C; Vitt et al. 1996), and in an area of “campos rupestres” in Minas Gerais (32.2°C; Van Sluys et al. 2004) also had warmer body temperatures than we observed (Table 1).

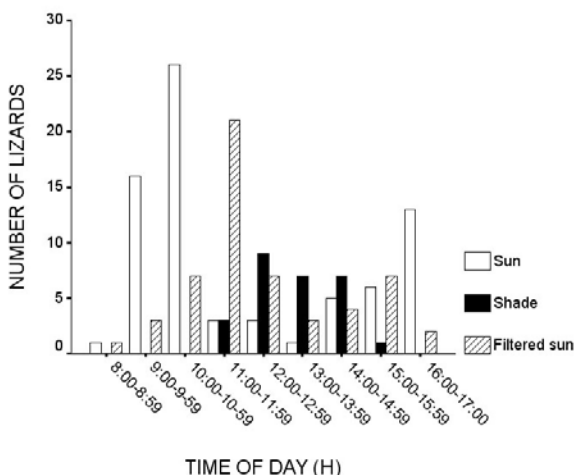
According to Brattstrom (1965) and Licht et al. (1966), phylogenetically related species of lizards tend to maintain similar body temperatures, even when living in different habitats. Nonetheless, the type of habitat used by these lizards is also an important factor that

influences their body temperatures (Pianka 1977; Magnusson 1993). In some cases a species living in habitats with cooler temperatures may have lower body temperatures than the conspecifics in warmer habitats (Fuentes and Jaksic 1979; Jaksic and Schwenk 1983). Thus, the relatively cooler temperatures typical of the state of Minas Gerais, especially at Zona da Mata Region may cause the differences in body temperature between this study and previous reports.

The lowest body temperatures previously recorded during activity for the Brazilian tropidurid lizards are found in species from forest habitats of the Amazon region, such as *Uranoscodon superciliosum* (26.6°C; Howland et al. 1990), *Plica plica* (30.7°C; Vitt 1991) and *P. umbra* (29.1°C; Vitt et al. 1997). The low mean body temperatures known for this species occurring in forested areas is probably due to the lower availability of sunlit areas used for thermoregulation. It is likely also a consequence of the lower temperatures of the

**TABLE 1.** Comparative data on mean active body temperature ( $T_b$ ) recorded for six Brazilian species of *Tropidurus* in areas of restinga (1) (marked with an asterisk, range of mean active body temperature of *Tropidurus torquatus* in ten restinga populations); oceanic islands (2); cerrado (3); “campos rupestres” (4); rock outcrops of the Mata Atlântica (5) and of the Amazon Forest (6); caatinga (7), from 1990 to 2005.

Species	$T_b$ (°C)	Locality	Source
<i>T. torquatus</i>	30.8–36.2*	Bahia; Espírito Santo; Rio de Janeiro (1)	Kiefer et al. (2005)
<i>T. torquatus</i>	34.0	Abrolhos, BA (2)	Rocha et al. (2002)
<i>T. torquatus</i>	34.8	Jurubatiba, RJ (1)	Hatano et al. (2001)
<i>T. torquatus</i>	34.0	Linhares, ES (1)	Gandolfi and Rocha (1998)
<i>T. torquatus</i>	35.3	Barra de Maricá, RJ (1)	Teixeira-Filho et al. (1996)
<i>T. torquatus</i>	35.6	Linhares, ES (1)	Bergallo and Rocha (1993)
<i>T. itambere</i>	33.0	Pirenópolis, GO (3)	Faria and Araújo (2004)
<i>T. itambere</i>	34.1	Valinhos, SP (5)	Van Sluys (1992)
<i>T. montanus</i>	31.7	Diamantina, MG (4)	Van Sluys et al. (2004)
<i>T. hispidus</i>	32.2	Diamantina, MG (4)	Van Sluys et al. (2004)
<i>T. hispidus</i>	34.1	Roraima (6)	Vitt et al. (1996)
<i>T. hispidus</i>	35.9	Pernambuco (7)	Vitt (1995)
<i>T. oreadicus</i>	33.4	Pirenópolis, GO (3)	Faria and Araújo (2004)
<i>T. oreadicus</i>	32.9	Pará (6)	Vitt (1993)
<i>T. oreadicus</i>	35.8	Pará (6)	Rocha and Bergallo (1990)
<i>T. semitaeniatus</i>	37.1	Pernambuco (7)	Vitt (1995)



**FIGURE 3.** Number of active *Tropidurus torquatus* with respect to position in sun, filtered sun or shade based on the original location where lizards were first sighted from 8:00-17:00 h, during both wet and dry seasons in the Toledos district, Juiz de Fora, Minas Gerais, Brazil.

microhabitat in these sites relative to open environments. The body temperature of sedentary foraging lizards tends to be lower and more variable than in the active foragers (Pianka 1977; Magnusson et al. 1985; Bowker et al. 1986; Menezes et al. 2000). In Toledos, *T. torquatus* remains active for long periods of the day. Generally lasting until at least 17:00, and their mean body temperatures during activity are considerably lower than that of other species of active foraging lizards (usually between 36.5 and 39.7°C) (Rocha 1994; Vitt 1995; Colli and Paiva 1997; Menezes et al. 2000; Dias and Rocha 2004). Thus, the low mean active body temperature recorded for this *T. torquatus* population in Toledos may be explained in part by the association between the effects of local environmental thermal patterns, the active period, and the foraging mode of this species.

The body temperatures of active *T. torquatus* did not differ between the sexes. This follows observations of *Liolaemus lutzae* (formerly belonging to the family Tropiduridae; Rocha 1995). Likewise, body temperature was not related to SVL. This suggests ontogenetic differences in this factor do not exist. This resembles observations of *T. torquatus* at the Abrolhos archipelago (Rocha et al. 2002) and in ten coastal restingas (Kiefer et al. 2005).

Three heat sources (direct solar radiation, substrate temperature, and air temperature) influence the body temperature of *T. torquatus*. The importance of direct solar radiation is to promote warming of the body during the early hours of the day when body temperatures are still low (around 20°C). At that time the lizards remain in direct sun for longer time periods, and after they warm to an adequate temperature for activity, they make only brief excursions into sunlit areas that exceed 40°C at noon. This is similar to the liolaemid *L. lutzae* (Rocha

1995). They exposed their heads to the sun in the morning until their body temperature rose to the required level.

Microhabitat (substrate and air) temperatures in the location where we first observed each lizard influenced the body temperature of *T. torquatus*. This thermal relation is similar to that reported for this species in a coastal restinga (Air temperature:  $r^2 = 0.44$ ; Substrate temperature:  $r^2 = 0.30$ ) (Hatano et al. 2001). However, the importance of this heat source may vary seasonally (Bogert 1948, 1959; Patterson and Davies 1978; Magnusson et al. 1985). Our study showed that substrate temperature may better explain body temperature variation during the rainy season, whereas air temperature better may be a better predictor during the dry season. This relationship not only characterizes heliothermy, but also reveals the thigmothermic behavior of *T. torquatus* when the substrate temperature is warm enough to serve as a heat source. This pattern of thermoregulation is similar to that reported for *T. oreadicus* (Rocha and Bergallo 1990) and *T. itambere* (Van Sluys 1992).

Seasonal variations in body temperature occur in various species of lizards, such as *Sceloporus occidentalis* (McGinnis 1966), *S. orcutti* (Mayhew and Weintraub 1971), *Amphibolurus isolepis* (Pianka 1971), *L. lutzae* (Rocha 1995) and *C. nativo* (Menezes et al. 2000). We suggest that such variations may be influenced by the distinct thermal conditions of each season and may result from the acclimation process for each species. Acclimation promotes physiological responses to changes in two or more environmental factors (Hutchison and Maness 1979).

In the rocky outcrop area in Toledos, the highest mean body temperature for *T. torquatus* occurred during the rainy season when we observed the microhabitat's highest mean temperatures. Conversely, we observed the lowest mean body temperature during the dry season when the microhabitat mean temperatures were lower. We conclude that the seasonal variation described for the mean active body temperatures of the Saxicolous Lizard *T. torquatus* probably reflects the variation in local environmental temperatures due to an acclimation mechanism. This study supports the need for additional investigations focusing on the thermal ecology of phylogenetically related species in other open areas to understand better how the local thermal environment influences lizard body temperatures and to what extent they reflect phylogenetic relationships.

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