

Thermal ecology and thermoregulatory behaviour of *Tropidurus hispidus* and *T. semitaeniatus* in a caatinga area of northeastern Brazil

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This study assessed the thermal ecology of *Tropidurus hispidus* and *T. semitaeniatus* in a caatinga area in the state of Rio Grande do Norte, Brazil. The mean activity body temperature of *T. semitaeniatus* (35.1 ± 2.0 °C) was significantly higher than that of *T. hispidus* (33.6 ± 2.3 °C). While there was no seasonal variation in the body temperature of *T. hispidus*, it was significantly higher for *T. semitaeniatus* in the wet season compared to the dry season. Substrate temperature was the best predictor of body temperature in *T. hispidus* in both seasons, whereas for *T. semitaeniatus* substrate and air temperatures were the best predictors of lizard temperature in the wet and dry season, respectively. During the dry season, both species spent more time in the shade or under filtered sunlight. In the wet season, *T. hispidus* did not prefer areas with specific light exposures, whereas *T. semitaeniatus* predominantly spent time exposed to the sun or under filtered sunlight. We conclude that the similarity in temperature ranges during activity of *T. hispidus* and *T. semitaeniatus* most likely reflects their common phylogenetic origin and foraging mode, whereas the differences in thermal behaviour may be due to their particular adaptations to their local, seasonal habitat.

Key words: body temperature, lizards, semiarid, Squamata, thermal biology, thermal behaviour, Tropiduridae

INTRODUCTION

Lizards, like other ectothermal animals, depend on external environmental sources to obtain the necessary heat to regulate their body temperatures (Bogert, 1959; Huey & Slatkin, 1976; Rocha & Van Sluys, 2007). Since ambient temperature is one of the most important physical factors in lizard ecology, a large part of the daily activity of various species is regulated by interactions with their thermal environment (Rocha et al., 2009). The intensity of activity varies across days and seasons (Huey et al., 1977; Ribeiro et al., 2008; Kolodiuk et al., 2009, 2010), and the body temperature changes according to daily activity patterns (Pianka, 1973; Bergallo & Rocha, 1993; Vitt et al., 2005).

Lizards of the genus *Tropidurus* are generally active from sunrise to sunset (Van Sluys, 1992; Teixeira-Filho et al., 1996; Hatano et al., 2001; Ribeiro et al., 2009). Species that start activity earlier in the day and remain active for longer periods often have lower and more variable body temperatures than species with shorter activity periods (Pianka et al., 1979; Rocha & Van Sluys, 2007). Given that foraging behaviour is correlated with temperature during activity, ambush-foraging lizards such as *Tropidurus* generally tend to have lower body temperatures during activity than those of active foragers like teiid lizards (Colli & Paiva, 1997). Studies on the thermal ecology of *T. hispidus* and *T. semitaeniatus* were previously conducted in one caatinga area in the state of Pernambuco (Vitt, 1995), and on *T. hispidus* in the Ama-

zon forest and savanna (Vitt & Carvalho, 1995; Vitt et al., 1996) and rocky fields in the state of Minas Gerais (Van Sluys et al., 2004).

Although intrageneric homogeneity suggests that phylogeny has a role in the expression of body temperature among species (Bogert, 1959), our initial prediction was that *T. hispidus* and *T. semitaeniatus* would differ in their thermal ecology depending on the environment. In this study, we analyse the variation in body temperature during activity and light exposure in *T. hispidus* and *T. semitaeniatus* in an area of the caatinga ecosystem in northeast Brazil, where both species live in sympatry.

MATERIALS AND METHODS

Study area

The study was conducted at the Ecological Station of the Seridó (ESEC Seridó, $06^{\circ}34'36.2''\text{S}$, $37^{\circ}15'20.7''\text{W}$, datum: WGS84; altitude: 192 m), which encompasses a caatinga area of 1,166.38 hectares located in the municipality of Serra Negra do Norte, Rio Grande do Norte, Brazil (Fig. 1). The climate is semiarid (Ab'Sáber, 1974), with a short wet season between March and May and rainfall ranging between 500 and 700 mm/year. Mean annual temperatures vary from 28 °C to 30 °C, and over the course of the year exceed 40 °C; the minimum ranges between 17 °C and 20 °C. Relative air humidity oscillates around 30–50% in the dry season, reaching 80–90% in the wet season (Nimer, 1972). The vegetation of ESEC Seridó is arboreal-bushy hyperxerophilous (Varela-Freire, 2002).

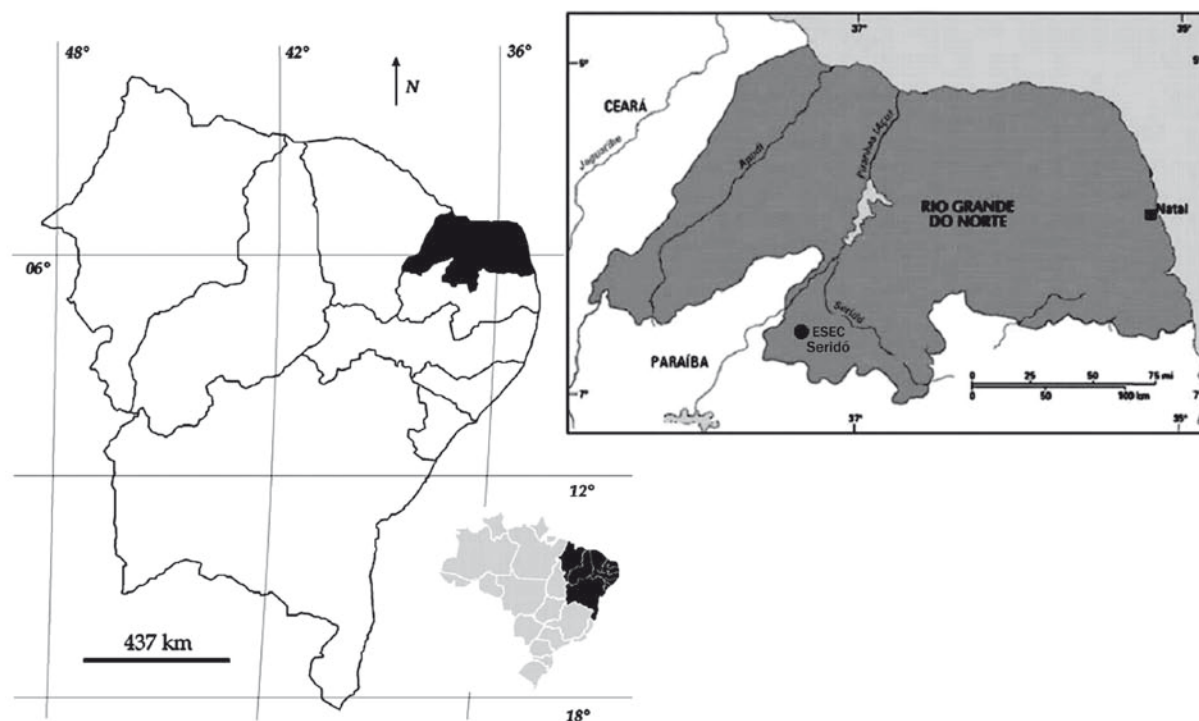


Fig. 1. Geographic location of the Ecological Station of the Seridó (black dot = ESEC Seridó) in the southwest portion of the state of Rio Grande do Norte, Brazil.

Amidst the arboreal-bushy vegetation various rocky extrusions are found that remain covered by the vegetation during the wet season, resulting in partially shaded areas. During the dry season they are exposed as large rocky outcrops after leaf fall (Velloso et al., 2002).

Collection methods and data analysis

Thermal ecology. Fieldwork was conducted on monthly excursions, each lasting three consecutive days, from April 2007 to May 2008. The dry season lasted from July 2007 to January 2008, and the wet season was between April and June 2007 and between February and May 2008. Mean monthly rainfall during the dry and wet season was 5.8 mm and 164.7 mm, respectively.

An area of ESEC Seridó composed of five rocky outcrops spaced on average 20 m apart was used for data collection. The lizards were collected from rocky surfaces between 0700 and 1800, using air rifles. Within 30 seconds after collection we measured the cloacal temperature of the lizards, substrate temperature at the point where they were sighted and air temperature 5 cm above the substrate, using a temperature sensor (Instrutherm® model S-02K) coupled to a digital thermometer (to the nearest 0.1 °C; Instrutherm® model HTR-160). Air temperature in the sun (at 150 cm above the substrate), of rocky surfaces in the sun and in the shade, and of ground surface temperature in the sun was measured with a digital thermometer (to the nearest 0.1 °C; Instrutherm® model HTR-160) every subsequent hour where the lizards were collected. We also recorded type of light exposure (sun, shade, filtered

sunlight and cloudy light), the time of collection, sex, and snout–vent length (SVL) measured with a manual caliper to the nearest 0.1 mm. The classification of individuals of *T. semitaeniatus* into adult and juvenile categories considered females with SVL ≥ 58 mm and males with SVL ≥ 64 mm (Vitt, 1995). For *T. hispidus*, size ranges were defined according to Ribeiro & Freire (2009), with females having SVL ≥ 65 mm and males having SVL ≥ 68 mm. The lizards were deposited in the Herpetological Collection of the Department of Botany, Ecology and Zoology (CHBEZ) of the Universidade Federal do Rio Grande do Norte.

The effects of interaction, species and seasonality on body temperatures were tested using a two-way ANOVA (Zar, 1999). A second two-way ANOVA with sex as one factor and maturity as the other was conducted to determine the effects on body temperature in each species. Interspecific and interseasonal body temperature differences as well as those between different light exposures were tested using one-way ANOVA. In each season we analysed the relationship of substrate and air temperatures to lizard temperatures using multiple regressions (Zar, 1999). The relationship between body temperature and SVL for each species was assessed using simple regressions. Bonferroni corrections were adopted for the one-way ANOVA and regression analyses, resulting in a significance level of 0.0055 (Zar, 1999). Lizard body temperatures were also compared to a null distribution of temperatures (cf. Hertz et al., 1993). Statistical analyses were conducted using SPSS 13.0.

Table 1. Mean activity body temperature for *Tropidurus hispidus* and *T. semitaeniatus* divided into types of light exposure at ESEC Seridó, Serra Negra do Norte municipality, Rio Grande do Norte, Brazil. The numbers in parentheses represent sample sizes.

Species	Types of exposure			
	Sun	Shade	Filtered sunlight	Cloudy light
<i>Tropidurus hispidus</i>	35.1±1.8 (13)	31.7±2.0 (10)	34.0±1.0 (9)	–
<i>Tropidurus semitaeniatus</i>	35.8±2.1 (26)	34.7±1.2 (14)	34.8±2.1 (17)	33.1±2.0 (4)

Thermoregulatory behaviour. For behavioural observations, five rocky outcrops were established surrounded by vegetation and located around 500 m from the lizard collection area. Observations were made from October to December 2006 (phase I; mean monthly rainfall: 1.6 mm), October to December 2007 (phase II; mean monthly rainfall: 1.2 mm) as part of the dry season, with the wet season represented between April and June 2007 (phase I; mean monthly rainfall: 68.7 mm) and April and June 2008 (phase II; mean monthly rainfall: 141.7 mm).

Given that body temperature regulation may involve shuttling between hotter (sunny) and cooler (shaded) areas (Vitt et al., 2005), the light exposure categories for *T. hispidus* and *T. semitaeniatus* were recorded as sun exposure time (TSu), shade exposure time (TSh), filtered sunlight exposure time (TFs) and cloudy light exposure time (TCI), measured in seconds of exposure. Data were collected on three consecutive days, from 0700 to 1000 and from 1400 to 1700, divided into six intervals of one hour each to obtain a homogeneous sample. The time intervals above were selected based on our preliminary observations and published data (Vitt, 1995) indicating that they correspond to highest lizard activity. During these intervals, 10-min focal sampling sessions were carried out (Altmann, 1974), alternating the species observed whenever possible, using a voice recorder and digital watch. After the lizard was sighted, the observation was initiated 5 minutes later to minimize observer interference.

The categories for light exposure (TSu, TSh, TFs, TCI) during thermoregulatory behaviour of *T. hispidus* and *T. semitaeniatus* were recorded and calculated for each lizard using the arithmetic mean by species and season following Vitt et al. (1996). The difference in length of stay under the various forms of exposure during thermoregulatory behaviour was tested for each species using one-way ANOVA coupled with a post-hoc Tukey-test (Zar, 1999).

RESULTS

Thermal ecology

All lizards were collected on rocky surfaces. Factors, species and seasonality interacted to affect the lizards' body temperatures ($F_{1,93}=6.870$, $P=0.010$). The body temperature of *T. hispidus* (33.6±2.3 °C, 28.1–37.8 °C, $n=33$) was significantly lower than that of *T. semitaeniatus* (35.1±2.0 °C, 29.1–38.3 °C, $n=61$; $F_{1,93}=9.903$, $P=0.002$). Seasonality did not affect the body tem-

perature of *T. hispidus*, which was similar in the rainy (33.1±2.2 °C, $n=19$) and dry seasons (34.1±2.5 °C, $n=14$; $F_{1,32}=1.478$, $P=0.233$), whereas for *T. semitaeniatus* body temperature in the rainy season (35.8±1.7 °C, $n=31$) was significantly higher than in the dry season (34.4±2.1 °C, $n=30$; $F_{1,60}=9.708$, $P=0.003$). The body temperature of *T. semitaeniatus* in the wet season was significantly higher than that of *T. hispidus* ($F_{1,49}=22.467$, $P=0.0001$), whereas in the dry season the body temperatures of both species were similar ($F_{1,43}=0.105$, $P=0.748$). Sex and maturity did not interact to affect the body temperature of *T. hispidus* ($F_{1,32}=0.777$, $P=0.385$) or of *T. semitaeniatus* ($F_{1,60}=0.700$, $P=0.406$). There was no significant relationship between body temperature and SVL in *T. hispidus* ($R^2=0.004$, $df=1$, $P=0.712$), or in *T. semitaeniatus* ($R^2=0.064$, $df=1$, $P=0.056$).

The mean activity body temperatures of *T. hispidus* differed according to the light category observed immediately after capture (Table 1). These differences occurred for the sun-shade types of exposure ($F_{2,29}=11.47$, $P<0.001$; Tukey-test: $P=0.0001$) and for shade-filtered sunlight ($F_{2,29}=11.47$, $P<0.001$; Tukey-test: $P=0.001$), when body temperature in the shade was significantly lower in both comparisons. For *T. semitaeniatus* there was no significant difference in body temperature (Table 1) between any of the exposure types ($F_{3,57}=2.61$, $P=0.06$).

In both seasons, only the interval between 0700 and 0800 had thermal means for rock in the shade above those of rock in the sun (Fig. 2). However, until mid afternoon, the temperature of rock in the sun rose rapidly to above 40 °C, representing the substrate with the highest temperatures by the end of the day (Fig. 2). The mean activity body temperatures of *T. hispidus* and *T. semitaeniatus* also varied over the day in the dry and wet seasons (Fig. 2).

Substrate temperature was higher than air temperature in both seasons (wet: air=28.6±2.8 °C, substrate=31.5±3.5 °C; $F_{1,99}=19.992$, $P<0.001$; dry: air=30.0±3.0 °C, substrate=32.7±3.7 °C; $F_{1,87}=13.452$, $P<0.001$), whereas substrate temperature in the wet season was similar to the dry season ($F_{1,93}=2.661$, $P=0.106$).

Most body temperatures of *T. hispidus* and *T. semitaeniatus* were above substrate and air temperatures (Fig. 3). In both seasons, body temperatures were related to micro-habitat temperatures for *T. hispidus* (wet: $R^2=0.31$, $df=2$, $P=0.003$; dry: $R^2=0.43$, $df=2$, $P=0.002$) and *T. semitaeniatus* (wet: $R^2=0.34$, $df=2$, $P=0.003$; dry: $R^2=0.50$, $df=2$, $P<0.001$). The largest $\beta_{\text{standardized}}$ coefficient showed that for *T. hispidus*, in the wet and dry seasons, substrate temperature was the best predictor of lizard body tem-

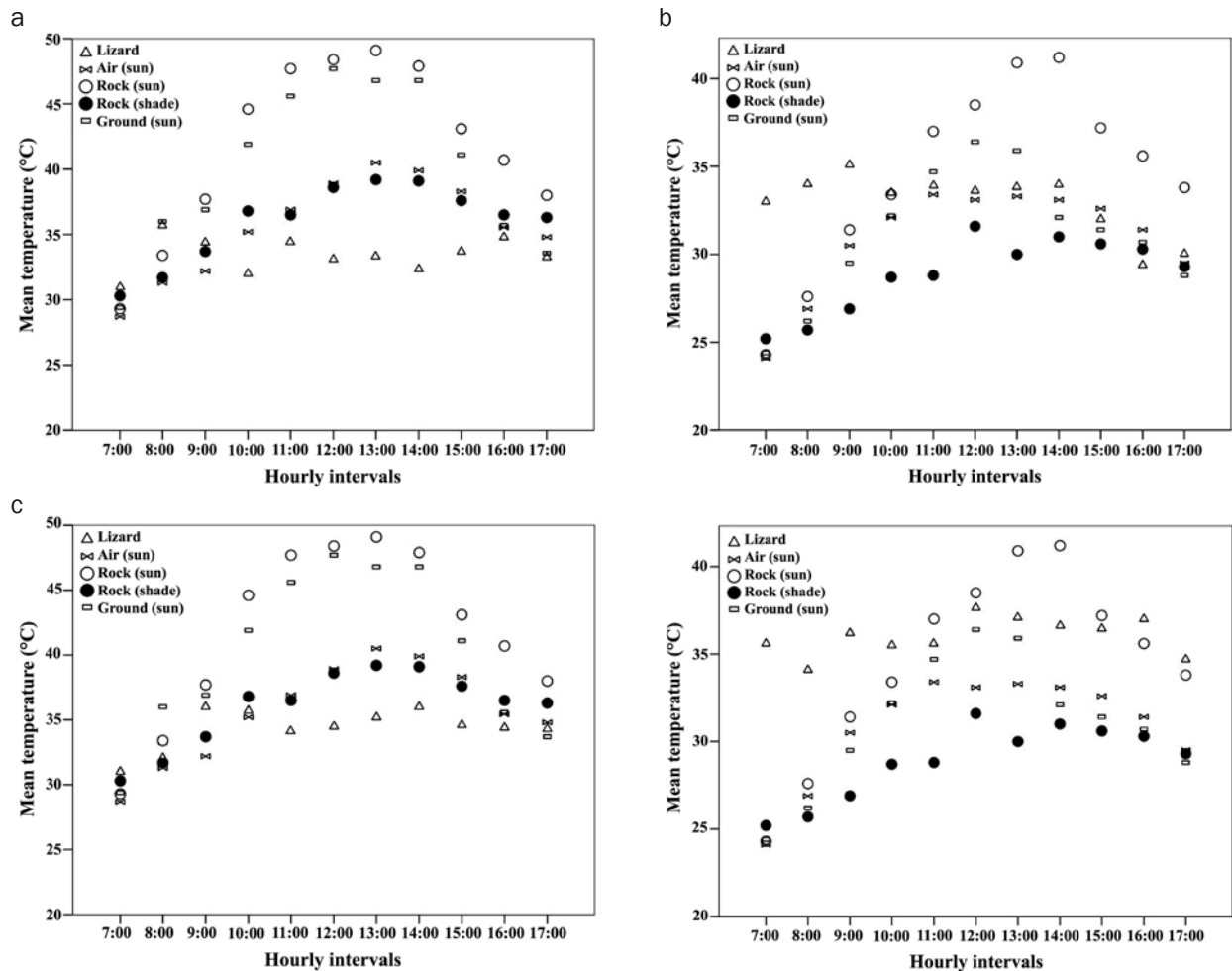


Fig. 2. Mean temperature of the lizards at hourly intervals, air at 150 cm above substrate (in the sun), rocky surface (in the sun and shade) and ground (in the sun). a and b) *Tropidurus hispidus*, in the dry and wet seasons, respectively. c and d) *T. semitaeniatus* in the dry and wet seasons.

peratures (wet: $\beta_{\text{standardized}} = 0.85$; dry: $\beta_{\text{standardized}} = 0.61$). For *T. semitaeniatus*, substrate temperature was also the best predictor of lizard temperature in the wet season ($\beta_{\text{standardized}} = 0.71$); however, in the dry season, the best predictor was air temperature ($\beta_{\text{standardized}} = 0.63$).

Thermoregulatory behaviour

We made 116 focal observations for thermoregulatory behaviour in phase I: 37 for *T. hispidus* (21 in the dry season and 16 in the wet) and 79 for *T. semitaeniatus* (38 in the dry season and 41 in the wet). In phase II there were 68 focal samplings: 25 for *T. hispidus* (13 in the dry season and 12 in the wet) and 43 for *T. semitaeniatus* (24 in the dry season and 19 in the wet).

There were significant differences for exposure time between sunny and shaded areas in the dry season (Table 2) for *T. hispidus* and *T. semitaeniatus* in phase I (*Th*: $F_{3,80} = 8.306$, $P = 0.0001$; *Ts*: $F_{3,148} = 12.435$, $P < 0.001$) and phase II (*Th*: $F_{3,48} = 10.125$, $P = 0.0001$; *Ts*: $F_{3,92} = 10.540$, $P < 0.001$). In this season, the comparison between pairs of exposure revealed that *T. hispidus* and *T. semitaeniatus* remained longer in cooler areas, either shade or filtered sunlight, as opposed to sun and cloudy light (Tukey-test, $P < 0.05$) (Table 2). On the other hand, during the wet season, *T. hispidus* remained for similar lengths of time

in the types of light exposure. This occurred for phase I ($F_{3,60} = 0.845$, $P = 0.475$) and II ($F_{3,44} = 1.053$, $P = 0.379$, Table 2). For *T. semitaeniatus* differences occurred between some of the light exposure pairs in phase I ($F_{3,160} = 2.904$, $P = 0.037$) and II ($F_{3,72} = 12.864$, $P < 0.001$), and for all the comparisons the longest exposure time was characterized by the use of hotter areas such as those with direct sun exposure on the rock or under filtered sunlight, as opposed to shaded areas (Tukey-test, $P < 0.05$) (Table 2).

DISCUSSION

The mean activity body temperatures of *T. hispidus* (33.6 °C) and *T. semitaeniatus* (35.1 °C) were lower than those recorded for the species (35.9 °C and 37.1 °C, respectively) by Vitt (1995) in the state of Pernambuco, although *T. semitaeniatus* again reached a higher body temperature than *T. hispidus*. The body temperature of *T. hispidus* resembled a population on a rock outcrop in the Amazon Forest (body temperature = 34.1 °C; Vitt et al., 1996) and of another population from an area with cooler temperatures (32.2 °C; Van Sluys et al., 2004). The small differences in body temperatures between species (32.2–35.9 °C for *T. hispidus* and 35.1–37.1 °C for *T. semitaeniatus*) might reflect the thermally conservative

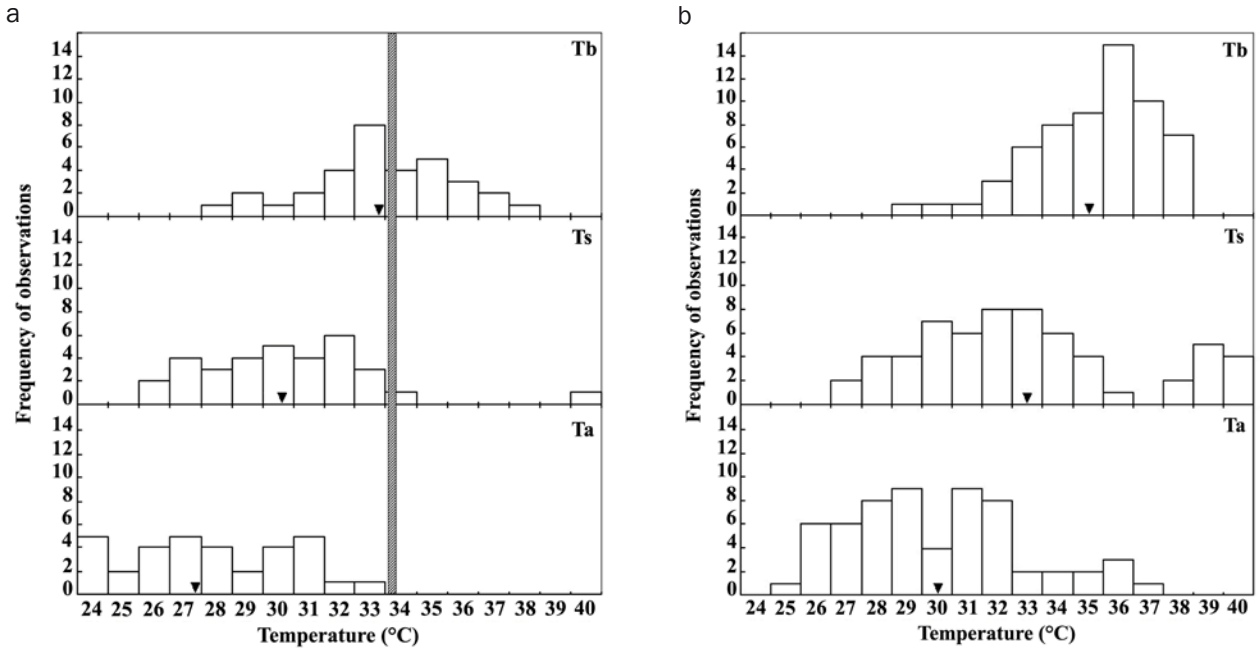


Fig. 3. Distributions of body temperature (Tb) and substrate (Ts) and air (Ta) temperatures in *Tropidurus hispidus* (a) and *T. semitaeniatus* (b) populations. Arrowheads indicate mean Tb, Ts and Ta. The cross-hatched vertical line indicates the selected body temperature (34.4 °C) for *T. hispidus* measured in the laboratory by Kohlsdorf & Navas (2006).

profile of congeneric species despite different environments (Colli & Paiva, 1997), with the subtle differences being due to adjustments to local thermal environments. Kiefer et al. (2005) studied ten populations of *T. torquatus* along the east coast of Brazil and also concluded that body temperatures of different populations (ranging between 34.4 and 36.2 °C) were influenced by environmental temperatures, while remaining within the characteristic thermal range of the species.

As shown by Kohlsdorf & Navas (2006), tropidurid lizards inhabiting sand dunes in the caatinga exhibit higher body temperatures during activity (e.g. *Eurolophosaurus divaricatus* = 38.0 °C and *T. psamonastes* = 37.5 °C) compared to species from the rocky cerrado (e.g. *T. torquatus* = 33.2 °C and *T. itambere* = 34.0 °C). Conversely, lower mean body temperatures for Brazilian tropidurid lizards were recorded for species from forest habitats, such as *Uranoscodon superciliosus* (26.6 °C; Howland et al., 1990), *Plica plica* (30.7 °C; Vitt, 1991) and *P. umbra* (29.1 °C; Vitt et al., 1997). According to these studies, the lower mean body temperature is due to a lack of opportunity for active thermoregulation, in addition to lower microhabitat temperatures. In the ESEC Seridó, rocky outcrops are the main thermoregulation sites for *T. hispidus* and *T. semitaeniatus*. Rocky surfaces provide areas of sunlight favouring thermoregulatory behaviour (Rocha & Bergallo, 1990; Van Sluys, 1992; Vitt et al., 1996). Evidence for active thermoregulation exists for *T. hispidus*, whose body temperatures approached the preferred temperature (34.4 °C) rather than reflecting substrate and air temperatures (Kohlsdorf & Navas, 2006). In

T. semitaeniatus, although the preferred temperature has yet to be determined, most body temperatures are well above substrate and air temperatures, evidencing active temperature regulation. Body temperatures of male and female *T. hispidus* and *T. semitaeniatus* during activity show no significant differences, as described for *Liolaemus lutzae* (Rocha, 1995) and *T. torquatus* (Ribeiro et al., 2008). Body temperatures of both lizard species showed no significant relationship with SVL, as recorded for insular, coastal and inland populations of *T. torquatus* (Rocha et al., 2002; Kiefer et al., 2005; Ribeiro et al., 2008).

The body temperature of some *Tropidurus* species inhabiting dry habitats has been shown to be positively correlated with air and substrate temperatures (Cruz, 1998; Faria & Araújo, 2004). The body temperature of *T. hispidus* showed no seasonal variation and was mostly influenced by substrate temperature, revealing the role of thigmothermic behaviour in *T. hispidus* in regulating its body temperature as previously suggested for *T. oreadicus* (Rocha & Bergallo, 1990; Faria & Araújo, 2004) and *T. itambere* (Van Sluys, 1992). The lower body temperature of *T. semitaeniatus* in the dry season was mostly linked to low air temperature, whereas in the wet season body temperature was more related to the substrate temperature. These relations show the seasonal alternation between heliothermic and thigmothermic basking for thermal control in *T. semitaeniatus*. Moreover, this change in thermal behaviour may explain the higher activity body temperature of *T. semitaeniatus* in the wet season. The same seasonal importance of these types of heat exchange was recorded for an inland population of *T. torquatus* inhabiting a

Table 2. Results of Tukey-tests for significant differences between *Tropidurus hispidus* and *T. semitaeniatus* for exposure time (mean±1 SE; in seconds) in the hottest (sunny) and coolest areas (shaded) during focal animal observations of thermoregulatory behaviour, in the dry and wet seasons of phases I and II of the study at ESEC Seridó, Serra Negra do Norte municipality, Rio Grande do Norte, Brazil. TSu = exposure time to the sun, TFs = exposure time to filtered sunlight, TSh = exposure time to shade, TCl = exposure time to cloudy light.

Phases	I		II	
Seasons	Dry	Wet	Dry	Wet
<i>Tropidurus hispidus</i>				
TSu	62.5±28.5 ^{1,2}	144.5±57.8	37.7±31.6 ²	230.8±65.6
TFs	222.7±45.7 ^{1,4}	80.5±37.8	192.2±66.0	137.0±46.0
TSh	266.8±53.4 ^{2,6}	165.2±58.5	361.1±73.2 ²	100.7±53.5
TCl	34.7±25.2 ^{4,6}	206.7±70.0	–	118.7±58.7
<i>Tropidurus semitaeniatus</i>				
TSu	58.8±15.3 ^{1,2}	122.4±30.8	84.8±23.5 ^{1,2}	339.0±48.2 ^{1,2,3}
TFs	234.7±30.0 ^{1,4}	211.7±35.7 ⁵	211.4±37.7 ¹	74.6±24.3 ¹
TSh	232.0±38.0 ^{2,6}	79.2±25.1 ⁵	232.8±51.0 ²	17.8±9.5 ²
TCl	58.8±26.3 ^{4,6}	174.0±42.1	–	143.7±55.5 ³

Pairs of significant differences ($P<0.05$) for ¹TSu–TFs; ²TSu–TSh; ³TSu–TCl; ⁴TFs–TCl; ⁵TFs–TSh; ⁶TSh–TCl.

rocky outcrop in the Atlantic Forest Domain (Ribeiro et al., 2008).

A series of studies has documented seasonal variations in body temperature for other species of lizards such as *Sceloporus occidentalis* (McGinnis, 1966), *S. orcutti* (Mayhew & Weintraub, 1971), *Amphibolurus isolepis* (Pianka, 1971), *L. lutzae* (Rocha, 1995), *Cnemidophorus natio* (Menezes et al., 2000) and *T. torquatus* (Ribeiro et al., 2008). According to these studies, variations in body temperatures are influenced by the distinct thermal conditions of each season, and result in an acclimatization process for each species to maintain body temperature within the appropriate range for behavioural and ecological performance.

In addition to phylogeny, habitat type and seasonality, other life-history parameters such as foraging mode and extent of activity also influence the body temperature of lizards (Pianka, 1977; Magnusson et al., 1985; Magnusson, 1993). The body temperature of ambush foragers such as *Tropidurus*, which normally initiate activity earlier and remain active for longer periods than do active foragers, tends to be low and variable (Magnusson et al., 1985; Bowker et al., 1986; Cruz et al., 1998). At ESEC Seridó, *T. hispidus* and *T. semitaeniatus* were observed active from dawn (approximately 0600) until around 1800, and their body temperatures during activity were indeed considerably lower than those of active foraging lizards such as the teiids *Ameiva ameiva*, *C. abaetensis*, *C. natio* and *C. ocellifer* (Rocha, 1994; Vitt, 1995; Menezes et al., 2000; Dias & Rocha, 2004). We conclude that the similarity in temperature ranges during activity of *T. hispidus* and *T. semitaeniatus* most likely reflects their phylogenetic proximity and foraging mode, with the differences in thermal behaviour being a result of particular adaptations to the local seasonal habitat where they live in sympatry.

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REFERENCES

Ab’Sáber, A. (1974). O domínio morfoclimático semiárido das caatingas brasileiras. *Geomorfologia* 43, 1–139.

Altmann, J. (1974). Observational study of behaviour: sampling methods. *Behaviour* 49, 227–267.

Bergallo, H.G. & Rocha, C.F.D. (1993). Activity patterns and body temperatures of two sympatric lizards with different foraging tactics in southeastern Brazil. *Amphibia–Reptilia*, 14, 312–315.

Bogert, C.M. (1959). How reptiles regulate their body temperature. *Scientific American* 22, 213–221.

Bowker, R.G., Damschroder, S., Sweet, A.M. & Anderson, D.K. (1986). Thermoregulatory behaviour of the North American lizards *Cnemidophorus velox* and *Sceloporus undulatus*. *Amphibia–Reptilia* 7, 335–346.

Colli, G.R. & Paiva, M.S. (1997). Estratégias de forrageamento e termorregulação em lagartos do cerrado e savanas amazônicas. In *Contribuição ao Conhecimento Ecológico do Cerrado*, 224–231. Leite, L.L. & Saito, C.H. (orgs). Brasília: Universidade de Brasília.

- Cruz, F.B. (1998). Natural history of *Tropidurus spinulosus* (Squamata: Tropiduridae) from the dry chaco of Salta, Argentina. *Herpetological Journal* 8, 107–110.
- Cruz, F.B., Silva, S. & Scrocchi, G.J. (1998). Ecology of the lizard *Tropidurus etheridgei* (Squamata: Tropiduridae) from the dry chaco of Salta, Argentina. *Herpetological Natural History* 6, 23–31.
- Dias, E.J.R. & Rocha, C.F.D. (2004). Thermal ecology, activity patterns, and microhabitat use by two sympatric whiptail lizards (*Cnemidophorus abietensis* and *Cnemidophorus ocellifer*) from northeastern Brazil. *Journal of Herpetology* 38, 586–588.
- Faria, R.G. & Araújo, A.F.B. (2004). Sintopy of two *Tropidurus* lizard species (Squamata: Tropiduridae) in a rocky cerrado habitat in central Brazil. *Brazilian Journal of Biology* 64, 775–786.
- Hatano, F.H., Vrcibradic, D., Galdino, C.A.B., Cunha-Barros, M., Rocha, C.F.D. & Van Sluys, M. (2001). Thermal ecology and activity patterns of the lizard community of the restinga of Jurubatiba, Macaé, RJ. *Revista Brasileira de Biologia* 61, 287–294.
- Hertz, P.E., Huey, R.B. & Stevenson, R.D. (1993). Evaluating temperature regulation by field active ectotherms: the fallacy of the inappropriate question. *American Naturalist* 142, 796–818.
- Howland, J.M., Vitt, L.J. & Lopez, P.T. (1990). Life on the edge: the ecology and life history of the tropidurine iguanid lizard *Uranoscodon superciliosus*. *Canadian Journal of Zoology* 68, 1366–1373.
- Huey, R.B. & Slatkin, M. (1976). Costs and benefits of lizard thermoregulation. *Quarterly Review of Biology* 51, 363–384.
- Huey, R.B., Pianka, E.R. & Hoffman, J.A. (1977). Seasonal variation in thermoregulatory behaviour and body temperature of diurnal Kalahari lizards. *Ecology* 58, 1066–1075.
- Kiefer, M.C., Van Sluys, M. & Rocha, C.F.D. (2005). Body temperatures of *Tropidurus torquatus* (Squamata, Tropiduridae) from coastal populations: do body temperatures vary along their geographic range? *Journal of Thermal Biology* 30, 449–456.
- Kohlsdorf, T. & Navas, C.A. (2006). Ecological constraints on the evolutionary association between field and preferred temperatures in Tropidurinae lizards. *Evolutionary Ecology* 20, 549–564.
- Kolodiuk, M.F., Ribeiro, L.B. & Freire, E.M.X. (2009). The effects of seasonality on the foraging behavior of *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata, Tropiduridae) living in sympatry in the Caatinga of northeastern Brazil. *Zoologia* 26, 581–585.
- Kolodiuk, M.F., Ribeiro, L.B. & Freire, E.M.X. (2010). Diet and foraging behavior of two species of *Tropidurus* (Squamata, Tropiduridae) in the caatinga of northeastern Brazil. *South American Journal of Herpetology* 5, 35–44.
- Magnusson, W.E. (1993). Body temperatures of field-active Amazonian savanna lizards. *Journal of Herpetology* 27, 53–58.
- Magnusson, W.E., Paiva, L.J., Rocha, R.M., Franke, C.R., Kasper, L.A. & Lima, A.P. (1985). The correlates of foraging mode in a community of Brazilian lizards. *Herpetologica* 41, 324–332.
- Mayhew, W.N. & Weintraub, J.D. (1971). Possible acclimatization in the lizard *Sceloporus orcutti*. *Journal of Physiology* 63, 336–340.
- McGinnis, S.M. (1966). *Sceloporus occidentalis*: preferred body temperature of the western fence lizard. *Science* 152, 1090–1091.
- Menezes, V.A., Rocha, C.F.D. & Dutra, G.F. (2000). Termorregulação no lagarto partenogenético *Cnemidophorus natio* (Teiidae) em uma área de restinga do nordeste do Brasil. *Revista de Etologia* 2, 103–109.
- Nimer, E. (1972). Climatologia da região nordeste do Brasil. Introdução à climatologia dinâmica. *Revista Brasileira de Geografia* 34, 3–51.
- Pianka, E.R. (1971). Ecology of the agamid lizard *Amphibolurus isolepis* in Western Australia. *Copeia* 1971, 527–536.
- Pianka, E.R. (1973). The structure of lizard communities. *Annual Review of Ecology and Systematics* 4, 53–74.
- Pianka, E.R. (1977). Reptilian species diversity. In *Biology of the Reptilia*, 1–34. Gans, C. & Tinkle, D.W. (eds). New York: Academic Press.
- Pianka, E.R., Huey, R.B. & Lawlor, L.R. (1979). Niche segregation in desert lizards. In *Analysis of Ecological Systems*, 67–115. Horn, D.J., Mitchell, R. & Stairs, G.R. (eds). Columbus: Ohio State University Press.
- Ribeiro, L.B. & Freire, E.M.X. (2009). *Tropidurus hispidus* (NCN). Minimum size at maturity; maximum body size. *Herpetological Review* 40, 350–351.
- Ribeiro, L.B., Gomides, S.C., Santos, A.O. & Sousa, B.M. (2008). Thermoregulatory behavior of the saxicolous lizard, *Tropidurus torquatus* (Squamata: Tropiduridae), in a rocky outcrop in Minas Gerais, Brazil. *Herpetological Conservation and Biology* 3, 63–70.
- Ribeiro, L.B., Sousa, B.M. & Gomides, S.C. (2009). Range structure, microhabitat use, and activity patterns of the saxicolous lizard *Tropidurus torquatus* (Tropiduridae) on a rock outcrop in Minas Gerais, Brazil. *Revista Chilena de Historia Natural* 82, 577–588.
- Rocha, C.F.D. (1994). Introdução à ecologia de lagartos brasileiros. In *Herpetologia no Brasil I*, 39–57. Nascimento, L.B., Bernardes, A.T. & Cotta, G.A. (eds). Minas Gerais: PUC/MG, Fundação Biodiversitas e Fundação Ezequiel Dias.
- Rocha, C.F.D. (1995). Ecologia termal de *Liolaemus lutzae* (Sauria: Tropiduridae) em uma área de restinga do sudeste do Brasil. *Revista Brasileira de Biologia* 55, 481–489.
- Rocha, C.F.D. & Bergallo, H.G. (1990). Thermal biology and flight distance of *Tropidurus oreadicus* (Sauria, Iguanidae) in an area of Amazonian Brazil. *Ethology, Ecology and Evolution* 2, 263–268.
- Rocha, C.F.D., Dutra, G.F., Vrcibradic, D. & Menezes, V.A. (2002). The terrestrial reptile fauna of the Abrolhos Archipelago: species list and ecological aspects. *Brazilian Journal of Biology* 62, 285–291.
- Rocha, C.F.D. & Van Sluys, M. (2007). Herpetofauna de restingas. In *Herpetologia no Brasil II*, 44–65. Nascimento, L.B. & Oliveira, M.E. (orgs). Belo Horizonte: Sociedade Brasileira de Herpetologia.
- Rocha, C.F.D., Van Sluys, M., Vrcibradic, D., Kiefer, M.C., Menezes, V.A. & Siqueira, C.C. (2009). Comportamento de termorregulação em lagartos brasileiros. *Oecologia Brasiliensis* 13, 115–131.

- Teixeira-Filho, P.F., Rocha, C.F.D. & Ribas, S.C. (1996). Ecologia termal e uso do habitat por *Tropidurus torquatus* (Sauria: Tropiduridae) em uma área de restinga do sudeste do Brasil. In *Herpetologia Neotropical*, 255–267. Péfaur, J.E. (ed.). Merida, Venezuela: Actas del II Congreso Latinoamericano de Herpetologia, Consejo de Publicaciones, Universidad de Los Andes.
- Van Sluys, M. (1992). Aspectos da ecologia do lagarto *Tropidurus itambere* (Iguanidae) em uma área do sudeste do Brasil. *Revista Brasileira de Biologia* 52, 181–185.
- Van Sluys, M., Rocha, C.F.D., Vrcibradic, D., Galdino, C.A.B. & Fontes, A.F. (2004). Diet, activity and microhabitat use of two syntopic *Tropidurus* species (Lacertilia: Tropiduridae) in Minas Gerais, Brazil. *Journal of Herpetology* 38, 606–611.
- Varela-Freire, A.A. (2002). *A Caatinga Hiperxerófila Seridó: A Sua Caracterização e Estratégias para Sua Conservação*. São Paulo: Academia de Ciências do Estado de São Paulo.
- Velloso, A.L., Sampaio, E.V.S.B. & Pareyn, F.G.C. (2002). *Ecorregiões: Propostas para o Bioma Caatinga*. Recife: Instituto de Conservação Ambiental/The Nature Conservancy do Brasil.
- Vitt, L.J. (1991). Ecology and life history of the scansorial arboreal lizard *Plica plica* (Iguanidae) in Amazonian Brazil. *Canadian Journal of Zoology* 69, 504–511.
- Vitt, L.J. (1995). The ecology of tropical lizards in the caatinga of northeast Brazil. *Occasional Papers of the Oklahoma Museum of Natural History* 1, 1–29.
- Vitt, L.J., Caldwell, J.P., Sartorius, S.S., Cooper, Jr, W.E., Baird, T.A., Baird, T.D. & Pérez-Mellado, V. (2005). Pushing the edge: extended activity as an alternative to risky body temperatures in a herbivorous teiid lizard (*Cnemidophorus murinus*: Squamata). *Functional Ecology* 19, 152–158.
- Vitt, L.J. & Carvalho, C.M. (1995). Niche partitioning in a tropical wet season: lizards in the Lavrado area of northern Brazil. *Copeia* 1995, 305–329.
- Vitt, L.J., Zani, P.A. & Ávila-Pires, T.C.S. (1997). Ecology of the arboreal tropidurus lizard *Tropidurus* (= *Plica*) *umbra* in the Amazon region. *Canadian Journal of Zoology* 75, 1876–1882.
- Vitt, L.J., Zani, P.A. & Caldwell, J.P. (1996). Behavioural ecology of *Tropidurus hispidus* on isolated rock outcrops in Amazonia. *Journal of Tropical Ecology* 12, 81–101.
- Zar, J.H. (1999). *Biostatistical Analysis*, 4th edn. New Jersey: Prentice-Hall, Inc.

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