

Thermal ecology and thermoregulatory behavior of *Coleodactylus natalensis* (Squamata: Sphaerodactylidae), in a fragment of the Atlantic Forest of Northeastern, Brazil

Pablo A. G. de Sousa^{1, 2} & Eliza M. X. Freire¹

¹ Laboratório de Herpetologia, Departamento de Botânica, Ecologia e Zoologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte. 59072-970 Natal, RN, Brazil. E-mail: pabloguitar2@hotmail.com; elizajuju@ufrnet.br

² Programa de Pós-Graduação em Psicobiologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte. 59072-970 Natal, RN, Brazil.

ABSTRACT. We studied the thermal ecology and thermoregulatory behavior of *Coleodactylus natalensis* Freire, 1999 in a remnant of a northern coastal patch of the Brazilian Atlantic Forest. Data were collected during four 20-day field excursions over the course of one year. We assessed the importance of substrate and air temperatures, in addition to time of exposure to sunlight, as relevant factors for the regulation of body temperature in this species. After each specimen was captured, body (T_b), substrate (T_s) and air (T_a) temperature were measured 10 cm above the ground, using a temperature sensor coupled to a fast response thermo-hygrometer. *Ad libitum* and focal animal methods were used to describe thermoregulatory behavior. The mean body temperature of *C. natalensis* was $31.3 \pm 3^\circ\text{C}$ (amplitude of 26.9 and 38.4°C, n = 20). A positive relationship was found between T_b and environmental temperatures; further, substrate temperature explained the additional variability of temperature variations in this species. With respect to environmental observations, individuals of *C. natalensis* did not expose themselves directly to the sun, moving equally between full and filtered sun. Our results indicate that *C. natalensis* is umbrophylic and a passive thermoregulator.

KEY WORDS. Atlantic Forest; behavior; umbrophylic species.

Like other ectothermal animals, lizards depend on environmental sources to absorb heat (PIANKA & VITT 2003). They use environmental mechanisms to adjust their body temperature and maintain it within a range that meets their physiological and ecological needs (COWLES & BOGERT 1944, HUEY 1982). The thermoregulatory behavior of a lizard involves costs and associated benefits, which reflect individual ecological and thermoregulatory priorities (HUEY & SLATKIN 1976, DOWNES & SHINE 1998).

Behavioral regulation of body temperature can be achieved through different mechanisms of sun exposure (COWLES & BOGERT 1944, BOGERT 1959, PIANKA 1971, HUEY *et al.* 1977, ROCHA 1988, ROCHA & BERGALLO 1990). These mechanisms play an important role in the active temperature regulation of individual animals (HUEY & SLATKIN 1976). In passive thermoregulation, body temperatures generally reflect environmental temperatures. Active and passive thermoregulation strategies can be considered as the two extremes of a continuum of thermoregulatory options (HUEY & SLATKIN 1976). Body temperature regulation is therefore a complex process, influenced not only by environmental heat sources, but also by the ecological and life history characteristics of the species (ROCHA 1994, KIEFER *et al.* 2005, 2007, ROCHA *et al.* 2009).

In Brazil, most thermal ecology studies have been conducted in open formations such as Restingas (ROCHA 1988, 1994, 1995, VAN SLUYS 1992, BERGALLO & ROCHA 1993, VRCIBRADIC & ROCHA 1996, 1998), Cerrado and in areas of Savanna in the Amazon territory (VITT 1991, COLLI & PAIVA 1997, MESQUITA & COLLI 2003, MESQUITA *et al.* 2006a, b) and Caatingas (VITT 1995, VITT & CARVALHO 1995, FREIRE *et al.* 2009, RIBEIRO & FREIRE 2010), while research in forest areas has concentrated on the Amazon Region (MAGNUSSON *et al.* 1985, ROCHA & BERGALLO 1990, VITT & ZANI 1998, VITT *et al.* 1997, 2000, 2005). There is an obvious scarcity of studies on the thermal ecology of lizards in the Atlantic Forest.

Coleodactylus natalensis Freire, 1999 (Fig. 1) was initially described as endemic to the Parque Estadual das Dunas de Natal, and is considered to be endemic to the Rio Grande do Norte Atlantic Forest. It is a diurnal lizard that inhabits leaf litter in shady areas (FREIRE 1999, CAPISTRANO & FREIRE 2009), making it a forest species restricted to the Atlantic Forest biome. Other than a description of the species (FREIRE 1999), few ecological studies have been conducted involving reproduction, habitat use, predation, activity period and diet (LISBOA *et al.* 2008, CAPISTRANO & FREIRE 2009, SOUSA & FREIRE 2010, SOUSA *et al.* 2010).

The aims of our study were to: (I) evaluate mean body temperature of active *C. natalensis* in an Atlantic Forest rem-

nant; (II) identify environmental factors involved in the thermoregulation process of this species, and (III) quantify exposure time to sunlight, as determinant factors for regulating body temperature.

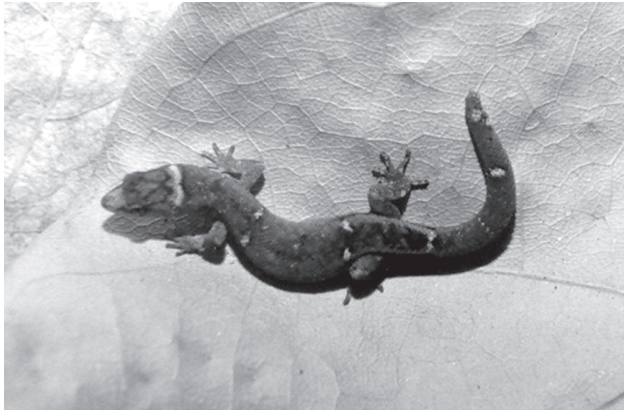


Figure 1. *Coleodactylus natalensis* Freire, 1999. Photo by Helianne de Niemeyer.

MATERIAL AND METHODS

Data were collected in a remnant of the Brazilian Atlantic Forest, the Parque Estadual Mata da Pipa (PEMP – 6°14'S and 35°03'W, Fig. 2). It is located in the Municipality of Tibau do Sul, state of Rio Grande do Norte, covering an area of approximately 290 ha (RIO GRANDE DO NORTE 2006) at 63 m above sea level.

The climate of the region is classified as sub-humid with a mean temperature of 26.5°C (maximum 32°C/minimum 21°C), mean annual relative humidity of 74% and highest rainfall levels in April and June. The soil is predominantly composed of dystrophic quartz sands, which are relatively flat and excessively drained and deep with extremely low natural fertility and a sandy texture (EMPARN 2010).

We conducted four 20-day field excursions (two in the rainy season: October 29 to November 18 2008 and October 8-28 2009 and two in the dry season: March 4-24 2008 and July 1-21 2008), totaling 80 days of daytime (between 0700 and 1800). Individuals were located by means of active searches in the high forest of PEMP. The percale area used during field work contains large trees (above 15 m) with diameters breast high

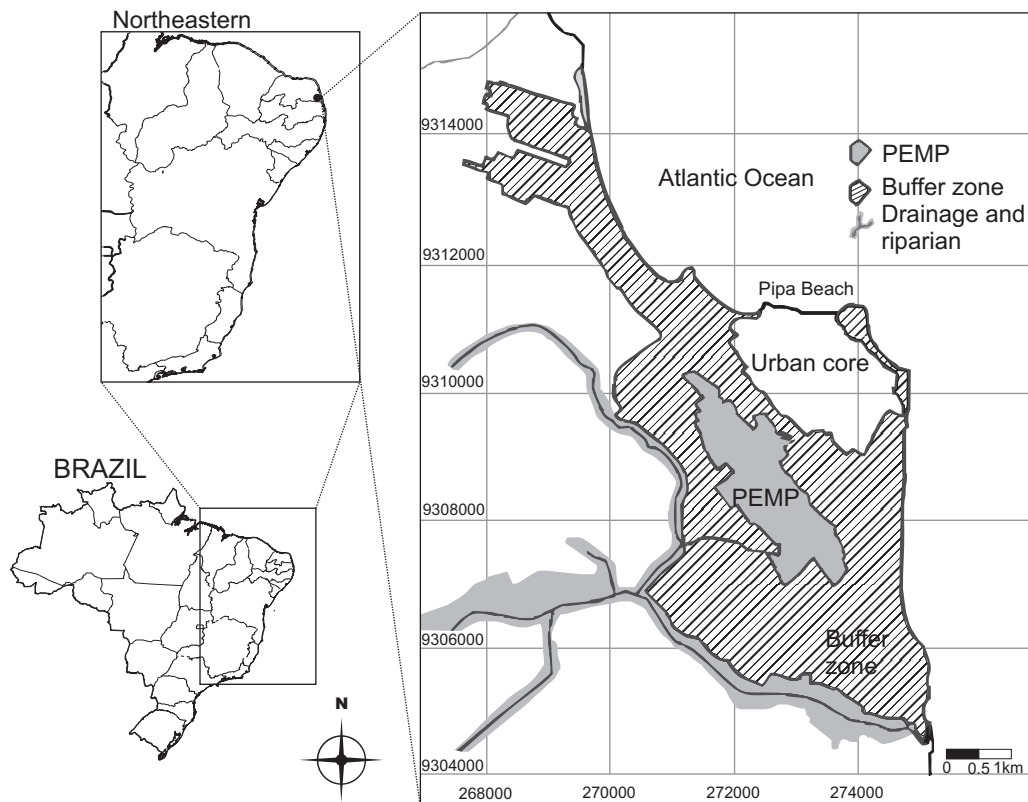


Figure 2. Location of the Parque Estadual Mata da Pipa (PEMP), municipality of Tibau do Sul, state of Rio Grande do Norte, northeastern Brazil.

(DBH) of over one meter and a canopy that blocks out most of the sunlight, except for some areas with clearings resulting from numerous tree falls. The litter is thick and abundant with extensive resprouting of the underbrush.

We explored four 500 m transects in the habitat. Those were located 50 m apart and crossed the area in a mainland-sea direction. Transects were traversed in a linear fashion, deviating 5 m to the right or left every 10 m in order to better cover the microhabitats used by these specimens. Individual animals were collected manually.

When studying *C. natalensis* specimens, behavioral observations were made *ad libitum* (ALTMANN 1974), to record behavioral activities at regular time intervals. The focal animal method (ALTMANN 1974), by which a single individual is observed for a given length of time to record behavior frequency and duration, was also used. We recorded the length of time the animals were exposed to three categories of sunlight: shade, filtered sun and direct sunlight (Figs 3, 4, and 5 respectively), as well as the length of time during which animals were motionless or moving. In both methods, 5-minutes observation intervals were established, followed by an additional five minutes for recordings.

At the moment of capture we measured cloacal temperature (considered as body temperature – T_b), as well as substrate (T_s) and air (T_a) temperature ($^{\circ}\text{C}$) 10 cm above ground. This procedure was performed with the help of a temperature sensor (Instruterm[®] model S-02K) coupled to a digital thermo-hygrometer (Instruterm[®] model HTR-160 – accurate to 0.1°C and 1-s response time). Only body temperatures obtained up to ten seconds after capture were considered. The collected specimens were deposited in the Coleção Herpetológica do Departamento de Botânica, Ecologia e Zoologia (CHBEZ), Universidade Federal do Rio Grande do Norte (UFRN).

We calculated mean body temperature of active *C. natalensis* as the arithmetic mean of cloacal temperatures recorded for all the lizards collected. The paired t-test was used to evaluate whether there was a significant difference between air and substrate temperatures recorded for the species. Body temperature dependency (T_b , dependent variable) in relation to that recorded in the microhabitat (T_s and T_a , independent variables) was determined by simple linear regression. If a significant correlation was found, multiple linear regression was carried out using the stepwise method to evaluate if either of the two environmental variables (T_a and T_s) explains an additional variation in the lizard's body temperature (DANCEY & REIDY 2006).

To estimate the degree of behavioral thermoregulation (passive or active thermoregulator), we used the absolute values of the differences between T_b and T_a (ΔT_A) and between T_b and T_s (ΔT_S) in the module (VRCIBRADIC & ROCHA 1998, KIEFER *et al.* 2007). The Wilcoxon non-parametric test was used to compare the ΔT_A and ΔT_S values (DANCEY & REIDY 2006). All statistical procedures were calculated with the aid of the software SPSS 15.0 for Windows.



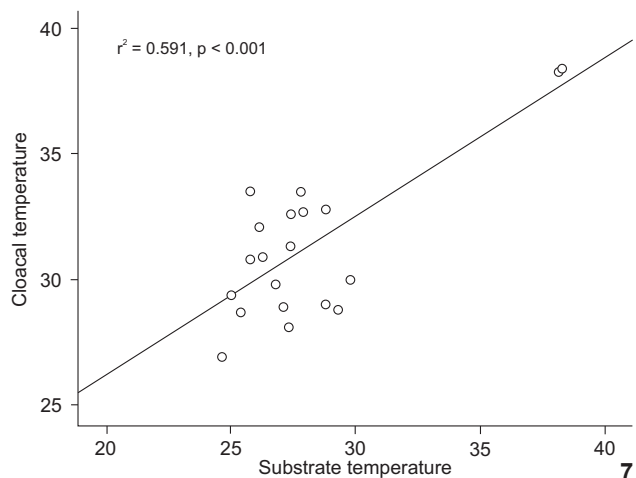
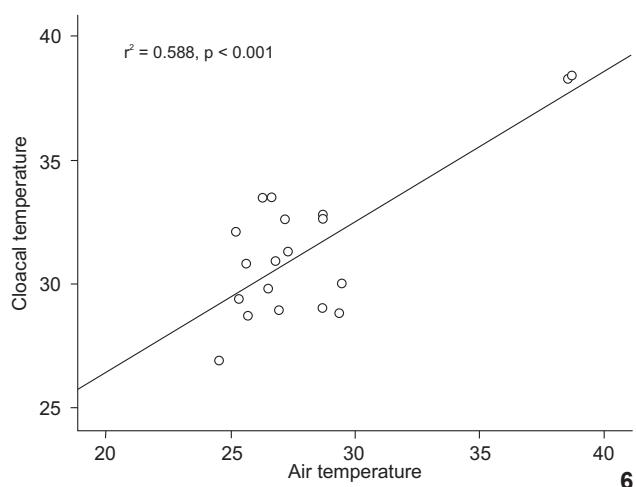
Figures 3-5. General aspect of the litter (3) in shade, (4) under filtered sun and (5) exposed to sunlight.

RESULTS

We observed 76 *Coleodactylus natalensis* individuals, all found in leaf litter (44 collected) during the four excursions; the body temperatures of 20 specimens were considered for analysis (Tab. I). Mean body temperature for the species during

activity was $31.3 \pm 3^\circ\text{C}$ ($26.9\text{--}38.4^\circ\text{C}$; $n = 20$) while mean air and substrate temperatures were $28.1 \pm 3.8^\circ\text{C}$ and $28.2 \pm 3.7^\circ\text{C}$, respectively (Tab. I). There was no significant difference between environmental temperatures (air and substrate – $t_{19} = -0.37$, $p = 0.713$, Tab. I).

A significant, positive correlation was found between body (Tb) and air temperatures (Ta, $r^2 = 0.588$, $p < 0.001$, Tab. I, Fig. 6). The same relationship was found between body (Tb) and substrate temperatures (Ts, $r^2 = 0.591$, $p < 0.001$, Tab. I, Fig. 7). However, after disregarding the effect of air temperature, substrate temperature explains part of the additional variation in body temperature during activity.



Figures 6-7. Relationships between body temperature of active *Coleodactylus natalensis* and environmental temperatures in the Parque Estadual Mata da Pipa, Tibau do Sul, Rio Grande do Norte, Brazil: (6) air temperature; (7) substrate temperature.

With respect to the degree of behavioral thermoregulation (Fig. 8), median ΔTA ($M = 3.6^\circ\text{C}$, $n = 20$, Tab. I) and ΔTS (3.6°C , $n = 20$, Tab. I) values were equal, with no significant difference among the remaining values (paired Wilcoxon, $T = 15.17$, $z = -0.525$, $p = 0.600$). The highest percentage of negative values was recorded for ΔTA (15%), while for ΔTS it was only 5%.

Table I. Mean body temperature (Tb) of active *Coleodactylus natalensis* ($n = 20$), mean air (Ta) and substrate (Ts) temperatures and median values of the module of differences between Tb and Ta (ΔTa) and between Tb and Ts (ΔTs) recorded in the lizard microhabitats, including a summary of paired t-test and simple and multiple linear regressions between the temperatures, as well as the paired Wilcoxon test between ΔTA and ΔTS .

Temperatures		Statistical tests	
Tb	$31.3 \pm 3^\circ\text{C}$	t-test	$t_{19} = -0.37$; $p = 0.713$
Ts	$28.2 \pm 3.7^\circ\text{C}$	Tb vs Ta	$r^2 = 0.588$; $p < 0.001$
Ta	$28.1 \pm 3.8^\circ\text{C}$	Tb vs Ts	$r^2 = 0.591$; $p < 0.001$
ΔTA	3.6°C	Tb vs Ta vs Ts	$r^2 = 0.484$; $F_{1,10} = 9.39$; $p = 0.012$; $p_{\text{Ta}} = 0.012$; $p_{\text{Ts}} = 0.961$
ΔTS	3.6°C	$\Delta\text{TA vs } \Delta\text{TS}$	$T = 15.17$; $Z = -0.525$; $p = 0.600$

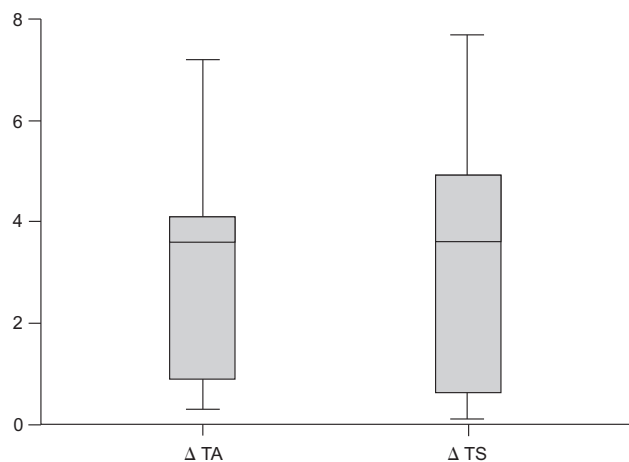


Figure 8. Absolute values of the differences between Tb and Ta (ΔTA) and between Tb and Ts (ΔTS) in the module for *Coleodactylus natalensis* ($N = 20$) in Parque Estadual Mata da Pipa, Tibau do Sul, Rio Grande do Norte, Brazil.

Our behavioral observations totaled 16 minutes and 20 seconds ($n = 9$; Tab. II). *Coleodactylus natalensis* individuals did not expose themselves directly to sunlight in the clearings and were primarily found moving between shade (72.4%) and filtered sun (27.6%, Tab. II). These observations were supplemented by the fact that 53.9% ($n = 41$) of the total number of

individuals of *C. natalensis* observed (n = 76) were found in shaded areas. The remaining animals (46.1%; n = 35) were spotted under filtered sun (Fig. 9).

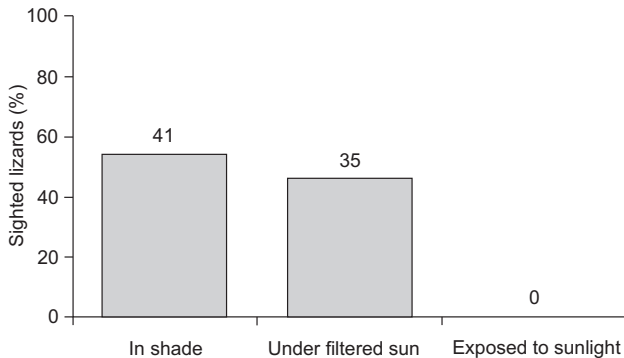


Figure 9. Frequency distribution of active *Coleodactylus natalensis* (n = 76) under different sunlight exposure conditions in Mata da Pipa State Park, Tibau do Sul, Rio Grande do Norte, Brazil. Numbers on top of bars indicate sample sizes.

DISCUSSION

The mean body temperature recorded for *C. natalensis* (Tab. I) was considered high when compared with estimates for an Amazonian congener, *C. amazonicus* (estimated in 27°C, based on temperatures in the microhabitats where they are found (VITT *et al.* 2005, 2008) and with other species of Sphaerodactylidae, such as *Gonatodes humeralis* (Guichenot, 1855) (28.4 and 30.3°C, VITT *et al.* 1997, VITT *et al.* 2000, respectively) and *G. hasemani* (30.6°C, VITT *et al.* 2000).

According to BRATTSTROM (1965) and LICHT *et al.* (1966), phylogenetically close lizard species tend to have similar body temperatures, even when living in different habitats. However, the type of habitat is also an important factor influencing body

temperature (PIANKA 1977, JAKSIC & SCHWENK 1983, MAGNUSSON 1993). In some cases, a species living in habitats with lower environmental temperatures may also have lower body temperatures than conspecifics in habitats where higher temperatures prevail (KIEFER *et al.* 2005, KOHLSDORF & NAVAS 2006). The body temperature recorded for *C. natalensis*, an umbrophile species, may be due to the fact that minute species such as the Sphaerodactylidae exhibit high rates of water loss in relation to their small size and, consequently, greater capacity to absorb heat (MACLEAN 1985, STEINBERG *et al.* 2007). Furthermore, this species shows tolerance to less shaded areas, as a pre-adaptive trait to warmer environments (FREIRE 1999), which might explain the high body temperatures recorded in two individuals who had body temperatures that possibly fled to the standard population (Figs 6 and 7). However, they were collected in a poorly shaded spot, near the forest edge, where the ambient temperatures were high, confirming that this species is tolerant to warmer environments.

To date, body temperature records for *Coleodactylus* are nonexistent, since species of this genus are the smallest among all lizards. Their small size hinders the use of methods routinely employed for lizards (VITT *et al.* 2005). However, the mean temperature recorded for the substrate used by *C. natalensis* (Tab. I) did not differ from that recorded for the substrate of Amazonian congeners (*C. amazonicus* and *C. septentrionalis* – VITT *et al.* 2005), or from the population of *C. natalensis* studied in its type-locality (CAPISTRANO & FREIRE 2009).

The body temperature of *C. natalensis* showed a significant relationship with the temperatures recorded at the capture site (Figs 6 and 7), which suggests that the individuals use behavior to maintain a certain degree of control over their temperature (VITT & CARVALHO 1992). Since substrate temperature offers the best explanation for body temperature variations, we suggest that this species has a thigmothermal behavior. The high proportion of individuals with T_b above T_s , along with the fact that no specimens were seen directly exposed to sunlight (Fig. 9), suggests that this species exhibits a certain degree

Table II. Length of exposure to light conditions and movement for *Coleodactylus natalensis* (n = 9).

Individual observed	In shade	Movement	Under filtered Sun	Movement	Total time
1	00:01:45 s	In motion	00:02:15 s	In motion	00:04:00 s
2	00:02:00 s	In motion	–	–	00:02:00 s
3	00:00:45 s/00:00:15 s	Motionless/In motion	–	–	00:01:00 s
4	–	–	00:01:00 s	In motion	00:01:00 s
5	00:00:30 s	In motion	–	–	00:00:30 s
6	00:02:00 s	In motion	–	–	00:02:00 s
7	00:02:10 s/00:00:50 s	In motion/Motionless	–	–	00:03:00 s
8	00:01:35 s	Motionless	–	–	00:01:35 s
9	–	–	00:02:15 s	In motion	00:02:15 s
Total	00:11:50 s (72.44%)		00:05:30 s (27.56%)		00:16:20 s (100%)

of thermoconformity (BOGERT 1949, 1959, PATTERSON & DAVIES 1978, MAGNUSON *et al.* 1985, KIEFFER *et al.* 2007), with ΔT_S values tending to be greater than those of ΔT_A (Fig. 8). *Coleodactylus natalensis* prefer forest habitats in shadier areas without direct sunlight, with milder temperatures, and more abundant litter (CAPISTRANO & FREIRE 2009). This preference for more mesologic habitats is shared with other *Coleodactylus* species in different biomes (VANZOLINI *et al.* 1980, VITT & ZANI 1998, COLLI *et al.* 2002, VITT *et al.* 2005).

The use of habitat by lizards has been mainly studied in the context of interspecific competition and niche partitioning, without considering the thermoregulatory restrictions in microhabitat use (GROVER 1996). However, some characteristics of habitats and (shade level and presence of water bodies) microhabitats used by lizards have an important influence on the food and thermal ecology of these animals (GANDOLFI & ROCHA 1998, HUEY 1982, ROCHA 1994, VAN SLUYS 1992, VRCIBRADIC & ROCHA 1998).

The thermal patterns of lizards may be influenced by phylogenetic and foraging factors, body size, activity period and habitat (HUEY & PIANKA 1983, PIANKA 1986, ROCHA 1994, ROCHA *et al.* 2009). The low mean temperature recorded during activity for lizard species from forest areas may be due to the lower availability of thermal sources for thermoregulation, as well as lower microhabitat temperatures, compared to open environments (HOWLAND *et al.* 1990, VITT 1991, VITT *et al.* 1997, 1998). Our data, therefore, corroborate findings that the thermal characteristics of species are a result of environmental factors and are regulated by behavioral strategies.

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