

Carla Piantoni

Efeitos do aquecimento global em populações do complexo de espécies *Tropidurus torquatus* (Squamata: Tropiduridae) no Brasil

The effects of climate warming on populations of the *Tropidurus torquatus* species complex (Squamata: Tropiduridae) in Brazil



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Orientador: Carlos A. Navas

Co-orientadora: Nora. R. Ibarzüengoytía

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A mis padres y a Felipe,  
por todo el apoyo y el amor



"Since natural selection demands only adequacy, elegance of design is not relevant; any combination of behavioural adjustment, physiological regulation, or anatomical accommodation that allows survival and reproduction may be favoured by selection. Since all animals are caught in a phylogenetic trap by the nature of past evolutionary adjustments, it is to be expected that a given environmental challenge will be met in a variety of ways by different animals. The delineation of the patterns of the accommodations of diverse types of organisms to the environment contributes much of the fascination of ecologically relevant physiology".

George A. Bartholomew  
[Symp. Soc. Exp. Biol., 1964]

"If you knew some of the experiments (if they may be so-called) which I am trying, you would have a good right to sneer, for they are so absurd even in my opinion that I dare not tell you".

Charles Darwin  
Letter to J.D. Hooker [April 14th, 1855]

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Male of *Troidurus torquatus* from Formoso do Araguaia river, Tocantins

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## INTRODUCTION

The term “climate change” was firstly used in a scientific publication in 1950s (Plass, 1956). The author explained how the extra, mainly industrial, CO<sub>2</sub> released into the atmosphere may had caused the temperature rise during the first half of last century and predicted that warming would continue for several centuries. Twenty years later, the term “global warming” appeared, making reference to the increasing average of the global surface temperature as a result of human emissions of greenhouse gases (Broecker, 1975). Global (climate) change entered the lexicon during the late 1980s, to encompass many other related issues, such as changes in precipitation patterns and sea level (Leiserowitz *et al.*, 2014). Since then, predicting models have estimated not only a rising in mean surface temperature of 1.5 to 4.5 °C by 2050 (Peters, 1988; Peters and Lovejoy, 1992; Schneider *et al.*, 1992; Schneider, 1993) and up to 6.4 °C over the 21<sup>st</sup> century (NRC, 2010), but also a decrease in the thermal amplitude of daily mean temperature in several regions (Aceituno *et al.*, 2007) and alteration in the precipitations along the seasons (Siqueira and Peterson, 2003; Mendonça, 2007; Nuñez and Solman, 2007). In Brazil, particularly in southern Amazonia and in the west central region of Brazil, mean air temperature and rainfalls are expected to increase by 6°C and decrease by 5-20%, respectively, by 2071-2100 (Marengo *et al.*, 2009). The impact of climate warming on biological diversity has been demonstrated in numerous studies for more than a decade (Hughes, 2000; Araujo *et al.*, 2006; Losos *et al.*, 2012; Weatherhead *et al.*, 2012). As postulated in the literature, an increase in ambient temperature ( $T_a$ ; also referred as environmental temperature) may cause shifts in the distribution of terrestrial species associated with changed in seasons' length (Easterling *et al.*, 2000; Meehl *et al.*, 2007; Trenberth and Shea 2005; Bradshaw and Holzapfel, 2008), interaction with other organisms (Buckley and Roughgarden, 2006; Pimm *et al.*, 2006; Gilman *et al.*, 2010; Harley, 2011), and habitat modifications or destruction (Catley, 2004; Sodhi and Brook, 2006; IPCC, 2013), but the further extinction is often a product of the synergy of several processes (Caughley, 1994 ; Oborny *et al.*, 2005, Brook *et al.*, 2006; Fagan and Holmes, 2006; Brook *et al.*, 2008). The amount of warming associated with climate change generally follows a latitudinal trend, with greater increases in temperature predicted in temperate regions (Addo-Bediako *et al.*, 2000; IPCC, 2007), but it ultimately affects individual behavioral and ecological performance (Huey

*et al.*, 2009; Sniegula and Johansson, 2010; Du *et al.*, 2014). Indeed, the literature largely demonstrates that temperature affects many aspects of the physiology, behavior and natural history of individuals (Huey, 1982; Cossins and Bowler, 1987; Angilletta *et al.*, 2006). Therefore, processes occurring at individual level assume central importance, either as a dominant or partial cause of more comprehensive models (Garland and Else, 1987; Andrews *et al.*, 2000; Adolph and Pickering, 2008).

Ectotherms' body temperature ( $T_b$ ) depends on the  $T_a$  and is particularly sensitive to thermal variation (Porter and Gates, 1969). Although variation in precipitation patterns may have an indirect effect on the phenology, development and diet (Somero, 2005),  $T_a$  affects most of the life-history aspects in lizards, from spatial patterns of body size, population density, and species diversity to temporal patterns of growth, survival, and reproduction (Huey and Stevenson 1979; Savage *et al.*, 2004; Angilletta *et al.*, 2002, 2004; Brown *et al.*, 2004; Piantoni *et al.*, 2006; Wiens *et al.*, 2006). While the temperature affects the whole organism's performance (Congdom, 1989; Huey, 1991; Sears, 2005; Huey and Slatkin, 1976), it also shapes the phenotype having a strong effect on the physiological processes (Angilletta, 2009) such as constraining the rates of biochemical reactions (Hochochka and Somero, 2002).

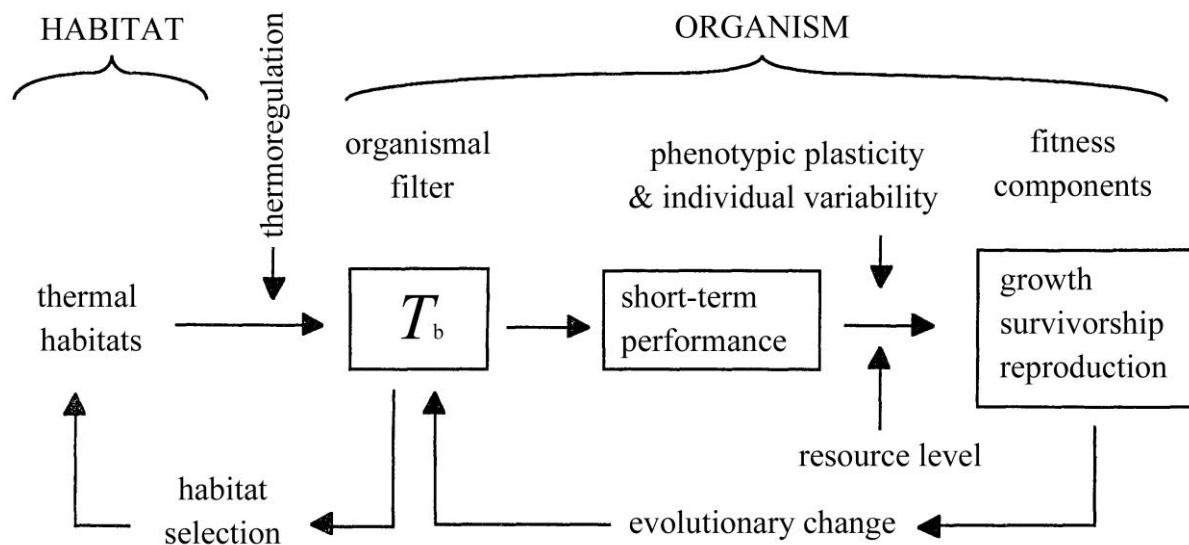


Figure 1. Conceptual summary of how habitat selection influences an organism's fitness by affecting the body temperature ( $T_b$ ) and, thus, performance. Buffer mechanisms such as thermoregulation become beneficial when coping with changes of  $T_a$  and phenotypic plasticity and individual variability, in for example performance, may also counteract the decrease of energy resources and lower the risk of extinction (modified from Huey, 1991).

Although many ectothermic vertebrates are likely to avoid lethal effects of  $T_a$  through behavioral thermoregulation (Huey and Tewksbury, 2009; Kearney *et al.*, 2009), habitat selection (Huey, 1991) and physiological acclimation (Feder, 1982; Angilletta 2009; Clusella-Trullas *et al.*, 2011; Donelson *et al.*, 2011) costs may cause a decline of the performance which may reach suboptimal levels (Miles, 1994b; Angilletta *et al.*, 2006; Seebacher and Franklin, 2012) and constrain the time for basking, foraging and reproducing (Figure 1; Grant, 1990; Dunham, 1993; Sinervo *et al.*, 2010; Moritz *et al.*, 2012). Reproductive success, thermoregulatory efficiency and habitat selection define fitness and, therefore, become crucial aspects in lizards' survival (Ibargüengoytía, 2005). Therefore, warming exerts a continuum of impacts among taxa which are not necessarily deleterious and may benefit some species in a short-run (Chamailé-Jammes *et al.*, 2006). In addition to the genetic differentiation among populations (Hertz *et al.*, 1979), buffering mechanisms, including behavioral (*e.g.* thermoregulation; Bogert, 1949a; Huey, 1982; Hertz *et al.*, 1983) and physiological (*e.g.* variation in thermal tolerances; Corn, 1971; Spellerberg, 1972; Hertz, 1981) plasticity have been registered to allow organisms to cope with drastic environmental changes. These mechanisms are analyzed hereafter.

### *1. The significance of ecophysiological variation in the adjustment to changing environments*

Although we recognize that genetic differentiation may explain large part of the morphological, behavioral and physiological variation encountered among the populations and species with wide geographic distributions (Moore, 1949; 1952; Berven, 1982; 1995; Partridge and Coyne, 1997) its latitudinal and altitudinal variation of life-history traits has been commonly explained as adaptive variation (Mayr, 1963). Nevertheless, comparative studies do not detect the causes and consequences of variation, and ignore potential biases as a result of within-species variation (Garamszegi and Moller, 2010). Whereas researchers mainly focus in finding phenotypic similarities due to common phylogenetic descent, intra-specific variation is commonly neglected. Phylogenetic corrections constrain the discrimination between causes and effects of the observed variation, since it is mostly due to phenotypic plasticity (Angilletta *et al.*, 2004). A considerable amount of studies has focused on variation of life-history traits along thermal clines in *Sceloporus* (Iguania: Phrynosomatidae). For example, *Sceloporus undulatus* lizards exhibit lower growth rates in colder environments (higher latitudes and altitudes; Sinervo and Adolph, 1994; Angilletta,

2001; Niewiarowski, 2001); thus, at these sites, sexual maturity in females is delayed as they need more time to reach a relatively large body size appropriate to reproduce. Although, common garden and reciprocal transplant experiments have demonstrated that growth may have a genetical basis (e.i. slow growth rates seems to be a fixed strategy of lizards from cooler environments which still show lower growth rate in comparison to lizards from warmer sites when transplanted to warmer environments; Ferguson and Brockman, 1980; Niewiarowski and Roosenburg, 1993; Niewiarowski, 1995), variation in growth among populations from different thermal locations was further explained as differences in the thermal and physiological constrains imposed by the environment (e.g. energy assimilation; Angilletta, 2001).

A counterpart of *Sceloporus* in South America would be the genus *Tropidurus*. Clines in several life-history traits are well documented for the genus (Rodrigues, 1987; Brandt and Navas, 2011), rendering it a good model for these kind of studies. Throughout an extensive distribution, these lizards occupy a variety of environments that range from forests to savannas, along wide latitudinal and altitudinal gradients. Random dispersion of the species due to unintentional human transportation and events of hybridization enhance the genetical variability and complexity of the genus (Sena, unpublished data). Moreover, some species are considered cryptic (e.g. *T. torquatus* and *T. etherigei* in Arinos, MG) which, in syntopic species, hinders their identification in the field but allows interesting comparisons with respect to, for example, shared or discrepant eco-physiology aspects.

According to Frost *et al.* (2001), the genus *Tropidurus*, spreads from southern Venezuela, eastern Guianas and northeastern Brazil, through the southwestern Amazon region to eastern Bolivia, northern Uruguay and central Argentina. Herein we focus our research on one of the four species groups recognized within the genus, the *T. torquatus* group (Rodrigues, 1987), and more precisely, on three populations of *T. torquatus*. *Tropidurus torquatus* (as currently recognized) is widespread in Brazil to the south of the Rio Amazonas (Rodrigues, 1987; see next section for details); it is distinguishable from most congeners on the basis of meristic and morphometric characters, except from *T. imbituba* and *T. catalanensis*, which are strictly defined by coloration characters that are only evident on adult males. From *T. catalanensis* it differs by lack of yellow coloration on chest and mental region, while from *T. imbituba* it differs by lack of orange-bronze coloration on the venter and flanks (Saraiva-Kunz and Borges-Martins, 2013). Thus, more conclusive taxonomic considerations on this regard

demand further studies that are already on course (Sena, in preparation).

Phenotypic plasticity "sensu strictu" is defined as "*the ability of a single genotype to produce more than one alternative form of morphology, physiological state, and/or behavior in response to environmental conditions*" (West-Eberhand, 1989). It comprises the variation, variability or individuality of any aspect of the phenotype (morphology, behavior, performance, growth rate) within an individual, a population or a species, and this variation may be studied on a spatial or temporal scale. Species that are geographically widespread generally exhibit variation in their life-history traits (Stearns, 1992). This variation is created and maintained by differences in the quality of resources and biotic interactions among the habitats, and indicates adaptive strategies for coping with contrasting environments (Sears and Angilletta, 2003). The differences in the responses within a taxon may result from various factors acting on the populations and have basis on the plasticity of the certain characters, the plastic response to environmental conditions or on the adaptation of different genotypes to different environments (Stearns, 1989; Angilletta, 2009). In all cases, the mechanisms that modulate the interaction between the environment and the variation of the expressed phenotype are difficult to discern and understand for which research needs to focus on taxa with broad distribution and geographical gradients (Dunham *et al.*, 1989; Niewiarowski *et al.*, 2004; Sears and Angilletta, 2003; Kearney and Porter, 2009). Variation has been reported for life-history strategies (Kingsolver, 1983; Dunham *et al.*, 1989; Sinervo, 1994; Angilletta, 2001; Jin and Liu, 2007), for thermal physiology among and within species (Hertz *et al.*, 1979; Crowley 1985; Van Damme *et al.*, 1989; Willett, 2010), and thermoregulatory patterns (Huey, 1974; Adolph, 1990; Freidenburg and Skelly, 2004). For example, in reaction to a shift in the  $T_a$ , some lizards may present acclimatory physiological responses (Corn, 1971; Spellerberg, 1972; Hertz, 1981; Somero, 2010) or may shift the hours of activity and basking (Bogert, 1949a; Huey, 1982).

### *1.1. Variation in the thermal microenvironment and the thermoregulatory behavior as predictors of populations' susceptibility in a warming scenario*

Like in many ectothermic vertebrates, the control of  $T_b$  in lizards depends upon the appropriate use of their thermal environment, a mechanism called thermoregulation [Mosauer, 1936; Cowles and Bogert, 1944; Saint-Girons and Saint-Girons, 1956; see Avery (1972) and Turner (1984) for a historical background on discoveries related to the thermal biology of

reptiles]. Whereas the  $T_b$  represents the field-active body temperature, the preferred temperature ( $T_p$ ) corresponds to the mean  $T_b$  and the thermoregulatory set-point range (lower- and upper- $T_{set}$ ; first and third interquartiles of the distribution of  $T_p$ ; Hertz *et al.*, 1993). The  $T_p$  is measured within an artificial thermal gradient where ecological costs (*e.g.* predation risk; Huey and Slatkin, 1976; Withers and Campbell, 1985; Figure 2) and constraints (*e.g.* availability of a heat source; Porter and Gates, 1969; Porter *et al.*, 1973) are minimized (for details of the methods used for recording these variables, see Hertz *et al.*, 1993). Although maintaining the  $T_b$  close or within the  $T_{set}$  range involves not only behavioral adjustments (Licht, 1968; Huey, 1982; Hertz *et al.*, 1993) but also physiological processes (Soulé, 1963; Seebacher and Franklin, 2005), behavioral thermoregulation is the predominant mechanism found in lizards. This active regulatory behavior can be demonstrated by showing that the lizards'  $T_b$  differ from hypothetical non-thermoregulating lizards (thermoconformers) which can be obtained by randomly mapping the thermal microenvironments with models of heat exchange. These models, when their heat exchange is calibrated with the one of the studied organisms, provide the predicted  $T_b$  of non-regulating ectotherms, known as operative temperature ( $T_e$ ), and provide a null model for calculating the degree of thermoregulation (Peterson, 1987; Grant and Dunham, 1988; Figure 2). Thereafter, the effectiveness of temperature regulation ( $E$ ) can be easily calculated as  $E = 1 - (\text{mean } d_b / \text{mean } d_e)$ , in which  $d_b$  is the degree to which a lizard experiences its  $T_b$  outside the  $T_{set}$  range (*i.e.* high  $d_b$  means low accuracy), and  $d_e$  is analogous to  $d_b$  but corresponds to the deviation between the  $T_e$  and the  $T_{set}$  (*i.e.* in a thermally ideal environment,  $d_e$  equals zero, whereas high values of  $d_e$  are of low thermal quality and lizards would need to thermoregulate to attain a  $T_b$  close or within the  $T_{set}$  range (see Hertz *et al.*, 1993, p 802).

Whereas  $T_p$  is generally variable at a genus level (Angilletta and Werner, 1998), most researchers assume that  $T_p$  is a stable variable at a population level (Bogert, 1949a, 1949b; Ushakov, 1964; Licht *et al.*, 1966). Nevertheless, recent publications have reported geographic (Du, 2006; Sagonas *et al.*, 2013) and individual (Withers and Campbell, 1985; Truter *et al.*, 2014; Leirião *et al.*, unpublished data) variation of  $T_p$ . Such findings highlight the substantial implications of the costs of thermoregulation over the individual adjustments (Huey, 1974; Huey and Slatkin, 1976; Lee, 1980; Hertz and Huey, 1981; Huey, 1982) and the different triggers of individual adjustment of  $T_p$  (*e.i.* seasonal: Christian and Bedford, 1995; health: Kluger *et al.*, 1975; diet shifts: Wall and Shine 2008; acclimation: Corn, 1971;





Figure 2. Methods for collecting data on lizards' thermal biology and performance. (A) Field body temperature ( $T_b$ ) measurement; (B) display of models to collect operative temperature ( $T_o$ ); (C) thermal gradients for registering preferred temperatures ( $T_p$ ); and (D) race track for performance trials.

neuroethology: Heath, 1970). Plasticity of the  $T_p$  and the  $T_b$  among populations (Ruibal and Philibos, 1970; Lee, 1980; Adolph, 1990; Diaz, 1997; Aubret and Shine, 2010), and of the thermoregulatory behavior (Huey and Pianka, 1977; Adolph, 1990) are expected to be

associated to environmental costs such as the habitat quality, food availability or predation. Precisely discovering which aspects of the environment determine the way the organism perceive an assemblage of physical conditions and how those conditions eventually affect fitness remains a challenge, especially when the nature and significance of those factors vary individually (Lewontin, 2000). Nevertheless, knowledge of variation in the thermal environment throughout the distribution of an ectothermic species and the way it copes with this variation can greatly contribute to our understanding of that species' ecology (Kearney and Porter 2009). It may also allow predictions on possible responses of some taxa to the rapid increase of  $T_a$  related to climate change.

Research on vulnerability of terrestrial ectotherms to warming suggests global patterns (Deutsch *et al.*, 2008; Huey *et al.*, 2009; Kearney *et al.*, 2009; Dillon *et al.*, 2010; Sinervo *et al.*, 2010). Most of these studies predict that tropical species are more susceptible than their temperate counterparts, as they already live in environments that are thermally closer to their upper thermal limits and they are commonly more passive with respect to thermoregulation which would behaviorally buffer themselves from even higher values of  $T_a$  (Huey *et al.*, 2010; Gunderson and Leal, 2012). As mentioned before, a rise in  $T_a$  will lead lizards, particularly the thermoconformers, to retreat within thermal refuges and shorten the hours of activity. Consequently the energy gain will be lower which will affect reproduction and consequently the survival of the population (Figure 3; Huey *et al.*, 2010). The geographic variation in thermal microenvironment as experienced by the organisms, in the thermoregulatory behavior and in the temperature-dependence of whole-organism performance, may explain possible increase or decrease of the susceptibility of the species to warming (Huey *et al.*, 2003; Kearney *et al.*, 2009).

### *1.2. Vulnerability as a function of the magnitude of variability in the performance curves within and among populations*

The behavior and physiology of ectothermic organisms transduce the thermal environment into a particular  $T_b$ , which directly influences performance and – ultimately – fitness (Huey and Kingsolver, 1989). Proxies for fitness associated to performance (*e.g.* optimal temperature for speed run) help to understand the interaction between the ecology of the organism and the whole-animal physiological performance (Huey and Slatkin, 1976). These proxies must be of clear ecological interpretation and allow circumvent the difficulty on quantifying the thermal

sensitivity of an organism's responses (Miles, 1994a, b; Irschick and Losos, 1999; Kingsolver and Gomulkiewicz, 2003; Kohlsdorf *et al.*, 2004). Whereas at physiological-biochemical levels, performance traits include functions such as heart rate, nerve conduction velocity and enzyme activity, the most commonly studied functions of performance at a whole-organisms level are fecundity, growth, metabolic rate, stamina and running speed. Anti-predatory behavior, foraging, social dominance and migration, among other ecological traits, depend on locomotor performance (Huey and Bennett, 1987; Autumn *et al.*, 1994; Perry *et al.*, 2004), which makes it one of the most commonly studied for the means of understanding the interaction between the thermal environment and the physiology at a whole-organism level (Hertz *et al.*, 1983; Huey and Dunham, 1987; Vanhooydonck *et al.*, 2001; Irschick, 2002; Pinch and Claussen, 2003). Additionally, different kinds of locomotor traits have different ecological meanings. For example, whereas speed sprints are linked to escape behavior, the endurance or the stamina are associated routine activities like foraging, reproduction, defensive or aggressive behavior (Irschick and Losos, 1999; Angilletta, 2009). Like in all performance traits, the effects of temperature on locomotion can be illustrated in a thermal bell-shaped performance curve (TPC; Figure 4A); performance gradually increases with temperature, from a minimum thermal extreme ( $CT_{\min}$ ), until it reaches a maximum ( $T_o$ ) and then rapidly decreases till the maximum thermal extreme ( $CT_{\max}$ ; Huey and Stevenson, 1979;

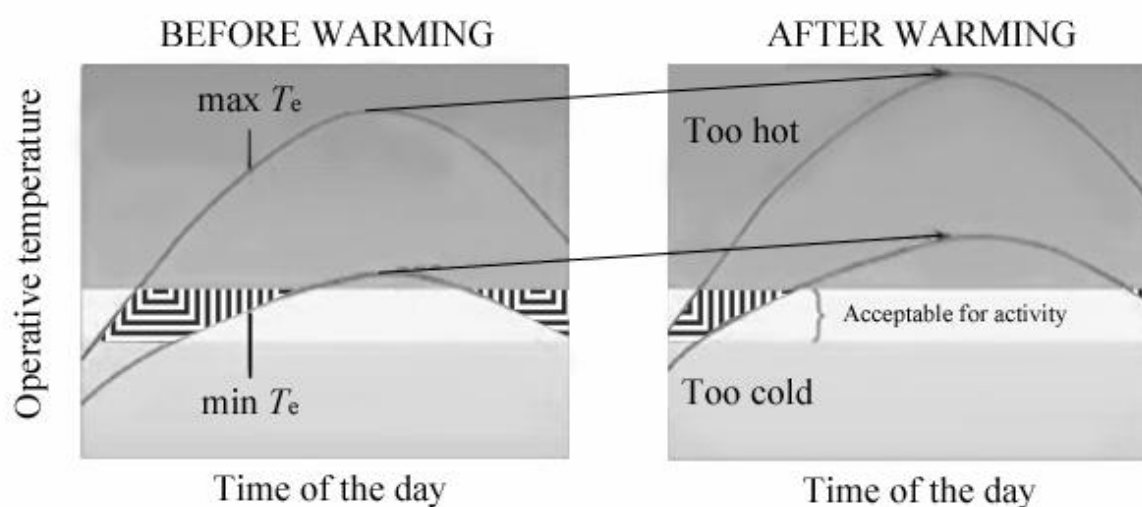


Figure 3. Hypothetical scenario of the effects of warming on the activity times of lizards. A shorten of the hours of activity are expected to reduce energy gains affecting reproduction and consequently causing extinction. (A) The maximum (upper curve) and minimum (bottom curve) operative temperatures ( $T_e$ ) of lizards during one day before global warming. Activity is constrained to a narrow range of  $T_e$ 's within an acceptable range and between the two curves; and (B)  $T_e$ 's in a warming scenario where activity time is considerably shortened (modified from Huey *et al.*, 2010).

Huey and Kingsolver, 1989, 1993; Angilletta *et al.*, 2002). The shape, the height (maximum performance), the position of the  $T_o$ , and the thermal breadths ( $B_{80}$  and  $B_{95}$ , range of  $T_b$ 's in which the performance reaches its 80% and 95%) of the TPC may change as a result of adaptive evolution or phenotypic plasticity (Huey and Kingsolver, 1989; Angilletta *et al.*, 2003; Izem and Kingsolver, 2005; Frazier *et al.*, 2006; Kingsolver, 2009). Knowing the function of the TPC, as well as the degree of plasticity of the TPCs, may help predict the responses of the species or populations to global warming (Deutsch *et al.*, 2008; Angert *et al.*, 2011; Dell *et al.*, 2011; Huey and Kingsolver, 2011).

Given a median (dominant)  $T_o$  in a population, vulnerability to warming can be estimated based on the distance between the  $T_b$  and the  $T_o$  of the individuals (Huey *et al.*, 2012) and on the thermal safety margin for physiological performance (the distance between the  $T_o$  and the  $T_a$ ; Huey *et al.*, 2009) which, in lizards, is lower in the tropics than in temperate-zones (due to lower capacities to tolerate warming in the tropics in comparison; Huey *et al.*, 2009). Therefore, more or less flexibility of  $T_o$  and of the thermal tolerance of lizards is generally associated to more or less stability of the habitat climate, respectively. For example, thermal specialists are often found in thermally stable tropical forests (Ghalambor *et al.*, 2006; Deutsch *et al.*, 2008; McCain, 2009; Sunday *et al.*, 2011; Clusella-Trullas *et al.*, 2011) thus, thermal breadth increases with latitude with the intensification of seasonal variation of  $T_a$  (Addo-Bediako *et al.*, 2000; Huey *et al.*, 2009; Sunday *et al.*, 2011). The thermal tolerance of a species may vary throughout its distribution and the life of the individuals due to plasticity (Bowler and Terblanche, 2008; Seebacher and Walter, 2012). Plasticity in thermal traits, such as thermal performance and behavior, is often correlated with the thermal environment experienced by the organisms (Kingsolver and Gomulkiewicz, 2003; Stillman, 2003; Chown *et al.*, 2004, 2010; Clusella-Trullas *et al.*, 2011; Sunday *et al.*, 2011) having a selective importance as it may buffer the impacts of raising  $T_a$ 's (Schulte *et al.*, 2011).

Optimal sprint temperature ( $T_o$ ) and heat tolerance ( $CT_{max}$ ) are positively associated with basking behavior (Huey *et al.*, 2009). In a thermally heterogeneous environment (*e.g.* open-habitat), lizards are expected to bask, thermoregulate and maintain a relatively elevated  $T_b$  (Hertz *et al.*, 1983; Huey *et al.*, 2009; 2012). When warming occurs, a thermoregulator can experience  $T_b$  near  $T_o$  for an extended period of time avoiding critical temperatures by means of behavior. As  $T_a$  continues rising  $T_b$  can exceed  $T_o$  and the survival of the organism will depend on the capacity to respond selection (Huey *et al.*, 2012). In contrast, in thermally

homogeneous habitats (e.g. forest-habitat) lizards tend to behave as poor thermoregulators or conformers (Hertz *et al.*, 1993; Huey *et al.*, 2009) and have low  $T_o$  and  $CT_{max}$  in comparison with the open-habitat congeners (Ruibal, 1961). Below the canopy  $T_e$ 's can be ideal (low and homogeneous; Huey *et al.*, 2009) for the thermoconformers but too low for the open-habitat thermoregulators. A prolonged rising of  $T_a$  will also increase  $T_e$  and thus, lizards'  $T_b$ . Hence, a stressful scenario for forest lizards could be suitable for the open-habitat

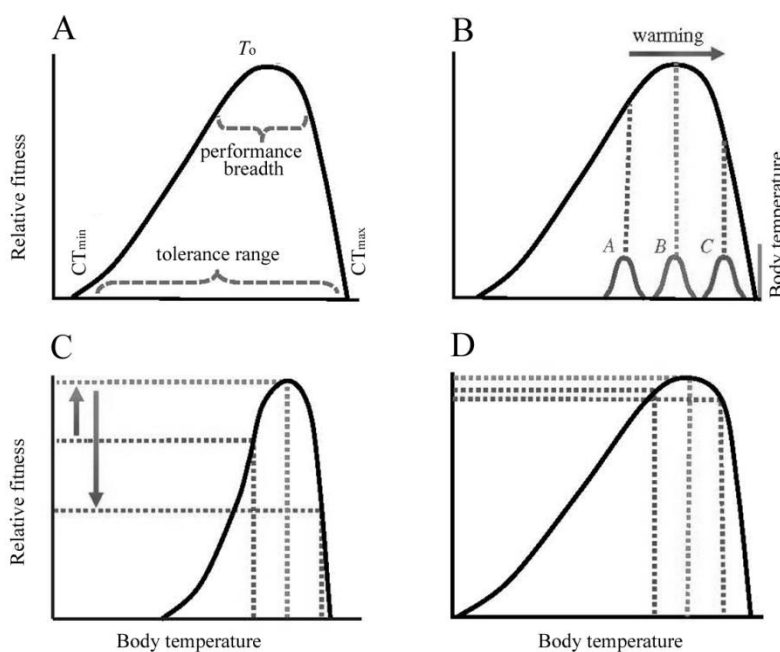


Figure 4. (A) Theoretical performance curve of a hypothetical ectotherm as a function of body temperature (e.g. maximum velocity or endurance vs.  $T_b$ ).  $CT_{min}$ : minimum or lower critical temperature;  $CT_{max}$ : maximum or upper critical temperature;  $T_o$ : optimal temperature (modified from Huey and Stevenson, 1979); (B)  $T_b$  distributions can shift higher with global warming. Warming should enhance fitness if it results in  $T_b$  getting closer to the  $T_o$  of the species (shift from A to B), but fitness will be reduced if warming raises  $T_b$  above  $T_o$  (shifts from B to C); (C, D) Impact of warming is expected to have more significant effects on thermal specialists (C) than on thermal generalists (D; modified from Huey *et al.*, 2012).

organisms. Additionally, in a performance curve, the maximum absolute performance of a species or population increases directly with its  $T_o$ , but there is also a trade-off between a maximal performance and performance breadth (open-habitat generalist vs. forest-habitat specialist). A given increase in  $T_b$  from warming will usually have a larger impact on a thermal specialist than on a thermal generalist (Figure 4B-C; Huey *et al.*, 2012). Following this trend, tropical lizards are expected to be particularly vulnerable to rapid changes (Huey *et al.*, 2009) and will probably suffer most of the extinctions (Sinervo *et al.*, 2010; Leal and Gunderson, 2012); particularly, forest lizards will soon experience selection for increased heat tolerance and the impact will depend on the organism's capacity of acclimatization (plasticity) and its ability for overcoming competitors from the open areas (Huey *et al.*, 2009).

### 1.3. Geographical and temporal variation in growth as a response to environmental temperature

Within the manifold life-history traits that respond to the fast increase in  $T_a$  (e.g. clutch size: Winkler *et al.*, 2002; breeding success: Sanz *et al.*, 2003; sex-ratio: Post *et al.*, 1999; and phenology: Visser *et al.*, 2003), individual growth variation due to global warming has been seldom studied (e.g. in geckos: Kubisch *et al.*, 2012; in lacertids: Chammaillé-Jammes *et al.*, 2006). These studies suggest that the effects of warming on life-history traits depend on species and populations, and that populations often respond in a nonlinear way.

The differences among populations or species lays on the activity  $T_b$  that better adjust to the environment and the thermoregulatory ability of individuals to compensate thermal shifts. Among the populations of one species, lizards may maintain a similar  $T_b$  during activity through thermoregulatory behavior, independently of any geographical or temporal variation (Bogert, 1949b). However, their  $T_b$  during inactivity and the hours per day of activity that lizards can spend experiencing a  $T_b$  near the  $T_p$  generally varies as a result of constrains of specific thermal environment (Adolph and Porter, 1993). The total time of exposure (e.g. to predators, solar radiation) and activity (e.g. foraging) generally differ among populations when the species occupy a broad geographical range along latitudinal or altitudinal gradients. More hours at a  $T_b$  within the optimal temperature range for activity will allow lizards to forage, find their food and consequently wait until digestion, absorption, and anabolism take place (Porter *et al.*, 1973; Huey *et al.*, 1977; Porter and Tracy, 1983; Sinervo and Adolph, 1989; Weiner, 1992). All these processes depend on each other and are sensitive in a different manner to  $T_b$  (Van Damme *et al.*, 1991; Ji *et al.*, 1996). Growth depends on the concerted performance of all these physiological processes as well as on locomotion which explains the high thermal sensitivity of the life-history trait and its variation across geographical and temporal thermal gradients (Grant and Dunham, 1990; Angilletta *et al.*, 2002). The manner in which the energy is used during the development and reproduction of the organisms will depend on biotic (sexual maturation, sex, age) and abiotic ( $T_a$ , photoperiod, hours of activity) factors, whereas the surplus of energy will be saved for periods of scarce resources (Barbault, 1991; Ghalambor *et al.*, 2006; Werneck *et al.*, 2009). Thus, longer activity seasons generally enhance growth rates and sexual maturity may be attained at younger age (Tinkle, 1972; Ballinger, 1983; Grant and Dunham, 1990). Additionally, lizards' clutch size (Winkler *et al.*, 2002; Angilletta *et al.*, 2006), reproductive success (Barbraud and Wimerskirch, 2001; Sanz

*et al.*, 2003; Angilletta *et al.*, 2006) and the sex ratio variation (Post *et al.*, 1999) increase with the raise of  $T_a$ . Recent studies have demonstrated a correlation between the warming reported for the last decades with the increase in body size, litter size, and total reproductive output in *Lacerta vivipara* (Chamaillé-Jammes *et al.*, 2006) and higher growth rate and earlier maturation in *Homonota darwini* (Kubisch *et al.*, 2012).

Global warming might benefit some lizard species, enhancing growth, reproduction success and, as a consequence, fitness. Yet, these may be short-term positive responses. If warming continues and  $T_a$  reaches values that constrain in a significant manner the activity time of a lizard, growth and reproduction will be firstly affected (Sinervo *et al.*, 2010). Most life-history traits are characterized by their plasticity, which may favor adjustments of the organisms along with the changing habitat (Radder, 2006). Hence, the long-term evolution and survival of a population or species will be determined by their change rate against the rate of global warming (Huey *et al.*, 2012).

## 2. Organization of dissertation

Environmental constrains and shifts affect organisms at different levels and with different strength, and may be buffer by phenotypic plasticity or genetic variability. Geographic and temporal variations of life-history traits reflect the interaction between the environment and the organisms. For example, precise thermoregulation is favored in habitats with low costs and risk of raising  $T_b$  (Ruibal, 1961; Regal, 1967; Hertz, 1974; Huey, 1974) highlighting a cost-benefit model. This model predicts the scope of thermoregulation that maximized energy gain (considering the costs and risks associated to achieving a particular  $T_b$ ; Huey, 1974) and the relative benefit of being a thermal generalists (eurytherm) vs. a thermal specialists (stenotherms; Huey and Slatkin, 1976). A clear-cut way for estimating the effects and physiological benefits of  $T_b$  on a whole-organism level is to measure the animal's performance over a spectrum of  $T_b$  and fit a curve function (TPC) to the data. The function for a TPC allows the calculation of the  $T_o$ , the thermal breadths and the relative performance at any  $T_b$  (Huey and Stevenson, 1979). The effect of rise of  $T_a$  on the animal's performance may be estimated based on this function. The knowledge of the interaction between  $T_a$  and the performance of a species provide fundamental elements to understanding the energetic balance and interpreting the effect of global warming over growth and reproduction. However, the susceptibility of a species results from a complex interaction of the habitat,



physiology and behavior, and these interactions may vary throughout its distribution. Knowledge of the thermal environment, physiology and ecology across a species' or close related species' range may contribute to our understanding of the impact of warming on these taxa (Kearney and Porter, 2009). This study aims to understand these interactions and estimate the impact of climate warming on six populations of lizards of the *Tropidurus torquatus* species complex (Wied-Neuwied, 1825) that inhabit different environments across the Cerrado biome (Figures 5, 6 & 7).

Chapter 1 brings a brief analysis of the patterns of vulnerability in Iguania, based on published data on the thermal ecology of *Sceloporus*, *Anolis* and *Liolaemus* distributed from Southern Patagonia to Mexico and the Caribbean, and unpublished data on *Tropidurus* from the Brazilian Cerrado. Based on an expanded data set, we examine how field body ( $T_b$ ),

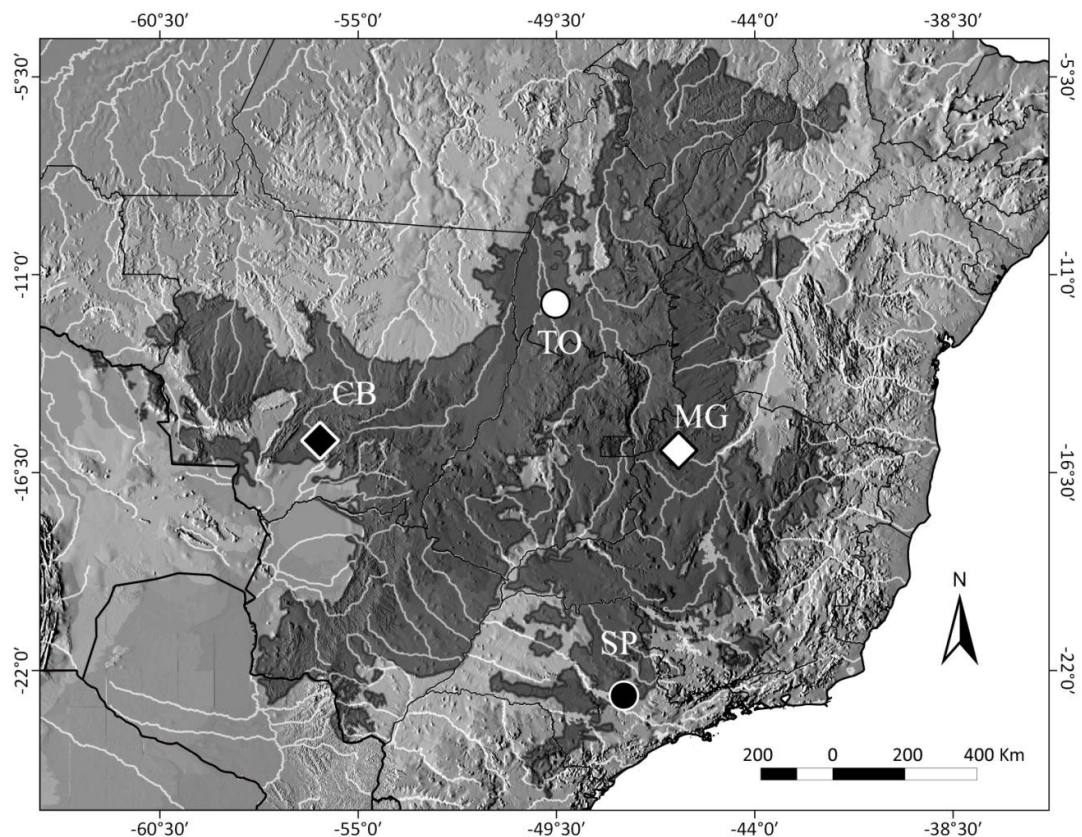


Figure 5. Study sites for *Tropidurus torquatus* (TOt) and *T. oreadicus* (TOo) from Formoso do Araguaia, Tocantins (TO, white circle), *T. torquatus* (MGt) and *T. etheridgei* (MGe) from Arinos, Minas Gerais (MG, white diamond), *T. torquatus* from Cuiaba, Mato Grosso (CB, black diamond), and *T. catalanensis* (SP) from Piracicaba, São Paulo (SP, black circles). The darker area delimits the Cerrado biome.



operative ( $T_e$ ), and preferred ( $T_p$ ) temperatures, as well as the thermoregulatory efficiency ( $E$ ) relate to (1) altitude and latitude and (3) whether vulnerability to global warming scenario decreases with latitude and altitude.

In Chapter 2 we focus on the effects of the environmental temperature ( $T_a$ ) on different thermal ( $T_b$ ,  $T_p$ , and  $T_{set-range}$ ) and behavioral ( $d_b$  and  $d_e$  indexes, and  $E$ ) traits of six populations of the *Tropidurus torquatus* species complex inhabiting different environments of the Brazilian Cerrado, and verify whether variability in thermal biology is higher among that within sites. We incorporate our findings in the context of a broader discussion under the light of data on about 60 populations of 21 species of tropidurids to discuss whether thermal differences among populations are compensated or tolerated. Finally, and under scenarios of compensation, we explore which aspects of thermal physiology and behavior are particularly relevant.

In Chapter 3 we examine the impact of warming (an increase of  $T_a$  by 3 °C) on five populations of the *Tropidurus torquatus* species based on the present thermal performance curves (TPC's). We analyze whether the vulnerability may be influenced by the magnitude of variability in thermal physiology that exists within populations of this lizard. We determine patterns of variability within populations (PVWP) compare them with patterns of variation among populations and analyze the impact of PVWP in the context of ecological climate change, to predict the response and vulnerability of the studied populations in a global warming scenario. We predict narrower performance breadths at the northern site due to a tropical environment and climate in comparison with the central and southern site (Huey and Bennett, 1987; Huey and Kingsolver, 1989), and a higher PVWP in the southern site than in the central and northern sites. At these latter populations we presume that stabilizing selection would reduce variation and consequently result in a low PVWP (Bolnick *et al.*, 2003). Finally, we expect the differences in sprint speed and endurance among the populations to follow a latitudinal pattern (Sinervo, 1990; Sinervo and Huey, 1990): for example, populations inhabiting open environments (southern and central sites) will exhibit higher sprint speed, which give a higher safety margin in a climate change scenario.

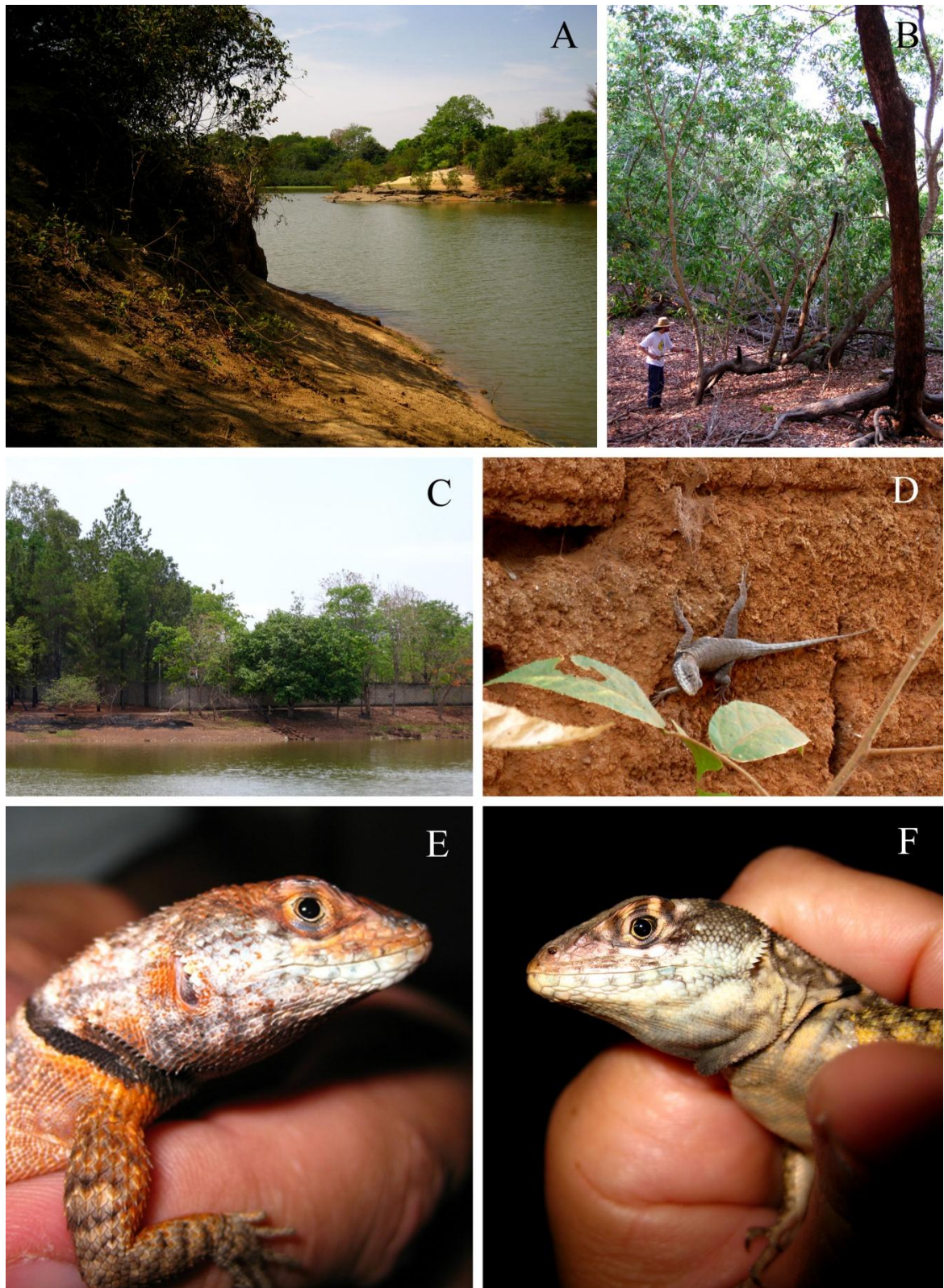


Figure 6. Gallery forests and urban Formoso do Araguaia, Tocantins, inhabited by *T. torquatus* (TOT) and *T. oreadicus* (TOO): (A) Formoso do Araguaia river (TOT's habitat); (B) gallery forest along the Córrego Papagaio (TOT's habitat); (C) downtown Formoso do Araguaia (TOO's habitat); (D) adult of TOO on typical substrate; (E) adults of TOO from downtown Formoso do Araguaia; and (F) adult of TOT collected by the Córrego Papagaio.



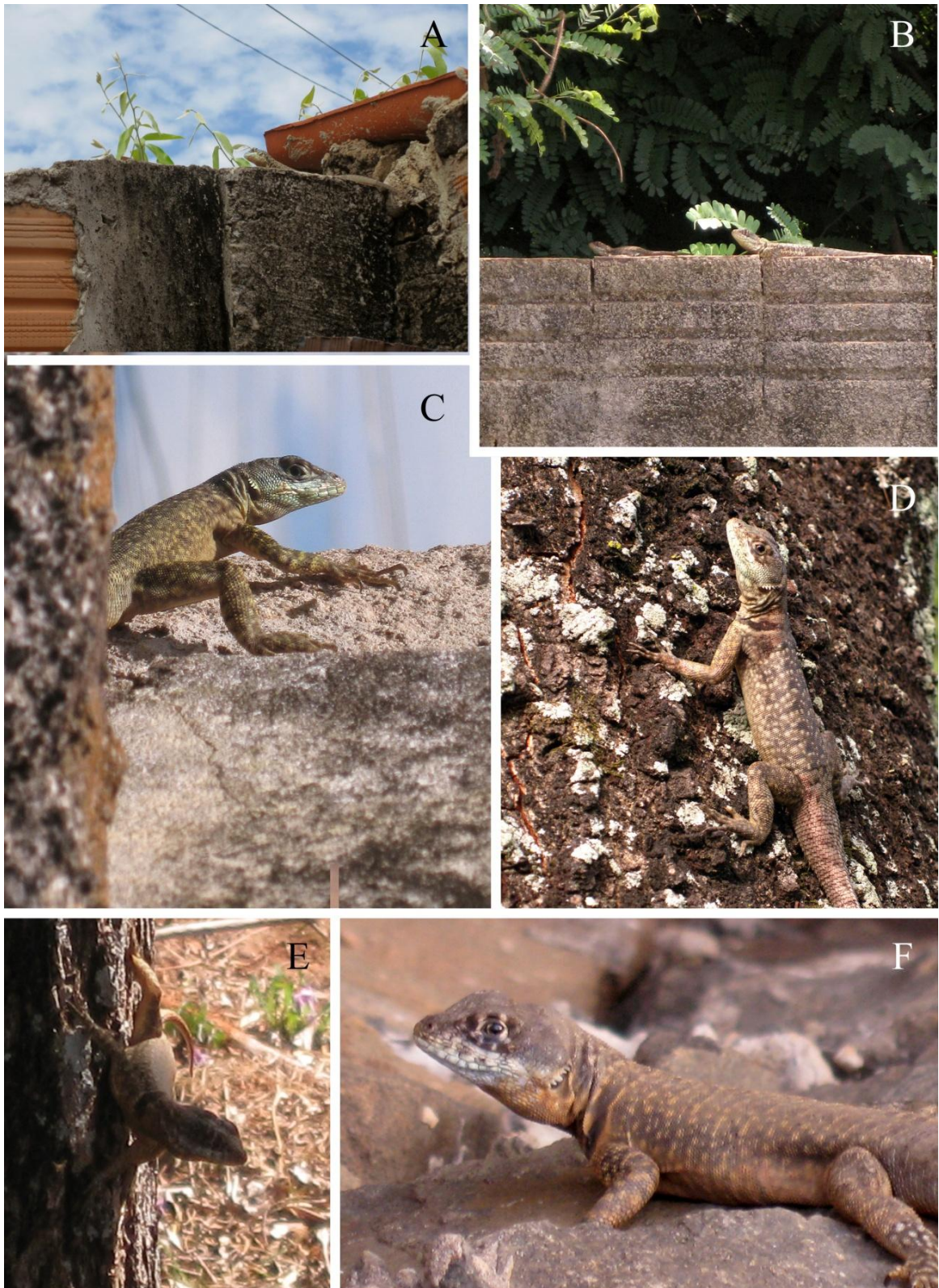


Figure 7. Specimens collected at the Central and southern sites in their typical environments or substrates: (A-B) Adults of *T. etheridgei* (MGe) and *T. torquatus* (MGt) from Arinos, Minas Gerais; (C-D) adults of *T. torquatus* (CB) from Cuiaba, Mato Grosso; (E-F) specimens of *T. catalanensis* (SP) from Piracicaba, São Paulo.

In Chapter 4, we ask whether growth patterns vary in relation to  $T_a$  in the widespread tropical lizards *T. torquatus*, and whether plasticity in phenology traits would allow the species to adjust to environmental changes associated to global warming. We take two approaches to answer these questions. Firstly, we estimate spatial variation of growth rates, age at sexual maturity, longevity, and bone growth during ontogeny among two populations sampled in northern and Central Brazilian Cerrado. Secondly, we estimate the variation of growth rates, age at sexual maturity, longevity, and bone growth during ontogeny within the two populations in over a 40 year period. More specifically, we hypothesize that rising temperatures and changing precipitation patterns over the last decades have constrained time of activity and consequently affect individual growth. The variation along the latitudinal gradient is expected to mimic the expected temporal change. In the last chapter we present results supporting the premise of temporal plasticity and suggest that an increment in  $T_a$  can benefit these populations in the short-run, but long-term consequences are unknown.



Female of *Tropidurus catalanensis* from Piracicaba, São Paulo

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## CHAPTER 1

### Vulnerability to climate warming of four genera of New World iguanians based on their thermal ecology

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*(Co-authored with Carlos A. Navas and Nora R. Ibarquengoytía)*

## ABSTRACT

We assess the vulnerability to global warming of four genera of iguanian lizards whose distributions include a broad range of environments from the Peninsula of Yucatán to southern Patagonia. Original data on body temperatures ( $T_b$ ), operative temperatures ( $T_e$ , "null temperatures" for nonregulating animals), the thermoregulatory set-point range (preferred body temperatures,  $T_{set}$ ), and quantitative indices of temperature regulation and quality of the thermal environment ( $d_b$ ,  $d_e$  and  $E$ ) for *Tropidurus* species are compared to published data for *Anolis*, *Liolaemus*, and *Sceloporus*. A general pattern suggests that thermoregulatory behavior increases with latitude and altitude (except for two southernmost liolaemids), and that tropical and lowland lizards behave as thermoconformers. Poor or no regulation of  $T_b$  and large proportions of  $T_b$  and  $T_e$  above  $T_{set}$ , as found in some of these populations, would preclude time of activity and augment the risk of overheating with an eventual raise of environmental temperature ( $T_a$ ). Our results highlight tropical populations, especially the ones inhabiting open and low elevation sites, as the most vulnerable to rising temperatures suggesting priorities in the conservation of these environments. In contrast, Patagonia and montane environments represent future thermal refuges for many northern or lowland lizards that would eventually be forced to retreat to these environments.

KEY-WORDS: Thermoregulatory efficiency, vulnerability, global warming, Iguania, operative and preferred temperatures.

## INTRODUCTION

Rising global temperatures is a dimension of climate change with major impacts on the biota (Peñuelas and Filella, 2001; Kerr, 2007; Sinervo *et al.*, 2010) through both direct and indirect effects (Hughes, 2000; Huey *et al.*, 2012). Temperature affects the biota at various levels of biological organization, but processes occurring at individual level have gained attention as a main mechanism of impact in animals (Garland and Else, 1987; Andrews *et al.*, 2000), particularly those whose body temperature depends heavily on environmental temperature. Terrestrial ectothermic vertebrates, for example, exhibit a close relationship between air (environmental;  $T_a$ ) and body temperatures ( $T_b$ ), thus tend to be sensitive to warming via effects on behavioral and physiological performance (Miles, 1994; Dunham, 1993; Angilletta, 2009; Seebacher and Franklin, 2012). In response to the increase in  $T_a$  small heliothermic lizards may shift the timing for activity and basking (Bogert, 1949; Huey, 1982), or alter their phenotype through physiological acclimation (Corn, 1971; Spellerberg, 1972; Hertz, 1981; Somero, 2010). According to the magnitude of climatic shifts and the physiology of organisms, warming may exert different impacts among taxa, eventually benefiting some lineages (Chamailé-Jammes *et al.*, 2006) and leading other to extirpation (local) or extinction (Sinervo *et al.*, 2010). Hence, climate warming may shift the distribution of lineages of ectothermic tetrapods, and impacts will vary according to physiological sensitivity (*e.g.* thermal tolerance) and temperature-dependent effects on ecological performance (Huey and Stevenson, 1979; Angilletta, 2009). Therefore, the vulnerability of a given taxon to climate warming may be framed as a compromise between sensitivity and resilience to changes in  $T_a$  (Huey *et al.*, 2012).

The concepts of sensitivity and resilience take into consideration the notion of adjustment, which occurs at various scales and levels of organization, from individual shifts to evolutionary adaptive potential (Williams *et al.*, 2008) that includes the plasticity of individual responses. The  $T_b$  range experienced, particularly during certain periods of life, may influence the integrated performance and fitness of an individual (Huey, 1991; Kingsolver *et al.*, 2004; Angilletta, 2009), but quantifying fitness is very difficult. Research relies on proxy variables such as variable-specific optimal temperatures ( $T_o$ ; *i.e.*, the body temperature in which the performance is highest or reaches 80% or 95% of maximum performance breath; Hertz *et al.*, 1983). However, in some lineages the absolute position and scope of thermal breadths may vary within individuals or across the geographical clines of a

population (Bowler and Terblanche, 2008). In contrast other lineages, particularly marked specialists, may exhibit inflexible  $T_o$  (e.g. tropical environments; Ghalambor *et al.*, 2006; Deutsch *et al.*, 2008; Huey *et al.*, 2009; McCain, 2009; Sunday *et al.*, 2011; Clusella-Trullas *et al.*, 2011). Therefore, flexibility may vary according to lineage specialization and environmental traits. Various hypotheses aiming to explain patterns of variation have been tested (Sunday *et al.*, 2011), but broad trends remain elusive. Whereas no latitudinal variation is observed for  $CT_{max}$ ,  $CT_{min}$  usually decreases with latitude (Addo-Bediako *et al.*, 2000; Ghalambor *et al.*, 2006; Huey *et al.*, 2009), and thermal tolerance breadths increase poleward, particularly in terrestrial organisms (Sunday *et al.*, 2011). High variation in seasonal temperature seems to be a significant driver of broadening the physiological thermal tolerances (Addo-Bediako *et al.*, 2000; Huey *et al.*, 2009; Sunday *et al.*, 2011). Conversely, warm specialists with low individual variability (e.g. tropical populations) would be more vulnerable to rapid changes (Huey *et al.*, 2009), with enhanced risk of extinction (Sinervo *et al.*, 2010; Leal and Gunderson, 2012).

In this paper, we ask whether vulnerability to climate warming in lizards is inversely related to latitude and altitude under scenarios of increased  $T_a$ . Our argument is based on thermal constraints, as deduced from the effects of rising  $T_a$  on key aspects of thermal biology. We present original data on four populations of two species in the genus *Tropidurus* from the Brazilian Cerrado and analyze our results in the context of published data on a sample of populations from the genera *Anolis*, *Liolaemus*, and *Sceloporus* distributed from Southern Patagonia to Mexico and the Caribbean. Based on this expanded data set, we examine how  $T_b$ ,  $T_e$ ,  $T_p$  and effectiveness of thermoregulation ( $E$ ) relate to (1) altitude and latitude and (3) whether vulnerability to global to warming scenario decreases with latitude and altitude.

## MATERIALS AND METHODS

This study includes field and laboratory temperatures, and thermoregulation indices (after Hertz *et al.*, 1993) for four iguanian families: Dactyloidae, Liolaemidae, Phrynosomatidae, and Tropiduridae (*sensu* Pyron *et al.*, 2013). We gathered data from the literature on the first three, particularly from the species *Anolis cooki*, *A. cristatellus*, *A. gundlachi* (Huey and Webster, 1976; Hertz, 1992a, 1992b; Hertz *et al.*, 1993), *Liolaemus albiceps*, *L. irregularis*, *L. multicolor* and *L. yanalcu* (Valdecantos *et al.*, 2013), *L. bibronii* (Medina *et al.*, 2009), *L. boulengeri* and *L. lineomaculatus* (Medina *et al.*, 2011), *L. elongatus* (Ibargüengoytía, 2005),



*L. magellanicus* and *L. sarmientoi* (Ibargüengoytía *et al.*, 2010), *L. pictus argentinus* (Gutiérrez *et al.*, 2010), and *Sceloporus mucronatus* and *S. serrifer* (Sinervo *et al.*, 2011). To these, we added unpublished data on *Tropidurus catalanensis*, *T. torquatus* "sensu lato" and *T. oreadicus* collected from 2011 until 2013 following the same methodology (Hertz *et al.*, 1993). This set of species encompasses a range of ecological settings such as the deserts of Yucatan, the Brazilian Cerrado, the lowlands of southern Patagonia steppe, the rainforests of Puerto Rico and the *Nothofagus* forests in Tierra del Fuego (Table S1).

### 1. Body and operative temperature data

Four populations of the genus *Tropidurus* were collected in three localities along a latitudinal gradient in the Cerrado biome: 22 lizards of *T. catalanensis* in Piracicaba, SP (554 m a.s.l; 22°43'30" S, 47°38'56" W; April, 2011 and September, 2013); 22 specimens of *T. torquatus* "sensu lato" in Arinos, MG (526 m a.s.l; 15°55'01" S, 46°06'21" W; March, 2012); 32 specimens of *T. torquatus* "sensu lato" in the gallery forests in the proximities of Formoso do Araguaia, TO (192 m a.s.l; 11°47'49" S, 49°31'44" W; September, 2012); and 26 *T. oreadicus* inhabiting the urban areas of Formoso do Araguaia, TO (265 m a.s.l; 11° 48' S, 46° 06' W; September, 2012).

Specimens were collected by hand or with the aid of a noose from 8 to 18 h only when active (outside the burrows, performing any behavior related to thermoregulation, feeding and/or breeding activities). Body temperatures ( $T_b$ ), which corresponds to field values measured during the hours of activity, were registered in the field immediately after specimens were captured (*sensu* Pough and Gans, 1982) using a Sper Scientific 4 Channel Datalogging thermometer (Mod. # 800024) and a catheter probe of 1.62 mm diameter (Sper Scientific Mod. # 800077). Individuals were handled by head to avoid heat transfer and temperature was recorded within 10 s of handling introducing ca. 1 cm inside the cloaca.

The distribution of the operative temperatures ( $T_e$ ) represent the "null" distribution of  $T_b$  that non-regulating animals would experience in their microhabitats (Heath, 1964) and were also collected during the hours of activity at each capture using plastic models made of gray PVC pipes of 10 to 15 cm filled with silicone [for a detailed description please see Sinervo *et al.* (2010)] that were connected to data loggers (HOBO U12 4-Channel External Data Logger - U12-008). Whereas 60 models were used to sample the distribution of  $T_e$  at the *Anolis*' sites (Hertz, 1992b) the other literature reviewed herein placed from 6 (Valdecantos *et al.*, 2013) to

20 (Gutiérrez *et al.*, 2010) models at each site. Based on this range, a minimum of 14 and a maximum of 22 models were deployed in potential microenvironments that lizards might occupy at the poleward ( $N = 14$ ), central ( $N = 22$ ) and equatorward ( $N = 22$ ) sites *Tropidurus* lizards. The size and color of the models were determined based on the calibration against real specimens for previous studies, using two catheter probes of 1.62 mm diameter (Sper Scientific Mod. # 800077) simultaneously to register the temperatures of both the models and the lizards. The best models for *Tropidurus catalanensis*, *T. torquatus* and *T. oreadicus* were selected by comparing the  $R^2$  obtained from the correlation between each model and specimens'  $T_b$ .

## 2. Preferred temperature and set-point range

Back in the laboratory lizards were conditioned in terraria with food (cockroaches and crickets) and water *ad libitum*. During the experiments, that lasted not more than three weeks, lizards were kept in average natural conditions of temperature and photoperiod. Preferred body temperature ( $T_p$ ) and set-point temperature range ( $T_{set}$ , which represents the "target"  $T_b$  range that animals would achieve in environments where the cost of thermoregulation is zero; Heath, 1965; Hertz *et al.*, 1993) were estimated using photothermal gradients of 100 x 45 x 16 cm where lizards were placed individually. A lamp was used as the heat source at one end of each terrarium and it was adjusted to achieve a linear  $T_a$  gradient of 23 °C to 45 °C (well above lethal limits). Ultra-thin catheter thermocouples (1 mm, Omega engineering Inc., Product code: 5SC-TT-T-40-72) were taped to the lizard's vent and body temperatures were recorded at 2 min intervals for 2 h, by connecting the thermocouple to a USB-based 8-channel TC input module (MCC DAQ Measurement Computing). Lizards would start thermoregulating after approximately 20 minutes of being placed in the gradients so these data were omitted in the calculations. Preferred temperatures and lower and upper  $T_{set}$  (the temperatures bounding the interquartile range of the observed  $T_p$ ) were estimated from the  $T_b$  recorded in the thermal gradients for each lizard and used to calculate the populations'  $T_p$  and  $T_{set}$ .

## 3. Effectiveness of temperature regulation

The efficiency of temperature regulation (*sensu* Hertz *et al.*, 1993) was calculated as:  $E = 1 - (\text{mean } d_b / \text{mean } d_e)$ , in which  $d_b$  is the average of the absolute distance of  $T_b$  from the set-point range of each individual and  $d_e$  is the deviations between  $T_e$  and  $T_{set}$  which specifies the

average thermal quality of a microenvironment from the organism's standpoint (Hertz *et al.*, 1993). Therefore, thermoregulation is considered effective when  $E$  is close to 1, thermoconforming when  $E$  is close to 0, and moderately effective if  $E$  is close to 0.5 (Hertz *et al.*, 1993; Bauwens *et al.*, 1996). Negative  $E$ -values occur if animals actively avoid favorable thermal microhabitats due to perhaps predation or prey availability (Hertz *et al.*, 1993).

#### 4. Comparison with other species

We analyzed all available data on field and selected body temperature for the iguanian species mentioned above together with the results on *Tropidurus torquatus* and *T. oreadicus* focusing on patterns of vulnerability associated to the environment they occupy and their thermal biology.

## RESULTS

### 1. Latitude and thermoregulation trends in *Liolaemus*, *Anolis* and *Sceloporus*

In Patagonia, *Liolaemus bibronii*, *L. boulengeri*, *L. lineomaculatus*, *L. magellanicus* and *L. sarmientoi* exhibit  $T_b$ 's ranging from 26 to 29°C but, their  $T_p$ 's are significantly higher, from 34 to 36°C (Medina *et al.*, 2009; Table S2). In the southernmost liolemids, *L. sarmientoi* and *L. magellanicus*, high percentages of the  $T_b$ 's, 92% and 100%, respectively, fall below the  $T_{set}$  (Figures S1A & S1B). Further North, interpopulational studies reveal the average extent to which *L. bibronii*, *L. boulengeri* and *L. lineomaculatus* experience  $T_b$  outside the  $T_{set}$  range ( $d_b$ ) increases with latitude (Medina *et al.*, 2009; Ibarzüengoytía *et al.*, 2010; Medina *et al.*, 2011; Table S2; Figure S2), whereas in *L. pictus argentinus* it increases with altitude (Gutiérrez *et al.*, 2010; Figure S3A). In open environments such as rocky lakeshore or the steppe outcrops, *L. p. argentinus*' and *L. elongatus*'  $T_b$  are not included in the  $T_{set}$  range (Ibarzüengoytía, 2005; Gutiérrez *et al.*, 2010; Table S2) and both species experience  $T_b$ 's that often exceed their thermal preference. For example, in *L. elongatus*, 26% of  $T_b$ 's were included in the  $T_{set}$  and 42% fell above this range (Ibarzüengoytía, 2005; Figure S3B). The indices obtained by comparing  $T_e$  and  $T_b$  with the  $T_{set}$  range, describe most of the southern species as moderate thermoregulators ( $E$  values range from 0.30 to 0.59; Table S2), whereas in open habitats in Patagonia liolemids behave as constrained thermoregulators (negative  $E$  values and close to zero; Table S2).

In the Puna, *Liolaemus albiceps*, *L. irregularis*, *L. multicolor*, and *L. yanalcu* achieve  $T_b$ 's that

range from 34.2 to 36.6°C; 39.5% to 63.6% (mean = 46.5) falling within the  $T_{set}$  range (Table S2; Figure S4). Mean percentages of 25 and 28 of  $T_b$ 's were below and above the  $T_{set}$  range (Figure S4).  $T_b$ 's were close to (low  $d_b$ ) and overall higher than the mean  $T_e$  registered in their environments (Table S2; Figure S4). In fact, 63.4-87.8% of the  $T_e$  recordings fall below the  $T_{set}$  range in all sites (Figure S4). Low  $d_b$ , given by the proximity of  $T_b$  and  $T_e$ , and high  $d_e$ , because of high percentages of  $T_e$  below the  $T_{set}$ , result in high values of  $E$  which range from 0.88 to 0.97 (Table S2).

In Puerto Rico, *Anolis* species experience  $T_b$  values (19.4-32.1 °C; Table S2) that are usually below the  $T_p$  (25.1-30.6°C; Table S2). More than 95%, 58-95% and 73-80% of the  $T_e$  recordings fall below the  $T_{set}$  range at high elevation (1130-1150 m a.s.l.), low elevation (90-210 m a.s.l.) and in the desert (5 m a.s.l.), respectively (Figure S5). For example, at 210 m a.s.l., *A. gundlachi* occupies microenvironments where almost 50% of all  $T_e$  readings are included within the  $T_{set}$  range whereas at 1130m a.s.l. more than 95% of the  $T_e$  readings are below the  $T_{set}$  range (Figure S5C). Moreover, lizards of this species thermoregulate more efficiently in summer ( $E = 0.14-0.21$ ), when mean  $T_e$  is above  $T_{set}$ , than in winter ( $E = 0.00-0.08$ ; Table S2). *A. cristatellus* also shows more efficiency in the desert in summer ( $E = 0.64$ ) than in mesic sites during either summer or winter (Table S2). In xeric lowlands, *Anolis cooki* also prefers and is active at high  $T_b$ 's but contrary to *A. gundlachi* and *A. cristatellus*, it appears to thermoregulate more effectively in winter than in summer (Table S2).

In Mexico, *Sceloporus mucronatus* from both upland (Ajusco - 3400 m a.s.l.) and montane (Tecocomulco - 2500 m a.s.l.) sites, and for *S. serrifer* from a lowland tropical forest site (Yucatan - 10 m a.s.l.) exceed their preferred temperature range ( $T_{set}$  range; Figure S6) although most registered values of  $T_e$  fall below the  $T_{set}$  range (Sinervo *et al.*, 2010).

## 2. Thermoregulation in four populations of the genus *Tropidurus*

In southern Brazilian Cerrado, *Tropidurus catalanensis* maintains its  $T_b$  within and close to its preferred temperature range (Table 1). Here, most of the  $T_b$  recordings fall below the  $T_{set}$  range, while most of the recordings of the central and northern sites of the biome exceed the  $T_{set}$  range by 0.9 to 1.7 °C (Table 1). Also in the southern site, 59% of the  $T_e$  values fall below the  $T_{set}$  range (Figure 1A). In the central site, most  $T_e$ 's exceed the upper- $T_{set}$  (Table 1; Figure 1B) while in the North 13% and the 58% of the  $T_e$ 's fall within and below this range, respectively (Table 1; Figure 1C). The index  $d_b$  was close to 2 in all populations but  $d_e$  was

significantly higher in the South which results in a higher efficiency in thermoregulation in this population ( $E = 0.69$ ). In the central and northern sites, *T. torquatus* behaves as a thermoconformer and as a constrained thermoregulator, respectively, reflected in their close to zero and/or negative  $E$  values (Table 1).

### 3. Variation of the thermoregulatory behavior with latitude and altitude

The  $d_b$  and  $d_e$  indices of the populations included herein, as well as their respective standard deviations, resulted positively correlated to latitude and altitude (with the exception of  $d_b$  and altitude; Table 2; Figures 2A & 2B). The correlation between  $E$  and latitude was significant when *L. magellanicus* was removed from the analyses, but became weak when included (Table 2; Figures 2C & 2D).

## DISCUSSION

The combined data on four iguanian lineages corroborate the hypotheses of increased susceptibility to warming in species from lower latitude and elevation, and contributes to debate climate-related risk of extinction in lizards (Deutsch *et al.*, 2008; Huey *et al.*, 2009). Lizards from cold regions face reduced opportunities for thermoregulation that, within limits, may be compensated by behavior (Fuentes and Jaksic, 1979; Ibagüengoytía *et al.*, 2008; Ibagüengoytía *et al.*, 2010), whereas lizards from warmer environments show a tendency to thermoconformity. Whereas most low-elevation Patagonian *Liolaemus* thermoregulate poorly (Medina *et al.*, 2009; Gutiérrez *et al.*, 2010; Medina *et al.*, 2011), their counterparts from the mountains and plateaus display moderate to high thermoregulatory efficiency (Gutiérrez *et al.*, 2010; Ibagüengoytía *et al.*, 2010; Valdecantos *et al.*, 2013). Given the high proportion of  $T_e$  below  $T_{set}$  observed in most of the cold and temperate environments inhabited by *Liolaemus* and *Anolis*, and the broad thermal tolerance described for the genus (Cruz *et al.*, 2005), warming could be neutral or beneficial to these populations, which are at lowest risk. *Anolis* also display variation in thermoregulation behavior. For example, *A. cooki* from xeric lowlands behaves as a moderate thermoregulator, whereas *A. cristatellus* exhibits an increasing efficiency of thermoregulation with altitude (Hertz *et al.*, 1993). Additionally, the thermoregulatory behavior of *Anolis* may vary seasonally (Hertz *et al.*, 1993), so the risk would not be homogenous through the year. The thermoregulation efficiency of *A. cooki* and *A. cristatellus*, at 5 and 90 m a.s.l respectively, decreases in summer, when the risk of overheating rises. Thus, the vulnerability of these lizards to climate warming is not only

linked to the efficiency of thermoregulation but also to the geographic and seasonal variation in their physiology (phenotypic plasticity).

Near the Equator, at low elevation, lizards experience minimum annual variations of  $T_a$  and both, open and forested environments are thermally stable. Under proper thermal conditions and physiological specialization, such environments may favor thermoconformity and, as seems the case of some *Tropidurus*, which show a relaxed capacity to adjust (Huey *et al.*, 2003; Sears *et al.*, 2011). Tropical environments, though, are not necessarily favorable. *Tropidurus* in the northern and southern limits of the Cerrado find buffering options against warming (gallery forests with low  $T_a$ 's, respectively), but central populations are exposed to  $T_e$ 's exceeding their upper- $T_{set}$ . Therefore, the latter are likely more vulnerable to warming. In addition, tropical-forest lizards may be particularly susceptible to climate change given a high tendency to physiological specialization, derived from thermal stability (Huey *et al.*, 2009). A parallel issue is that tropical low elevations may more often display overheating substrate temperatures, so that access to low  $T_a$  shelters may be beneficial as a short-term key factor because of the expected compromise between sheltering and activity time.

Overheating is a concrete risk in some environments, both as a direct driver of death or as a limiting factor for activity (Sinervo *et al.*, 2010). For example, the ground surface temperature of deserts inhabited by *S. merriami* exceeds the species lethal temperature during most of the day (Grant and Dunham, 1990). Accordingly, Dunham (1993) predicted that a 2°C increase in  $T_a$  would severely restrict lizard activity, energy gain and population growth. Furthermore, Sinervo *et al.* (2010) emphasized the vulnerability of *S. merriami*, *S. mucronatus*, and *S. serrifer* due to energetic constraints during the reproductive season, reporting the extinction of 24 populations of this genus between 1975 and 2009. Whereas *T. torquatus* and *Sceloporus* species from forested environments may avoid overheating in cool refuges (Huey *et al.*, 2009), the central population of *T. torquatus*, *A. gundlachi*, and the desert populations of *A. cristatellus*, cannot access such refuges and therefore are in high risk of suffering the effects of warming. Although a recent study on *A. sagrei* confirmed that some tropical populations might be capable of adapting to warmer and thermally variable environments (Logan *et al.*, 2014), for most ectotherms, it remains unclear whether they have the genetic plasticity to overrun the rate of global warming (Chevin *et al.*, 2010). Climate change likely promotes natural selection on behavior, physiology and niche preferences in lizard taxa, but further

consequences remain unclear given the few studies on the evolutionary rates for these traits (Kellermann *et al.*, 2012; Muñoz *et al.*, 2014; Sunday *et al.*, 2014; Logan *et al.*, 2014).

A proposed generalization based on shifts in thermal physiology across latitudinal gradients is that the more sensitive populations and species to variation in  $T_a$  (*e.g.* close to the Equator) may be in greatest danger from continued global warming (Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008). Moreover, upper tolerances seem conservative across species (Addo-Bediako *et al.*, 2000; Sunday *et al.*, 2011; Kellermann *et al.*, 2012; Grigg and Buckley 2013; Hoffmann *et al.*, 2013), so populations facing high  $T_a$  may fail to evolve physiological tolerances to warming (Araujo *et al.*, 2013). Note that, whereas  $T_a$  is generally exceeded by the physiological thermal-tolerance limits,  $T_e$  matches or surpasses them, which suggests that predictions based on rising  $T_a$  generally underestimates the effects of climatic variation on ectotherms (Sunday *et al.*, 2014).

It must be noted that the sensitivity of populations to warming, as viewed by Williams *et al.* (2008), may vary across lineages. Whereas some taxa may adapt to environmental changes (Logan *et al.*, 2014) adaptive trends are unlikely to outrun global warming (Miles, 1994; Sinervo *et al.*, 2010). Besides, habitat fragmentation and transformation may constrain the possibilities to disperse to cooler environments accelerating the extinctions, particularly in montane populations that would also face the upward progress of lowland species (Huey *et al.*, 2009). Understanding the processes of adaptation, acclimation and phenotypic plasticity that determine the variation in the physiology among taxa would help assessing lizard vulnerability to climate warming. This challenge entails an integration of physiological, behavioral, and evolutionary approaches, and will not be settled unless specific predictions for different traits and lineages are tested.

As a final comment, we must acknowledge the challenging ecological context in which some of the studied populations are located. Sheep overgrazing together with soil and water pollution by oil and mining companies represent the main threats to the biodiversity of Patagonia. Nevertheless, this region concentrates more than 2,2 ha. in National Parks (Hopkins, 1995). In Puerto Rico and Mexico, fragmentation of the landscapes represents the major conservation problem. Species like *A. cooki*, for example, which used to inhabit the dry forests, have been slowly displaced to areas in sympatry with *A. cristatellus* (Genet, 2002). However, despite being considered as a hotspot for conservation (Myers *et al.*, 2000), the

worst scenario is observed in the Brazilian Cerrado as the savanna is gradually replaced by soy fields and cattle ranches and less than 3% of the biome is under protection (Ratter *et al.*, 1997). Paradoxically, the results presented herein suggest that species with the highest vulnerability inhabit the less protected areas, which highlights the urgent need of mitigation measures as the increase in conservation units to protect their underestimated biodiversity.

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Table 1. Mean  $\pm$  standard error or median and range ( $N$ ) of body ( $T_b$ ) and preferred ( $T_p$ ) temperatures, set-point range (lower and upper  $T_{set}$ ), operative temperatures ( $T_e$ ),  $d_b$  and  $d_e$  indices, and effectiveness of thermoregulations ( $E$ ) of *Tropidurus catalanensis*, *T. torquatus* "sensu lato" and *T. oreadicus*. Sample size is indicated between brackets.

	$T_b$	$T_p$	lower- $T_{set}$	upper- $T_{set}$	$T_e$	$d_b$	$d_e$	$E$
<i>Tropidurus catalanensis</i> - Brazil								
Savanna, 22°S	36.1 (30.6-39.3; 43)	34.4 $\pm$ 0.02 (43)	33.6 $\pm$ 0.2 (43)	35.2 $\pm$ 0.2 (43)	37.3 $\pm$ 0.3 (14)	1.6 $\pm$ 0.2 (41)	5.3 $\pm$ 1.3 (13)	0.69
<i>T. torquatus</i> "sensu lato"								
Savanna, 15°S	35.8 (30.4-39.3; 22)	33.9 $\pm$ 0.01 (22)	33.1 $\pm$ 0.2 (22)	34.7 $\pm$ 0.2 (22)	36.1 $\pm$ 0.6 (20)	1.9 $\pm$ 0.3 (22)	0.9 (0-6.6; 20)	0.06
Gallery forest in savanna, 11°S	36.2 $\pm$ 0.3 (32)	34.6 (30.3-37; 32)	34.1 (30-36.3; 32)	35.3 (30.4-39.1; 32)	33.5 (31.5-39.4; 7)	1.7 $\pm$ 0.2 (32)	1.7 $\pm$ 0.7 (7)	-0.01
<i>T. oreadicus</i>								
Savanna, 11°S	38.1 (30.1-41.3; 26)	35.3 (30.7-37; 26)	34.8 (29.6-37; 26)	36 (30.8-37.5; 26)	39.6 $\pm$ 1.2 (15)	3.2 $\pm$ 0.4 (26)	4.5 $\pm$ 0.9 (15)	0.29

Table 2. Results of the correlation (Spearman rank order statistic and *P* value) and regressions (when the correlations were significant (*P* < 0.05); *b* coefficient, *t*-test and analysis of variance statistics and equation) among latitude, altitude, indices of thermoregulation (*d<sub>b</sub>*, *d<sub>e</sub>*, and *E*), and the correspondent standard deviation (SD).

		Correlation		Regression						
		<i>S</i>	<i>P</i>	<i>b</i>	<i>t</i> -test	<i>P</i>	<i>r</i> <sup>2</sup>	<i>F</i>	<i>P</i>	Equation
Latitude	<i>d<sub>b</sub></i>	0.382	< 0.05	0.111	<i>t</i> <sub>33</sub> = 5.039	< 0.001	0.442	<i>F</i> <sub>1,32</sub> = 25.388	< 0.001	<i>d<sub>b</sub></i> = -0.325 + (0.111 * Lat.)
	SD of <i>d<sub>b</sub></i>	0.618	< 0.05	0.0105	<i>t</i> <sub>33</sub> = 0.855	<b>0.399</b>	0.0223	<i>F</i> <sub>1,32</sub> = 0.73	0.399	SD of <i>d<sub>b</sub></i> = 0.38 + (0.0105 * Lat.)
	<i>d<sub>e</sub></i>	0.678	< 0.05	0.150	<i>t</i> <sub>33</sub> = 3.122	<b>0.004</b>	0.239	<i>F</i> <sub>1,32</sub> = 9.746	0.004	<i>d<sub>e</sub></i> = 2.262 + (0.15 * Lat.)
	SD of <i>d<sub>e</sub></i>	0.706	< 0.05	0.818	<i>t</i> <sub>33</sub> = 0.975	<b>0.334</b>	0.0424	<i>F</i> <sub>1,32</sub> = 0.975	0.334	SD of <i>d<sub>e</sub></i> = 0.818 + (0.0656 * Lat.)
	<i>E</i>	0.27	<b>0.127</b>	-	-	-	-	-	-	-
Altitude	<i>d<sub>b</sub></i>	-0.16	<b>0.365</b>	-	-	-	-	-	-	-
	SD of <i>d<sub>b</sub></i>	0.629	< 0.05	0.0003	<i>t</i> <sub>33</sub> = 3.49	0.001	0.276	<i>F</i> <sub>1,32</sub> = 12.177	0.001	SD of <i>d<sub>b</sub></i> = 0.295 + (0.0003 * Lat.)
	<i>d<sub>e</sub></i>	0.673	< 0.05	0.00181	<i>t</i> <sub>33</sub> = 4.987	< 0.001	0.445	<i>F</i> <sub>1,32</sub> = 24.872	< 0.001	<i>d<sub>e</sub></i> = 4.295 + (0.00181 * Lat.)
	SD of <i>d<sub>e</sub></i>	0.799	< 0.05	0.00183	<i>t</i> <sub>33</sub> = 21.18	< 0.001	0.953	<i>F</i> <sub>1,32</sub> = 448.607	< 0.001	SD of <i>d<sub>e</sub></i> = -0.118 + (0.00183 * Lat.)
	<i>E</i>	0.423	< 0.05	0.00017	<i>t</i> <sub>33</sub> = 5.622	< 0.001	0.505	<i>F</i> <sub>1,32</sub> = 31.611	< 0.001	<i>E</i> = 0.238 - (0.00017 * Lat.)



## FIGURE LEGENDS

Figure 1. Distribution of body temperatures ( $T_b$ ; upper graphs) and operative temperatures ( $T_e$ ; lower graphs) distributions of *Tropidurus catalanensis* in (A) Piracicaba (southern site), and *T. torquatus* in (B) Arinos (central site), and (C) Formoso de Araguaia (northern site). The black and grey arrows indicate the mean  $T_b$  and mean  $T_p$ , respectively. The grey area indicates the lower and upper set-points ( $T_{set}$ ) of the preferred body temperature. Percentages of the observation below and above the  $T_{set}$  range are specified.

Figure 2. Variation of thermoregulatory indices (*sensu* Hertz *et al.*, 1993) with latitude (A) and altitude (B) for the populations of *Anolis*, *Liolaemus*, *Sceloporus* and *Tropidurus* included in the paper. Index  $d_b$ , solid circles and lines; standard deviation of  $d_b$ , empty circles and dotted lines;  $d_e$ , solid triangles and medium dashed lines; standard deviation of  $d_e$ , empty triangles and dash-dot-dotted lines; and the effectiveness of thermoregulations ( $E$ ), solid squares and long-dashed lines.

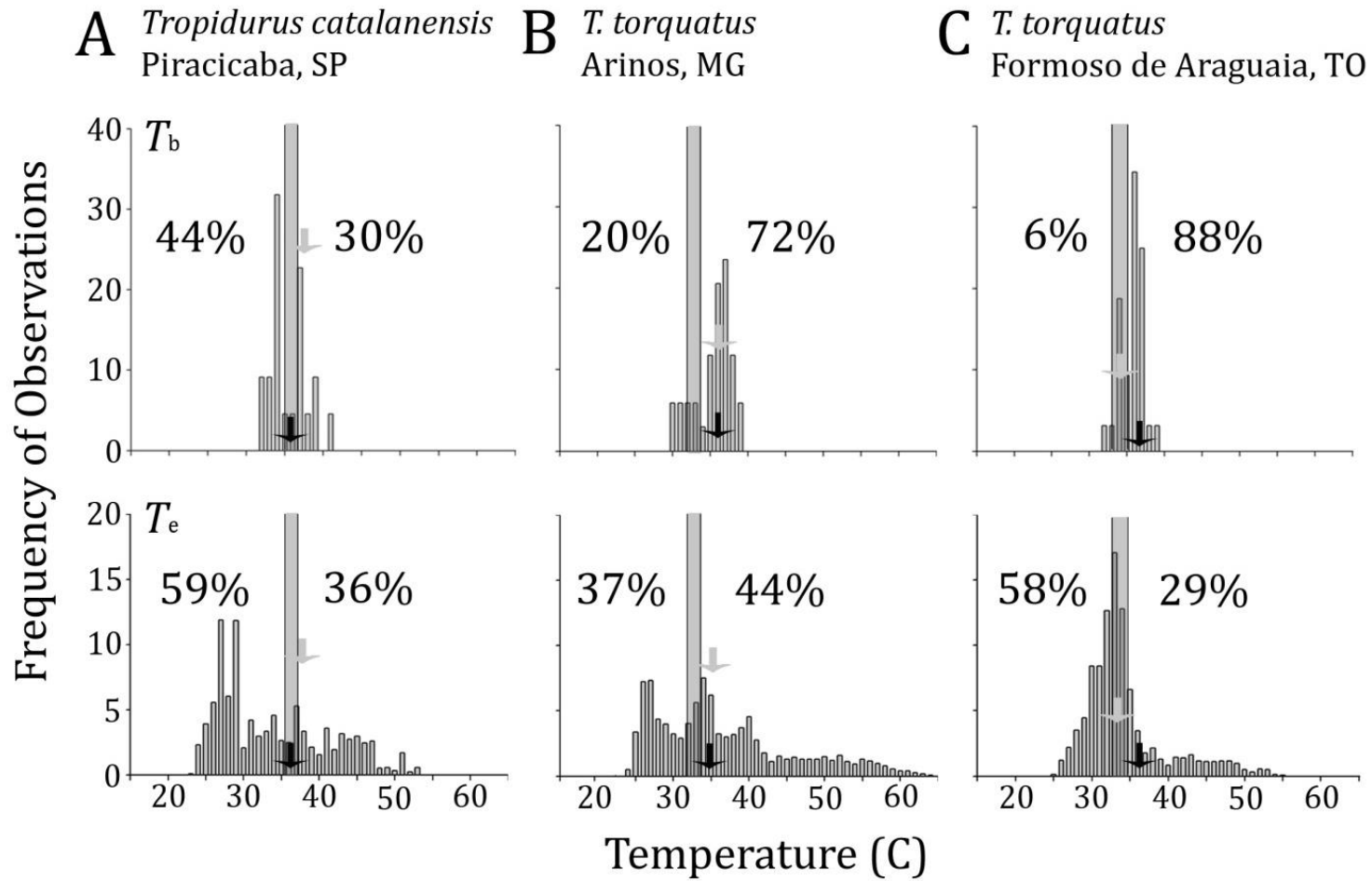


Figure 1.

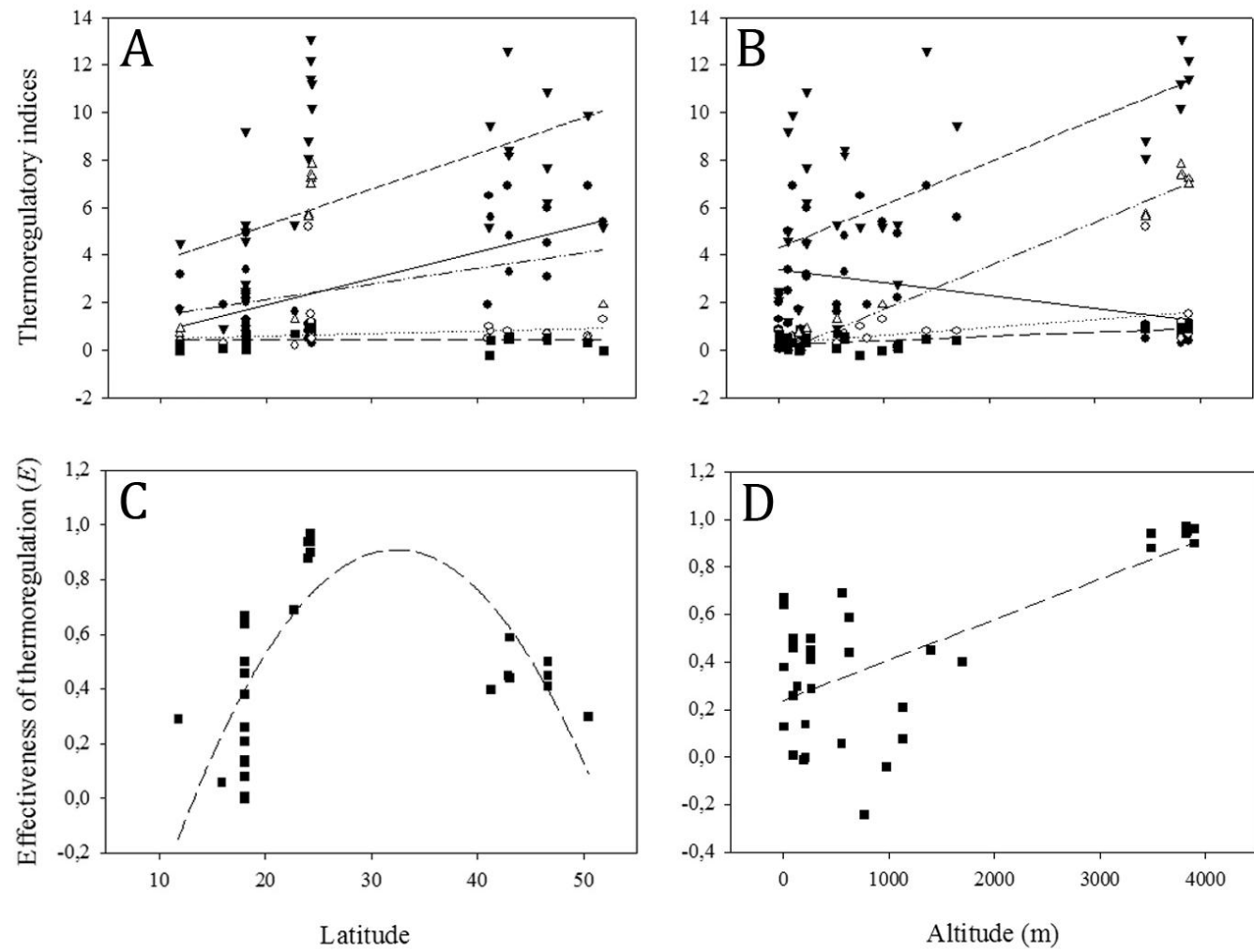


Figure 2.

## SUPPLEMENTAL MATERIAL

Table S1. Data on the study sites of the species/populations included in the study.

Species	Study sites	Coordinates	Elevation (m a.s.l)	Habitat	Authors
<i>Anolis cooki</i>	SW Puerto Rico	18°01'N, 67°04'W	5	Desert	Hertz, 1992a; 1992b; Huey and Webster, 1976
<i>A. cristatellus</i>	SW Puerto Rico	18°01'N, 67°04'W	5	Desert	Hertz, 1992a; 1992b; Huey and Webster, 1977
	SW Puerto Rico	18°01'N, 67°04'W	90	Lowland mesic	Hertz, 1992a; 1992b; Huey and Webster, 1978
	SW Puerto Rico	18°01'N, 67°04'W	1150	Upland mesic	Hertz, 1992a; 1992b; Huey and Webster, 1979
<i>A. gundlachi</i>	SW Puerto Rico	18°01'N, 67°04'W	210	Lowland mesic	Hertz, 1992a; 1992b; Huey and Webster, 1980
	SW Puerto Rico	18°01'N, 67°04'W	1130	Upland mesic	Hertz, 1992a; 1992b; Huey and Webster, 1981
<i>Liolaemus albiceps</i>	San Antonio de los Cobres, Salta, Argentina	24°16'S, 66°13'W	3816	Puna desert	Valdecanto <i>et al.</i> , 2013
<i>L. bibronii</i>	Esquel, Chubut, Argentina	43°01'S, 70°47'W	626	Patagonian steppe	Medina <i>et al.</i> , 2009
	Perito Moreno, Santa Cruz, Argentina	46°37'S, 71°15'W	263	Patagonian steppe	Medina <i>et al.</i> , 2009
<i>L. boulengerie</i>	Esquel, Chubut, Argentina	43°01'S, 70°47'W	626	Patagonian steppe	Medina <i>et al.</i> , 2011
	Perito Moreno, Santa Cruz, Argentina	46°37'S, 71°15'W	263	Patagonian steppe	Medina <i>et al.</i> , 2011
<i>L. elongatus</i>	Pilcaniyeu, Rio Negro, Argentina	41-41.5°S, 70- 71.4°W	840	Patagonian steppe	Ibargüengoytía., 2005
<i>L. irregularis</i>	San Antonio de los Cobres, Salta, Argentina	24°15'S, 66°21'W	3824	Puna desert	Valdecanto <i>et al.</i> , 2013
	San Antonio de los Cobres, Salta, Argentina	24°00'S, 66°14'W	3478	Puna desert	Valdecanto <i>et al.</i> , 2013
	San Antonio de los Cobres, Salta, Argentina	24°13'S, 66°15'W	3886	Puna desert	Valdecanto <i>et al.</i> , 2013
	San Antonio de los Cobres, Salta, Argentina	24°16'S, 66°13'W	3816	Puna desert	Valdecanto <i>et al.</i> , 2013
<i>L. lineomaculatus</i>	Esquel, Chubut, Argentina	42°52'S, 71°12'W	1400	Patagonian steppe	Medina <i>et al.</i> , 2011
	Perito Moreno, Santa Cruz, Argentina	46°37'S, 71°15'W	263	Patagonian steppe	Medina <i>et al.</i> , 2011
<i>L. magellanicus</i>	Santa Cruz, Argentina	51°56'S, 70°24'W	980	Patagonian steppe	Ibargüengoytía <i>et al.</i> , 2010
<i>L. multicolor</i>	San Antonio de los Cobres, Salta, Argentina	24°00'S, 66°14'W	3478	Puna desert	Valdecanto <i>et al.</i> , 2013
<i>L. pictus argentinus</i>	Co. Challhuaco, Rio Negro, Argentina	41°15'S, 71°17'W	1615– 1769	<i>Nothofagus</i> forest	Gutiérrez, Krenz and Ibargüengoytía, 2010
	Melipal Beach, Rio Negro, Argentina	41°07'S, 71°20'W	771	Lake coast	Gutiérrez, Krenz and Ibargüengoytía, 2010

Species	Study sites	Coordinates	Elevation (m a.s.l)	Habitat	Authors
<i>L. sarmientoi</i>	Santa Cruz, Argentina	50°28'S, 72°16'W	133	Patagonian steppe	Ibargüengoytía <i>et al.</i> , 2010
<i>L. yanalcu</i>	San Antonio de los Cobres, Salta, Argentina	24°13'S, 66°15'W	3886	Puna desert	Valdecanto <i>et al.</i> , 2013
<i>Tropidurus catalanensis</i>	Piracicaba, São Paulo, Brazil	22°42'S, 47°38'W	553	Brazilian savanna	This study
<i>T. torquatus</i>	Arinos, Minas Gerais, Brazil	15°54'S, 46°06'W	522	Brazilian savanna	This study
	Formoso do Araguaia, Tocantins, Brazil	11°47'S, 49°45'W	192	Gallery forest in Brazilian savanna	This study
<i>T. oreadicus</i>	Formoso do Araguaia, Tocantins, Brazil	11°48'S, 46°06'W	265	Brazilian savanna	This study

Table S2. Mean  $\pm$  standard error and, in some cases, range of body ( $T_b$ ) and preferred ( $T_p$ ) temperatures, set-point range (lower and upper  $T_{set}$ ), operative temperatures ( $T_e$ ),  $d_b$  and  $d_e$  indices, and effectiveness of thermoregulations ( $E$ ) of species/populations included in the study. Sample size is indicated between brackets.

	$T_b$	$T_p$	lower- $T_{set}$	upper- $T_{set}$	$T_e$	$d_b$	$d_e$	$E$	
<b><i>Anolis cooki</i> - Puerto Rico, 18°N</b>									
Desert, 5 m asl, January	30.8 $\pm$ 0.3 (58)*					29.9 $\pm$ 0.1*	0.8 $\pm$ 0.1 (58)*	2.4 $\pm$ 0.1 (58)*	0.67*
Desert, 5 m asl, August	32.1 $\pm$ 0.2 (68)*	30.6 $\pm$ 0.38 (6)**	29.6 $\pm$ 0.4 (6)**	31.6 $\pm$ 0.5 (6)**		32.8 $\pm$ 0.1*	1.3 $\pm$ 0.1 (68)*	2.1 $\pm$ 0.1 (68)*	0.38*
<b><i>A. cristatellus</i> - Puerto Rico, 18°N</b>									
Desert, 5 m asl, January	27.3 $\pm$ 0.9 (15)*					29.9 $\pm$ 0.1*	2.0 $\pm$ 0.8 (15)*	2.3 $\pm$ 0.1 (15)*	0.13*
Desert, 5 m asl, August	30.8 $\pm$ 0.4 (25)*	29.6 $\pm$ 0.9 (6)**	28.6 $\pm$ 1.0 (6)**	30.9 $\pm$ 0.3 (6)**		32.8 $\pm$ 0.1*	0.9 $\pm$ 0.2 (25)*	2.5 $\pm$ 0.1 (25)*	0.64*
Lowland mesic, 90 m asl, January	25.7 $\pm$ 0.4 (115)*					24.2 $\pm$ 0.1	3.4 $\pm$ 0.3 (115)*	4.6 $\pm$ 0.1 (115)*	0.26*
Lowland mesic, 90 m asl, August	28.9 $\pm$ 0.2 (125)*	29.6 $\pm$ 0.59 (6)**	28.6 $\pm$ 0.7 (6)**	30.7 $\pm$ 0.4 (6)**		28.2 $\pm$ 0.1	1.1 $\pm$ 0.1 (125)*	1.2 $\pm$ 0.1 (125)*	0.08*
Upland mesic, 1150 m asl, January	23.5 $\pm$ 0.4 (105)*					23.4 $\pm$ 0.1*	5.0 $\pm$ 0.4 (105)*	9.2 $\pm$ 0.1 (105)*	0.46*
Upland mesic, 1150 m asl, August	27.2 $\pm$ 0.3 (159)*	29.0 $\pm$ 0.4 (6)**	28.1 $\pm$ 0.5 (6)**	29.7 $\pm$ 0.2 (6)**		19 $\pm$ 0.1	2.5 $\pm$ 0.3 (159)*	5.0 $\pm$ 0.3 (159)*	0.50*
<b><i>A. gundlachi</i> - Puerto Rico, 18°N</b>									
Puerto Rico		25.1 $\pm$ 0.6 (6)*	24.3 $\pm$ 0.7 (6)*	26.1 $\pm$ 0.8 (6)*					
Lower site, 210 m asl, January	23.9 $\pm$ 0.2 (117)*					23.9 $\pm$ 0.1*	0.9 $\pm$ 0.1 (117)*	0.9 $\pm$ 0.1 (117)*	0.00*
Lower site, 210 m asl, August	25.7 $\pm$ 0.1 (140)*					25.1 $\pm$ 0.1*	0.6 $\pm$ 0.1 (140)*	0.7 $\pm$ 0.1 (140)*	0.14*
Higher site, 1130 m asl, January	19.4 $\pm$ 0.2 (72)*					19 $\pm$ 0.1*	4.9 $\pm$ 0.2 (72)*	5.3 $\pm$ 0.1 (72)*	0.08*
Higher site, 1130 m asl, August	22.2 $\pm$ 0.1 (138)*					21.6 $\pm$ 0.1*	2.2 $\pm$ 0.1 (138)*	2.8 $\pm$ 0.1 (138)*	0.21*
<b><i>Liolaemus albiceps</i><sup>♂</sup> - Argentina</b>									
Puna desert, 3824 m asl, 24°S	36.2 $\pm$ 1.9; (29.4–39.5; 35)	36.2 $\pm$ 0.7 (10)	35.45		37.2	25.6 $\pm$ 9.5 (288)	0.7 $\pm$ 1.2	11.2 $\pm$ 7.8	0.94

	$T_b$	$T_p$	lower- $T_{set}$	upper- $T_{set}$	$T_e$	$d_b$	$d_e$	$E$
<b><i>L. bibronii</i><sup>θ</sup> - Argentina</b>								
Patagonian steppe, 43°S	28.3 ± 0.5 (86)	34.1 ± 0.6 (46)	31.9 ± 1 (46)	37.7 ± 0.4 (46)	22.6 ± 0.8 (107)	4.8 ± 0.7 (46)		8.42 0.44
Patagonian steppe, 46°S	27.7 ± 0.6 (47)	34.1 ± 0.4 (47)	32.3 ± 0.9 (47)	37.7 ± 0.2 (47)	20 ± 0.6 (83)	6 ± 0.7 (47)		10.87 0.45
<b><i>L. boulengerie</i><sup>ϕ</sup> - Argentina</b>								
Patagonian steppe, 43°S	28.9 ± 0.5 (98)	33.8 ± 0.17 (45)	30.8 ± 0.9 (44)	35.9 ± 0.6 (44)	23.3 ± 0.8 (120)	3.3 ± 0.5 (44)		8.2 0.59
Patagonian steppe, 46°S	27.8 ± 0.54 (60)	32.9 ± 0.2 (46)	29.3 ± 0.9 (46)	36.9 ± 0.3 (45)	24.4 ± 0.6 (120)	3.1 ± 0.5 (46)		6.2 0.5
<b><i>L. elongatus</i><sup>υ</sup> - Argentina</b>								
Patagonian steppe, 41°S	30.3 ± 0.8 (41)	29.9 ± 0.3 (14)	28.9 (14)	31.1 (14)		1.9 ± 0.5		
<b><i>L. irregularis</i><sup>ω</sup> - Argentina, 24°</b>								
Puna desert, 3824 m asl	36.1 ± 1.8 (28.3–39.4; 43)	36.4 ± 1.3 (10)	35.7	37.2	24.2 ± 9.6 (380)	0.6 ± 1.2	13.1 ± 7.4	0.95
Puna desert, 3478 m asl	36.6 ± 1.4 (33.1–39.3; 52)	36.2 ± 1.2 (12)	35.3	37.3	32.2 ± 10.5 (283)	1.1 ± 5.2	8.8 ± 5.7	0.88
Puna desert, 3886 m asl	36.4 ± 1.5 (33.4–38.9; 22)	36.6 ± 0.2 (5)	35.6	37.6	25.3 ± 9.9 (283)	0.4 ± 0.7	12.2 ± 7.2	0.96
Puna desert, 3816 m asl	36.4 ± 1.04(34–38.5; 36)	35.4 ± 0.6 (10)	34.07	36.57	25.6 ± 9.5 (288)	0.3 ± 0.5	10.2 ± 7.3	0.97
<b><i>L. lineomaculatus</i><sup>ϕ</sup> - Argentina</b>								
Patagonian steppe, 43°S,	25.8 ± 0.7 (52)	34.5 ± 0.4 (60)	32.1 ± 0.8 (60)	37.8 ± 0.2 (60)	15.9 ± 0.8 (105)	6.9 ± 0.8 (53)	12.6	0.45
Patagonian steppe, 46°S	26.1 ± 0.4 (90)	32 ± 0.5 (73)	28.9 ± 0.7 (73)	35.9 ± 0.4 (73)	24.9 ± 0.6 (132)	4.5 ± 0.4 (73)	7.7	0.41
<b><i>L. magellanicus</i><sup>ο</sup> - Argentina</b>								
Patagonian steppe, 51°S	23.4 ± 0.8 (16)	31.8 ± 0.7 (12)	28.6 ± 1.0 (12)	35.7 ± 0.5 (12)	23.3 ± 0.6 (36)	5.4 ± 1.3	5.2 ± 1.9 (36)	-0.04
<b><i>L. multicolor</i><sup>ω</sup> - Argentina</b>								
Puna desert, 3478 m asl, 24°S	36.5 ± 1.3 (33.7–39.1; 28)	35.2 ± 0.5 (12)	34	36.6	32.2 ± 10.5 (283)	0.5 ± 0.8	8.1 ± 5.6	0.94
<b><i>L. pictus argentinus</i><sup>⋈</sup> - Argentina,</b>								
<i>Nothofagus</i> forest, 1692 m asl, 41°S	28.9 ± 0.8 (30)	36.2 ± 0.4 (27)	34.3 ± 0.7 (27)	38.2 ± 0.3 (27)	24.9 (20.6-37.9; 44)	5.6 ± 0.8 (27)	9.47 (40)	0.40

	$T_b$	$T_p$	lower- $T_{set}$	upper- $T_{set}$	$T_e$	$d_b$	$d_e$	$E$
Lake beach, 771 m asl, 41°S	32.6 ± 0.9 (33)	35.6 ± 0.5 (30)	34.6 ± 0.6 (30)	38 ± 0.3 (30)	31.3 (17.7-59.5; 77)	6.5 ± 1.0 (30)	5.20 (77)	-0.24
<i>L. sarmientoi</i> ° - Argentina								
Patagonian steppe, 50° S	26.2 ± 0.6 (69)	34.4 ± 0.3 (63)	32.7 ± 0.4 (63)	36.8 ± 0.2 (63)	22.2 ± 0.5 (53)	6.9 ± 0.6	9.9 ± 0.5 (53)	0.30
<i>L. yanalcu</i> <sup>θ</sup> - Argentina								
Puna desert, 3886 m asl, 24°S	34.2 ± 2.2 (31–36.8; 9)	35.8 ± 0.8 (3)	34.6	37.6	25.3 ± 9.9 (283)	1.2 ± 1.5	11.4 ± 7.0	0.90

\* Hertz, 1992a; 1992b; \*\* Huey and Webster, 1976; <sup>υ</sup> Ibarzüengoytía, 2005; <sup>∫</sup> Gutiérrez, Krenz and Ibarzüengoytía, 2010; <sup>°</sup> Ibarzüengoytía *et al.*, 2010;

<sup>θ</sup> Medina *et al.*, 2009; <sup>ϕ</sup> Medina *et al.*, 2011; <sup>ω</sup> Valdecanto *et al.*, 2013.



## FIGURE LEGENDS

Figure S1. Distribution of body temperature ( $T_b$ ; upper graph) and operative temperatures ( $T_e$ ; lower graph) of (A) *L. sarmientoi*, and (B) *L. magellanicus*. The black and grey arrows indicate the mean  $T_b$  and mean  $T_e$ , respectively. The grey areas indicate the lower and upper set-points ( $T_{set}$ ) of the preferred body temperature (modified from Ibarzüengoytía *et al.*, 2010). Percentages of the observation below and within the  $T_{set}$  range are specified.

Figure S2. Distribution of body temperature ( $T_b$ ) of (A) *Liolaemus bibronii*, (B) *L. boulengeri*, and (C) *L. lineomaculatus* from Esquel (northern site; upper graphs) and Perito Moreno (southern site; lower graphs). The black and grey arrows indicate the mean  $T_b$  and mean operative temperatures ( $T_e$ ), respectively. The grey area indicates the lower and upper set-points ( $T_{set}$ ) of the preferred body temperature (modified from Medina *et al.*, 2011). Percentages of the observation below and above the  $T_{set}$  range are specified.

Figure S3. Distribution of body temperature ( $T_b$ ) of (A) *Liolaemus pictus argentinus* at 1615-1769 m a.s.l. (Chalhuaco Mountain; upper graph) and at 771 m a.s.l. (Melipal Beach, Lake Nahuel Huapi; lower graph; modified from Gutiérrez, Krenz and Ibarzüengoytía (2010), and for (B) *L. elongatus* at 840 m a.s.l. (modified from Ibarzüengoytía, 2005). The black and grey arrows indicate the mean  $T_b$  and mean operative temperatures ( $T_e$ ), respectively. The grey area indicates the lower and upper set-points ( $T_{set}$ ) of the preferred body temperature. Percentages of the observation below and above the  $T_{set}$  range are specified.

Figure S4. Distributions of body temperature ( $T_b$ ; upper graphs) and operative temperatures ( $T_e$ ; lower graphs) of (A) *L. irregularis* from the four sites studied and of (B) *L. multicolor* (left), *L. albiceps* (center) and *L. yanalco* (right) from sympatric sites with *L. irregularis* (modified from Valdecantos *et al.*, 2013). The black and grey arrows indicate the mean  $T_b$  and mean  $T_e$ , respectively. The grey area indicates the lower and upper set-points ( $T_{set}$ ) of the preferred body temperature. Percentages of the observation below and above the  $T_{set}$  range are specified.

Figure S5. Distributions of body temperature ( $T_b$ ; upper graphs) and operative temperatures ( $T_e$ ; lower graphs) of (A) *Anolis cristatellus* from 1150 m a.s.l. collected in August, (B) the same population collected in January, and of (C) *A. gundlachi* from 210 m a.s.l. collected in August. The black and grey arrows indicate the mean  $T_b$  and mean  $T_e$ , respectively. The grey area indicates the lower and upper set-points ( $T_{set}$ ) of the preferred body temperature

(modified from Hertz *et al.*, 1993). Percentages of the observation below and above the  $T_{\text{set}}$  range are specified.

Figure S6. Distribution of operative temperature ( $T_e$ ) for (A) *Sceloporus mucronatus* lizards from an upland site (2500 m a.s.l.), (B) *S. mucronatus* from a montane site (3400 m a.s.l.), and (C) *S. serrifer* from a lowland tropical forest site (10 m a.s.l.). The black and grey arrows indicate the mean body temperatures ( $T_b$ ) and mean  $T_p$ , respectively. The grey area includes the lower and upper set-points ( $T_{\text{set}}$ ) of the preferred body temperature (modified from Sinervo *et al.*, 2011). Percentages of the observation below and above the  $T_{\text{set}}$  range are specified.

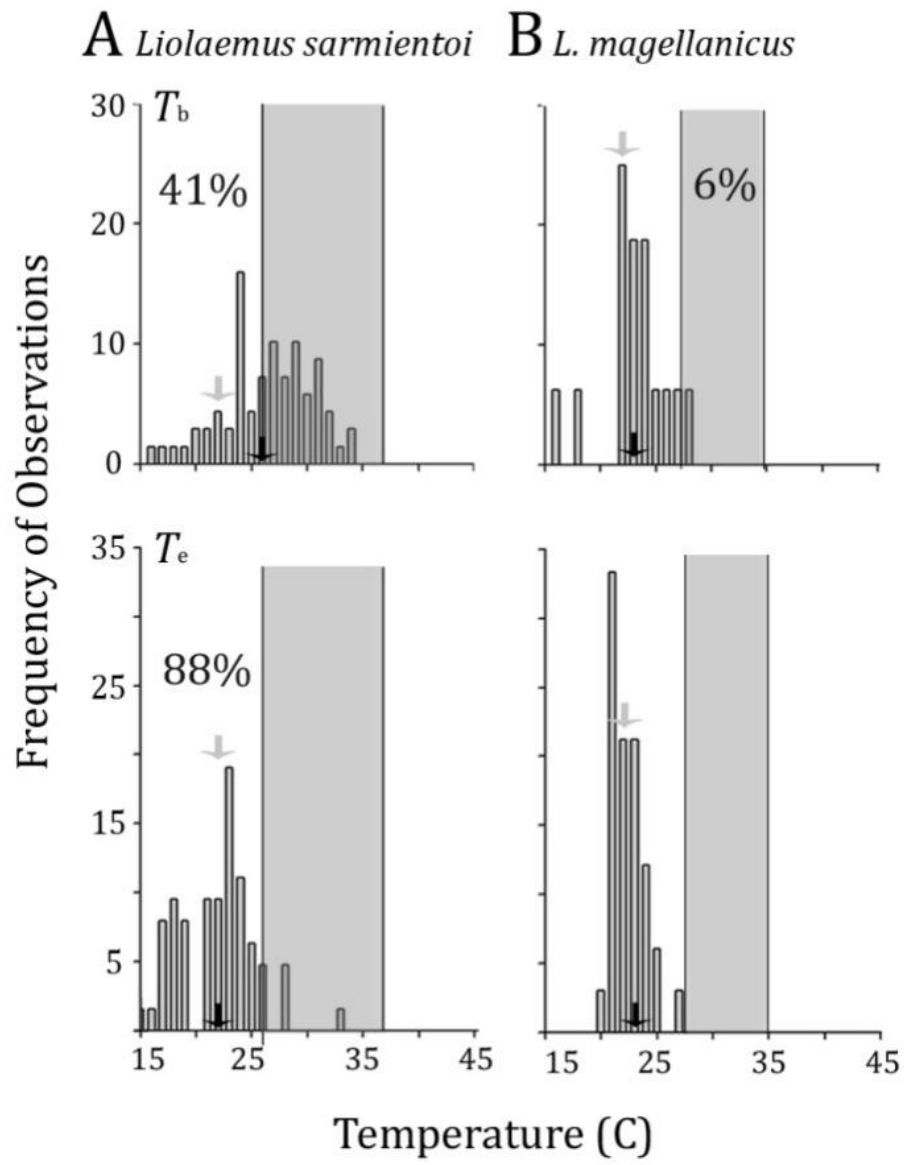


Figure S1.

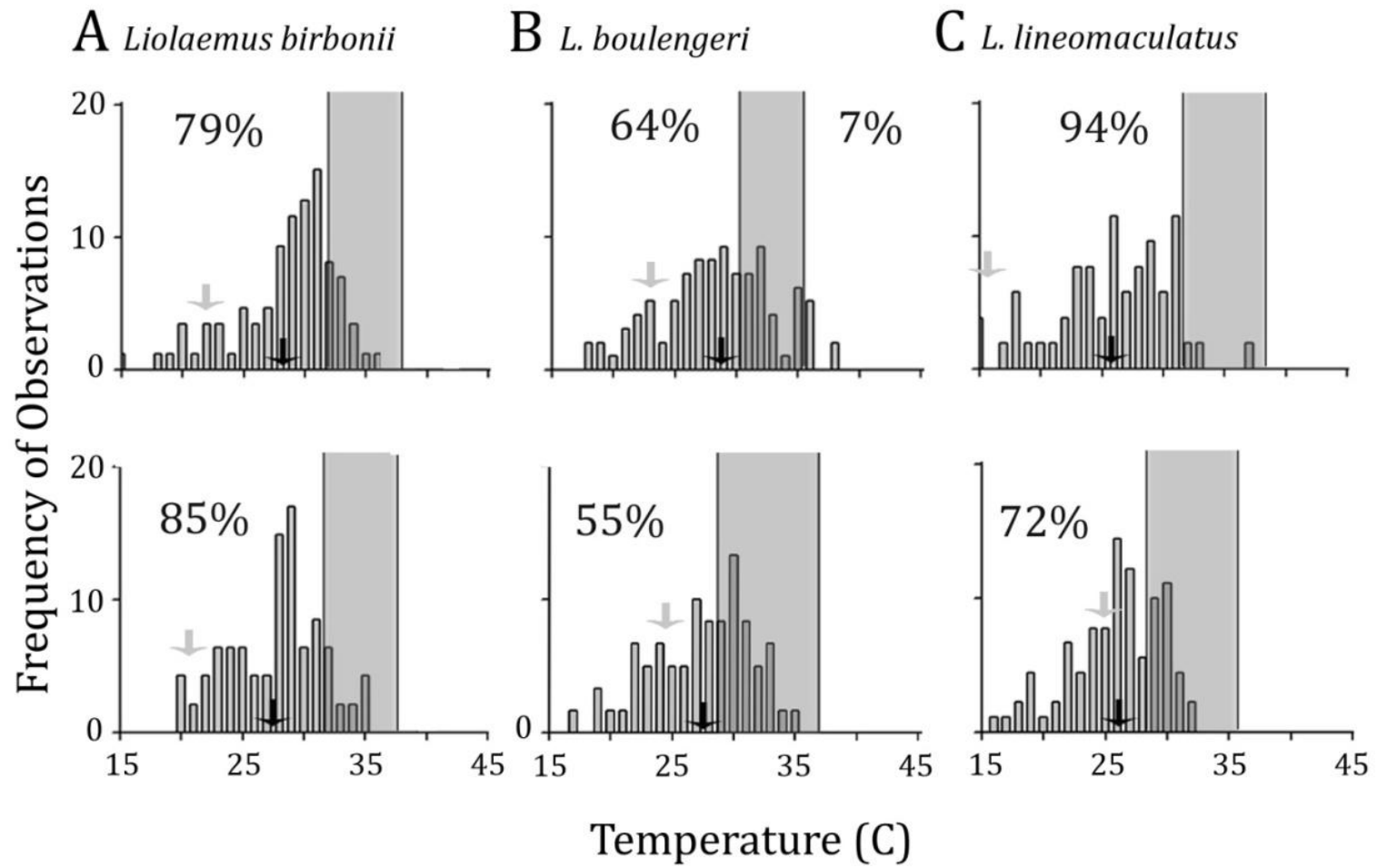


Figure S2.

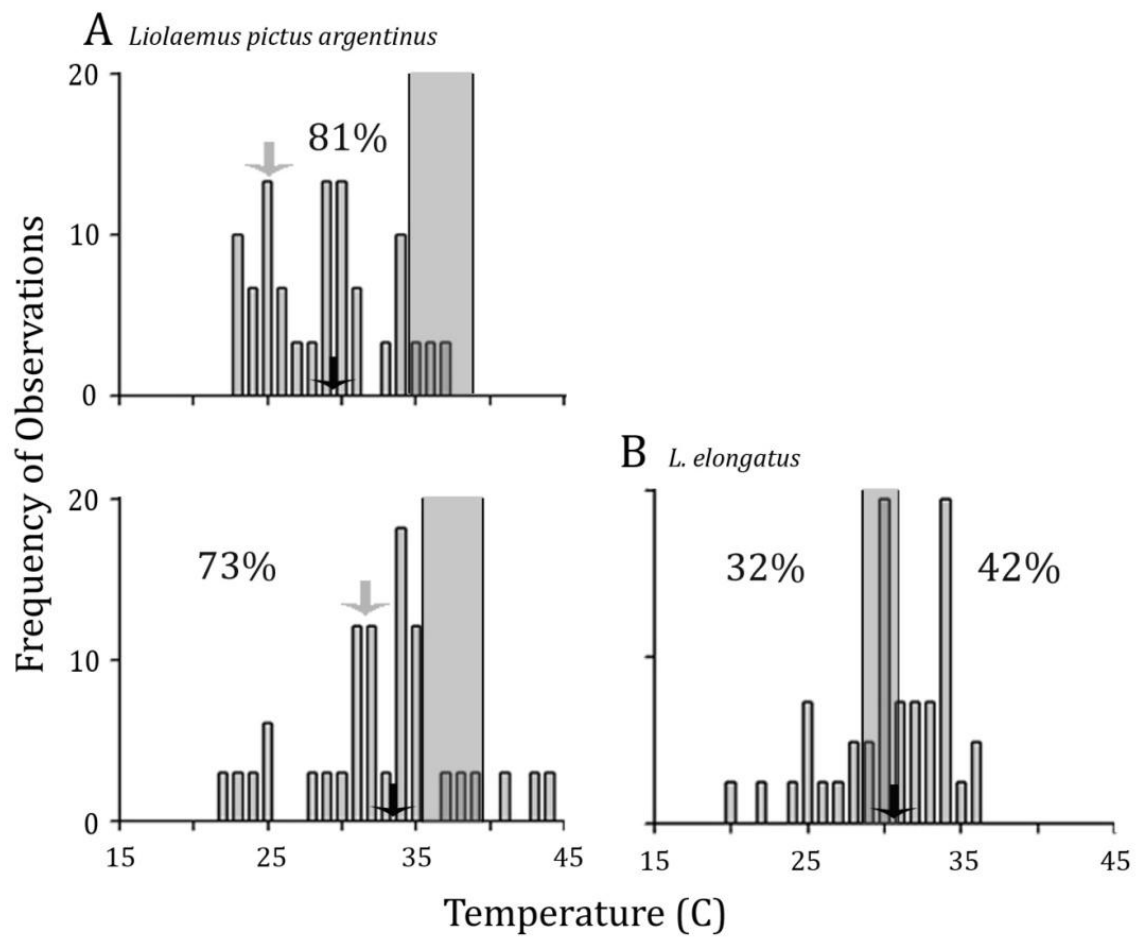


Figure S3.

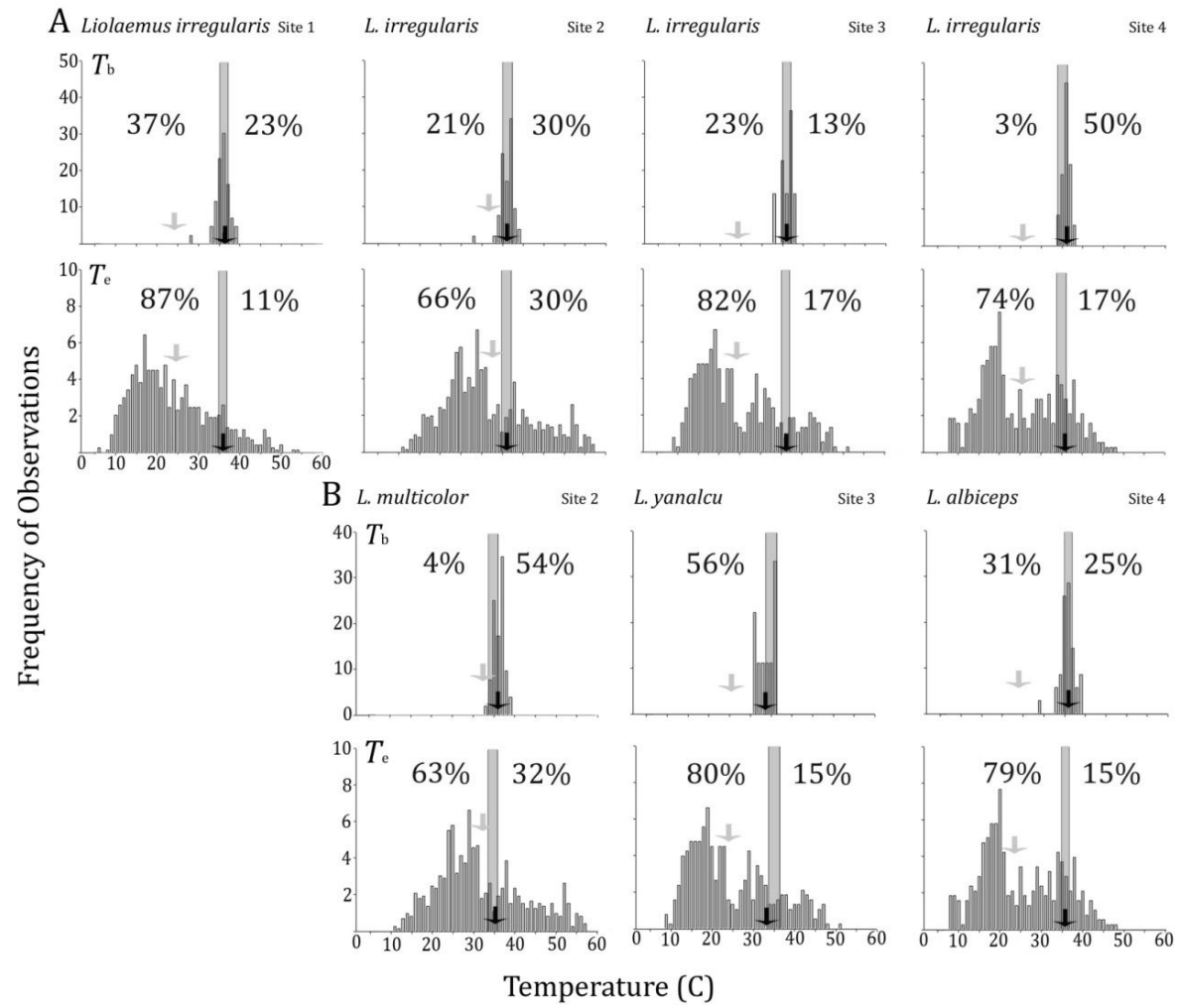


Figure S4.

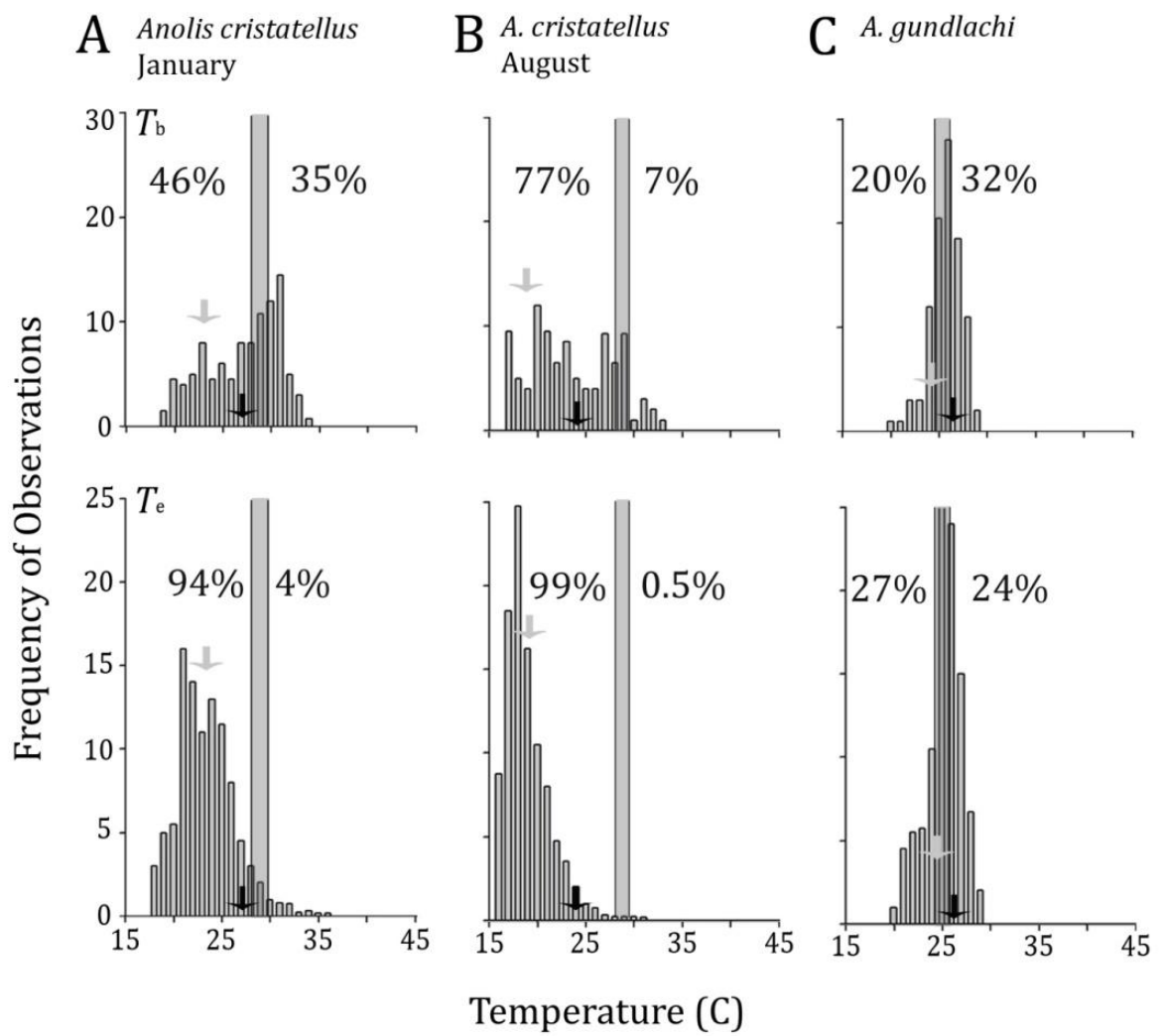


Figure S5.

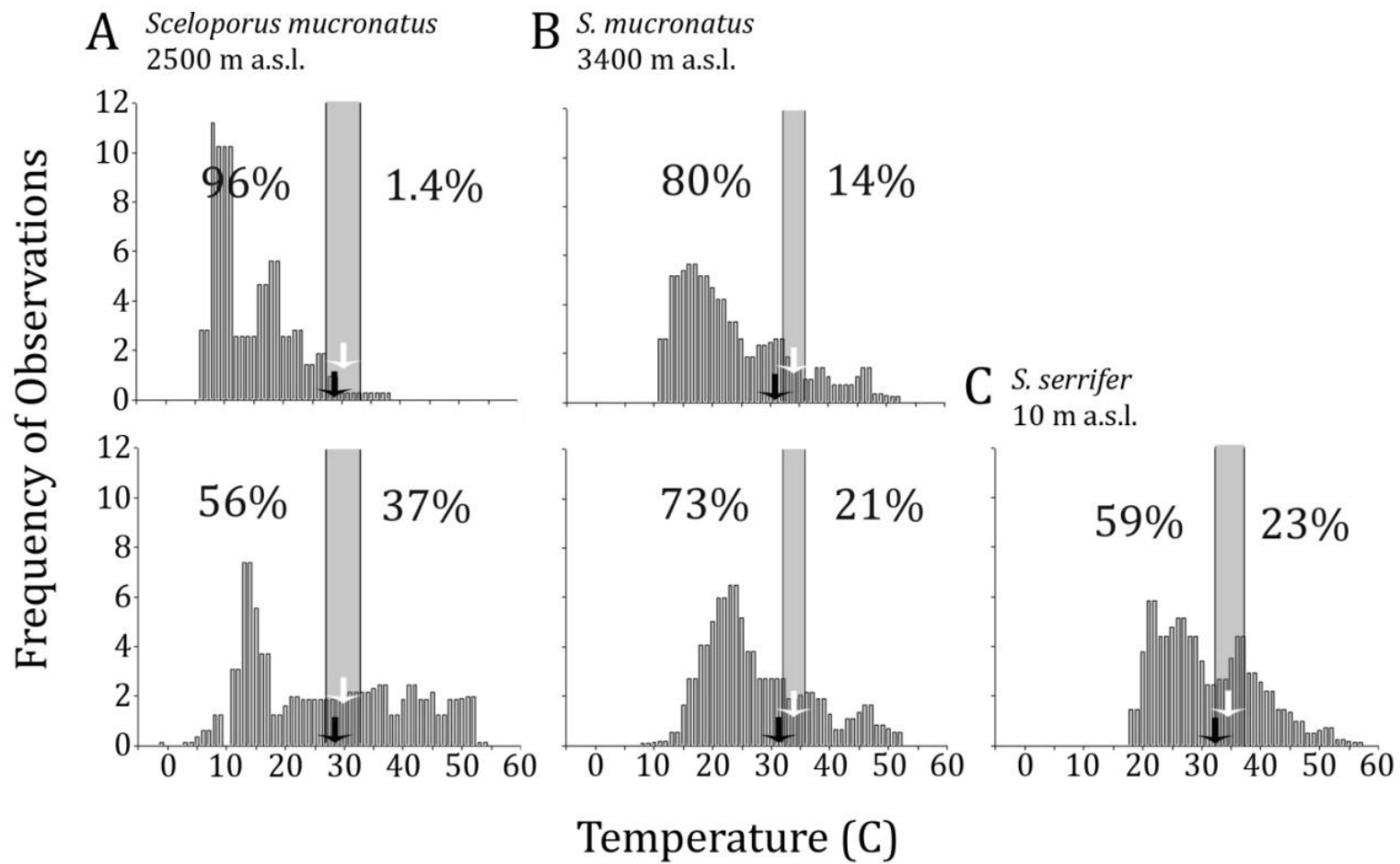


Figure S6.



## CHAPTER 2

Geographic variation of the thermal sensitivity of six populations of the *Tropidurus torquatus* species complex (Squamata: Tropiduridae) in the Brazilian savanna

*(Co-authored with Nora R. Ibarzüengoytía and Carlos A. Navas)*

## ABSTRACT

We herein examine the thermal biology of six populations of the *Tropidurus torquatus* species complex in a latitudinal gradient of the Brazilian Cerrado in order to assess their vulnerability in the context of global warming. We analyze the variability of body ( $T_b$ ) and operative temperatures ( $T_e$ , "null temperatures" for nonregulating animals), the thermoregulatory set-point range (range of preferred body temperatures,  $T_{set}$ -range of  $T_p$ ) and quantitative indexes of temperature regulation ( $d_b$ ,  $d_e$  and  $E$ ). We also analyzed data on  $T_b$  and  $T_p$  for 60 populations of 21 species of tropidurids from the Caatingas, Amazonia, Cerrado, Chaco, and other regions as the coast of Peru and Galapagos Islands gathered from the literature, in order to find geographical patterns that could help understand the evolution of these variables along the group. A general pattern suggests that the thermoregulatory behavior decreases towards the Equator, particularly due to environmental constrains and probably to the low environmental variation. In most tropidurids,  $T_b$  and  $T_p$  are similar and higher than  $T_a$  pointing to a plesiomorphic condition, probably related to earlier forested environments. Poor or null thermoregulation and large proportions of  $T_b$  and  $T_e$  above the  $T_{set}$  of the central and northernmost populations would augment the risk of overheating and preclude time of activity with an eventual raise of environmental temperature.

KEY-WORDS: Environmental variation, geographical patterns, lizards' thermoregulation, thermal ecology.

## INTRODUCTION

Through influences on body temperature ( $T_b$ ) and thermoregulation, environmental temperature ( $T_a$ ) affects most aspects of lizard biology, including life-history traits such as growth, survival, and reproduction (Angilletta, 2009). The impact of  $T_a$  on life-history traits is evident from intrageneric comparisons among populations across geographical gradients encompassing changes in  $T_a$  (Huey and Stevenson 1979; Savage *et al.*, 2004; Wiens *et al.*, 2006; Niewiarowski and Angilletta, 2008). Gradients of  $T_a$  may affect thermal biology through various processes and underlying mechanisms that are induced by thermal experience, for example the profile of exposure to episodes of suboptimal thermal conditions (Huey, 1991; Dunham, 1993; Sinervo and Huey, 1990; Angilletta, 2009; Kearney *et al.*, 2009; Moritz *et al.*, 2012; Seebacher and Franklin, 2012). Conversely, geographical variation in  $T_a$  may be buffered to extents related to thermoregulation (Ibargüengoytía, 2005). Thus, both behavioral thermoregulation and physiological adjustments interplay to maintain lizard  $T_b$  close near preferred-optimal temperatures ("set-point range" of  $T_p$ ; Heath, 1970; Huey, 1982; Pough and Gans, 1982), but several patterns may emerge. For example, in thermoconforming lineages,  $T_b$  matches field operative temperatures ( $T_e$ ), and both relate positively to  $T_a$ , thus varying daily and seasonally, and across latitudinal and altitudinal clines (Angilletta, 2009). However, a positive correlation between  $T_b$  and  $T_a$  can emerge also in thermoregulating species (Huey and Slatkin, 1976), particularly when thermal constraints restrict animals' activity and costs of thermoregulation are high (Andrews, 1998). Similarly, whereas  $T_p$  is expected to co-evolve with the thermal range granting performance optima ( $T_o$ ), exceptions may exist (Huey and Bennet, 1987), particularly if precise thermoregulation is costly due to scant heat sources (see references in Huey and Slatkin, 1976; p. 364).

Because of the geographic variation in the availability of thermal resources (Damme *et al.*, 1987), species with broad distributions generally compensate environmental thermal variation with different physiological and behavioral responses (Avery, 1976; Garland and Adolph, 1991; Hertz, 1992a, 1992b; Hertz and Huey, 1981), such as acclimatory adjustments of thermal physiology (Corn, 1971; Spellerberg, 1972; Hertz, 1981; Somero, 2010), and by modifying the timing for activity and basking (Bogert, 1949; Huey, 1982). When environmental changes are compatible with the generation time of a species, populations may accommodate such changes through a combination of adaptive evolution, and behavioural and/or physiological plasticity (Davis and Shaw, 2001). However, during extreme

unpredictable changes in ambient temperature ( $T_a$ ) and/or precipitation, survival may depend mainly on two factors: displacement (Parmesan, 2006; Chen *et al.*, 2011) or adjustment (Alberto *et al.*, 2013). If displacement is not an option, and phenotypic evolution is slower than the change rate of the environment, then local extinctions are to be expected (Chown *et al.*, 2010). Understanding to which extent genetical and phenotypical variation allow predicting possible responses of organisms to climate change may help forecasting their future (Hoffmann, 2010). The analysis of the genetic differentiation among the populations transcends the scope of this study, but we examine the variation of the thermal biology and behavior, due to phenotypic plasticity or adaptation, in lineages of the genus *Tropidurus* Wied-Neuwied, 1825, with wide geographical distributions and highly heterogeneous habitats (from open sand-dunes to dense forests; Rodrigues, 1987). Comparisons within and among species of the thermal biology traits may further explain the role of environmental costs and physiological and behavioral adjustments in the evolution and radiation of the genus, as well as the prospect persistence over time. Lizards which distribution includes diverse environments indicate a large plasticity and becomes useful models for understanding physiological and ecological adjustments of ectothermic vertebrates. We take advantage of the diversity within the genus. We focus on six populations (operational units) located in the Brazilian savanna known as Cerrado, but inhabiting thermally diverse localities (from gallery to open urban areas), to ask whether and how populations of such diverse species complex differ in thermoregulatory traits. Environment have a main role in the determination of the plasticity of thermal physiology and behavior of lizards and therefore, we predict inter- and intraspecific variation in the thermal biology of the chosen populations.

Even though molecular differentiation among the populations is well supported, all species except *T. oreadicus* share a similar, almost cryptic, morphology. Such similarities in the morphology may reflect a shared thermal physiology, but physiological characters, more flexibly than morphology, generally vary as a product of environmental changes or constrains. Therefore we expect and specifically verify whether variability in the thermal biology of these lizards is higher among than within sites. Variation within the populations may result from the body size (SVL), sexual dimorphism and the reproductive state. For example, during the reproductive season, lizards are expected to allocate more energy into mating and defending their territories undermining thermoregulation (Hertz *et al.*, 1993). It may also vary may

throughout the hours of the day as a function of the  $T_a$  that may restrict activity when reaching too high or low values.

For elements of analysis, we sampled a) three populations of *T. torquatus* "sensu lato" [recent molecular data suggests that these may belong to different clades (Sena, unpublished data); hereafter named only as '*T. torquatus*'), b) one population of *T. catalanensis* in the southern Cerrado, during the reproductive and non-reproductive seasons, c) one population of *T. etheridgei* living in complete syntopy with *T. torquatus*, and c) one population of *T. oreadicus* in an urban area 20 km distant from a gallery forests population of *T. torquatus*. To understand the patterns of geographic variation that may explain the collected data herein, we incorporate our findings in the context of a broader discussion under the light of thermal data on about 60 populations of 21 species of tropidurids. We analyzed data on  $T_b$ ,  $T_p$ ,  $T_e$ , and the thermoregulation indices  $d_b$ ,  $d_e$  and  $E$  to describe the thermal biology and behavior of each population. We further discuss whether thermal differences among populations are compensated or tolerated, and we finally explore which aspects of the thermal physiology and behavior are particularly relevant under scenarios of compensation.

## MATERIALS AND METHODS

### 1. Model organisms

The *Tropidurus torquatus* species group (Frost *et al.*, 2001) currently comprises 13 species among which *T. torquatus* stands out for its broad geographic range in South America, and for reported clines in several aspects of life-history (Rodrigues, 1987; Brandt and Navas, 2011). The species, as currently known, is distributed from southern Rio de Janeiro to the Rio Amazonas (Sena, 2015), but present at least two morphologically heterogeneous groups, one inhabiting the Atlantic Forest and a second group occupying the Cerrado (Rodrigues, 1987; Sena, 2015). The last, being a mosaic of physiognomies, ranges from open grass fields to forested formations (wooded savannas and gallery forests) with climate seasonally determined by dry winters and wet summers (Wiederhecker *et al.*, 2002).

### 2. Study area and collecting material

We sampled three populations of *T. torquatus* "sensu lato": 32 specimens in the proximities of Formoso do Araguaia, Tocantins (230 m a.s.l; 11°47'49" S, 49°31'44" W; September, 2012; hereafter referred as TOt), 21 specimens in Cuiaba, Mato Grosso (211 m a.s.l; 15°55'01" S,

46°06'21" W; February, 2014; CB) and 22 in Arinos, Minas Gerais (526 m a.s.l; 15°55'01" S, 46°06'21" W; March, 2012; MGt). In addition, we sampled a population of *T. etheridgei* ( $n = 14$ ; MGe), in complete syntopy with MGt, and a population of *T. oreadicus* ( $n = 26$ ; TOo) 20 km East from TOt, in Formoso do Araguaia, TO. In southern Cerrado we sampled a population of *T. catalanensis* Saraiva-Kunz and Borges-Martins (2013; until recently considered *T. torquatus* and only differentiated from this last species by its yellow ventral patches) from Piracicaba, São Paulo (554 m a.s.l; 22°43'30" S, 47°38'56" W; April, 2011 and September, 2013). At this site, specimens and environmental data were sampled in the non-reproductive ( $n = 24$ ; SPnr) as well as in the reproductive season ( $n = 47$ ; SPr). Data collected in both seasons were compared to further estimate possible effects of the reproductive state on the physiological and behavioral biology at this locality.

Specimens were collected only when found active by hand or with the aid of a noose from 8 to 18 h. The snout-vent length (SVL) and body mass were registered for each lizard immediately after capture, using a caliper Mitutoyo CD-6" CX ( $\pm 0.01$  mm) and Pesola spring scales of 10 and 100 ( $\pm 0.5$  g), respectively. Reproductive condition and sex were determined by the presence of black ventral patches on thighs in males and by the minimum SVL for adult females and males following Wiederhecker *et al.* (2002) and Meira *et al.* (2007). In the cases of doubts, sexual maturity was confirmed by the observation of the gonads and the reproductive tracts after autopsy.

Lizards were transported to the laboratory facilities at the Department of General Physiology, Bioscience Institute, University of São Paulo (IB-USP), where experiments of thermal physiology and performance were conducted during the following three weeks. Here, lizards were conditioned in terraria with water *ad libitum* (approximately five lizards per terrarium) and fed everyday with cockroaches and crickets. Temperature and photoperiod followed natural conditions during the time of captivity and lizards were allowed to thermoregulate under light spots available in each terrarium. After the experiments were concluded, lizards were euthanized for further studies following the protocol of the Research Ethics Committee of the Department of Physiology of Bioscience Institute of the University of São Paulo (IB-USP), fixed in Bouin's solution for 24 h, and preserved in 70% ethanol. The specimens are stored at the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, and at the Coleção Herpetológica de Ribeirão Preto (CHRP), Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo (FFCLRP/USP), Ribeirão Preto, São

Paulo State, Brazil.

### 3. Recording of data on thermal biology ( $T_b$ and $T_e$ ) and associated thermal niche ( $T_s$ and $T_a$ )

Substrate ( $T_s$ ) and air ( $T_a$ ) temperatures were registered immediately after specimens were captured (*sensu* Pough and Gans, 1982) using a Sper Scientific 4 Channel Datalogging thermometer (Mod. # 800024) and specific probes (Sper Scientific Mod. # 800073 and # 800076, respectively).

Operative temperatures ( $T_e$ , which represents the "null" distribution of  $T_b$  that non-regulating animals would experience in their microhabitats; Bakken, 1992; Hertz, 1992b; Dzialowski, 2005) were also collected during the hours of activity and at each capture sites, spreading plastic models (gray PVC pipes filled with silicone of 10 to 15 cm) connected to data loggers (HOBO U12 4-Channel External Data Logger - U12-008) in potential microenvironments that lizards might occupy. The size and color of the models were determined based on the calibration against real specimens for previous studies, using two catheter probes of 1.62 mm diameter (Sper Scientific Mod. # 800077) simultaneously to register the temperatures of both the models and the lizards.

Body temperature ( $T_b$ ; *sensu* Pough and Gans, 1982) was recorded using a catheter probe of 1.62 mm diameter (Sper Scientific Mod. # 800077). Individuals were handled by head to avoid heat transfer and temperature was recorded within 10 s of handling introducing ca. 1 cm inside the cloaca. Time of day at capture was also registered.

### 4. Laboratory protocol to estimate preferred body temperature ( $T_p$ , $T_{set}$ ) and the efficiency of thermoregulation (E)

Preferred body temperature ( $T_p$ ) and set-point temperature range ( $T_{set}$ , which represents the ideal "target"  $T_b$  range that animals would achieve in environments where the cost of thermoregulation is zero; Heath, 1965; Licht *et al.*, 1966; Hertz *et al.*, 1993) were estimated using thermal gradients of 100 x 45 x 16 cm where lizards were placed individually. A lamp was used as the heat source at one end of each terrarium and it was adjusted to achieve a linear substratum gradient of 23 °C to 45 °C (well above lethal limits). Ultra-thin catheter thermocouples (1 mm, Omega engineering Inc., Product code: 5SC-TT-T-40-72) were taped to the lizard's vent and body temperatures were recorded at 2 min intervals for 2 h, by connecting the thermocouple to a USB-based 8-channel TC input module (MCC DAQ

Measurement Computing). Lizards would start thermoregulating after approximately 20 minutes of being placed in the gradients so these data were omitted in the calculations. Preferred temperatures and lower and upper  $T_{\text{set}}$  (the temperatures bounding the interquartile range of the observed  $T_p$ ) were estimated from the  $T_b$  recorded in the thermal gradients for each lizard and used to calculate the populations'  $T_p$  and  $T_{\text{set}}$ .

The effectiveness of temperature regulation (*sensu* Hertz *et al.*, 1993) was calculated as:  $E = 1 - (\text{mean } d_b / \text{mean } d_e)$ , in which  $d_b$  is the mean of the absolute distance of  $T_b$  from the set-point range of each individual and  $d_e$  is the deviations between  $T_e$  and  $T_{\text{set}}$  which specifies the average thermal quality of a microenvironment from the organism's standpoint (Hertz *et al.*, 1993). Therefore, thermoregulation is considered effective when  $E$  is close to 1, thermoconforming when  $E$  is close to 0, and moderately effective if  $E$  is close to 0.5 (Hertz *et al.*, 1993; Bauwens *et al.*, 1996). Negative  $E$ -values occur if animals actively avoid favorable thermal microhabitats due to any ecological constraint (Hertz *et al.*, 1993).

#### 5. Behavioral compensation or physiological mechanisms to cope with environmental thermal changes

The thermoregulatory behavior was analyzed calculating variation (*i.e.* coefficient of variation - CV) of the residuals of the regressions of  $T_b$  vs.  $T_a$  that fell below and above the  $T_{\text{set}}$  range of each population. To analyze the figures these were divided the plots in quadrants determined by the regression  $T_b$  vs.  $T_a$  and the  $T_{\text{set}}$  range and  $T_p$ : (I) above the regression and below the lower- $T_{\text{set}}$  and  $T_p$ ; (II) below the regression and below the lower- $T_{\text{set}}$  and  $T_p$ ; (III) above the regression and above the lower- $T_{\text{set}}$  and  $T_p$ ; and (IV) below the regression and below the lower- $T_{\text{set}}$  and  $T_p$ .

#### 6. Comparison with other tropidurid species

All available data on  $T_b$  and  $T_p$  of 60 populations and 21 species of tropidurids were gathered from the literature. If coordinates or elevation were not given for particular sites, these data were determined by searching the locality in Google Earth Plus. We organize the populations in different environments based on the characteristics of the described biome, macro and microhabitats that they occupy. The order was set up based on the variation of environmental temperatures gathered from the nearest weather stations (1 indicating the environment with less variation and 5 with the highest variation). The analyzed biomes were: (1) Chaco; (2)



Caatinga; (3) Rainforest; (4) Cerrado; and (5) Coastal. Macrohabitats were divided in: (1) Chaco and montane; (2) Caatinga; (3) gallery forests in the Cerrado, Amazonian and Atlantic rainforests and restinga; (4) savanna and urban areas of the Cerrado; and (5) Coastal sites. Based on their microhabitats and ecological use of the landscape the populations were also separated the populations into: (1) herbaceous/shrub specialists; (2) sand specialist; (3) generalists; (4) rock/trunk specialists; and (5) soil/trunk specialists.

We gathered historical climate data collected at the nearest (less than 500 km) weather stations for each population from the sites <http://www.inmet.gov.br/portal/index.php?r=bdmep/bdme> and <http://www.tutempo.net>. We performed regressions between the precipitation (mm), maximum mean and minimum air temperature ( $T_{a \text{ max}}$ ,  $T_{a \text{ mean}}$  and  $T_{a \text{ min}}$ ; °C) from August 1<sup>st</sup>, 1977, until May 31<sup>st</sup>, 2009, and latitude to analyze possible patterns of geographic variation. The coefficients of variations (CV) were calculated using the published information.

### 7. Statistical analyses

Data were analyzed using one way analysis of variance (ANOVA), unpaired and paired Student's t-test, multiple stepwise or simple regressions, and Spearman's correlations. Normality and variance-homogeneity were tested with the one-sample Kolmogorov-Smirnov and Levene tests, respectively. When the assumptions were violated, non-parametric Kruskal-Wallis One Way ANOVA, Mann-Whitney Rank Sum test, Holm-Sidak or Dunn's methods were used. Means are given  $\pm$  SD. Due the striking sexual dimorphism of *Tropidurus* (Pinto *et al.*, 2005) and for comparative purposes, when the regressions of the thermal variables against SVL were significant, the data were adjusted according to individual SVL using the residuals of the regression of the  $\text{Log}T_b$ ,  $\text{Log}T_p$ ,  $\text{Log}T_{\text{set}}$ ,  $\text{Logupper-}T_{\text{set}}$  and  $\text{Loglower-}T_{\text{set}}$  vs.  $\text{LogSVL}$ . When no difference was found between the data collected in Piracicaba, SP, in 2011 and in 2013, these were pooled for further analyses. Coefficient of variation (CV) were calculated as the ratio of the SD to the mean and expressed as a percentage in all cases.

## RESULTS

### 1. Variation of SVL within *T. torquatus* and among species

Juveniles of *T. torquatus* were scarce at all localities (none was collected in TOt) but they presented a consistent size range and same CV between CB and MGt (Table S1). Among adults, the SVL differed (MGt > CB  $\geq$  TOt), but not when compared only among females or

among males within the species (Tables S1, S2 & S3). Overall, adults' SVL differed among the studied populations and species ( $MGt \geq MGe \geq CB \geq TOt \geq SP \geq TOo$ ; Tables S1, S2 & S3). Only females of TOo were significantly smaller than the females of the other studied tropidurids ( $MGe \geq MGt \geq SP \geq CB \geq TOt > TOo$ ; Tables S1, S2 & S3). Males also differed in SVL among the populations ( $MGe \geq MGt \geq TOt \geq CB \geq TOo \geq SP$ ; males of SP were smaller than the males of MGt and TOt but similar to CB's; Tables S1, S2 & S3).

## 2. Microenvironmental and body temperatures

### 2.1. Variation within *T. torquatus* and among all species and populations

The substrate ( $T_s$ ) and air ( $T_a$ ) temperatures were different among the sites occupied by *T. torquatus* ( $TOt > MGt > CB$ , only  $T_s$  of CB and MGt were similar; Figure 1A-C. For detailed information data on A, B and C, see Tables S2, S4 & S5). Nevertheless, lizards of the three populations showed similar  $T_b$ 's ( $TOt \geq MGt \geq CB$ ; Tables 1; statistical test results on Table S6). Variation of  $T_b$  (CV) was higher in CB and in MGt and lower in TOt than within the species (Table 1).

Recorded  $T_s$ ,  $T_a$  and  $T_b$  differed among the populations ( $T_s$ :  $MGe > TOo > TOt > SPnr > MGt > SPPr > CB$ ;  $T_a$ :  $MGe > TOt > TOo > SPnr > MGt > SPPr > CB$ ;  $T_b$ :  $TOo > MGe = TOt > SP > CB > MGt$ ; Table 1; Figure 1; statistical test results on Tables S3 & S6). The CV of  $T_s$ ,  $T_a$  and  $T_b$  also differed among the populations ( $T_s$ :  $SPnr > TOo > MGe > MGt > SPPr > CB > TOt$ ;  $T_a$ :  $TOo > SPnr > MGe > SPPr = MGt > CB > TOt$ ;  $T_b$ :  $MGe > TOo > MGt > SPnr > CB > SPPr > TOt$ ; Table 1). In most populations, females and males were collected with a similar  $T_b$ ; only in MGt and TOo females were 1-4°C warmer than males (Tables 1).

$T_s$  and  $T_a$  could only predict the  $T_b$  of MGe (Tables 1; Figure 1D). In most of the other species the increment of  $T_b$  depended mainly on  $T_s$  (Multiple regression, SP:  $F_{2,21} = 9.378$ ; MGt:  $F_{2,19} = 26.042$ ; TOt:  $F_{2,29} = 19.358$ ; TOo:  $F_{2,23} = 73.838$ ;  $P \leq 0.001$ ), whereas the main heat source for CB was  $T_a$  (Multiple regression,  $F_{2,17} = 9.751$ ;  $P = 0.002$ ; Figure 1).

*Tropidurus torquatus* was found active during the day for 10 to 11 h in CB, 6-7 h in MGt and 7-8 h in TOt (Figure 1). In spite of the sympatry with MGt, MGe was active one hour earlier (Figure 1). The hours of activity of TOo also differed from the ones of TOt as they appeared to be active mostly in the morning, retreating to their burrows when  $T_a$  exceeded their thermal tolerances (Figure 1). Similar to its congeners, lizards in SP were active for 6 h during the

non-reproductive season and 7 h in the reproductive months. Details on the collecting sites and the variation of  $T_s$ ,  $T_a$  and  $T_b$  during the day are presented as supplemental material.

### 2.2. Common trends to all species and populations

Among all populations and species there was a positive correlation ( $s = 0.786$ ,  $P = 0.0251$ ) between the CV's of  $T_b$  and  $T_a$ , while the correlation between the CV's of  $T_b$  and  $T_s$  was not significant ( $s = 0.714$ ,  $P = 0.0545$ ). The variation of  $T_b$  was considerably lower among the sites than the variation within the sites. The variation  $T_s$  and  $T_a$  was as low as in the gallery forest of TOt (Table S4). No correlation was found between the variation (SD and CV) of the populations  $T_b$  and the variation of the environmental temperatures ( $T_{a \text{ min}}$ ,  $T_{a \text{ mean}}$  and  $T_{a \text{ max}}$ ) obtained from the nearest weather stations (Table S8).

## 3. Preferred and operative temperatures, and efficiency of thermoregulation

### 3.1. Variation within *T. torquatus* and among all species and populations

Whereas mean  $T_p$  and the lower- and upper- $T_{\text{set}}$  differed among the populations of *T. torquatus* ( $T_p$  and upper- $T_{\text{set}}$ : CB  $\geq$  TOt  $\geq$  MGt, CB  $\neq$  MGt; lower- $T_p$ : TOt  $\geq$  CB  $>$  MGt; Table 1), the  $T_{\text{set}}$  range was similar in all three (Kruskal-Wallis One Way Analysis of Variance on Ranks,  $H_2 = 5.414$ ,  $P = 0.067$ ; Table 1). Mean  $T_p$  was significantly lower than mean  $T_b$  only in TOt (Tables 1). In addition, in the three sites most of the  $T_b$  recordings (45-75%) fell above the  $T_{\text{set}}$ -range, whereas from 4.5 to 25 % and only from 3.1 to 36.4 % fell within and below it, respectively (Figure 2A-C). Different  $d_e$ 's and  $T_e$ 's were recorded in the three sites ( $d_e$ : CB  $\geq$  MGt  $\geq$  TOt;  $T_e$ : MGt  $>$  TOt  $>$  CB, and MGt  $\neq$  CB; Tables S4, S9 & S10)

The distribution of the  $T_e$  recordings in *T. torquatus*' sites differed among the sites (below the lower- $T_{\text{set}}$ : CB  $>$  TOt  $>$  MGt; within the  $T_{\text{set}}$  range: TOt  $>$  MGt  $>$  CB; above the upper-  $T_{\text{set}}$ : MGt  $>$  TOt  $>$  CB; Figure 2 A-C). Sexual dimorphism in relation to  $T_p$ , and the lower- and upper- $T_{\text{set}}$  was only present among the males of the species (Tables 1). Differences within *T. torquatus* with respect to the index  $d_b$  were also absent but  $E$  varied as CB resulted an efficient thermoregulator whereas the MGt and TOt were mainly constrained to thermoregulate (Tables 1; statistical test results on Tables S9 & S10). CV of  $T_p$ , lower- and upper- $T_p$  within the populations, in comparison with the variation within the species, was lower in CB and MGt, whereas in TOt the variation was higher (Table 1).

Mean  $T_p$  differed among all different species and populations of studied tropidurids, but in all

cases  $T_p$  was lower than  $T_b$  ( $CB \geq TOo \geq SP > TOt = MGt \geq MGe$ ; Tables 1). The lower- and upper- $T_{set}$  and the  $T_{set}$  range also differed among the populations (lower- $T_{set}$ :  $CB \geq TOo \geq SP \geq TOt \geq MGt \geq MGe$ ; upper- $T_{set}$ :  $TOo \geq CB \geq SP \geq TOt = MGt = MGe$ ;  $T_{set}$  range:  $SP \geq MGt \geq MGe \geq CB \geq TOo \geq TOt$ ,  $SP \neq TOt$  and  $TOo$ ; Tables 1). Overall, annual  $T_e$ ,  $T_e$ ,  $d_b$  and  $d_e$  indices, and  $E$  also differed among all sites and seasons (annual  $T_e$ :  $SP > CB > MG > TOt$ ;  $T_e$ :  $MG > SPnr > SPr > TOo > CB > TOt$ ;  $d_b$ :  $TOo > MGe > SPr > TOt > MGt > SPr > CB$ ;  $d_e$ :  $SPnr > TOo > SPr > CB > MGt > MGe > TOt$ ;  $E$ :  $SPnr > CB > SPr > TOo > MGt > TOt > MGe$ ; Tables 1). Whereas most of the  $T_b$  values fell above the  $T_{set}$ -range in all populations, a considerable proportion of  $T_b$  fell within the  $T_{set}$ -range in SPnr (61.5%; Figure 2F) and CB (25%; Figure 2A). The population that exhibited the largest proportions of  $T_e$  below and within the  $T_{set}$ -range were SPnr (53.7%; Figure 2F) and CB (76.8%; Figure 2A), and TOt (24.7%; Figure 2C), respectively. The largest proportions of  $T_e$  above the  $T_{set}$ -range were recorded for TOo (54.2%; Figure 2E) and for SPr (58.6%; Figure 2G). More details in intersite variation of  $T_e$  and  $T_b$  with respect to the  $T_{set}$ -range in the supplemental material.

The CV of  $T_e$ ,  $d_b$  and  $d_e$  were higher within the different populations than the overall variation of all of them (Tables 1). The lowest CV of  $d_b$  was obtained from the MGe and the highest from CB and SPnr (Table 1). A contrasting pattern was observed in the variation of  $d_e$  as the lowest CV's were seen in CB and SP and the highest, TOt (Table S4). The index  $E$  varied considerably also in this last species (CV = 583.3) whereas the lowest CV was found in SP and CB (Table 1). The  $E$  ranged from high in SP and CB to moderate in TOo, whereas MGt, and TOt and MGe behaved as thermoconformers or constrained thermoconformers, respectively (Table 1).

### 3.2. Common trends to all species and populations

The variation of  $T_p$  was low in all the populations (SD = 0.5-1.6), which was also confirmed by the CV's ( $TOt > SPnr > MGe \geq TOo = SPr > CB \geq MGt$ ; Tables 1). The variation of  $T_p$  and the lower- and upper- $T_{set}$  among the seven populations (CV = 2.2-4.2) was overall lower than the variation within the sites (CV = 4.1; Table 1). Like  $T_b$ , the variation (SD and CV) of  $T_p$  showed no correlation with the variation of the  $T_a$  obtained from the nearest weather stations (Table S8).

There was no correlation between  $E$  of the studied populations and variation of the  $T_{a \min}$ ,  $T_{a \text{ mean}}$  and  $T_{a \max}$  gathered from the nearest weather stations. Only  $T_p$  was positively correlated to

$E$ , as well as the  $T_e$  with longitude. With respect to  $T_a$ , the variation (SD and CV) of  $T_{a \text{ max}}$ ,  $T_{a \text{ mean}}$ , and  $T_{a \text{ min}}$  were positively correlated with the variation (SD and CV) of  $T_e$  (Correlations results on Table S11).

#### 4. Behavioral compensation or physiological mechanisms to cope with environmental thermal changes

##### 4.1. Variation within *T. torquatus* and among all species and populations

In CB, no values of  $T_b$  fell above the  $T_p$ , which limited the analysis of the variation of the residuals that fell below this value, resulting  $CV_I > CV_{II}$  (Figure 3A). Differently, in MGt,  $CV_{II} > CV_I$  and  $CV_{IV} > CV_{III}$  (Figure 3B). Opposite to CB, most values of  $T_b$  fell above the  $T_p$  in TOt, and similarly to MGt,  $CV_{IV} > CV_{III}$  (Figure 3C). In MGe, most values of  $T_b$  fell above the  $T_p$ , and  $CV_{IV} > CV_{III}$  (Figure 3D). In TOo,  $CV_{II} > CV_I$  and  $CV_{III} > CV_{IV}$  (Figures 3E) and in SPrn and SPn was  $CV_I > CV_{II}$  and  $CV_{III} > CV_{IV}$ , and  $CV_I > CV_{II}$  and  $CV_{IV} > CV_{III}$ , respectively (Figure 3F-G; for detailed information data on the Figure 3, see Tables S12 & S13).

##### 4.2. Common trends to all species and populations

When comparing the variation of the residuals below and above the  $T_{\text{set}}$  range, SPnr was the only population that exhibited a higher variation below the lower- $T_{\text{set}}$  than above the upper- $T_{\text{set}}$ . The rest of the populations showed the opposite pattern. When comparing the CV of the residuals below and above the  $T_p$ , all populations except TOo showed a higher variation below than above  $T_p$ . The regressions of  $T_b$  vs.  $T_a$  below and above  $T_p$  indicated positive  $b$  coefficients in most cases, except in SPr and TOt; in both species, the negative  $b$  values occurred when  $T_a$  exceeded  $T_p$  (Figures 3C & 3E).

#### 5. Comparison with other tropidurid species

No difference was found between the mean  $T_b$  and mean  $T_p$  of the tropidurids reported in the literature ( $T_b = 35.5 \pm 1.7$ ;  $T_p = 34.8 \pm 1.1$ ; Paired t-test,  $t_{15} = 1.647$ ,  $P = 0.120$ ) but the variation of  $T_b$  was significantly larger than the variation of  $T_p$  (Wilcoxon Signed Rank Test, SD:  $Z = -1.785$ ,  $P = 0.079$ ; CV:  $Z = -1.706$ ,  $P = 0.093$ ). The data gathered from the weather stations ( $N = 26$ ) suggested that there was a no significant correlation between latitude and precipitation amount ( $S = 0.137$ ,  $P = 0.5$ ), precipitation standard deviation ( $S = 0.274$ ,  $P =$

0.174) or range ( $S = 0.223$ ,  $P = 0.27$ ). On the contrary, there was a latitudinal pattern with respect to the  $T_a$  and the thermal variation:  $T_{a \text{ max}}$ ,  $T_{a \text{ mean}}$  and  $T_{a \text{ min}}$  increase whereas the standard deviation and the range ( $T_{a \text{ max}} - T_{a \text{ min}}$ ) of  $T_a$  decreased considerably from latitudes  $30^\circ$  to  $0^\circ$  S (Figure 4A-C). Like precipitation,  $T_b$ ,  $T_p$ , SD and CV  $T_b$  were not correlated with latitude, the biomes, macro or microhabitats (Figure 4D-F). Nevertheless, the SD and CV of  $T_p$  were significantly correlated with the microhabitats that the lizards occupy (Figure 4F). Mean  $T_{a \text{ min}}$  decreases, whereas CV of  $T_{a \text{ mean}}$ , and the SD and CV of  $T_{a \text{ min}}$  increase from longitude  $45^\circ$  to  $90^\circ$  W (westward).

The biomes, macro and microhabitats that the species occupy were not correlated with latitude but were correlated among themselves. Environmental temperature ( $T_{a \text{ max}}$ ,  $T_{a \text{ mean}}$  and  $T_{a \text{ min}}$ ) were not correlated with the type of biomes, micro or macrohabitats.

In most tropidurids,  $T_b$  and  $T_p$  exceed the  $T_a$ . The correlations between the variation of  $T_b$  and  $T_p$  and the variation of the environmental temperature ( $T_{a \text{ max}}$ ,  $T_{a \text{ mean}}$  and  $T_{a \text{ min}}$ ) were not significant (for detailed information data on the statistical analyses on this section and Figure 4, see Table S14-S19).

## DISCUSSION

Across our study, the body temperature ( $T_b$ ) of tropidurids differed among the populations but was independent from either mean or variance of ambient temperature ( $T_a$ ). This pattern seems explained by thermoregulation, given that basking lizards experienced  $T_b$  higher or similar to nearby environmental temperatures, but within a narrow range. The variation in  $T_b$  within populations in comparison with the overall variation among them coincided with the pattern of variation of the annual operative temperature ( $T_e$ ), is higher in the Central urban areas and lower in the gallery forest at the northern site. Whereas  $T_{a \text{ max}}$ ,  $T_{a \text{ mean}}$  and  $T_{a \text{ min}}$  and their variation respectively increase and decreases with latitude, mean  $T_b$  and its variation do not follow a specific pattern.  $T_{a \text{ max}}$ ,  $T_{a \text{ mean}}$  and  $T_{a \text{ min}}$  do not necessarily reflect the temperature that lizards experience and may achieve in their environments. In fact, based on our results, the  $T_a$  and  $T_s$  are different from  $T_e$  at each site. On the contrary,  $T_e$  was affected directly by the thermal variability of the environment ( $T_e$  was positively correlated to longitude and the variation of  $T_e$  increase with the variation of  $T_{a \text{ max}}$ ,  $T_{a \text{ mean}}$  and  $T_{a \text{ min}}$ ) and reached extreme values at all sites. Our results imply that behavioral and physiological mechanisms are involved in the adjustment of the populations to certain environments, being responsible for

the absence of pattern of most of the lizards' thermal variables.

Although a more homogeneous and predictable environment generally leads to low variation in ecological traits (Roff, 1992; Stearns, 1992),  $T_p$  and the lower- and upper- $T_{set}$  in *T. torquatus* at the gallery forest appeared to vary more than in the open urban areas in Central Cerrado. Interestingly, different species of a same latitude shared a similar upper- $T_{set}$  (northern species < central species), which suggests a geographic pattern possibly associated to the tolerance to high temperatures, environmental thermal variation or different physical landscapes. In fact, the analysis of the thermal physiology of a broader range of tropidurids highlighted the correlation between the variation of  $T_p$  and the microhabitats but no pattern was observed in a macrohabitat or biome level. Most of the species seem to cope with the thermal variation and constrains selecting environments where temperatures are close to optimal. For example, whereas in the southern and central sites, lizards were found basking on wall and in open areas with a  $T_b$ 's range of 35-36.3 °C, in the northern locality *T. torquatus* was restrained to the gallery forest. Even being the coolest available environment for the species,  $T_b$ 's were at the upper limit of its  $T_{set}$  range. In the urban areas nearby, 73.3 % of the  $T_e$ 's exceeded *T. torquatus*' upper- $T_{set}$  and reached values 5 °C higher that in the forest. The high thermal tolerance of *T. oreadicus* allow the species to occupy such environment, but lizards' activity was restricted from early morning until 14:00 h whereas in the other sites activity would last until 18:00 h with few breaks at midday to avoid the highest  $T_a$ 's. Upon an increase in  $T_a$ , lizards like *T. oreadicus* may be able to disperse into the forest finding lower  $T_a$ 's whereas others like *T. torquatus* will be limited to its site and will have to cope with the invasive species and adjust to the changing environment.

However, thermoregulatory efficiency may buffer the risk to overheating in the face of climate warming (Kearney *et al.*, 2008; Huey and Tewksbury, 2009). A moderate thermoregulator such as *T. oreadicus* exhibits a narrow range of  $T_b$ 's relative to the fluctuations of thermal environment. On the other hand, in environments where thermal variation is low, lizards tend to behave as thermal specialists (Dobzhansky, 1950), and also present narrow ranges of  $T_b$ 's, but similar to the ones of the  $T_a$ 's. In some cases, such as in TOt, lizards are constraint to thermoregulate because thermal microenvironments may not be available or predation risk is too high for lizards' activity (Hertz *et al.*, 1993). Constrained thermoregulation may also be observed in lizards from open habitats like in Central Cerrado, where avoiding high temperatures and seeking cooler borrows represents high costs and are

commonly impossible to achieve. Our results suggest that the efficiency of thermoregulation ( $E$ ) declines from the center of the Cerrado towards the Equator, probably due to the increase in environmental constraints (e.i. high  $T_a$ 's and few borrows in the central region and extensive tree cover in the North) and the low variation of  $T_a$  which leads lizards to thermal specialization and low versatility. Adverse impacts of sudden environmental changes may therefore affect populations adapted to low seasonal variation (e.g. in tropical forests) than populations that experience seasonality (e.g. in temperate regions; Deutsch *et al.*, 2008; Bonebrake and Mastrandrea, 2010), which highlights the vulnerability of the central and northern populations. At the southern site and contrary to what expected, lizards thermoregulated similarly during the reproductive and the non-reproductive seasons. Nevertheless, during the reproductive months, the accuracy slightly decreased as part of the time and energy were also allocated into mating and protecting the territory. In fact, the  $E$  of the juveniles did not vary along the year. The two species at the Central site shared the same microenvironments and adults exhibited a similar  $E$ . The higher  $d_b$  index in *T. etheridgei*, though, indicates that this species experienced more difficulties maintaining its  $T_b$  close to the  $T_{set}$  range.

In agreement with previous studies, thermoregulatory behavior differed among the *Tropidurus* populations (Teixeira-Filho *et al.*, 1996; Kiefer *et al.*, 2007). This is not only due to genetical or physiological differences but also to differences in external factors (e.g. environmental costs). The thermal physiology and behavior compensate for differences among habitats which enables lizards to adjust to different environments. Apparently, when  $T_p$  is low the need of thermoregulating more efficiently is not as important as when  $T_p$  is high. When possible, like most heliothermic lizards, *Tropidurus* thermoregulates actively with the main objective of maintaining their body within optimal  $T_b$ 's and avoiding lethal temperatures. Recent studies demonstrated that either constant or fluctuating thermal regimes might affect the capacity to acclimate to environmental variations (Hadamová and Gvozdík, 2011). Our results suggest that the inhabiting the forest, where variation of  $T_s$  and  $T_a$  is low, the adjustments would result in a thermoconformer rather than in a thermoregulator behavior. Interestingly, of all the presented variables, only the variation of  $E$  was higher among the populations than within them, which suggests that  $E$  is closely associated to the environment than to the individual variability within the sites.

This hypothesis was reinforced when data from the literature and weather station was



incorporated to the analyses: the variation of  $T_a$  decreases with latitude, being less variable closer to the Equator. In most tropidurids,  $T_b$  and  $T_p$  are similar and higher than  $T_a$  suggesting a relation with a plesiomorphic condition, probably linked to earlier semiarid environments such as the Caatinga (Carvalho *et al.*, 2013). Only the variation of  $T_p$  was correlated with the variation of the microhabitats: a fluctuating microenvironment may lead to a narrower range and more similar  $T_p$  among the lineages. Plasticity of  $T_p$  can be attributed to seasonal or developmental responses (Gvozdík, 2012). In *Tropidurus*, both kinds seem to contribute: seasonal plasticity was corroborated between the reproductive and non-reproductive season in *T. catalanensis*, whereas developmental plasticity was observed, for example, in relation to the efficiency of thermoregulation that varied between juveniles and adults of MGt. Behavioral plasticity was observed with respect to thermoregulation. For example, when  $T_a$  fell below  $T_p$ , lizards from SP and CB actively looked for maintaining their  $T_b$  as close as possible to  $T_p$ . On the other hand, when  $T_a$  exceeded the  $T_p$ , the variation augmented above the regression line, which suggests that even at higher  $T_a$ 's lizards thermoregulate. Lizards during the reproductive season showed a different behavior at high  $T_a$ 's, probably associated with hiding in cooler borrows to keep  $T_b$  within the  $T_{set}$  range. On the contrary, MGt showed low variation above the regression when  $T_a$  was below the  $T_p$  indicating possible environmental constrains limiting the correct thermoregulation, which results in lower  $T_b$ 's. When  $T_a$  exceeded  $T_p$ , MGt showed a similar pattern of residual variation than SP and CB, but the  $b$  value was close to zero, suggesting an active thermoregulation. At the same site, the  $b$  value of the regression obtained for MGe was close to one, which suggests a poor or null behavior of thermal regulation. In TOt, all value of  $T_b$  above the regression  $T_b$  vs.  $T_a$  fell within the  $T_{set}$  range but most was below the regression. The variation of the residuals below the regression was higher at all  $T_a$ 's than above the regression, probably because of the few options for basking at the site. In TOo, thermoregulation appears to be relevant, especially at high  $T_a$ 's where the risk of overheating becomes more probable. Although plasticity of  $T_p$  is often denied or neglected, it might turn out to be a relevant trait for coping with climate changes. Low efficiency of thermoregulation (*e.g.* in the tropical forests) may be compensated by a higher scope of  $T_p$  plasticity (*e.g.* also closer to the Equator) and vice versa, which may determine the persistence particularly of the populations with limited dispersal (Gvozdík, 2012) and exposed to low seasonal fluctuation (Angilletta, 2009).

With the present data, any conclusion on the cause of the variability would be speculative.

Indeed, an increment in the costs of thermoregulation may also increase the variation of  $T_p$  (Huey and Slatkin, 1976; Withers and Campbell, 1985). Previous experiments with specimens of *T. catalanensis* and *T. torquatus* determined that the efficiency of thermoregulation decreases when the costs augment, but it also confirmed that individual variability plays an important role in the mean behavior of the population (Leirião *et al.*, unpublished data). Two different strategies are observed in these species: whereas some always chose higher  $T_p$ 's, others opt for lower  $T_p$ 's. Individual variation in lizards has been previously reported with respect to reproduction and growth (Middendorf and Simon, 1988; Christian and Bedford, 1995; Stapley, 2006) but very few authors have analyzed the individuality in behavior associated to thermoregulation (Bowker, 1984). Like reported for African lizards (Bowker, 1984), *Tropidurus* showed that not only costs may affect lizards thermoregulation but also individuality. Furthermore,  $T_p$  may be an individual-dependent and context-dependent feature of the specie (Cowles and Bogert, 1944; Avery, 1982).

Several factors confirm that heliothermic lizards' vulnerability to climate warming increases towards the Equator such as the higher  $T_b$ 's at these sites in relation to the counterparts in southern locations, the high percentages of  $T_e$ 's that fall above the upper- $T_{set}$  of the species, and the low possibilities of dispersal that some populations have in the present. It is well known climate change may over-run adaptation rates (Etterson and Shaw, 2001; Huey *et al.*, 2003; Molina-Montenegro and Naya, 2012), thus when dispersal is not an option, plasticity may be the last mechanism for a species to adjust to a new scenario (Hahn *et al.*, 2012; Frei *et al.*, 2014). Thermoregulation may also be a buffer mechanism to cope with warming in a short-run, as the efficiency of thermoregulation is affected not only by the physiological adjustments but also by the environmental costs that may also augment. Plasticity of the behavior associated to thermal adjustment and costs may contribute to the genus' adaptive capacity and may be one of the main factors responsible for the survival of its populations.

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Table 1. Mean  $\pm$  standard deviation (SD), median (range) and coefficient of variation (CV) of body ( $T_b$ ) and preferred temperature ( $T_p$ ), lower- and upper- $T_{set}$  points, indices  $d_b$  and  $E$  for juveniles, adults, females, males, and overall individuals of *T. torquatus* from Cuiaba, MT (CB), Arinos, MG (MGt), and Formoso do Araguaia, TO (TOt), *T. etheridgei* from Arinos, MG (MGe), *T. oreadicus* from Formoso do Araguaia, TO (TOo), and *T. catalanensis* from Piracicaba, SP, collected in the non-reproductive (SPnr) and reproductive (SPr) seasons. Values for all overall specimens of *T. torquatus* and for all studied specimens are also presented to compare the variation of the thermal traits within and among groups.

Species/populations	Categories	$T_b$ (°C)	CV	$T_p$ (°C)	CV	lower- $T_{set}$ (°C)	CV	upper- $T_{set}$ (°C)	CV	$d_b$ (n)	CV	$E$	CV
CB	Juveniles (1)	-	-	34.3	-	33.3	-	35	-	-	-	-	-
	Adults (20)	$35.4 \pm 2.1$	5.9	$34.8 \pm 0.8$	2.4	$34.0 \pm 1.1$	3.2	$35.6 \pm 0.7$	2.0	$1.1 \pm 1.2$	109.8	$0.58 \pm 0.5$	78.4
		34.6 (32.5-40.2)		34.6 (33.3-36.3)		33.8 (31.5-36)		35.6 (34.4-37.1)		0.9 (0-3.9)		0.67 (-0.5-1)	
	♀ (11)	$35.4 \pm 2.2$	6.2	$34.8 \pm 0.8$	2.3	$34.1 \pm 0.9$	2.7	$35.5 \pm 0.8$	2.1	$1.1 \pm 1.2$	109.4	$0.61 \pm 0.43$	70.6
		34.6 (32.5-40.2)		34.6 (33.8-36.3)		33.9 (33.1-36)		35.4 (34.4-36.7)		1.1 (0-3.6)		0.6 (-0.4-1)	
	♂ (9)	$35.4 \pm 2.1$	5.9	$34.8 \pm 0.9$	2.6	$33.9 \pm 1.3$	3.9	$35.7 \pm 0.7$	1.9	$1.2 \pm 1.4$	116.0	$0.55 \pm 0.51$	94.0
34.5 (32.5-39)			34.7 (33.3-36.1)		33.6 (31.5-35.9)		35.6 (34.9-37.1)		0.8 (0-3.9)		0.7 (-0.46-1)		
Overall (21)	$35.4 \pm 2.1$	5.9	$34.8 \pm 0.8$	2.3	$34 \pm 1.1$	3.2	$35.6 \pm 0.71$	2.0	$1.1 \pm 1.2$	109.8	$0.58 \pm 0.46$	78.4	
	34.6 (32.5-40.2)		34.6 (33.3-36.3)		33.8 (31.5-36)		35.5 (34.4-37.1)		0.9 (0-3.9)		0.67 (-0.46-1)		
MGt	Juveniles (8)	$34.5 \pm 2.2$	6.3	$33.8 \pm 0.5$	1.6	$32.8 \pm 0.7$	2.1	$34.6 \pm 0.6$	1.8	$1.0 \pm 1.1$	108.6	$0.45 \pm 0.59$	130.6
		34.8 (31.4-37.5)		33.7 (33.1-34.6)		33 (32-33.7)		34.6 (33.5-35.5)		0.6 (0-3.1)		0.68 (-0.67-1)	
	Adults (14)	$35.3 \pm 2.8$	7.9	$33.9 \pm 0.8$	2.5	$33.1 \pm 1.0$	3.1	$34.9 \pm 1.0$	2.9	$2.1 \pm 1.4$	65.4	$-0.12 \pm 0.73$	629.3
		36.4 (30.4-39.3)		33.9 (32.6-35.7)		33.3 (30.8-34.7)		34.8 (33.7-37)		2.2 (0-4.6)		-0.15 (-1.5-1)	
	♀ (6)	$37.5 \pm 1.0$	2.7	$34.2 \pm 0.9$	2.7	$33.6 \pm 0.9$	2.8	$35.2 \pm 1.0$	2.8	$1.9 \pm 1.3$	66.2	$-0.03 \pm 0.69$	2032.6
		37.4 (36.4-39.3)		34.1 (33.1-35.7)		33.5 (32.1-34.7)		35.3 (33.7-36.7)		2.2 (0-3.6)		-0.2 (-0.9-1)	
♂ (8)	$33.7 \pm 2.7$	8.0	$33.6 \pm 0.8$	2.3	$32.8 \pm 1.0$	3.2	$34.7 \pm 1.1$	3.1	$2.3 \pm 1.3$	68.4	$-0.23 \pm 0.84$	371.2	
	33.6 (30.4-37.3)		33.6 (32.6-34.8)		33 (30.8-34)		34.2 (33.7-37)		1.9 (0.6-4.7)		0.01 (-1.5-0.67)		
Overall (22)	$35.0 \pm 2.59$	7.4	$33.8 \pm 0.7$	2.2	$33 \pm 0.9$	2.8	$34.8 \pm 0.9$	2.6	$1.70 \pm 1.36$	79.8	$0.09 \pm 0.72$	794.1	
	35.8 (30.4-39.3)		33.8 (32.6-35.7)		33.2 (30.8-34.7)		34.7 (33.5-37)		1.78 (0-4.65)		0.047 (-1.49-1)		

Species/populations	Categories	$T_b$ (°C)	CV	$T_p$ (°C)	CV	lower- $T_{set}$ (°C)	CV	upper- $T_{set}$ (°C)	CV	$d_b$ (n)	CV	$E$	CV
TOt	Juveniles (1)	-	-	-	-	-	-	-	-	-	-	-	-
	Adults (32)	$36.2 \pm 1.5$	4.1	$33.9 \pm 1.6$	4.8	$33.2 \pm 2.0$	6.0	$34.8 \pm 1.6$	4.7	$1.7 \pm 1.3$	73.4	$-0.14 \pm 0.84$	583.3
		36.3 (32.2-39.2)		34.3 (30.9-36.8)		34.0 (29.4-36)		35.1 (30.3-37.4)		1.6 (0-5.7)		$-0.1 (-2.8-1)$	
	♀ (18)	$36.5 \pm 1.4$	3.8	$34.2 \pm 1.5$	4.5	$33.7 \pm 1.9$	5.5	$35.0 \pm 1.7$	4.7	$1.8 \pm 0.9$	52.1	$-0.18 \pm 0.62$	336.6
		36.6 (33.6-39.2)		34.5 (30.7-36.5)		34.2 (29.6-36)		35.2 (31.1-37.4)		1.9 (0-3.5)		$-0.28 (-1.3-1)$	
	♂ (14)	$35.7 \pm 1.5$	4.2	$33.4 \pm 1.6$	4.8	$32.5 \pm 2.0$	6.2	$34.4 \pm 1.6$	4.6	$1.6 \pm 1.6$	99.4	$-0.09 \pm 1.09$	1161.3
36 (32.2-37.8)			33.9 (29.8-35.4)		33.1 (29.4-34.9)		35 (30.3-35.8)		1.0 (0-5.7)		$0.3 (-2.8-1)$		
Overall (32)	$36.2 \pm 1.5$	4.1	$33.8 \pm 1.6$	4.7	$33.2 \pm 2.0$	6.0	$34.8 \pm 1.6$	4.7	$1.7 \pm 1.3$	73.5	$-0.14 \pm 0.84$	583.3	
	36.3 (32.2-39.2)		34.3 (29.8-36.5)		34.0 (29.4-36.0)		35.2 (30.3-37.4)		1.6 (0-5.7)		$-0.09 (-2.8-1)$		
Overall <i>T. torquatus</i> (CB, MGt, TOt)	Juveniles (9)	$34.5 \pm 2.2$	6.4	$33.8 \pm 0.5$	1.5	$32.9 \pm 0.7$	2.1	$34.6 \pm 0.6$	1.7	$1.02 \pm 1.1$	107.8	$0.45 \pm 0.59$	131.1
		34.8 (31.4-37.5)		33.9 (33.1-34.6)		33.2 (32-33.7)		34.7 (33.5-35.5)		0.6 (0-3.1)		$0.68 (-0.67-1)$	
	Adults (66)	$35.8 \pm 2$	5.6	$34.1 \pm 1.3$	3.8	$33.4 \pm 1.6$	4.8	$35 \pm 1.3$	3.7	$1.6 \pm 1.3$	81.3	$0.07 \pm 0.79$	1179.1
		36.2 (30.4-40.2)		34.3 (29.8-36.5)		33.7 (29.4-36)		35.2 (30.3-37.4)		1.5 (0-5.7)		$0.17 (-2.8-1)$	
	♀ (35)	$36.3 \pm 1.7$	4.7	$34.4 \pm 1.2$	3.5	$33.8 \pm 1.5$	4.4	$35.2 \pm 1.3$	3.7	$1.7 \pm 1.2$	70.7	$0.04 \pm 0.7$	1750
		36.4 (32.5-40.2)		34.5 (30.7-36.5)		34 (29.6-36)		35.3 (31.1-37.4)		1.5 (0-4.7)		$0.1 (-1.49-1)$	
♂ (31)	$35.1 \pm 2.1$	6.0	$33.9 \pm 1.4$	4.1	$33 \pm 1.7$	5.2	$34.9 \pm 1.3$	3.7	$1.6 \pm 1.5$	91.1	$0.1 \pm 0.89$	890	
	35.9 (30.4-39)		34.1 (29.8-36.1)		33.4 (29.4-35.9)		35.1 (30.3-37.1)		1.4 (0-5.7)		$0.3 (-2.8-1)$		
Overall (75)	$35.6 \pm 2.1$	5.9	$34.1 \pm 1.3$	3.8	$33.4 \pm 1.5$	4.5	$35 \pm 1.3$	3.7	$1.6 \pm 1.3$	81.3	$0.11 \pm 0.77$	703.6	
	36.2 (30.4-40.2)		34.3 (29.8-36.5)		33.5 (29.4-36)		35.1 (30.3-37.4)		1.5 (0-5.7)		$0.205 (-2.8-1)$		
MGe	Juveniles (1)	37.5	-	33.4	-	32.6	-	34.7	-	28	-	-0.541	-
	Adults (14)	$36.2 \pm 3.8$	10.5	$33.8 \pm 1.5$	4.3	$32.8 \pm 2.3$	7.0	$34.8 \pm 1.0$	2.8	$2.8 \pm 1.6$	57.1	$-0.53 \pm 0.87$	165.6
		37.4 (26.1-39.5)		33.8 (31-36.8)		33.3 (28-36.2)		34.6 (33.6-37.2)		2.5 (0-5.9)		$-0.4 (-2.2-0.9)$	
♀ (7)	$35.7 \pm 4.4$	12.3	$33.6 \pm 1.5$	4.3	$32.7 \pm 1.1$	7.1	$34.8 \pm 0.8$	2.4	$2.9 \pm 1.8$	64.2	$-0.55 \pm 1.0$	180.9	
	37.4 (26.1-38.8)		34.3 (31-34.9)		33.6 (28-34.8)		35.3 (33.6-35.7)		2.6 (0-5.9)		$-0.43 (-2.2-0.9)$		

Species/populations	Categories	$T_b$ (°C)	CV	$T_p$ (°C)	CV	lower- $T_{set}$ (°C)	CV	upper- $T_{set}$ (°C)	CV	$d_b$ (n)	CV	$E$	CV
TOo	♂ (6)	36.7± 3.2	8.7	33.9 ± 1.6	4.7	32.9 ± 2.5	7.6	34.8 ± 1.2	3.5	2.8 ± 1.5	53.1	-0.5 ± 0.8	159.6
		37.4 (30.9-39.5)		33.6 (32.1-36.8)		33.1 (28.5-36.2)		34.5 (33.8-37.2)		2.5 (1.3-4.9)		-0.33 (-1.7-0.3)	
	Overall (14)	36.3 ± 3.6	10.0	33.7 ± 1.4	4.2	32.8 ± 2.2	6.7	34.8 ± 0.9	2.7	2.8 ± 1.5	54.8	-0.53 ± 0.84	158.8
		37.0 (26.1-39.5)		33.6 (31-36.8)		33.1 (28-36.2)		34.6 (33.6-37.2)		2.6 (0-5.9)		-0.414 (-2.2-0.9)	
	Juveniles (1)	40.9	-	34.6	-	33.8	-	35.8	-	3.9	-	0.31	-
	Adults (25)	37 ± 3.3	8.9	34.6 ± 1.4	4.0	33.8 ± 2.1	6.1	35.8 ± 1.5	4.2	3.0 ± 2.0	66.1	0.32 ± 0.45	143.04
		38 (30.1-41.3)		34.8 (30.5-36.9)		34.4 (29.6-36.6)		35.8 (30.7-37.4)		3.3 (0-8)		0.25 (-0.81-1)	
	♀ (12)	37.5 ± 3.5	9.3	34.7 ± 1.5	4.3	33.6 ± 2.5	7.5	36.2 ± 1.4	3.9	3.1 ± 1.8	59.0	0.29 ± 0.42	145
		38.1 (30.1-41.3)		34.9 (30.9-36.7)		34.5 (29.6-36.2)		36.3 (32.2-37.4)		3.3 (0-5.8)		0.24 (-0.33-1)	
	♂ (13)	36.6 ± 3.2	8.7	34.5 ± 1.4	4.2	33.9 ± 1.6	4.7	35.4 ± 1.5	4.3	2.9 ± 2.2	75.3	0.34 ± 0.5	146.2
37.8 (30.2-39.4)		34.7 (30.5-36.9)		34.4 (30.3-36.6)		35.6 (30.7-37.2)		3.3 (0-8)		0.25 (-0.8-1)			
Overall (26)	37.2 ± 3.31	8.9	34.6 ± 1.4	4.1	33.9 ± 2.1	6.1	35.8 ± 1.5	4.1	3.1 ± 2	64.3	0.31 ± 0.45	144.5	
	38.1 (30.1-41.3)		34.8 (30.5-36.9)		34.4 (29.6-36.6)		35.9 (30.7-37.4)		3.4 (0-8)		0.24 (-0.81-1)		
SPnr	Juveniles (15)	36.3 ± 2.7	7.4	34.4 ± 1.1	3.2	33.1 ± 1.2	3.6	36.2 ± 1.6	4.5	1.8 ± 2.3	128.8	0.64 ± 0.46	72.1
		36.6 (32.3-41.6)		34.6 (31.8-35.8)		33.4 (30.4-34.7)		36.2 (32.9-39.8)		1.1 (0-8.7)		0.78 (-0.7-1)	
	Adults (9)	35.4 ± 2.1	5.9	34.9 ± 1.3	3.7	33.7 ± 1.5	4.3	36.2 ± 1.4	3.8	1.2 ± 1.1	94.5	0.77 ± 0.22	28.3
		34.8 (32.5-38.9)		34.6 (32.6-37.6)		34 (31.1-36.5)		35.9 (34-38.6)		0.8 (0-3.0)		0.83 (0.4-1)	
	♀ (8)	35.5 ± 2.2	6.2	35.2 ± 1.1	3.1	34.0 ± 1.2	3.4	36.4 ± 1.2	3.3	1.2 ± 1.2	97.0	0.76 ± 0.23	30.5
		35.1 (32.5-38.9)		34.8 (34.2-37.6)		34 (32.8-36.5)		36.3 (35-38.6)		1.1 (0-3)		0.78 (0.4-1)	
	♂ (1)	34.8	-	32.6	-	31.1	-	34	-	0.8	-	0.83	-
	Overall (24)	36.0 ± 2.5	6.8	34.9 ± 1.6	4.5	33.7 ± 1.8	5.4	36.2 ± 1.5	4.2	1.6 ± 2.0	124.5	0.69 ± 0.38	55.6
		35.2 (32.3-41.6)		34.8 (31.5-39.6)		33.8 (30.4-39.6)		36.0 (33-39.8)		0.8 (0-1)		0.83 (-0.7-1)	
	SPr	Juveniles (12)	35.3 ± 2.0	5.6	35.0 ± 1.0	2.9	34.4 ± 1.0	3.0	35.9 ± 1.1	3.0	1.9 ± 1.3	68.0	0.53 ± 0.32
35.9 (32.1-37.9)			35 (33.7-36.8)		34.5 (32.5-36.1)		35.8 (34.9-38.3)		2.0 (0-4)		0.5 (-0.004-1)		
Adults (29)		35.9 ± 1.9	5.2	33.9 ± 1.5	4.4	33 ± 1.4	4.3	34.7 ± 1.3	3.8	1.9 ± 1.4	73.4	0.53 ± 0.47	130.3
		36.2 (30.6-39.3)		34.1 (30.8-36)		33.2 (30-35.8)		35.1 (31.2-36.2)		1.9 (0-5)		0.36 (-0.7-1)	
♀ (14)		36 ± 2.4	6.6	33.6 ± 1.6	4.8	32.7 ± 1.8	5.4	34.5 ± 1.6	4.6	2.3 ± 1.4	60.1	0.43 ± 0.34	81.4

Species/populations	Categories	$T_b$ (°C)	CV	$T_p$ (°C)	CV	lower- $T_{set}$ (°C)	CV	upper- $T_{set}$ (°C)	CV	$d_b$ (n)	CV	$E$	CV
		36.4 (30.6-39.3)		34.1 (30.8-36)		33.1 (30-35.8)		34.9 (31.2-36.2)		2 (0-5)		0.5 (-0.05-1)	
	♂ (15)	35.8 ± 1.3 36 (33.1-37.7)	3.6	34.1 ± 1.0 34.5 (31.7-35.1)	2.9	33.4 ± 1.0 33.5 (31.1-34.5)	2.9	34.9 ± 1.0 35.4 (32.5-36)	2.8	1.5 ± 1.3 1.3 (0-3.8)	91.6	0.64 ± 0.33 0.68 (0.29-1)	51.6
	Overall (41)	35.7 ± 1.9 36.1 (30.6-39.3)	5.4	34.1 ± 0.2 34.4 (30.8-36.9)	3.9	33.4 ± 1.5 33.8 (30-36.2)	4.4	35.0 ± 1.4 35.3 (31.2-38.3)	3.9	1.9 ± 1.3 1.9 (0-5.02)	70.7	0.53 ± 0.33 0.53 (-0.25-1)	62.5
SP nr & r	Juveniles (27)	35.9 ± 2.4 36.1 (32.1-41.6)	6.7	35 ± 1.5 (22) 34.9 (31.8-39.6)	4.3	33.9 ± 1.8 34 (30.4-39.6)	5.2	36.1 ± 1.4 35.9 (32.9-39.8)	4.0	1.8 ± 2.0 1.6 (0-8.7)	107.9	0.60 ± 0.41 0.66 (-0.7-1)	68.5
	Adults (38)	35.8 ± 1.9 36.1 (30.6-39.3)	5.3	34.1 ± 1.4 (34) 34.5 (30.8-37.6)	4.1	33.2 ± 1.5 33.2 (30-36.5)	4.4	35.1 ± 1.5 35.4 (31.2-38.6)		1.7 ± 1.3 1.7 (0-5)	79.6	0.6 ± 0.33 0.64 (-0.25-1)	54.7
	♀ (22)	35.8 ± 2.3 36.2 (30.6-39.3)	6.4	34.2 ± 1.6 34.5 (30.8-37.6)	4.7	33.2 ± 1.7 33.2 (30-36.5)	5.0	35.2 ± 1.7 35.4 (31.2-38.6)	4.9	1.8 ± 1.4 1.8 (0-5)	74.8	0.57 ± 0.34 0.57 (-0.25-1)	59.1
	♂ (16)	35.7 ± 1.2 35.9 (33.1-37.7)	3.4	34.0 ± 1.0 34.4 (31.7-35.1)	2.9	33.2 ± 1.1 33.3 (31.1-34.5)	3.4	34.8 ± 1.0 35.3 (32.5-36)	2.8	1.4 ± 1.3 1.3 (0-3.8)	91.3	0.66 ± 0.32 0.69 (-0.05-1)	48.3
	Overall (52)	35.8 ± 2.1 36.1 (30.6-41.6)	5.9	34.5 ± 1.4 34.6 (31-39.6)	4.1	33.6 ± 1.6 33.9 (30.4-39.6)	4.8	35.6 ± 1.5 35.5 (31.2-39.8)	4.2	1.7 ± 1.6 1.6 (0-8.7)	94.1	0.51 ± 0.45 0.55 (-0.7-1)	88.2
Overall spp./pops	Juveniles (33)	35.8 ± 2.5 35.7 (31.4-41.6)	7.0	34.6 ± 1.4 34.5 (31.8-39.6)	4.0	33.7 ± 1.6 33.7 (30.4-39.6)	4.7	35.7 ± 1.4 35.5 (32.9-39.8)	3.9	1.7 ± 1.8 1.6 (0-8.7)	105.9	0.47 ± 0.51 0.64 (-0.7-1)	108.5
	Adults (138)	36 ± 2.5 36.3 (26.1-41.3)	6.9	34.2 ± 1.4 34.4 (29.8-37.6)	4.1	33.4 ± 1.7 33.7 (28-36.6)	5.1	35.2 ± 1.4 35.3 (30.3-38.6)	4.0	2 ± 1.6 1.9 (0-8)	80	0.15 ± 0.73 0.29 (-2.8-1)	486.7
	♀ (75)	36.3 ± 2.6 36.7 (26.1-41.3)	7.2	34.3 ± 1.4 34.5 (30.7-37.6)	4.1	33.5 ± 1.8 33.9 (28-36.5)	5.4	35.3 ± 1.5 35.4 (31.1-38.6)	4.2	2.1 ± 1.5 1.9 (0-5.9)	71.4	0.13 ± 0.69 0.25 (-2.22-1)	530.8
	♂ (63)	35.7 ± 2.3 36.1 (30.2-39.5)	6.4	34 ± 1.3 34.2 (29.8-36.9)	3.8	33.2 ± 1.7 33.5 (28.5-36.6)	5.1	35 ± 1.3 35.2 (30.3-37.2)	3.7	2 ± 1.7 1.8 (0-8)	85	0.17 ± 0.78 0.3 (-2.8-1)	458.8
	Overall (171)	36 ± 2.5 36.3 (26.1-41.6)	6.9	34.3 ± 1.4 34.4 (29.8-39.6)	4.1	33.4 ± 1.7 33.7 (28-39.6)	5.1	35.3 ± 1.4 35.3 (30.3-39.8)	4.0	2 ± 1.6 1.8 (0-8.7)	80	0.21 ± 0.7 0.32 (-2.8-1)	333.3

## FIGURE LEGENDS

Figure 1. Linear regressions of body temperature ( $T_b$ ; solid lines and circles) and microenvironmental temperatures, substrate ( $T_s$ ; dotted lines and empty circles), and air temperatures ( $T_a$ ; dashed lines and solid triangles) vs. the time of capture for: (A) *Tropidurus torquatus* from Cuiaba, MT (CB); (B) *T. torquatus* from Arinos, MG (MGt); (C) *T. torquatus* from Formoso do Araguaia, TO (TOt); (D) *T. etheridgei* from Arinos, MG (MGe); (E) *T. oreadicus* from Formoso do Araguaia, TO (TOo); and (F & G) *T. catalanensis* from Piracicaba, SP, collected in the non-reproductive and reproductive season, respectively. The horizontal dashed lines indicate the lower and upper set-points of the preferred body temperature ( $T_p$ ).

Figure 2. Frequency of body ( $T_b$ ; solid bars) and operative ( $T_e$ ; light bars) temperatures of: (A) *Tropidurus torquatus* from Cuiaba, MT (CB); (B) *T. torquatus* from Arinos, MG (MGt); (C) *T. torquatus* from Formoso do Araguaia, TO (TOt); (D) *T. etheridgei* from Arinos, MG (MGe); (E) *T. oreadicus* from Formoso do Araguaia, TO (TOo); and (F & G) *T. catalanensis* from Piracicaba, SP, collected in the non-reproductive and reproductive season, respectively. The vertical dashed lines indicate the lower and upper set-points of the preferred body temperature ( $T_p$ ). Percentages values correspond to the  $T_b$  (above) and  $T_e$  (below) that fell below (left) and above (right) the  $T_{set}$  range.

Figure 3. Body temperature [ $T_b$ ; circles (below the correspondent  $T_p$ ) and dashed and dotted lines (above the correspondent  $T_p$ )] and preferred temperature ( $T_p$ ; white triangles and dashed-dotted line) vs. air temperature ( $T_a$ ) for: (A) *Tropidurus torquatus* from Cuiaba, MT (CB); (B) *T. torquatus* from Arinos, MG (MGt); (C) *T. torquatus* from Formoso do Araguaia, TO (TOt); (D) *T. etheridgei* from Arinos, MG (MGe); (E) *T. oreadicus* from Formoso do Araguaia, TO (TOo); and (F & G) *T. catalanensis* from Piracicaba, SP, collected in the non-reproductive and reproductive season, respectively. The horizontal and vertical dashed lines indicate the set-point range of  $T_p$ . The histograms correspond to the distribution of the operative temperatures ( $T_e$ ) recorded at each site and the arrows indicate the mean  $T_p$ .

Figure 4. Geographic variation of the environmental temperature parameters: mean values (A), standard deviation (SD; B), and mean range between the lowest and the highest values (C) of maximum ( $T_{a\ max}$ ; solid circles and line), mean ( $T_{a\ mean}$ ; empty circles and dotted line), and minimum ( $T_{a\ min}$ ; solid triangles and dashed line) temperature, and  $T_{a\ max}-T_{a\ min}$  range

(empty triangles and dotted-dashed line) vs. latitude; and the distribution of body ( $T_b$ ; grey boxes) and preferred temperature ( $T_p$ ; white boxes) along the Biomes [D; Chaco (1), Caatinga (2), Rainforest (3), Cerrado (4) and Coastal (5)], macrohabitats [E; Chaco and montane (1), Caatinga (2), gallery forests in the Cerrado, Amazonian and Atlantic rainforests and restinga (3), savanna and urban areas of the Cerrado (4), and Coastal (5)]; and microhabitats and use of the landscape [(F; herbaceous/shrub specialists (1), sand specialist (2), generalists (3), rock/trunck specialists (4), and soil/trunck specialists (5)].



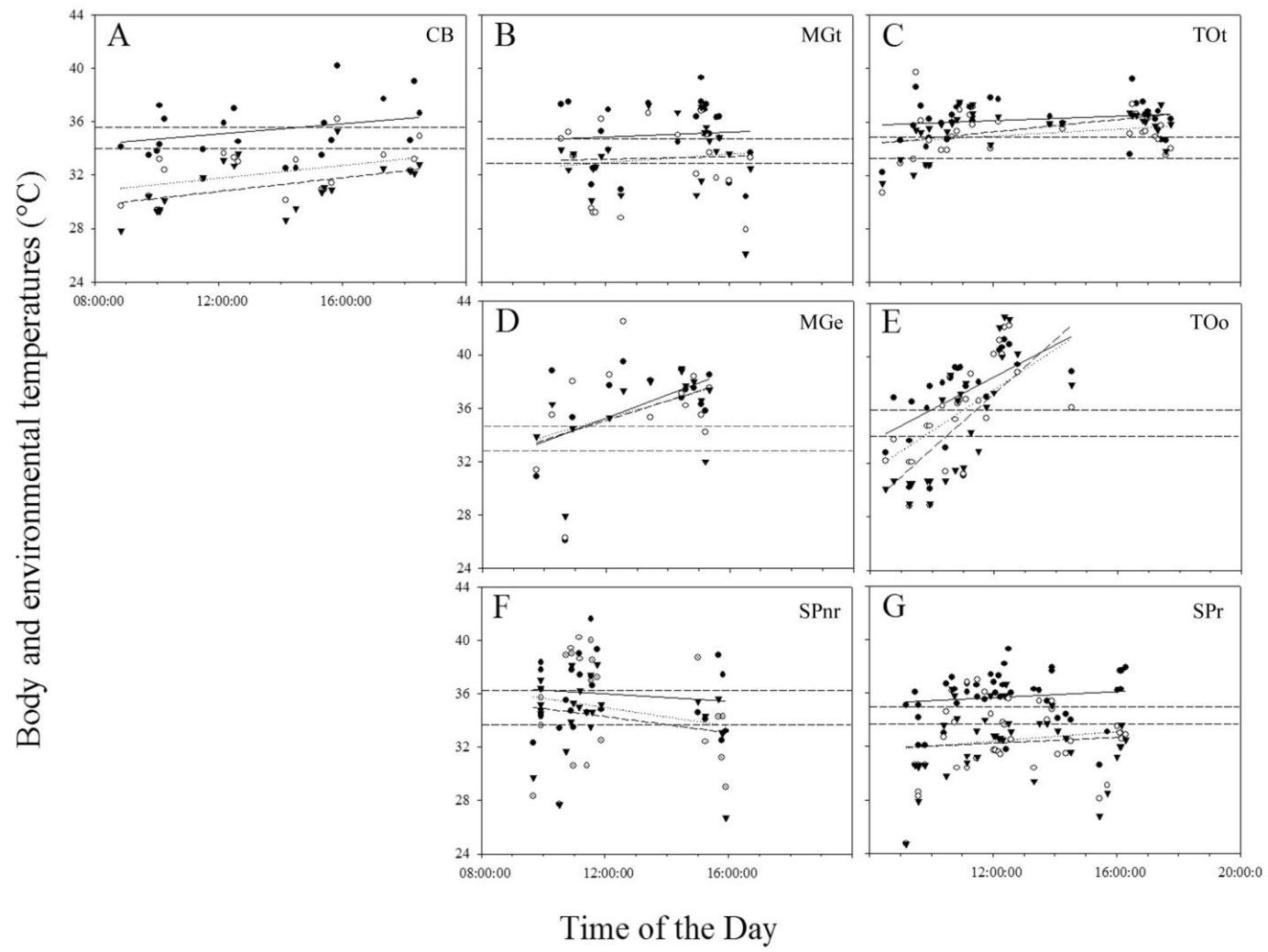


Figure 1.

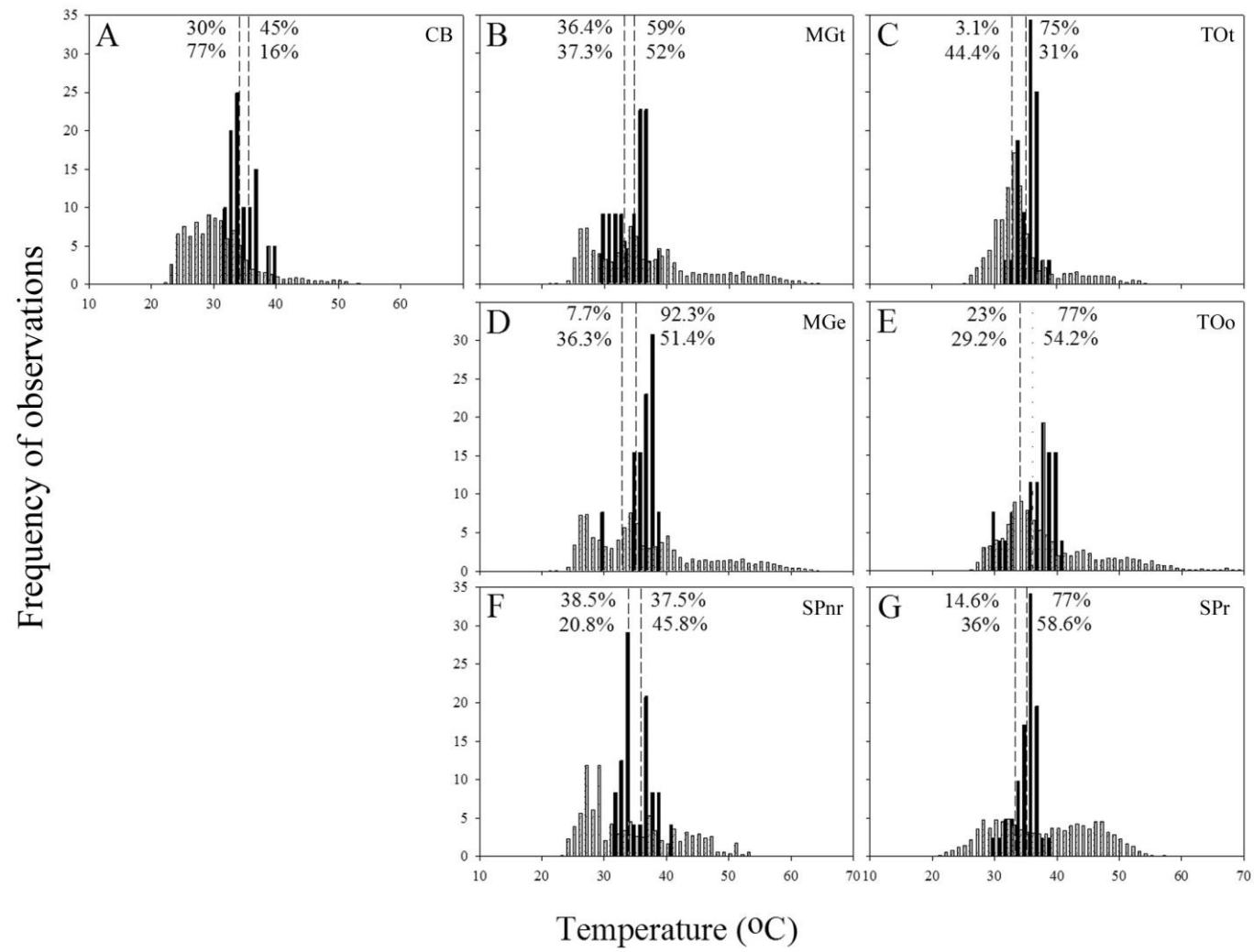


Figure 2.

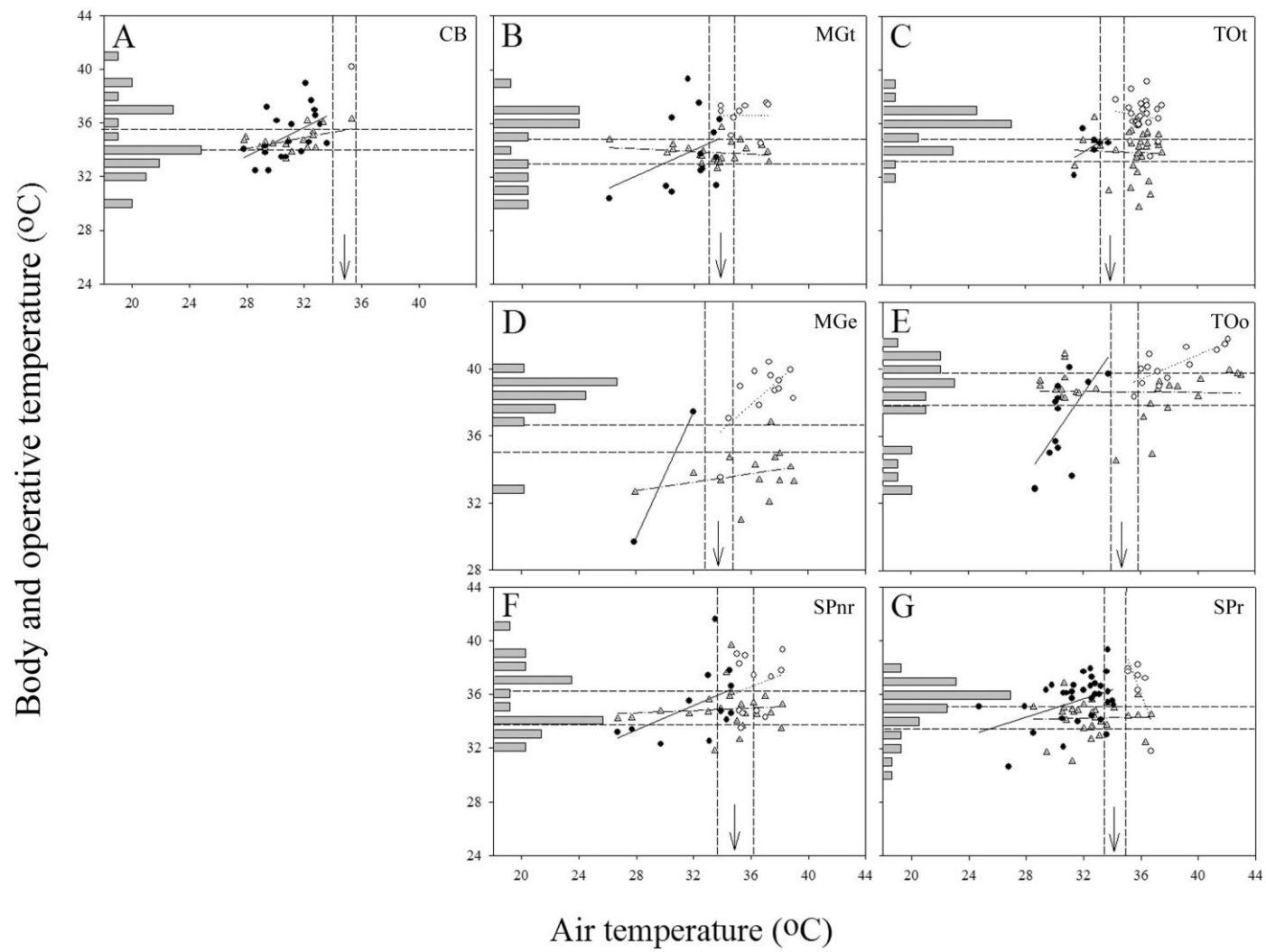


Figure 3.

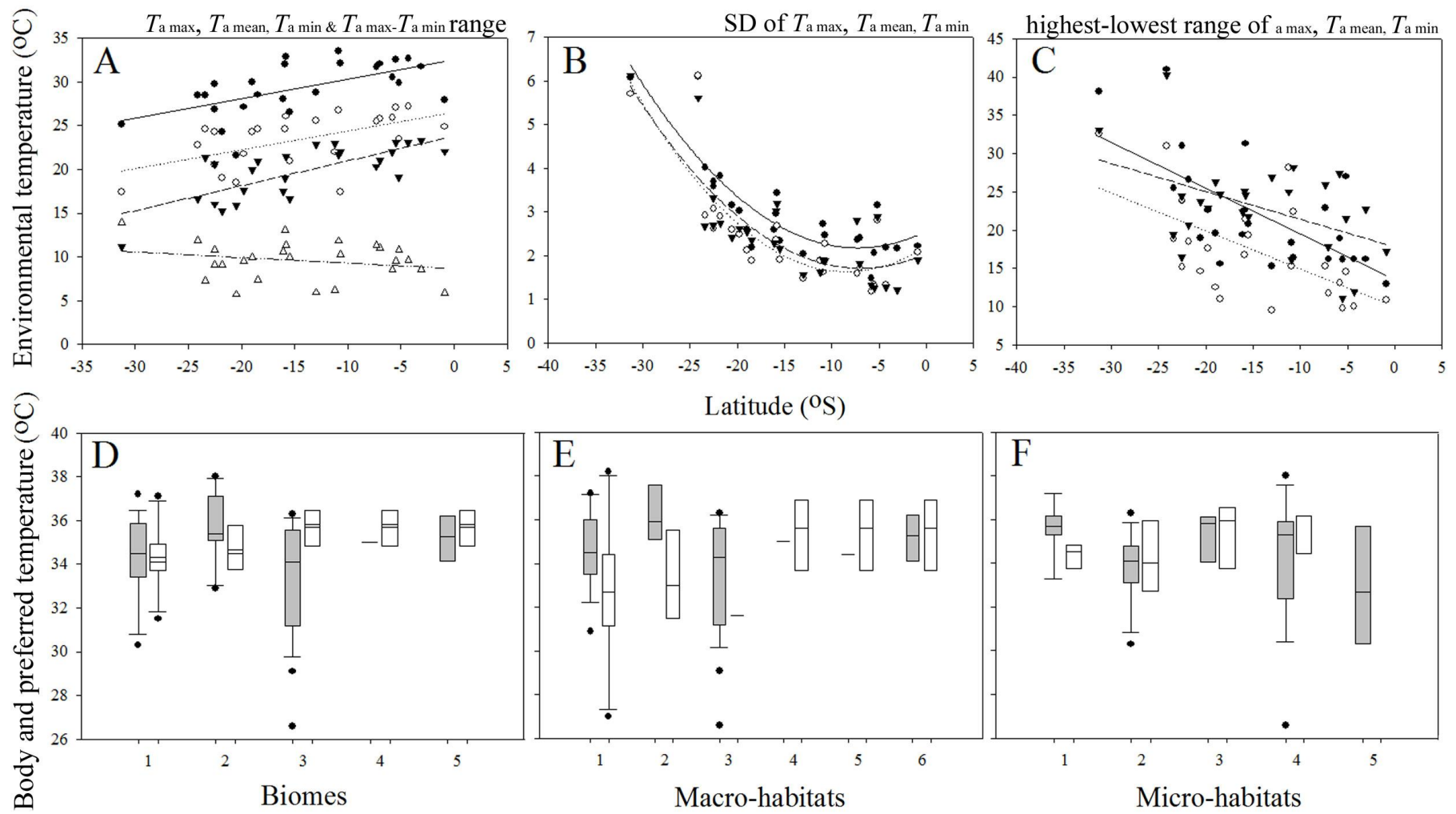


Figure 4.

## SUPPLEMENTAL MATERIAL

*1. Collecting material - Description of the sites*

CB chose similar habitats than in MGt, basking on walls and sidewalks, or on the pavement where the substrate temperature exceeded 50 °C. They were collected from 8:50 h until 18:30 h and often found in couples, thus, the sex ratio was 1.2 females per male. As in the other sites, females ( $n = 11$ ) were smaller than males ( $n = 9$ ; Tables S1 & S2). Whereas juveniles were observed in areas with vegetation, adults of MGt were generally exposed to the sun, like CB, on warmer substrates with nearby shrubs and plants used as burrows. Only one adult of MGt was collected on a tree. MGt was collected between 10:30 h and 16:40 h and its sex ratio was 0.7 female per male. Differently from CB and MGt, TOt was only found in the gallery forests along the Rio Formoso, Gameleira and Córrego Papagaio. The rivers were no more than 25 km from the town but the environment was completely different as they presented more humidity, exuberant vegetation and lower temperatures. Lizards were found on trunks and generally in couples. In fact the sex ratio was 1.3 female ( $n = 18$ ) per male ( $n = 14$ ). Juveniles were harder to find than adults and none for TOt was collected.

In Arinos, MG, MGt was seen in complete sympatry with MGe, although the later was found active one hour earlier, from 9:45 until 15:20 h, than the former. Sex ratios for MGe was 1.2 females per males but overall adults, females and males were similar in SVL to MGt's (Tables S1, S2 & S3). In the northernmost site, TOo was seen and captured in sympatry with TOt only in one location while basking on a termite mound by the highway, next to the Córrego Papagaio. Its  $T_b$  (37.8 °C) was almost 2 °C higher than its congeners' at the same riverside (35.96 °C; range = 34.8 - 37.7 °C). All other TOo were collected in the urban area, basking particularly on grey concrete walls. Observations of both TOt and TOo were recorded from 8:00 until 17:55 h, with a gap between 14:15 until 16:30 h. Most males of TOo were in an aggressive combat mode and many of them were captured while confronting with other contenders. The sex ratio for TOo was 0.5 females per male. Interestingly, half of the males did not present the red coloration and the body proportions were similar to the females'. Considering only the red males the sex ratio would be 2 females per red male. Only one juvenile TOo was collected. Adults of TOt were larger in snout-vent length (SVL) than adults of TOo (Tables S1 & S2). Females and males of TOt were both larger than females and males of TOo (Tables S1 & S2). In both species females were significantly smaller than males

(Tables S1 & S2).

In Piracicaba, SP, *T. catalanensis* were collected at the sports campus of the Escola Superior de Agricultura Luiz de Queiroz (ESALQ) while basking on walls and trees. SP<sub>r</sub> were collected between 9:45 and 16:00 h and exhibited a pattern of harem, the sex ratio was eight females per male. Fifteen juveniles were captured in the periphery. In contrast, lizards in SP<sub>r</sub> were found in couples. In fact, the sex ratio was 0.94 females ( $n = 16$ ) per male ( $n = 17$ ). Lizards' behavior as well as the activity hours (from 9:11 to 16:18 h) were similar in SP<sub>r</sub> and SP<sub>nr</sub>. Adults from both seasons displayed similar size (Tables S1 & S2). Differently from the other species, *T. catalanensis* did not show sexual differences in SVL although sexual dimorphism was noticeable (Tables S1 & S2).

## 2. Microenvironmental and body temperatures

### 2.1. Relationship between $T_s$ , $T_a$ and $T_b$ vs. the time of the day

Neither  $T_s$  nor  $T_a$  from the microenvironments occupied by CB, were related to the time of the day (Regression,  $F_{T_s 1,18} = 6.278$ ;  $F_{T_a 1,18} = 7.094$ ;  $P \leq 0.022$ ; Table S4) but  $T_b$  did (Regression,  $F_{1,18} = 7.094$ ;  $P = 0.016$ ; Figure 1A). Both  $T_s$  and  $T_a$  collected at both MGt's and MGe's microhabitats showed no relationship with the time of the day (Regression, MGt:  $F_{T_s 1,20} = 0.125$ ;  $F_{T_a 1,20} = 0.0138$ ; MGe:  $F_{T_s 1,12} = 1.812$ ;  $F_{T_a 1,12} = 3.840$ ;  $P \geq 0.074$ ; Table S4). Also,  $T_b$  and time of the day were independent (Regression, MGt:  $F_{1,20} = 0.0539$ ; MGe:  $F_{1,12} = 3.866$ ;  $P \geq 0.073$ ; Table S4; Figure 1B & 1D). The  $T_b$  of both MGt and MGe had a significant and positive relationship with  $T_s$  and  $T_a$ . However, whereas the increment of  $T_b$  in MGt depended mainly on  $T_s$  (Multiple regression,  $F_{2,19} = 26.042$ ;  $P \leq 0.001$ ), the increment of  $T_b$  in MGe related better to  $T_s$  or  $T_a$  (Multiple regression,  $F_{2,11} = 30.433$ ;  $P \leq 0.001$ ; Figure 3D). In MGt,  $T_b$  differed from both  $T_s$  and  $T_a$  (Tables 1 & S4; Figures 1B & 3B), contrasting to MGe, species in which  $T_b$  was similar to both  $T_s$  and  $T_a$  (Tables 1 & S4; 1D & 3D).

In the gallery forest, only  $T_a$  increased with the time of the day (Regression,  $F_{T_s 1,30} = 0.1438$ ,  $P = 0.240$ ;  $F_{T_a 1,30} = 6.336$ ,  $P = 0.017$ ; Figure 1C). Downtown, in TOo's microenvironments neither  $T_s$  nor  $T_a$  increased with the time of the day (Regression,  $F_{T_s 1,24} = 21.261$ ;  $F_{T_a 1,24} = 35.473$ ;  $\leq 0.001$ ; Figure 1C). Whereas the  $T_b$  of TOt bared no relationship with the time of the day (Regression,  $F_{1,30} = 0.815$ ,  $P = 0.374$ ; Figure 1C) the  $T_b$  of TOo did (Regression,  $F_{1,24} = 15.401$ ;  $P \leq 0.001$ ; Figure 1E). The  $T_b$  of both TOt and TOo had a significant and positive relationship with  $T_s$  and  $T_a$ , but in both species the increment of  $T_b$  depended mainly on  $T_s$

(Multiple regression, TOt:  $F_{2,29} = 19.358$ ; TOo:  $F_{2,23} = 73.838$ ;  $P \leq 0.001$ ; Tables 1 & S4; Figure 3C & 3E).

In Piracicaba, SP,  $T_s$  and  $T_a$  were unrelated under all sampled circumstances (Regression, SPnr:  $F_{T_s 1,22} = 0.641$ ;  $F_{T_a 1,22} = 0.902$ ; SPr:  $F_{T_s 1,39} = 1.157$ ;  $F_{T_a 1,39} = 0.237$ ;  $P \geq 0.289$ ; Figure 3F & 3G), and lizard  $T_b$  was never a function of time of the day (Regression, NRs:  $F_{1,22} = 0.242$ ; Rs:  $F_{1,39} = 0.900$ ;  $P \geq 0.349$ ; Tables 1 & S4; Figure 2F & 2G).

### 3. Preferred and operative temperatures, and efficiency of thermoregulation

#### 3.1. Variation within *T. torquatus* and among all species and populations

##### 3.1.1. Variation of $T_p$ between sexes, within and among all species and populations

Similar values of  $T_p$ , and lower- $T_{set}$  were observed among the females, as well as among the males, of all populations while the upper- $T_{set}$  differed considerably (Tables 1, S6, & S7). Among females differences in the upper- $T_{set}$  were registered between TOo and MGe (Tables 1, S6, & S7). Among males, differences in the upper- $T_{set}$  were between the high values of TOo and SP, and the lower values of the rest of the populations, with the exception of the similarities between SP and MGt (Tables 1, S6, & S7).

Both the  $T_p$  and the  $T_{set}$ -range were similar in MGt and MGe (Tables 1 & S6). In both species,  $T_b$  values exceeded  $T_p$  values but the difference was only significant in of MGe (Tables 1 & S6). When analyzed separately for interspecific comparisons, the  $T_p$  and the  $T_{set}$ -range of juveniles, adults, females and males result similar as well (Tables 1 & S6). When comparing within the species, the only differences appeared between juveniles and adults in MGt, and between females and males of MGe (Tables 1 & S6). Values of  $T_p$  and lower- and upper- $T_{set}$  in juveniles of MGt were lower than adults' values (Table 1). In MGe, both sexes presented similar higher  $T_p$  and lower-  $T_{set}$ , but and a higher upper- $T_{set}$  in females (Tables 1 & S6).

All values of  $T_p$ , lower- and upper- $T_{set}$  were higher in TOo than in TOt although differences in the lower- $T_{set}$  were not significant (Tables 1 & S6). In both species,  $T_b$  exceeded  $T_p$  by more than 2.3 and 3.2°C in TOt and TOo, respectively (Tables 1 & S6). Values of  $T_p$  and the  $T_{set}$ -range were higher in females and males of TOo although females of both species presented similar  $T_p$  and lower- $T_{set}$  (Tables 1 & S6).

Higher values of  $T_p$  and lower- and upper- $T_{set}$  were collected in SPnr than in SPr (Tables 1 & S6). Overall the  $T_b$  of the species was higher than the  $T_p$  throughout the year, although

significant differences were only found in SPr (Tables 1 & S6). Juveniles'  $T_p$  and  $T_{set}$ -range were higher and narrower, respectively, during in SPr than in SPnr while adults' records showed only seasonal differences in the higher upper- $T_{set}$  of the SPnr (Tables 1 & S6). Mean  $T_p$  in juveniles were lower than adults' in SPnr and higher than adults' in the SPr (Tables 1 & S6). Females chose higher  $T_p$  and upper- $T_{set}$  during the SPnr than in the SPr (Tables 1 & S6). On the contrary, males presented higher  $T_p$  and  $T_{set}$ -range in SPr than in SPnr (Tables 1 & S6). No difference in  $T_p$  was found between the females and males in SPr (Tables 1 & S6).

### 3.1.2. Variation of $T_e$ and $T_b$ with respect to the $T_{set}$ range within sites

During the collecting trip in Arinos, MG, 36.3-37.3, 10.7-12.4 and 51.4-52 % of the  $T_e$  recordings fell below, within and above the  $T_{set}$ -range, respectively (Figures 2B & 2D). In MGe 7.7 % and 92.3 % of the  $T_b$  recordings fell below and above the  $T_{set}$ -range, respectively (Figure 2D). As both species were in complete sympatry,  $T_e$  and  $d_e$  were the same (Table S4). Nevertheless,  $d_b$  was higher in MGe than in MGt (Tables 1, S9 & S10). The species also differed with respect to  $E$  being positive and close to zero in MGt and negative MGe (Tables 1, S9 & S10). The  $d_b$  and  $E$  indexes were similar between the adults (Tables 1 & S9). Both indexes were also similar between females of MGt and of MGe (Tables 1 & S9). Males of both species also shared similar indexes (Tables 1 & S9).

In TOt's environment, 55.6 and 23.4 % of  $T_e$  were below and above the  $T_{set}$ -range of TOo, respectively. In the urban area, inhabited by TOo, 23.5, 13.9 and 62.6 % of the  $T_e$  readings were below, within and above the  $T_{set}$ -range of TOt, respectively. Here, 54.2 % were above the  $T_{set}$ -range of TOo and the rest 29.2 and 16.6 % below and within the  $T_{set}$ -range of the species, respectively (Figure 2E). In this environment TOo presented 76.9 % of the  $T_b$  exceeding the species upper- $T_{set}$  while the rest was below the lower- $T_{set}$  (Figure 2E). Mean  $T_e$  in the gallery forest was 4.9°C lower than in the urban area (Table S4). In addition, its coefficient of variation was lower in the forest (Table S4). Despite the differences in the  $T_e$ , the  $d_e$  indexes of TOt and TOo in the two environments were similar (Tables S4 & S6). Nevertheless,  $d_b$  was higher in TOo than in TOt (Tables 1, S6 & S7). The species also differed with respect to  $E$  being positive and close to zero in TOo and negative in TOt (Tables S4 & S6). The  $d_b$  and  $E$  indices differed between the adults of TOt and TOo (Tables 1 & S6). Both  $E$  were close to zero but TOt's was negative and TOo's was positive (Table 1). The  $d_b$  and  $E$  indices differed between females of TOt and of TOo (Tables 1, S9 & S10). On the contrary,



males of both species shared similar indexes (Tables 1 & S9). Females and males presented similar  $d_b$  and  $E$  indices within both species (Tables 1 & S9).

In SPnr, 53.7 % and 37.5% of the  $T_e$  recordings were below and above the  $T_{set}$ -range, respectively, and only 8.8 % fell within the range (Figure 2F). 38.5 and 84.6 % of the lizards'  $T_b$  were below and above the  $T_{set}$ -range, and 61.5 % were included in the range (Figure 2F). The values of  $T_e$  in SPr were overall higher than in SPnr but the difference was not significant (Tables S4 & S9). Only 35.7 and 5.6 % of the  $T_e$  fell below and within the  $T_{set}$ -range, respectively, whereas 58.6% exceeded the upper- $T_{set}$  (Figure 2G). With respect to the  $T_b$ , 14.6, 9.8 and 75.6 % of the recordings fell below, within and above the  $T_{set}$ -range, respectively (Figure 2G). The  $d_b$  and  $d_e$  indices were similar in both seasons (Tables 1, S4 & S6). The  $E$  was higher in SPnr than in SPr but the difference was not significant (Table 1 & S9). Juveniles'  $d_b$  index and  $E$  were similar in the SPnr and SPr (Tables 1 & S9). In adults, the  $d_b$  index was similar throughout the year but the  $E$  decreased in the SPr (Tables 1 & S9). In SPnr both indexes,  $d_b$  and  $E$ , were similar between juveniles and adults (Tables 1 & S9). In SPr, juveniles and adults also exhibited similar  $db$  and  $E$  (Tables 1 & 16). The index  $db$  in females was similar in SPnr and SPr but the  $E$  was lower in SPr (Tables 3 & 15). Based on the descriptive data for males,  $E$  also decreased in SPr (Table 2). Females and males presented similar  $db$  and  $E$  indexes in SPr (Tables 2 & 16).

Adults'  $d_b$  and  $E$  differed among the populations (Tables 1, S9 & S10). The  $d_b$  and  $E$  indexes in females differed among the populations (Tables 1, S9 & S10). The highest  $d_b$  in females was in TOo (3.1; Table 1). The index  $d_b$  in males were similar among the populations but  $E$  values differed (Tables 1, S9 & S10). Males of MGt and MGe presented negative  $E$  values and in TOo and TOt the values were positive but closer to zero. In SP and CB, males'  $E$  exceeded 0.6.

Table S1. Mean  $\pm$  standard deviation (SD;  $n$ ), median (range) and coefficient of variation (CV) of lizards' snout-vent length (SVL; mm) for juveniles, adults, females, males, and overall individuals of *T. torquatus* from Cuiaba, MT (CB), Arinos, MG (MGt), and Formoso do Araguaia, TO (TOt), *T. etheridgei* from Arinos, MG (MGe), *T. oreadicus* from Formoso do Araguaia, TO (TOo), and *T. catalanensis* from Piracicaba, SP, collected in the non-reproductive (SPnr) and reproductive (SPr) seasons. Values for all overall specimens of *T. torquatus* and for all studied specimens are also presented to compare the variation of the thermal traits within and among groups.

Species/populations	Juveniles		Adults		♀		♂		Overall	
	SVL (mm)	CV	SVL (mm)	CV	SVL (mm)	CV	SVL (mm)	CV	SVL (mm)	CV
CB	36 $\pm$ 5.7 (2)	15.8	92.2 $\pm$ 10.8 (20)	11.7	86.7 $\pm$ 9.6 (12)	11.1	97.7 $\pm$ 10.4 (9)	10.7	87.1 $\pm$ 19.5 (22)	22.4
	36 (32-40)		91 (75-119)		85 (75-106)		98 (86-119)		90 (32-119)	
MGt	41.8 $\pm$ 6.6 (8)	15.8	102.3 $\pm$ 11.1 (14)	10.8	93.1 $\pm$ 6.9 (6)	7.4	109.2 $\pm$ 8.2 (8)	7.5	80.3 $\pm$ 31.2 (22)	38.9
	43 (32-53.8)		(85.1-119.4)		92.4 (85.1-101.3)		111.7 (94.6-119.4)		92.4 (32-119)	
TOt	-	-	90.5 $\pm$ 13 (32)	14.4	83.9 $\pm$ 8.1 (18)	9.7	99.1 $\pm$ 13.3 (14)	13.4	90.5 $\pm$ 13 (32)	16.1
			90.3 (69.7-127.8)		83 (73.8-103.2)		96 (69.7-127.8)		90.3 (69.7-127.8)	
Overall <i>T. torquatus</i>	40.7 $\pm$ 6.6 (10)	16.2	93.5 $\pm$ 12.7 (66)	13.6	86.7 $\pm$ 8.8 (35)	10.1	101.3 $\pm$ 12 (31)	11.8	86.6 $\pm$ 21.6 (76)	24.9
	41.3 (32-53.8)		92.6 (69.7-127.8)		85 (73.8-106)		100 (69.7-127.8)		90.9 (32-127.8)	
MGe	48.7 (1)	-	97.8 $\pm$ 9.2 (13)	9.4	93.2 $\pm$ 7.1 (7)	7.6	103.1 $\pm$ 8.9 (6)	8.7	94.3 $\pm$ 15.8 (14)	16.8
			97.1 (80.4-113.9)		95.6 (80.4-101)		102.7 (88.8-113.9)		96.7 (48.7-113.9)	
TOo	60.9 (1)	-	70.9 $\pm$ 8.9 (13)	12.6	71.8 $\pm$ 4.7 (12)	6.5	85.3 $\pm$ 6.5 (13)	7.6	78.2 $\pm$ 9.4 (26)	12.0
			78.1 (62.3-100.4)		73.1 (62.3-78.7)		83.3 (77.1-100.4)		77.6 (60.9-100.4)	
SPnr	44 $\pm$ 6.2 (12)	14.1	84.2 $\pm$ 8.9 (9)	10.6	85.9 $\pm$ 7.8 (8)	9.1	70.5 (1)	-	61.2 $\pm$ 21.7 (21)	35.5
	44 (30.7-54.2)		80.7 (70.5-96.1)		85.1 (77.5-96.1)				49.9 (30.7-96.1)	
SPr	58.1 $\pm$ 6.6 (1)	11.4	85 $\pm$ 13.2 (13)	15.5	87.9 $\pm$ 7.8 (14)	8.9	82.5 $\pm$ 20 (16)	16.5	76.4 $\pm$ 17.1 (44)	22.4
	57.6 (44.3-70)		81.4 (67.2-115.6)		90.8 (71.8-95.8)		74.9 (67.2-115.6)		73.1 (44.3-115.6)	

	Juveniles	Adults	♀	♂	Overall					
SP nr & r	51.6 ± 9.5 (1)	18.4	84.8 ± 12.3 (13)	14.5	87.2 ± 7.7 (22)	8.8	81.8 ± 16.3 (17)	19.9	71.5 ± 19.9 (65)	27.8
	52.6 (30.7-70)		81.3 (67.2-115.6)		89.8 (71.8-96.1)		73.4 (67.2-115.6)		71.8 (30.7-115.6)	
Overall spp./pops	48.9 ± 10 (38)	20.4	89 ± 13.2 (143)	14.8	85.1 ± 9.8 (76)	11.5	93.4 ± 15.1 (67)	16.2	80.6 ± 20.6 (181)	25.6
	47.7 (30.7-70)		88.8 (62.3-127.8)		85 (62.3-106)		93.9 (67.2-127.8)		83 (30.7-127.8)	

Table S2. Comparisons within (Paired and Student  $t$ -test,  $t$  statistic; Wilcoxon Signed Rank Test,  $Z$  statistic; Mann-Whitney Rank Test,  $U$  statistic) and among (One Way ANOVA,  $F$  statistic; Kruskal-Wallis On Way ANOVA on Ranks,  $H$  statistic) population of snout-vent length (SVL) of adults, females and males, microenvironmental temperatures (air and substrate temperature -  $T_a$  and  $T_s$ ), field body temperature ( $T_b$ ) vs.  $T_a$  and  $T_s$ ,  $T_b$  vs. preferred temperature ( $T_b$ ) for *T. torquatus* from Cuiaba, MT (CB), Arinos, MG (MGt), and Formoso do Araguaia, TO (TOt), and *T. etheridgei* from Arinos, MG (MGe), and *T. oreadicus* in Formoso do Araguaia, TO (TOo), and *T. catalanensis* collected in Piracicaba, SP, during the reproductive (SPr) and non-reproductive (SPnr) seasons.

Comparisons	Statistic	$P$ -values	
<b>Snout-vent length - SVL</b>			
<i>Among T. torquatus (CB, MGt, TOt)</i>			
Overall specimens	$H_2 = 0.00389$	0.998	
Adults <i>T. torquatus</i>	$F_{2,} = 2.890$	0.011	
♀ <i>T. torquatus</i>	$F_{2,34} = 2.890$	0.07	
♂ <i>T. torquatus</i>	$F_{2,30} = 2.619$	0.091	
<i>Among all populations</i>			
Overall Adults' SVL	$F_{5,142} = 10.843$	$\leq 0.001$	
<i>Within populations comparisons</i>			
♀ CB	♂ CB	$t_{18} = -2.256$	0.037
Adults MGt	Adults MGe	$t_{25} = 1.143$	0.264
♀ MGt	♀ MGe	$t_{11} = -0.0253$	0.980
♂ MGt	♂ MGe	$t_{12} = 1.313$	0.214
♀ MGt	♂ MGt	$t_{12} = -3.874$	0.002
♀ MGe	♂ MGe	$t_{11} = -2.238$	0.047
Adults TOt	Adults TOo	$t_{55} = -3.846$	$\leq 0.001$
♀ TOt	♀ TOo	$t_{28} = 4.629$	$\leq 0.001$
♂ TOt	♂ TOo	$U = 160, n = 13, n = 14$	$\leq 0.001$
♀ TOt	♂ TOt	$t_{30} = -4.009$	$\leq 0.001$
♀ TOo	♂ TOo	$t_{23} = -5.899$	$\leq 0.001$
Adults SPnr	Adults SPr	$U = 131, n = 9, n = 30$	0.907
♀ SP	♂ SP	$t_{37} = -1.368$	0.180
<b>Microenvironmental temperatures - <math>T_s</math>, <math>T_w</math>, <math>T_e</math> and annual <math>T_e</math></b>			
<i>Among T. torquatus (CB, MGt, TOt)</i>			
$T_s$		$H_2 = 20.167$	$\leq 0.001$
$T_a$		$H_2 = 34.593$	$\leq 0.001$

Comparisons		Statistic	P-values
<i>Among sites comparisons</i>			
$T_s$		$H_6 = 39.08$	$\leq 0.001$
$T_a$		$H_6 = 48.809$	$\leq 0.001$
$T_e$			
Annual $T_e$		$H_3 = 3531.771$	$\leq 0.001$
<i>Within sites comparisons</i>			
$T_s$ MGt	$T_s$ MGe	$t_{34} = -2.514$	$\leq 0.017$
$T_a$ MGt	$T_a$ MGe	$t_{34} = -2.783$	$\leq 0.017$
$T_s$ TOt	$T_s$ TOo	$U = 346, n = 26 \ n = 32$	0.277
$T_a$ TOt	$T_a$ TOo	$U = 428, n = 26 \ n = 32$	0.277
$T_s$ SPnr	$T_s$ SPr	$U = 305.5, n = 24 \ n = 41$	$\leq 0.011$
$T_a$ SPnr	$T_a$ SPr	$U = 260, n = 24 \ n = 41$	$\leq 0.011$
<b><math>T_b</math> vs. <math>T_s</math> &amp; <math>T_a</math></b>			
<i>Within sites comparisons</i>			
$T_b$ CB	$T_s$ CB	$t_{19} = 9.781$	$\leq 0.001$
$T_b$ CB	$T_a$ CB	$t_{19} = 10.886$	$\leq 0.001$
$T_b$ MGt	$T_s$ MGt	$t_{21} = 5.715$	$\leq 0.003$
$T_b$ MGt	$T_a$ MGt	$t_{23} = 3.349$	$\leq 0.003$
$T_b$ TOt	$T_s$ TOt	$t_{31} = 5.655$	0.009
$T_b$ TOt	$T_a$ TOt	$t_{31} = 2.798$	0.009
$T_b$ MGe	$T_s$ MGe	$t_{13} = 0.592$	0.514
$T_b$ MGe	$T_a$ MGe	$t_{13} = 0.675$	0.514
$T_b$ TOo	$T_s$ TOo	$t_{25} = 4.507$	0.009
$T_b$ TOo	$T_a$ TOo	$t_{25} = 3.972$	0.009
$T_b$ SPnr	$T_s$ SPnr	$t_{23} = 1.785$	0.006
$T_b$ SPnr	$T_a$ SPnr	$t_{23} = 3.033$	0.006
$T_b$ SPr	$T_s$ SPr	$t_{40} = 8.237$	$\leq 0.001$
$T_b$ SPr	$T_a$ SPr	$t_{40} = 8.532$	$\leq 0.001$
<b>Field vs. Preferred body temperature - <math>T_b</math> vs. <math>T_p</math></b>			
<i>Within populations comparisons</i>			
$T_b$ CB	$T_p$ CB	$t_{17} = 2.108$	0.050
$T_b$ MGt	$T_p$ MGt	$t_{21} = 2.068$	0.051
$T_b$ TOt	$T_p$ TOt	$t_{31} = 7.8$	0.001
$T_b$ MGe	$T_p$ MGe	$t_{13} = 2.629$	0.021
$T_b$ TOo	$T_p$ TOo	$t_{13} = 2.629$	0.021
$T_b$ SPnr	$T_p$ SPnr	$t_{22} = 1.440$	0.164
$T_b$ SPr	$T_p$ SPr	$Z = -2.692$	0.007

Table S3. Pairwise multiple comparisons (Holm-Sidak and Dunn's methods;  $P$ -values or \* indicating significant differences,  $P \leq 0.05$ ) of snout-vent length (SVL) among adults of *T. torquatus* from Cuiaba, MT (CB), Arinos, MG (MGt), and Formoso do Araguaia, TO (TOt), and among overall adults, females and males of CB, MGt, TOt, *T. etheridgei* from Arinos, MG (MGe), and *T. oreadicus* in Formoso do Araguaia, TO (TOo), and *T. catalanensis* collected in Piracicaba, SP (SP).

	SP	MGt	MGe	TOt	TOo	CB
(A) Adults <i>T. torquatus</i>						
MGt				3.054; 0.630		2.412*
TOt						0.484*
(B) Overall adults' and females' SVL						
SP		5.171*	3.808*	2.487; 0.0141	1.670; 0.0972	2.676; 0.008
MGt	1.686; 0.0962		1.009; 0.315	3.164*	6.064*	2.499; 0.0136
MGe	1.819; 0.0731	1.542; 0.0944		1.901; 0.0594	4.783*	1.354; 0.178
TOt	1.350; 0.181	2.557; 0.0127	2.735; 0.0079		3.785*	0.502; 0.617
TOo	5.584*	5561*	5874*	4226*		3.845*
CB	0.180; 0.858	1.682; 0.0969	1.796; 0.0768	0.978; 0.332	4751*	
(C) Males' SVL						
SP		4.328*	2.993*	3.001*	0.470	2.473
MGt			0.804	1.743	3.744*	1.721
MGe				0.694	2.529	0.763
TOt					2.362	0.149
TOo						1.951

Table S4. Mean  $\pm$  standard error (SD), median and range and coefficient of variation of the mean (CV) of substrate ( $T_s$ ), air ( $T_a$ ), and operative ( $T_e$ ) temperatures, and the  $d_e$  index of *T. torquatus* from Cuiaba, MT (CB), Arinos, MG (MGt), and Formoso do Araguaia, TO (TOt), *T. etheridgei* from Arinos, MG (MGe), and *T. oreadicus* in Formoso do Araguaia, TO (TOo), and *T. catalanensis* collected in Piracicaba, SP, during the reproductive (SPr) and non-reproductive (SPnr) seasons. The  $T_e$  corresponds to the data collected during the field trips and the annual  $T_e$  was calculated based on the daily mean  $T_e$  registered during 12 months at each site. Data for overall populations of *T. torquatus* and other species are also exhibited.

Populations / Species (n) Site	$T_s$ (°C)	CV	$T_a$ (°C)	CV	$T_e$ (°C)	CV	$d_e$	CV	Annual $T_e$ (°C)	CV
CB / <i>T. torquatus</i> Cuiaba, MT	32.1 $\pm$ 1.9 (20) 32.4 (29.4-36.2)	5.8	31.2 $\pm$ 1.9 (20) 31 (35.3-35.3)	6.1	31.3 $\pm$ 5.8 (2836) 30.3 (22.7-57.2)	18.5	2.7 $\pm$ 1.84 (6) 2.549 (0.726-5.06)	68.2	27.4 $\pm$ 1.6 (1417) 27.3 (22.3-31.3)	13.8
MGt / <i>T. torquatus</i> Arinos, MG	33.2 $\pm$ 2.8 (22) 33.8 (27.9-36.9)	8.5	33.3 $\pm$ 2.6 (22) 33.6 (27.9-39)	7.7	37 $\pm$ 9 (3425) 35 (21.2-65.4)	24.5	1.87 $\pm$ 2.118 (20) 0.768 (0-6.452)	113.3	26.2 $\pm$ 2.4 (1460) 26.2 (20.1-34.6)	9.0
TOt / <i>T. torquatus</i> (32) Formoso do Araguaia, TO	35 $\pm$ 1.7 (32) 35.2 (30.7-39.7)	4.9	35.5 $\pm$ 1.6 (32) 35.9 (31.4-37.5)	4.4	34.7 $\pm$ 5.3 (1995) 33.5 (25.7-55.1)	15.2	1.49 $\pm$ 1.93 (7) 0.475 (0-4.631)	129.8	30.8 $\pm$ 4.2 (2008) 30.3 (24.4-38.3)	5.7
Overall sites/populations of <i>T. torquatus</i>	33.7 $\pm$ 2.4 (73) 33.9 (27.9-39.7)	7.1	33.5 $\pm$ 2.7 (74) 33.8 (26.1-37.5)	8.1	34.5 $\pm$ 7.6 (8256) 33.1 (21.2-65.4)	22	1.94 $\pm$ 2.013 (33) 0.956 (0-6.52)	103.8	26.4 $\pm$ 2.9 (3914) 26.5 (10.9-35.8)	11.0
MGe / <i>T. etheridgei</i> Arinos, MG	36 $\pm$ 3.7 (14) 36.7 (26.3-42.5)	10.4	35.9 $\pm$ 3.0 (14) 37 (27.9-39)	8.4	37 $\pm$ 9 (3425) 35 (21.2-65.4)	24.5	1.84 $\pm$ 2.1 (20) 0.744 (0-6.427)	114.5	26.2 $\pm$ 2.4 (1460) 26.2 (20.1-34.6)	9.0
TOo / <i>T. oreadicus</i> Formoso do Araguaia, TO	35.9 $\pm$ 3.8 (26) 36.3 (28.8-42.3)	10.6	35 $\pm$ 4.6 (26) 35.3 (29-43)	13	38.9 $\pm$ 8.1 (2554) 36.3 (25.8-69.6)	20.9	4.41 $\pm$ 3.748 (15) 3.79 (0-9.563)	85		
SPnr / <i>T. catalanensis</i> Piracicaba, SP	34.9 $\pm$ 3.9 (24) 35.1 (27.7-40.2)	11.3	34.3 $\pm$ 2.9 (24) 34.8 (26.7-38.2)	8.5	34.5 $\pm$ 7.5 (1835) 32.3 (23.6-53.5)	21.7	5.081 $\pm$ 3.61 (29) 4.585 (0-14.47)	71	21.5 $\pm$ 3.6 (1328) 21.8 (11-31.1)	16.7
SPr / <i>T. catalanensis</i> Piracicaba, SP	32.5 $\pm$ 2.6 (41) 32.6 (24.7-37)	8.1	32.4 $\pm$ 2.5 (41) 32.7 (24.7-36.6)	7.7	37.8 $\pm$ 8 (14560) 37.9 (18.3-62.2)	21.2	4.03 $\pm$ 2.829 (44) 3.402 (0-13)	70.2	21.5 $\pm$ 3.6 (1328) 21.8 (11-31.1)	16.7
Overall sites/populations	34.2 $\pm$ 1.6 (7) 34.9 (32.1-36)	4.7	33.9 $\pm$ 1.7 (7) 34.3 (31.2-35.9)	5.1	35.7 $\pm$ 2.7 (7) 35.8 (18.3-69.6)	7.7	2.9 $\pm$ 1.37 (7) 2.7 (1.5-5.1)	47.1	26.4 $\pm$ 3.9 (4) 26.8 (11-44)	14.8

Table S5. Results of the pairwise comparison (Dunn's method;  $Q$  values and \* indicating significant differences,  $P \leq 0.05$ ) of: air ( $T_a$ : below the diagonal) and substrate ( $T_s$ : above the diagonal) temperatures among *T. torquatus*' sites (A) and among all sites (B); and operative ( $T_e$ ) temperature (C) collected during the collecting campaigns (above the diagonal) and during one year between 2012 and 2013 (below the diagonal) among SP, MG, CB and TOt. Collecting sites: Cuiaba, MT (CB), Arinos, MG (MGt), and Formoso do Araguaia, TO (TOt), *T. etheridgei* from Arinos, MG (MGe), and *T. oreadicus* in Formoso do Araguaia, TO (TOo), and *T. catalanensis* collected in Piracicaba, SP, during the reproductive (SPr) and non-reproductive (SPnr) seasons.

	SPnr	SPr	MGt	MGe	TOt	TOo	CB
(A) Among <i>T. torquatus</i> sites							
MGt					2.452*		1.884
TOt			3.09*				4.424*
CB			2.597*		5.817*		
(B) Among all sites							
SPnr		2.968	1.685	1.199	0.324	0.736	3.303*
SPr	2.616		1.004	3.767*	3.604*	3.873*	0.870
MGt	1.308	1.083		2.634*	2.112	2.436	1.627
MGe	1.671	3.988*	2.774		0.985	0.588	4.027*
TOt	1.455	4.517*	2.813	0.528		0.457	3.816*
TOo	0.00852	2.673	1.325	1.703	1.497		4.063*
CB	3.756*	1.704	2.431	4.876*	5.368*	3.815*	
(C) Among all sites							
	SP	SPnr	SPnr	MG	TOt	TOo	CB
SPnr				9.739*	3.451*	18.9*	13.667*
SPr			18.267*	8.998*	14.282*	5.845*	41.965*
MG	23.653*				6.041*	111.346*	27.226*
TOt	34.301*			11.078*		15.621*	17.833*
TOo							36.212*
CB	57.874*			32.298*	19.497*		



Table S6. Comparisons (One Way ANOVA,  $F$  statistic; Kruskal-Wallis One Way ANOVA on Ranks;  $H$  statistic; Student  $t$ -test,  $t$  statistic, Mann-Whitney Rank Test,  $U$  statistic) of  $T_b$ ,  $T_p$ , and lower- and upper- $T_{set}$  of: (1) Overall specimens, juveniles (Juv.), adults (Ad.), females (♀) and males (♂) among the populations of *T. torquatus* from Cuiaba, MT (CB), Arinos, MG (MGt), and Formoso do Araguaia, TO (TOt); (2) Overall specimens, adults, females and males among the populations of *T. torquatus* (CB; MGt; TOt), *T. etheridgei* from Arinos, MG (MGe), *T. oreadicus* in Formoso do Araguaia, TO (TOo), and *T. catalanensis* collected in Piracicaba, SP (SP); (3) Juveniles vs. adults, and females vs. males at each population (including reproductive and non-reproductive seasons *T. catalanensis*, SP<sub>r</sub> and SP<sub>nr</sub>, respectively); and (4) Overall specimens, juveniles, adults, females, and males between the populations at each site (MGt vs. MGe in Arinos, MG; TOt vs. TOo in Formoso do Araguaia, TO, and SP<sub>r</sub> vs. SP<sub>nr</sub> in Piracicaba, SP). \* Indicates that the comparisons were performed using transformed data (residuals).  $P$  values are expressed in bold when the difference is significant.

	$T_b$		$T_p$		Lower- $T_{set}$		Upper- $T_{set}$	
	Statistic	$P$	Statistic	$P$	Statistic	$P$	Statistic	$P$
<i>Among populations of T. torquatus</i>								
Overall specimens	$H_2 = 3.688$	0.158	$H_2 = 9.68$	<b>0.008</b>	$H_2 = 6.465$	<b>0.039</b>	$H_2 = 8.848$	<b>0.012</b>
Ad.	$F_{2,63} = 1.411$	0.252	$F_{2,63} = 3.585$	<b>0.034</b>	$H_2 = 3.524$	0.172	$H_2 = 5.706$	0.058
♀	$F_{2,34} = 3.428$	0.055	$F_{2,34} = 0.755$	0.478	$F_{2,34} = 0.375$	0.691	$F_{2,34} = 0.393$	0.678
♂	$F_{2,30} = 2.604$	0.092	$F_{2,30} = 3.489$	<b>0.044</b>	$F_{2,30} = 2.259$	0.123	$H_2 = 8.652$	<b>0.013</b>
<i>Among populations comparisons</i>								
Overall specimens	$H_5 = 14.59$ $n = 172$	<b>0.01*</b>	$H_5 = 32.26$ $n = 171$	$\leq$ <b>0.001*</b>	$H_5 = 12.116$ $n = 171$	<b>0.033</b>	$H_5 = 30.51$ $n = 171$	$\leq$ <b>0.001*</b>
Ad.	$F_{5,138} = 10.08$	$\leq$ <b>0.001*</b>	$F_{5,140} = 11.29$	$\leq$ <b>0.001*</b>	$F_{5,139} = 11.08$	$\leq$ <b>0.001*</b>	$F_{5,139} = 10.6$	$\leq$ <b>0.001*</b>
♀	$F_{5,72} = 10.94$	$\leq$ <b>0.001*</b>	$H_5 = 4.714$ $n = 77$	0.452	$H_5 = 4.222$ $n = 77$	0.52	$H_5 = 11.76$ $n = 77$	<b>0.038</b>
♂	$F_{5,63} = 7.67$	$\leq$ <b>0.001*</b>	$H_5 = 10.467$ , $n = 63$	0.063	$H_5 = 8.211$ $n = 63$	0.15	$F_{5,62} = 9.3$	$\leq$ <b>0.001*</b>

		$T_b$	$T_p$	Lower- $T_{set}$	Upper- $T_{set}$
<i>Within populations comparisons</i>					
CB	Juv. vs. Ad.	-	- -	- -	- -
	♀ vs. ♂	$t_{16} = 0.06$	0.96 $t_{18} = 0.08$	0.94 $U = 56$ $n = 9$ $n = 11$	0.649 $t_{18} = 0.66$ 0.52
MGt	Juv. vs. Ad.	$U = 67$ $n = 8$ $n = 14$	0.473 $t_{20} = -16.58$	$\leq 0.001^*$ $t_{20} = -14.78$	$\leq 0.001^*$ $t_{20} = -13.66$ $\leq 0.001^*$
	♀ vs. ♂	$t_{12} = -2.57$	<b>0.02*</b> $t_{12} = 1.27$	0.23 $t_{12} = -1.414$	0.18 $t_{12} = 0.85$ 0.41
TOt	Juv. vs. Ad.	-	- -	- -	- -
	♀ vs. ♂	$U = 170$ $n = 14$ $n = 18$	0.094 $U = 167$ $n = 14$ $n = 18$	0.124 $U = 176$ $n = 14$ $n = 18$	0.06 $U = 161$ $n = 14$ $n = 18$ 0.19
MGe	Juv. vs. Ad.	-	- -	- -	- -
	♀ vs. ♂	$U = 17$ $n = 6$ $n = 7$	0.628 $t_{11} = -0.32$	0.75 $U = 22$ $n = 6$ $n = 7$	0.945 $t_{11} = -2.72$ <b>0.02*</b>
TOo	Juv. vs. Ad.	-	- -	- -	- -
	♀ vs. ♂	$t_{23} = -5.87$	$\leq 0.001^*$ $U = 64$ $n = 12$ $n = 13$	0.463 $U = 74$ $n = 12$ $n = 13$	0.849 $U = 36$ $n = 12$ $n = 13$ <b>0.024</b>
SPnr	Juv. vs. Ad.	$t_{21} = 0.75$	0.46 $t_{19} = -9.62$	$\leq 0.001^*$ $t_{19} = -9.61$	$\leq 0.001^*$ $t_{21} = 0.13$ 0.90
	♀ vs. ♂	-	- -	- -	- -
SPr	Juv. vs. Ad.	$t_{39} = 0.83$	0.41 $t_{31} = -5.15$	$\leq 0.001^*$ $t_{31} = 0.03$	0.978* $t_{31} = -5.17$ $\leq 0.001^*$
	♀ vs. ♂	$t_{24} = -1.13$	0.27* $U = 62$ $n = 12$ $n = 13$	0.399 $t_{23} = 1.15$	0.262 $U = 67$ $n = 12$ $n = 13$ 0.568
<i>Within sites comparisons</i>					
MGt	Overall	$U = 94$ $n = 14$ $n = 22$	0.053 $t_{34} = 0.285$	0.78 $U = 145$ $n = 14$ $n = 22$	0.783 $t_{34} = -0.08$ 0.94
vs.	Juv.	-	- -	- -	- -
MGe	Ad.	$U = 92$ $n = 14$ $n = 22$	0.085 $t_{25} = 1.319$	0.20* $t_{25} = 1.27$	0.22* $U = 159$ $n = 13$ $n = 14$ 0.28*
	♀	$U = 19.5$ $n = 6$ $n = 7$	0.836 $t_{11} = 0.83$	0.43 $t_{11} = 0.86$	0.41 $t_{11} = 0.739$ 0.48
	♂				
TOt	Overall	$t_{12} = -1.13$	0.30* $t_{12} = 0.43$	0.70 $t_{12} = -0.08$	0.94 $U = 32$ $n = 6$ $n = 8$ 0.11*
vs.	Juv.				
TOo	Ad.	$U = 255$ $n = 26$ $n = 32$	<b>0.012</b> $U = 275$ $n = 26$ $n = 32$	<b>0.028</b> $U = 316$ $n = 26$ $n = 32$	0.122 $U = 191$ $n = 26$ $n = 32$ $\leq 0.001$

		$T_b$	$T_p$	Lower- $T_{set}$	Upper- $T_{set}$	
	♀	-	- -	- -	- -	-
	♂	$U = 255$ $n = 25$ $n = 32$	<b>0.02</b> $U = 273$ $n = 25$ $n = 32$	<b>0.042</b> $U = 316$ $n = 25$ $n = 32$	0.182 $U = 190$ $n = 25$ $n = 32$	$\leq$ <b>0.001</b>
SPnr	Overall	$t_{58} = -0.06$	0.95 $U = 433$ $n = 21$ $n = 33$	<b>0.005*</b> $U = 467$ $n = 21$ $n = 33$	<b>0.002*</b> $U = 501$ $n = 21$ $n = 33$	<b>0.010*</b>
vs.	Juv.	$t_{24} = 0.92$	0.37 $U = 11$ $n = 9$ $n = 12$	<b>0.002</b> $t_{19} = -3.863$	<b>0.001*</b> $t_{19} = -4.22$	$\leq$ <b>0.001*</b>
SPr	Ad.	$t_{33} = -1.06$	0.30 $U = 214$ $n = 9$ $n = 25$	$\leq$ <b>0.001*</b> $t_{33} = 0.26$	0.80 $t_{32} = 2.823$	<b>0.08</b>
	♀	$t_{19} = 1.21$	0.24 $U = 98$ $n = 8$ $n = 14$	<b>0.001</b> $t_{19} = 0.26$	0.13 $t_{19} = -2.995$	<b>0.007</b>
	♂	-	- -	- -	- -	-

Table S7. Results of the pairwise tests (Holm-Sidak and Dunn's methods expressed with statistics  $t$  and  $Q$ , respectively; \* indicates significant differences,  $P \leq 0.05$ ) of the inter-sites comparisons among: (A) overall specimens' preferred body temperature ( $T_p$ ; above the diagonal) and adults'  $T_p$  (below the diagonal) of the three populations the *T. torquatus*; (B) males'  $T_p$  (above the diagonal) and overall specimens' lower interquartile of  $T_p$ -range (lower- $T_{set}$ ; below the diagonal) of the three populations the *T. torquatus*; (C) overall specimens' upper interquartile of  $T_p$ -range (upper- $T_{set}$ ; above the diagonal) and males upper- $T_{set}$  (below the diagonal); (D) overall specimens' body temperature ( $T_b$ ; above the diagonal) and adults'  $T_b$  (below the diagonal); (E) females' (above the diagonal) and males'  $T_b$  (below the diagonal); (F) overall specimens' preferred body temperature ( $T_p$ ; above the diagonal) and adults'  $T_p$  (below the diagonal); (G) overall specimens' lower interquartile of  $T_p$ -range (lower- $T_{set}$ ; above the diagonal) and adults' lower- $T_{set}$  (below the diagonal); (H) overall specimens' upper interquartile of  $T_p$ -range (upper- $T_{set}$ ; above the diagonal) and adults' upper- $T_{set}$  (below the diagonal); (I) females' upper- $T_{set}$  (above the diagonal) and among males' upper- $T_{set}$  (below the diagonal). Populations and sites: *T. torquatus* of Cuiaba, MT (CB), Arinos, MG (MGt), and Formoso do Araguaia, TO (TOt), *T. etheridgei* from Arinos, MG (MGe), and *T. oreadicus* in Formoso do Araguaia, TO (TOo), and *T. catalanensis* collected in Piracicaba, SP, during the reproductive (SPr) and non-reproductive (SPnr) seasons.

	SP	MGt	MGe	TOt	TOo	CB
(A) Overall specimens' and adults' $T_p$ of <i>T. torquatus</i>						
MGt					1.262	3.076*
TOt		0.068; 0.0483				2.097
CB		2.014; 0.946		2.539*		
(B) Males' $T_p$ and overall specimens' lower- $T_{set}$						
MGt				0.486; 0.631		1.832; 0.077
TOt		1.741				2.588*
CB		2.498*		0.997		
(C) Overall specimens' and males' upper- $T_{set}$						
MGt					1.387	2.964*
TOt		0.634				1.852
CB		2.707*		2.421*		

	SP	MGt	MGe	TOt	TOo	CB
<i>(D) Overall specimens' and adults' <math>T_b</math></i>						
SP		0.915	1.621	0.561	2.858	0.566
MGt	4.857*		2.075	1.267	3.104*	0.239
MGe	3.95*	0.651; 0.516		1.119	0.572	1.778
TOt	2.75; 0.007	2.684; 0.008	1.853; 0.066		2.076	0.933
TOo	1.136; 0.258	5.447*	4.584; $\leq 0.05$	3.589*		2.685
CB	2.936*	1.909; 0.058	1.180; 0.240	0.611; 0.543	3.681*	
<i>(E) Females' and males' <math>T_b</math></i>						
SP		2.636*	2.213; 0.0302	0.182; 0.857	3.684*	1.126; 0.264
MGt	4.771*		0.456; 0.65	2.453; 0.167	5.073*	1.520; 0.133
MGe	3.870*	0.406; 0.686		2.027; 0.0465	4.800*	1.078; 0.285
TOt	3.946*	1.405; 0.007	0.826; 0.412		3.703*	0.942; 0.349
TOo	1.110; 0.01	3.713*	2.936*	2.715; 0.009		4.091*
CB	3.417*	1.186; 0.009	0.691; 0.492	0.0669; 0.947	2.393; 0.02	
<i>(F) Overall specimens' and adults' <math>T_p</math></i>						
SP		2.451	4.004*	3.63*	0.824*	4.014*
MGt	4.915*		1.695	0.677	1.455	1.345
MGe	3.695*	0.915; 0.362		1.224	3.020	0.491
TOt	2.356; 0.02	3.044*	1.894; 0.061		2.306	0.793
TOo	1.779; 0.077	6.051*	4.868*	3.902*		2.835
CB	3.049*	2.002; 0.047	0.969; 0.334	0.975; 0.331	4.399*	
<i>(G) Overall specimens' and adults' lower- <math>T_{set}</math></i>						
SP		1.713	1.044	0.141	1.847	1.132
MGt	5.066*		0.348	1.669	3.002*	2.362
MGe	3.78*	0.968; 0.335		1.071	2.264	1.744
TOt	2.514; 0.0131	3.074*	1.861; 0.0649		1.542	0.92
TOo	1.534; 0.127	5.977*	4.745*	3.785*		0.507
CB	3.034*	2.151; 0.0332	1.058; 0.292	0.825; 0.411	4.152*	
<i>(H) Overall specimens' and adults' upper- <math>T_{set}</math></i>						
SP		2.423	3.983*	3.577*	1.077	3.919*
MGt	5.023*		1.698	0.661	1.223	1.288
MGe	3.808*	0.908; 0.05		1.241	2.820	0.544
TOt	2.39; 0.0183	3.126*	1.982; 0.0496		2.035	0.748
TOo	1.355; 0.178	5.797*	4.636*	3.497*		2.547

	SP	MGt	MGe	TOt	TOo	CB
CB	3.041*	2.106; 0.0371	1.058; 0.292	0.939; 0.349	4.003*	
<i>(I) Females' and males' upper-T<sub>set</sub></i>						
SP		0.512	1.234	0.327	2.49	0.0217
MGt	5.521*		0.536	0.279	2.242	0.478
MGe	4.071*	0.873; 0.387		0.964	2.984*	1.118
TOt	4.186*	1.959; 0.06	0.814; 0.419		2.655	0.29
TOo	1.188; 0.24	4.484*	3.127*	2.977*		2.105
CB	3.663*	1.836; 0.07	0.799; 0.428	0.0562; 0.955	2.589; 0.01	

Table S8. Spearman rank order correlations between mean and standard deviation (SD) of body temperature at the field ( $T_b$ ) and preferred body temperature at the laboratory ( $T_p$ ) vs. means and SD of maximum, mean and minimum air temperature ( $T_a$ ) obtained at the nearest weather stations for each site using the data of all tropidurids found in the literature, Cerrado and Caatinga populations, Cerrado populations and this study populations. \*Indicates that the comparisons were performed using transformed data (residuals).  $P$  values are expressed in bold when the difference is significant. \*Indicates that the comparisons were performed using transformed data (residuals).  $P$  values are expressed in bold when the difference is significant.

	All <i>Tropidurus</i>		Cerrado & Caatinga		Cerrado		Populations in this study	
	Statistic ( $S$ )	$P$ -value	Statistic ( $S$ )	$P$ -value	Statistic ( $S$ )	$P$ -value	Statistic ( $S$ )	$P$ -value
$T_b$ vs. $T_{a \text{ max}}$	0.304	$\leq \mathbf{0.001}^*$	0.707	$\leq \mathbf{0.001}^*$	0.788	$\leq \mathbf{0.001}^*$	0.404	0.341
$T_b$ vs. $T_{a \text{ mean}}$	0.0463	0.751	0.143	0.521	0.602	$\mathbf{0.0359}^*$	0.404	0.341
$T_b$ vs. $T_{a \text{ min}}$	0.127	0.369	0.31	0.147	0.571	$\mathbf{0.0391}^*$	0.404	0.341
SD $T_b$ vs. SD $T_{a \text{ max}}$	0.094	0.562	-0.0507	0.837	-0.257	0.402	-0.202	0.602
SD $T_b$ vs. SD $T_{a \text{ mean}}$	0.0421	0.793	0.0357	0.883	-0.223	0.484	-0.202	0.602
SD $T_b$ vs. SD $T_{a \text{ min}}$	0.143	0.365	0.118	0.617	-0.207	0.498	-0.202	0.602
$T_p$ vs. $T_{a \text{ max}}$	-0.174	0.523	0.137	0.651	-0.0987	0.775	-0.167	0.66
$T_p$ vs. $T_{a \text{ mean}}$	-0.317	0.224	-0.159	0.591	-0.0129	0.948	-0.167	0.66
$T_p$ vs. $T_{a \text{ min}}$	-0.281	0.282	-0.089	0.764	-0.0129	0.948	-0.167	0.66
SD $T_p$ vs. SD $T_{a \text{ max}}$	-0.612	$\mathbf{0.0188}^*$	-0.711	$\mathbf{0.0127}^*$	-0.466	0.207	-0.259	0.545
SD $T_p$ vs. SD $T_{a \text{ mean}}$	0.0421	0.793	-0.516	0.0795	-0.466	0.207	-0.259	0.545
SD $T_p$ vs. SD $T_{a \text{ min}}$	-0.725	$\leq \mathbf{0.001}^*$	-0.739	$\leq \mathbf{0.001}^*$	-0.466	0.207	-0.259	0.545

Table S9. Comparisons (One Way ANOVA,  $F$  statistic; Kruskal-Wallis One Way ANOVA on Ranks;  $H$  statistic; Student  $t$ -test,  $t$  statistic, Mann-Whitney Rank Test,  $U$  statistic) of the operative temperatures ( $T_e$ ), the  $d_b$  and  $d_e$  indices (the mean of the absolute values obtained from the deviations of  $T_b$  from  $T_{set}$  of each individual and of each  $T_e$  from  $T_{set}$ , respectively) and the efficiency of thermoregulation ( $E=1-(\text{mean } db/\text{mean } de)$ ) of: (1) Overall specimens, juveniles (Juv.), adults (Ad.), females ( $\text{♀}$ ) and males ( $\text{♂}$ ) among the populations of *T. torquatus* from Cuiaba, MT (CB), Arinos, MG (MGt), and Formoso do Araguaia, TO (TOt); (2) Overall specimens, adults, females and males among the populations of *T. torquatus* (CB; MGt; TOt), *T. etheridgei* from Arinos, MG (MGe), *T. oreadicus* in Formoso do Araguaia, TO (TOo), and *T. catalanensis* collected in Piracicaba, SP (SP); (3) Juveniles vs. adults, and females vs. males at each population (including reproductive and non-reproductive seasons *T. catalanensis*, SPr and SPnr, respectively); and (4) Overall specimens, juveniles, adults, females, and males between the populations at each site (MGt vs. MGe in Arinos, MG; TOt vs. TOo in Formoso do Araguaia, TO, and SPr vs. SPnr in Piracicaba, SP). \* Indicates that the comparisons were performed using transformed data (residuals).  $P$  values are expressed in bold when the difference is significant.

	$T_e$		$d_b$		$d_e$		$E$	
	Statistic	$P$	Statistic	$P$	Statistic	$P$	Statistic	$P$
<i>Among populations of T. torquatus</i>								
Overall specimens	$H_2 = 13.497$	<b>0.001</b>	$F_{2,71} = 1.368$	0.261	$H_2 = 2.438$	0.296	$F_{2,71} = 5.767$	<b>0.005</b>
Ad.			$F_{2,63} = 2.364$	0.103			$F_{2,63} = 6.301$	<b>0.003</b>
$\text{♀}$			$F_{2,33} = 2.474$	0.101			$F_{2,33} = 6.053$	<b>0.006</b>
$\text{♂}$			$F_{2,29} = 0.481$	0.623			$F_{2,29} = 1.515$	0.238
<i>Among populations comparisons</i>								
Overall specimens	$H_6 = 20.164$ $n = 141$	<b>0.003</b>	$H_6 = 23.878$ $n = 164$	$\leq$ <b>0.001</b>	$H_6 = 22.329$ $n = 141$	<b>0.001</b>	$H_6 = 43.490$ $n = 180$	$\leq$ <b>0.001</b>
Ad.			$F_{5,126} = 4.353$	$\leq$ <b>0.001</b>			$H_6 = 32.26$ $n = 133$	$\leq$ <b>0.001</b>
$\text{♀}$			$F_{5,65} = 3.151$	$\leq$ <b>0.009</b>			$H_6 = 26.736$ $n = 72$	$\leq$ <b>0.001</b>
$\text{♂}$			$F_{5,53} = 1.864$	0.116			$F_{5,53} = 3.12$	<b>0.015</b>



		$T_e$	$d_b$	$d_e$	$E$
<i>Within populations comparisons</i>					
CB	♀ vs. ♂		$t_{16} = -0.247$	0.808	$t_{16} = 0.247$ 0.808
MGt	Juv. vs. Ad.		$t_{20} = -1.878$	0.075	$t_{19} = 1.878$ 0.075
	♀ vs. ♂		$t_{12} = -0.473$	0.645	$t_{12} = 0.473$ 0.645
TOt	Juv. vs. Ad.		-	-	- -
	♀ vs. ♂		$t_{30} = 0.293$	0.771	$t_{30} = -0.293$ 0.771
MGe	Juv. vs. Ad.		-	-	- -
	♀ vs. ♂		$t_{11} = 0.104$	0.919	$t_{11} = -0.104$ 0.919
TOo	Juv. vs. Ad.		-	-	- -
	♀ vs. ♂		$t_{11} = 0.277$	0.784	$t_{11} = -0.277$ 0.784
SPnr	Juv. vs. Ad.		$t_{21} = 0.773$	0.448	$t_{21} = -0.773$ 0.448
	♀ vs. ♂		-	-	- -
SPr	Juv. vs. Ad.		$t_{27} = -0.0178$	0.986	$t_{27} = -0.0178$ 0.986
	♀ vs. ♂		$t_{19} = 1.415$	0.173	$t_{19} = -1.415$ 0.173
<i>Within sites comparisons</i>					
MGt	Overall		$t_{34} = -0.228$	<b>0.029</b>	$t_{34} = 2.349$ <b>0.025</b>
vs.	Juv.		-	-	- -
MGe	Ad.		$t_{25} = -1.265$	$\geq 0.196$	$t_{25} = 1.329$ $\geq 0.196$
	♀		$t_{13} = -1.143$	$\geq 0.257$	$t_{13} = 1.185$ $\geq 0.257$
	♂		$t_{10} = -0.532$	$\geq 0.577$	$t_{10} = 0.576$ $\geq 0.257$
TOt	Overall	$t_{20} = -2.619$	<b>0.016</b> $t_{56} = -3.161$	<b>0.003</b> $t_{17} = -0.914$	0.373 $U = 276$ $n = 26$ $n = 32$ <b>0.029</b>
vs.	Juv.		-	-	- -
TOo	Ad.		$t_{56} = -3.088$	<b>0.003</b>	$U = 263$ $n = 25$ $n = 32$ <b>0.028</b>
	♀		$U = 56$ $n = 12$ $n = 18$	<b>0.029</b>	$t_{28} = 2.315$ $\leq 0.029$

		$T_e$	$d_b$	$d_e$	$E$
	♂		$t_{25} = -1.727$	$\geq 0.096$	$t_{25} = -1.316$ $\geq 0.096$
SPnr	Overall	$U = 796$ $n = 29$ $n = 44$	0.076 $U = 406$ $n = 23$ $n = 29$	0.183 $U = 516$ $n = 29$ $n = 44$	0.171 $t_{50} = -1.614$ 0.113
vs.	Juv.		$t_{20} = -0.0657$	0.948	$t_{20} = 0.586$ 0.564
SPr	Ad.		$t_{28} = -1.375$	0.180	$t_{28} = 1.912$ 0.066
	♀		$t_{17} = -1.787$	0.092	$t_{17} = 2.357$ <b>0.031</b>

Table S10. Results of the pairwise tests (Holm-Sidak and Dunn's methods expressed with statistics  $t$  and  $Q$ , respectively; \* indicates significant differences,  $P \leq 0.05$ ) of the inter-sites comparisons among: (A) the operative temperatures ( $T_e$ ) at *T. torquatus*' sites (above the diagonal) and the efficiency of thermoregulation ( $E$ ) of the overall specimens of the species (below the diagonal); (B) adults' (above the diagonal) and females'  $E$  (below the diagonal) in *T. torquatus*; (C) overall specimens'  $T_e$  values (above the diagonal) and the deviation of mean  $T_e$  from  $T_{set}$  ( $d_e$  index; below the diagonal); (D) overall specimens'  $d_b$  index (above the diagonal) and efficiency of thermoregulation ( $E$ ; below the diagonal); (E) adults'  $d_b$  index (above the diagonal) and  $E$  (below the diagonal); (F) females'  $d_b$  index (above the diagonal) and  $E$  (below the diagonal); and (G) males'  $d_b$  index (above the diagonal) of all sites where the studied populations were collected. Populations and sites: *T. torquatus* of Cuiaba, MT (CB), Arinos, MG (MGt), and Formoso do Araguaia, TO (TOt), *T. etheridgei* from Arinos, MG (MGe), and *T. oreadicus* in Formoso do Araguaia, TO (TOo), and *T. catalanensis* collected in Piracicaba, SP, during the reproductive (SPr) and non-reproductive (SPnr) seasons.

	SPnr	SPnr	MGt	MGe	TOt	TOo	CB
(A) $T_e$ at <i>T. torquatus</i> ' sites and overall specimens' $E$ in the species							
MGt					1.484		3.621*
TOt			1.167				1.859
CB			2.129		3.393*		
(B) Adults' and females' $E$ in <i>T. torquatus</i>							
MGt					0.118		3.387*
TOt			0.150				2.694*
CB			2.636*		3.272*		
(C) Overall specimens' $T_e$ and $d_e$							
SPnr		2.143	1.158	1.158	0.234	2.968	1.938
SPr	1.28		0.653	0.653	1.502	1.443	3.175*
MGt	3.33	2.454		0	0.991	1.778	2.591
MGe	3.423	2.554	0.0852		0.991	1.778	2.591
TOt	2.797	2.142	0.478	0.417		2.278	1.385
TOo	0.813	0.16	2.077	2.156	2.009		3.754*
CB	1.157	0.488	0.965	1.023	1.185	0.539	



Table S11. Spearman rank order correlations between mean, standard deviation (SD) and coefficient of variation (CV) of body temperature at the field ( $T_b$ ) and preferred body temperature at the laboratory ( $T_p$ ), latitude, longitude, maximum, mean and minimum air temperature ( $T_a$ ) and the mean, SD, and CV of the operative temperature ( $T_e$ ), index de and the mean, SD, and CV of the efficiency of thermoregulation ( $E$ ) obtained at the nearest weather stations for each studied population ( $N = 6$ ).  $P$  values are expressed in bold when the difference is significant.

	$T_e$		SD & CV $T_e$		$d_e$	$E$		SD $E$		CV $E$		
	$S$	$P$	$S$	$P$	$S$	$P$	$S$	$P$	$S$	$P$		
$T_b$	0.493	0.297	0.667	0.136	0.143	0.803	-0.371	0.497	-0.0294	0.919	0.0857	0.919
SD & CV $T_b$	0.841	0.0333	0.261	0.564	0.257	0.658	-0.371	0.497	-0.0588	0.919	0.657	0.175
$T_p$	-0.338	0.497	-0.456	0.356	0.725	0.103	0.928	<b>0.0167</b>	-0.851	0.0333	-0.754	0.103
SD $T_p$	-0.191	0.714	0.309	0.564	-0.203	0.658	-0.232	0.658	0.0896	0.803	-0.348	0.497
CV $T_p$	-0.232	0.658	0.232	0.658	-0.314	0.564	-0.314	0.564	0.206	0.658	-0.314	0.564
Latitude	-0.118	0.803	0.588	0.242	-0.232	0.658	-0.145	0.714	0.254	0.658	-0.116	0.803
Longitude	0.955	<b>0.00278</b>	0.524	0.297	0.152	0.714	-0.516	0.297	0.0	1.0	0.88	<b>0.0333</b>
$T_{a \text{ max}}$	0.000	1.000	0.627	0.175	-0.0883	0.803	-0.0883	0.803	0.136	0.803	-0.0883	0.803
SD & CV $T_{a \text{ max}}$	-0.418	0.419	-0.925	<b>0.0167</b>	0.265	0.564	0.559	0.242	-0.348	0.497	-0.441	0.356
$T_{a \text{ mean}}$ & $T_{a \text{ min}}$	0.000	1.000	0.627	0.175	-0.0883	0.803	-0.0883	0.803	0.136	0.803	-0.0883	0.803
SD & CV $T_{a \text{ mean}}$ , & SD $T_{a \text{ min}}$	-0.418	0.419	-0.925	<b>0.0167</b>	0.265	0.564	0.552	0.242	-0.348	0.497	-0.441	0.356
CV $T_{a \text{ min}}$	0.000	1.000	-0.627	0.175	0.0883	0.803	0.0883	0.803	-0.136	0.803	0.0883	0.803

Table S12. Residuals of  $T_b$  vs.  $T_a$  [Mean  $\pm$  SD ( $n$ );  $^{\circ}$ C] and the observed variation (CV; %) of the residuals in each quadrant determined by the regression and the  $T_{set}$  range or  $T_p$ : (I) above the regression and below the lower- $T_{set}$  and  $T_p$ ; (II) below the regression and below the lower- $T_{set}$  and  $T_p$ ; (III) above the regression and above the lower- $T_{set}$  and  $T_p$ ; and (IV) below the regression and below the lower- $T_{set}$  and  $T_p$ . CV<sub>i</sub>: variation of the residuals for the quadrant i. CV<sub>ii/i</sub>: variation of quadrant ii with respect to i. (CV<sub>iv/iii</sub>)/(CV<sub>ii/i</sub>): overall variation with respect to the  $T_{set}$  range and  $T_p$ . In all three cases, values lower and higher than 1 indicate that the variation is more significant below than above, or, above than below the  $T_{set}$  range and  $T_p$ , respectively. Populations: *T. torquatus* of Cuiaba, MT (CB), Arinos, MG (MGt), and Formoso do Araguaia, TO (TOt), *T. etheridgei* from Arinos, MG (MGe), and *T. oreadicus* in Formoso do Araguaia, TO (TOo), and *T. catalanensis* collected in Piracicaba, SP, during the reproductive (SPr) and non-reproductive (SPnr) seasons.

.Residuals of $T_b$ vs. $T_a$ [Mean $\pm$ SD ( $N$ )] with respect to the lower- and upper- $T_{set}$											
	I	CV <sub>I</sub>	II	CV <sub>II</sub>	CV <sub>II/I</sub>	III	CV <sub>III</sub>	IV	CV <sub>IV</sub>	CV <sub>IV/III</sub>	(CV <sub>IV/III</sub> )/(CV <sub>II/I</sub> )
CB	1.29 $\pm$ 1.11 (9)	86	1.36 $\pm$ 0.78 (10)	57.5	0.67	--	--	--	--	--	--
MGt	3.72 $\pm$ 1.31 (3)	35.2	1.50 $\pm$ 0.71 (5)	47.3	1.34	0.84 $\pm$ 0.46 (5)	55	1.55 $\pm$ 1.26 (2)	81.3	1.48	1.65
TOt	1.25 (1)	--	0.8 $\pm$ 0.82 (4)	102.3	--	0.81 $\pm$ 0.83 (13)	102.3	0.84 $\pm$ 1.01 (12)	121	1.18	--
MGe	3.47 (1)	--	2.11 (1)	--	--	1.7 $\pm$ 0.65 (4)	38.2	0.88 $\pm$ 0.86 (6)	98.2	2.57	--
TOo	2.49 $\pm$ 0.94 (6)	37.7	2.54 $\pm$ 1.39 (6)	54.7	1.45	0.83 $\pm$ 0.59 (5)	71.7	0.72 $\pm$ 0.27 (8)	37.4	0.52	1.18
SPnr	1.73 $\pm$ 2.46 (5)	142.3	2.45 $\pm$ 0.82 (2)	33.5	0.24	0.68 $\pm$ 0.75 (4)	109.7	2.41 $\pm$ 0.52 (2)	21.7	0.2	0.75
SPr	1.02 $\pm$ 0.61 (18)	59.8	1.91 $\pm$ 0.13 (9)	7	0.12	1.01 $\pm$ 0.49 (5)	48.2	2.8 $\pm$ 3.37 (2)	120.2	2.5	2.52

Residuals of $T_b$ vs. $T_a$ [Mean $\pm$ SD ( $N$ )] with respect to $T_p$											
	I	CV <sub>I</sub>	II	CV <sub>II</sub>	CV <sub>II/I</sub>	III	CV <sub>III</sub>	IV	CV <sub>IV</sub>	CV <sub>IV/III</sub>	(CV <sub>IV/III</sub> )/(CV <sub>II/I</sub> )

CB	1.37 ± 1.11 (9)	81	1.23 ± 0.6 (10)	48.7	0.6	--	--	--	--	--	--
MGt	2.76 ± 1.88 (5)	68.1	1.73 ± 1 (8)	52	0.76	0.63 ± 0.25 (6)	39.2	1.26 ± 0.98 (3)	78.1	1.99	0.98
TOt	1.08 ± 1 (2)	91.2	0.54 ± 0.56 (4)	103.3	1.13	0.86 ± 0.73 (13)	84.8	0.86 ± 0.84 (13)	97.3	1.15	0.94
MGe	--	--	--	--	--	1.51 ± 0.81 (5)	53.4	1.08 ± 1.29 (7)	119.3	2.22	--
TOo	2.16 ± 1.18 (6)	54.8	1.85 ± 1.47 (7)	79.4	1.45	0.7 ± 0.55 (6)	79.4	0.6 ± 0.41 (7)	69.5	0.87	1.1
SPnr	1.47 ± 1.98 (7)	134.9	2.06 ± 0.69 (5)	33.6	0.25	1.5 ± 1.09 (7)	72.9	2.1 ± 0.6 (5)	28.7	0.39	0.6
SPr	1.22 ± 0.73 (19)	60.2	1.54 ± 1.54 (15)	74.8	1.24	1.42 ± 0.61 (3)	42.9	1.07 ± 0.87 (4)	81.7	1.91	0.92

Table S13. Results of the regressions ( $b$  coefficient,  $t$ -test and analysis of variance statistics and equation) between body temperature ( $T_b$ ) and air temperature ( $T_a$ ), below and above the preferred temperature ( $T_p$ ) of each population. Last column includes the variation between the  $b$  coefficients above and below the regressions: values close to 1 indicate a similarity between  $b$  below and above  $T_p$ ; values close to 0 indicate that  $b$  below  $T_p$  is more significant than above it; negative values of  $b$  indicate a shift from a positive  $b$  to a negative  $b$ , below and above  $T_p$ , respectively. Populations: *T. catalanensis* collected in the non-reproductive (SP11) and reproductive season (SP13) Piracicaba, SP, *T. torquatus* (MGt) and *T. etheridgei* (MGe) from Arinos, MG, *T. torquatus* (TOt) and *T. oreadicus* (TOo) from Formoso do Araguaia, TO, and of *T. torquatus* (CB) from Cuiaba, MT. The letters between brackets next to the populations' abbreviations indicate the correspondent plot of Figure 2.

		$b$	$t$ -test	$r^2$	$F$	$P$	Equation	$b$ Above $T_p$ / $b$ Below $T_p$
CB	Below $T_p$	0.53	$t_{17} = 2.31$	0.239	$F_{1,17} = 5.334$	<b>0.034</b>	$T_b = 18.840 + (0.526 * T_a)$	--
	Above $T_p$	--	--	--	--	--	--	--
MGt	Below $T_p$	0.48	$t_{11} = 1.288$	0.131	$F_{1,11} = 1.658$	0.224	$T_b = 18.713 + (0.479 * T_a)$	0.02
	Above $T_p$	0.01	$t_7 = 0.0342$	0.0002	$F_{1,7} = 0.00117$	0.974	$T_b = 36.206 + (0.0108 * T_a)$	
TOt	Below $T_p$	0.62	$t_4 = 1.018$	0.206	$F_{1,4} = 1.037$	0.366	$T_b = 14.066 + (0.620 * T_a)$	<b>-0.32</b>
	Above $T_p$	<b>-0.20</b>	$t_{24} = -0.621$	0.0158	$F_{1,24} = 0.385$	0.541	$T_b = 43.830 - (0.200 * T_a)$	
MGe	Below $T_p$	--	--	--	--	--	--	--
	Above $T_p$	0.94	$t_{10} = 2.825$	0.444	$F_{1,10} = 7.981$	<b>0.018</b>	$T_b = 2.575 + (0.937 * T_a)$	
TOo	Below $T_p$	1.51	$t_{11} = 2.943$	0.440	$F_{1,11} = 8.660$	0.013	$T_b = -11.663 + (0.1507 * T_a)$	0.28
	Above $T_p$	0.43	$t_{11} = 4.253$	0.622	$F_{1,11} = 18.091$	<b>0.001</b>	$T_b = 22.443 + (0.433 * T_a)$	
SPnr	Below $T_p$	0.45	$t_{10} = 1.69$	0.222	$F_{1,10} = 2.856$	0.002	$T_b = 20.551 + (0.457 * T_a)$	0.98
	Above $T_p$	0.44	$t_{10} = 0.783$	0.058	$F_{1,10} = 0.612$	0.452	$T_b = 20.882 + (0.435 * T_a)$	
SPr	Below $T_p$	0.34	$t_{32} = 2.518$	0.165	$F_{1,32} = 6.339$	0.017	$T_b = 24.714 + (0.342 * T_a)$	<b>-8.24</b>
	Above $T_p$	<b>-2.80</b>	$t_5 = -2.415$	0.538	$F_{1,5} = 5.834$	0.060	$T_b = 136.672 - (2.794 * T_a)$	



Table S14. General information on biome and macrohabitat, localities, latitude (Lat.) and longitude (Long.), microhabitat, mean  $\pm$  SD of body ( $T_b$ ) and preferred ( $T_p$ ) temperatures and the respective coefficients of variation (CV; when possible) for the species and/or populations of tropidurids available in the literature. The populations are organized by biome or habitat, and secondly, alphabetically by the name of the species.

Species / Populations (source, endnote)	Biome/Macrohabitat	Locality	Lat. (S)	Long.(W)	Elev. (m)	Microhabitat	$T_b$ (°C)	CVT <sub>b</sub>	$T_p$ (°C)	CVT <sub>p</sub>
<i>Tropidurus catalanensis</i> , SPnr (1)	Cerrado/Urban areas	Piracicaba, São Paulo, Brazil	22.7	47.63	553	Generalist	36.0 $\pm$ 2.5	6.94	34.9 $\pm$ 1.5	4.30
<i>T. catalanensis</i> , SPr (1)	Cerrado/Urban areas	Piracicaba, São Paulo, Brazil	22.7	47.63	553	Generalist	35.7 $\pm$ 1.9	5.32	34.1 $\pm$ 1.3	3.81
<i>T. etheridgei</i> , MGe (1)	Cerrado/Urban areas	Arinos, Minas Gerais, Brazil	15.9	46.1	522	Generalist	36.3 $\pm$ 3.6	9.92	33.7 $\pm$ 1.4	4.15
<i>T. insulanus</i> (2)	Cerrado	Brasília, Distrito Federal, Brazil	15.8	47.87	1070	Rock specialist	34.5 $\pm$ 2.4	6.96		
<i>T. insulanus</i> (3)	Cerrado	Serra do Cachimbo, Amazonas, Brazil	8.39	56.07	510	Rock specialist			31.5 $\pm$ 2.2	6.98
<i>T. itambere</i> (3)	Cerrado	Atibaia, São Paulo, Brazil	23.12	46.55	800	Rock specialist	30.9 $\pm$ 2.7	8.74	33.2 $\pm$ 1.8	5.42
<i>T. itambere</i> (4)	Cerrado					Rock specialist	34.1 $\pm$ 4.0	1.17		
<i>T. itambere</i> (5)	Cerrado/Montane	Serra dos Pirineus, Pirenópolis, Goiás, Brazil	15.85	48.95	1100	Rocks	33.1 $\pm$ 2.8	8.46		
<i>T. itambere</i> (6)	Cerrado	Valinhos, São Paulo, Brazil	22.98	47.01	740	Soil	34.1 $\pm$ 2.0	5.867		
<i>T. oreadicus</i> (4)	Cerrado					Rock/trees	34.0 $\pm$ 3.5	1.03		
<i>T. oreadicus</i> (3)	Cerrado	Palmas, Tocantins, Brazil	10.18	48.33	260	Rock/trees			37.1 $\pm$ 2.2	5.93
<i>T. oreadicus</i> (5)	Cerrado	"Serra dos Pirineus", Pirenópolis, Goiás, Brazil	15.85	48.95	1100	Rocks	33.5 $\pm$ 2.1	6.27		
<i>T. oreadicus</i> , TOo (1)	Cerrado/Urban areas	Formoso do Araguaia, Tocantins, Brazil	11.8	46.1	265	Generalist	37.2 $\pm$ 3.3	8.87	34.6 $\pm$ 1.4	4.05
<i>T. spinulosus</i> (6)	Cerrado/ Forest	Tanti, Punilla Department, Cordoba, Argentina	31.33	64.62	700	Trunks/rocks	30.3			
<i>T. torquatus</i> (3)	Cerrado	Brasília, Distrito Federal, Brazil	15.8	47.87	1070	Generalist	33.3 $\pm$ 2.2	6.61	36.1 $\pm$ 2.8	7.76
<i>T. torquatus</i> , CB (1)	Cerrado/Urban areas	Cuiabá, Mato Grosso, Brazil	15.61	56.06	179	Generalist	35.4 $\pm$ 2.1	5.88	34.8 $\pm$ 0.8	2.3

Species / Populations (source, endnote)	Biome/Macrohabitat	Locality	Lat. (S)	Long.(W)	Elev. (m)	Microhabitat	T <sub>b</sub> (°C)	CVT <sub>b</sub>	T <sub>p</sub> (°C)	CVT <sub>p</sub>
<i>T. torquatus</i> , MGt (1)	Cerrado/Urban areas	Arinos, Minas Gerais, Brazil	15.9	46.1	522	Generalist	35.0 ± 2.6	7.43	33.8 ± 0.7	2.07
<i>T. torquatus</i> , TOt (1)	Gallery Forest	Formoso do Araguaia, Tocantins, Brazil	11.78	49.75	192	Trunks/Soil	36.2 ± 1.5	4.14	33.8 ± 1.6	4.73
<i>Eurolophosaurus divaricatus</i> (3)	Caatinga	Ibiraba, Bahia, Brazil	10.79	42.82	400	Sand specialist	38.0 ± 2.2	5.78	36.2 ± 3.4	9.39
<i>T. psamonastes</i> (3)	Caatinga	Ibiraba, Bahia, Brazil	10.79	42.82	400	Sand specialist	37.6 ± 2.0	5.32	34.5 ± 2.1	6.09
<i>T. hispidus</i> (4)	Caatinga				192	Generalist	36.0 ± 1.6	4.44		
<i>T. hispidus</i> (3)	Caatinga	Sítio do Conde, Bahia, Brazil	11.82	37.68	80	Sand specialist			34.5 ± 2.4	6.96
<i>T. hispidus</i> (7)	Caatinga	Rio Grande do Norte, Brazil	6.58	37.26	192	Rock specialist	33.6 ± 2.3	6.85		
<i>T. hispidus</i> (8)	Caatinga	Exu, Pernambuco, Brazil	7.42	40.17	840		35.9 ± 0.1			
<i>T. hygomi</i> (3)	Caatinga	Salvador, Bahia, Brazil	12.97	38.48	20	Rock specialist	35.4 ± 2.6	7.34	33.5 ± 1.9	5.67
<i>T. hygomi</i> (9)	Restinga	Abaeté, Salvador, Bahia, Brazil	12.97	38.38	5	Sandy soil/shrubs	32.9 ± 2.0	6.08		
<i>T. hygomi</i> (10)	Restinga	Costa Azul, Jandaíra, Bahia, Brazil	11.67	37.48	15	Sandy soil	35.3 ± 2.2	6.23		
<i>T. hygomi</i> (10)	Restinga	Pirambu, Sergipe, Brazil	10.73	36.85	8	Herbaceous/shrubs	35.2 ± 2.0	5.68		
<i>T. semitaeniatus</i> (8)	Cerrado	Exu, Pernambuco, Brazil	7.42	40.18	840		37.1 ± 0.2			
<i>T. semitaeniatus</i> (7)	Caatinga	Rio Grande do Norte, Brazil	6.58	37.26		Rock specialist	35.1 ± 2.0	0.57		
<i>T. torquatus</i> (11)	Restinga	Reserva Florestal Vale do Rio Doce, Linhares, Espírito Santo, Brazil	19.29	40.09	50	Generalist	35.6 ± 1.9	5.34		
<i>T. torquatus</i> (12)	Atlantic Forest	Trancoso, Bahia, Brazil	16.65	39.22	10	Sandy soil/shrubs	35.6 ± 1.8	5.05		
<i>T. torquatus</i> (12)	Atlantic Forest	Prado, Bahia, Brazil	17.3	39.22	8	Sandy soil/shrubs	33.2 ± 3.0	9.01		
<i>T. torquatus</i> (12)	Atlantic Forest	Guriri, Espírito Santo, Brazil	18.68	39.75	10	Sandy soil/shrubs	36.2 ± 1.5	4.13		
<i>T. torquatus</i> (12)	Atlantic Forest	Setiba, Espírito Santo, Brazil	20.58	40.45	20	Sandy soil/shrubs	34.4 ± 2.9	8.41		
<i>T. torquatus</i> (12)	Atlantic Forest	Praia das Neves, Espírito Santo, Brazil	21.25	40.97	7	Sandy soil/shrubs	30.8 ± 4.5	1.46		
<i>T. torquatus</i> (12)	Atlantic Forest	Grussaí, Rio de Janeiro, Brazil	21.73	41.03	6	Sandy soil/shrubs	35.8 ± 1.7	4.74		
<i>T. torquatus</i> (12)	Atlantic Forest	Jurubatiba, Rio de Janeiro, Brazil	22.28	41.68	11	Sandy soil/shrubs	35.6 ± 1.5	4.20		

Species / Populations (source, endnote)	Biome/Macrohabitat	Locality	Lat. (S)	Long.(W)	Elev. (m)	Microhabitat	T <sub>b</sub> (°C)	CVT <sub>b</sub>	T <sub>p</sub> (°C)	CVT <sub>p</sub>
<i>T. torquatus</i> (12)	Atlantic Forest	Massambaba, Rio de Janeiro, Brazil	22.93	42.2	7	Sandy soil/shrubs	36.2 ± 2.3	6.34		
<i>T. torquatus</i> (12)	Atlantic Forest	Barra de Marica, Rio de Janeiro, Brazil	22.95	42.83	1	Sandy soil/shrubs	35.2 ± 2.3	6.52		
<i>T. torquatus</i> (13)	Atlantic Forest	Barra de Marica, Rio de Janeiro, Brazil	22.95	42.83	1	Sandy soil/shrubs	35.4 ± 2.1	5.93		
<i>T. torquatus</i> (12)	Atlantic Forest	Grumari, Rio de Janeiro, Brazil	23.08	43.5	10	Sandy soil/shrubs	35.3 ± 2.1	7.65		
<i>T. torquatus</i> (14 & 15)	Atlantic Forest	Toledos, Juiz de Fora, Minas Gerais, Brazil	21.81	43.59	697	Sandy soil/rocks/shrubs	31.2 ± 3.1	9.94		
<i>T. torquatus</i> - wet season (14 & 15)	Atlantic Forest	Toledos, Juiz de Fora, Minas Gerais, Brazil	21.81	43.59	697	Sandy soil/rocks/shrubs	32.4 ± 2.7	8.33		
<i>T. torquatus</i> - dry season (14 & 15)	Atlantic Forest	Toledos, Juiz de Fora, Minas Gerais, Brazil	21.81	43.59	697	Sandy soil/rocks/shrubs	30.4 ± 3.0	9.86		
<i>T. oreadicus</i> (16)	Amazonia/ Rainforest	Serra Norte, Carajas, Para, Brazil	5.9	49.88	170	Rocks/shrubs	35.8 ± 1.5	4.19		
<i>Uranoscodon superciliosum</i> (17)	Amazonia/ Rainforest	Río Xingu, Pará, Brazil	4	52.6	170	Soil	26.6 ± 1.3	4.89		
<i>Plica plica</i> (18)	Amazonia/ Rainforest	Río Xingu, Pará, Brazil	3.56	51.8	150	Trunk specialist	30.7 ± 1.5	4.89		
<i>P. umbra</i> (19)	Amazonia/ Rainforest	Porto Walter Area, Acre, Brazil	8.54	72.8	230	Trunk specialist	29.1 ± 2.8	9.55		
<i>Uracentron flaviceps</i> (20)	Amazonia/ Rainforest	Reserva de Produccion Faunistica Cuyabeno, Sucumbios Province, Quito, Ecuador	0.02	76.3	260	Branch Specialist	31.2 ± 2.8	9.02		
<i>T. hispidus</i> (21)	Amazonia/ Rainforest	Caracaraí, Roraima, Brazil	2.83	60.67	11	Rocks	34.1 ± 3.7	10.88		
<i>T. melanopleurus</i> (22)	Rainforest	Samaipata, Santa Cruz, Bolivia	18.17	63.83	1600	Rocks	♂: 33.1 ± 1.9; ♀: 31.6 ± 3.5	5.74; 11.08		
<i>T. montanus</i> (23)	Montane	Serra do Cipó, Minas Gerais, Brazil	19.37	43.53	1100	Rocks	34.7			
<i>E. nanuzae</i> (24)	Montane	Serra do Cipó, Minas Gerais, Brazil	19.37	43.53	1100	Rocks	34.1			
<i>Microlophus quadrivittatus</i> - summer (25)	Coast	Chucumata, 36 km south of Iquique, Chile	20.53	70.17	70	Soil	36 ± 1.2	3.33	36.6 ± 17	4.64
<i>M. quadrivittatus</i> (winter) (25)	Coast	Chucumata, 36 km south of	20.53	70.17	70	Soil	34 ± 1.8	5.29	36 ± 0.9	2.5

Species / Populations (source, endnote)	Biome/Macrohabitat	Locality	Lat. (S)	Long.(W)	Elev. (m)	Microhabitat	T <sub>b</sub> (°C)	CVT <sub>b</sub>	T <sub>p</sub> (°C)	CVT <sub>p</sub>
		Iquique, Chile								
<i>M. peruvianus</i> (26)	Coast	Bayovar, Piura Department, Peru	5.83	81.03	5	Rocks/driftwood	36.3 ± 1.6	4.41	35.6 ± 1.3	3.59
<i>T. albemarlensis</i> (27)	Coast	Academy Bay, Santa Cruz Island, Galápagos Archipelago, Ecuador	0.74	90.3	15	Rocks/driftwood	34.5 ± 4.1	11.95	34.6 ± 2.1	6.13
<i>T. spinulosus</i> (28)	Chaco	Ranch "Los Colorados", Salta, Argentina	24.58	63.18	245	Trunks	34.2 ± 1.8	5.26		
<i>T. etheridgei</i> (29)	Chaco	Anta, Salta, Argentina	24.58	63.18	245	Trunks/soil	35.8 ± 2.5	6.98		
Overall tropidurids							34.3 ± 2.2	6.41	34.7 ± 1.4	4.03

<sup>1</sup> This study; <sup>2</sup> Colli unpublished data; <sup>3</sup> Kohlsdorf and Navas, 2006; <sup>4</sup> Colli and Paiva, 1997; <sup>5</sup> Faria and Araujo, 2004; <sup>6</sup> Martori and Aun, 1994; <sup>7</sup> Ribeiro and Freire, 2010; <sup>8</sup> Vitt, 1995; <sup>9</sup> Vargens *et al.*, 2008; <sup>10</sup> Martins, 2011; <sup>11</sup> Bergallo and Rocha, 1993; <sup>12</sup> Kiefer *et al.*, 2005; <sup>13</sup> Teixeira-Filho *et al.*, 1996; <sup>14</sup> Ribeiro and Souza, 2006; <sup>15</sup> Ribeiro *et al.*, 2008; <sup>16</sup> Rocha and Bergallo, 1990; <sup>17</sup> Howland *et al.*, 1990; <sup>18</sup> Vitt, 1991; <sup>19</sup> Vitt *et al.*, 1997; <sup>20</sup> Vitt and Zani, 1996; <sup>21</sup> Vitt *et al.*, 1996; <sup>22</sup> Pérez-Mellado and De la Riva, 1993; <sup>23</sup> Kiefer, 1998; <sup>24</sup> Kiefer, 2003; <sup>25</sup> Báez and Cortez, 1990; <sup>26</sup> Huey, 1974; <sup>27</sup> Stebbins *et al.*, 1967; <sup>28</sup> Cruz, 1998; <sup>29</sup> Cruz *et al.*, 1998.

Table S15. Climate data from the nearest weather stations from the populations of tropidurids from the literature included in this study. Weather stations: Ara - Aracajú, BA; Ari: Arinos, MG; Ba: Barbalha, CE; Be: Belo Horizonte, MG; Br: Brasilia, DF; Cam: Campos, RJ; Car: Caravelas, BA; Ce: Ceara Mirim, CE; Cor: Córdoba, Argentina; Cru: Cruzeiro do Sul, AC; For: Formosa, GO; Iq: Iquique, Chile; It: Itaituba, PA; Ju: Juiz de Fora, RJ; Man: Manaus, AM; Mar: Maraba, PA; Pet: Petrolina, BA; Piu: Piura, Perú; Por: Porto Nacional, TO; Rio: Rio de Janeiro, RJ; Riv: Rivadavia, Salta, Argentina; Sal: Salvador, BA; San: San Cristobal, Galápagos, Ecuador; Sc: São Carlos, SP; Sm: São Mateus, ES.

Abr	Elev. (m)	Lat. (S)	Long. (W)	N	Prec.	SD	Range	N	$MT_{max}$	SD	Range	N	$MT_{mean}$	SD	Range	N	$MT_{min}$	SD	Range	N
Ara	4.72	11.2	37.1	8947	3.601	9.698	157					7557	21.973	1.889	28.2	7833	22.966	1.634	25	7800
Ari	519.00	15.9	46.05	10007	3.417	10.196	152.5	9365	32.055	2.971	22.6	9332	24.651	2.365	16.72	9386	19.005	3.03	25.1	9349
Ba	409.03	7	39.3	8174	2.975	10.306	163.9	8144	32.076	2.413	16.2	7453	25.774	1.711	11.76	8076	21.07	1.812	17.8	8062
Be	915.00	19.8	43.9	10012	4.373	11.811	164.2	10017	27.136	3.025	22.6	9917	21.763	2.501	17.6	10015	17.631	2.624	22.9	10012
Br	1159.54	15.5	47.9	11489	4.081	10.144	131	11481	26.591	2.341	20.8	11469	20.969	1.916	19.32	11496	16.66	2.165	21.7	11478
Cam	11.20	22.5	41.3	7884	2.698	8.338	146.6	10813	29.74	3.702	23.8	8049	24.264	2.615	15.2	10775	20.65	2.695	16.5	10755
Car	2.88	18.5	39.3	8291	3.917	10.743	195.2	7091	28.532	2.196	15.6	6216	24.607	1.89	11.04	7351	20.973	2.356	24.7	6158
Ce	61.35	5.8	35.4	7274	3.497	10.698	153.8	7191	30.537	1.49	18.9	5941	25.945	1.186	13.1	7200	22.012	1.332	27.4	7151
Cor	484	31.31	64.21	12066	1013.8	6.498	47.4	12084	25.145	6.076	38.1	12085	17.415	5.702	32.6	12081	11.195	6.11	33.1	12080
Cru	156.85	7.3	72.7	10507	5.915	12.522	160.6	10364	31.671	2.368	22.9	10191	25.503	1.588	15.3	10389	20.345	2.807	25.9	10314
Cu	151.34	15.8	56.1	8655	3.969	10.747	134.3	8534	32.847	3.443	31.3	8365	26.068	2.687	21.46	8475	21.473	3.203	24.6	8449
For	935.19	16.1	47.3	11380	3.959	10.337	124.6	10287	28.037	2.603	19.4					10168	17.459	2.282	22.4	9694
Iq	52	20.53	70.18	10899	1015.1	2.17	18.8	10971	21.577	3.167	19	10972	18.471	2.607	14.6	10970	15.881	2.418	23.7	10945
It	45	4.3	56	10856	5.58	12.629	164.2	10885	32.668	2.19	16.2	10653	27.203	1.339	10.04	10660	23.09	1.276	11.9	10652
Ju	939.96	21.8	43.3	10089	4.36	11.1	147.4	9957	24.307	3.824	26.6	9755	18.991	2.901	18.46	9963	15.262	2.746	20.6	9820
Man	67	3.1	60	11184	6.268	13.305	155	10992	31.754	2.171	16.2					10994	23.246	1.213	22.7	10973
Mar	95	5.5	49.2	11229	5.187	13.447	309	11040	32.565	2.068	16.1	11086	27.083	1.34	9.75	11258	23.035	1.263	11.1	11034

Abr	Elev. (m)	Lat. (S)	Long. (W)	N	Prec.	SD	Range	N	$MT_{\max}$	SD	Range	N	$MT_{\text{mean}}$	SD	Range	N	$MT_{\min}$	SD	Range	N
Pet	370.46	10.7	40.5	9026	1.354	6.781	151.3	8952	32.172	2.467	16.4	10168	17.459	2.282	22.4	7557	21.973	1.889	28.2	7475
Piu	49	5.18	80.6	8236	1013.2	2.179	34.7	8360	29.887	3.164	27	8360	23.493	2.821	14.5	8359	19.124	2.891	21.5	8359
Por	239.2	10.9	48.4	9764	4.532	11.386	140.6	9793	33.516	2.736	18.4	9671	26.743	1.621	15.26	10287	21.721	1.903	16.1	9748
Rio	11.10	23.4	43.2	4395	2.694	8.648	151.3	6934	28.443	4.02	25.5	4603	24.644	2.918	18.8	6137	21.366	2.68	19.4	6134
Riv	205	24.16	62.3	4146	1010.1	6.67	46.3	4297	28.508	6.1	41	286	22.804	6.13	31	4295	16.625	5.61	40.3	4294
Sal	51.41	13	38.5	9148	5.212	12.685	232.5	9174	28.827	2.046	15.3	9013	25.609	1.485	9.54	8076	22.893	1.574	26.9	8069
San	6	0.9	89.6	253	1011.7	1.952	9.8	1196	27.942	2.224	13	1196	24.888	2.077	10.9	1195	22.06	1.903	17.2	1196
Sc	856.00	22.5	47.9	10962	4.247	10.717	143.1	10802	26.831	3.58	31	10394	20.565	3.075	23.9	10878	16.052	3.326	24.5	10798
Sm	25.04	19	39.9	8342	3.829	11.017	175.3	9849	29.947	2.605	19.6	7757	24.304	2.132	12.52	9870	19.992	2.557	26.3	9837

Table S16. Results of the correlation ( $n$ ; Spearman's statistic  $S$ ;  $P$ -value) and of the regressions ( $b$  coefficient,  $t$ -test and analysis of variance statistics and equation) between latitude, and the means, standard deviation ( $SD$ ) and range of the maximum ( $T_{a \text{ max}}$ ), the mean ( $T_{a \text{ mean}}$ ) and the minimum temperature ( $T_{a \text{ min}}$ ) gathered at the nearest weather stations from the populations of tropidurids (**Table S15**).  $P$  values are expressed in bold when the difference is significant.

	$n$	$S$	$P$	$b$	$t$ -test	$P$	$r^2$	$F$	$P$	Equation
Latitude vs. $T_{a \text{ max}}$	25	0.578	<b>0.003</b>	0.223	$t_{23} = 3.577$	0.002	0.357	$F_{1,23} = 12.792$	0.002	$T_{a \text{ max}} = 32.553 + (0.223 * \text{Latitude})$
Latitude vs. $SD_{T_{\text{max}}}$	25	-0.791	<b>&lt;0.001</b>	-0.106	$t_{23} = -5.562$	<0.001	0.574	$F_{1,23} = 30.931$	<0.001	$SD = 1.468 - (0.106 * \text{Latitude})$
Latitude vs. $\text{Range}_{T_{\text{max}}}$	25	-0.655	<b>&lt;0.001</b>	-0.598	$t_{23} = -4.336$	<0.001	0.45	$F_{1,23} = 18.803$	<0.001	$\text{Range} = 13.510 - (0.598 * \text{Latitude})$
Latitude vs. $T_{a \text{ mean}}$	24	0.592	<b>0.0023</b>	0.215	$t_{22} = 3.172$	0.004	0.314	$F_{1,22} = 10.059$	0.004	$T_{a \text{ mean}} = 26.544 + (0.215 * \text{Latitude})$
Latitude vs. $SD_{T_{\text{mean}}}$	24	-0.751	<b>&lt;0.001</b>	-0.108	$t_{22} = -4.68$	<0.001	0.499	$F_{1,22} = 21.905$	<0.001	$SD = 0.861 - (0.108 * \text{Latitude})$
Latitude vs. $\text{Range}_{T_{\text{mean}}}$	24	-0.592	<b>0.0023</b>	-0.495	$t_{22} = -3.474$	0.002	0.354	$F_{1,22} = 12.068$	0.002	$\text{Range} = 9.976 - (0.495 * \text{Latitude})$
Latitude vs. $T_{a \text{ min}}$	26	0.732	<b>&lt;0.001</b>	0.285	$t_{24} = 5.253$	<0.001	0.535	$F_{1,24} = 27.598$	<0.001	$T_{a \text{ min}} = 23.831 + (0.285 * \text{Latitude})$
Latitude vs. $SD_{T_{\text{min}}}$	26	-0.696	<b>&lt;0.001</b>	-0.108	$t_{24} = -5.236$	<0.001	<b>0.535</b>	$F_{1,24} = 27.415$	<0.001	$SD = 0.969 - (0.108 * \text{Latitude})$
Latitude vs. $\text{Range}_{T_{\text{min}}}$	26	-0.313	0.117	-0.363	$t_{24} = -2.592$	0.016	0.219	$F_{1,24} = 6.716$	0.016	$\text{Range} = 17.790 - (0.363 * \text{Latitude})$

Table S17. Spearman rank order correlations between latitude, biomes, macro and microhabitats and the mean, standard deviation (SD) and coefficient of variation (CV) of body temperature at the field ( $T_b$ ), preferred body temperature ( $T_p$ ), maximum, mean and minimum air temperature ( $T_a$  - obtained at the nearest weather stations from each site) for all populations of tropirudids gathered from the literature.  $P$  values are expressed in bold when the difference is significant.

	Latitude vs.			Longitude vs.			Biomes vs.			Macrohabitats vs.			Microhabitats vs.		
	$n$	$S$	$P$	$n$	$S$	$P$	$S$	$P$	$P$	$n$	$S$	$P$	$n$	$S$	$P$
$T_b$	52	0.00165	0.991	51	0.2	0.16	58	-0.0835	0.532	58	-0.109	0.414	57	-0.162	0.229
SD $T_b$	47	-0.0188	0.899	47	-0.008	0.956	53	-0.153	0.273	53	-0.258	0.0619	53	-0.131	0.348
CV $T_b$	47	-0.0069	0.963	47	-0.0536	0.719	53	-0.141	0.311	53	-0.245	0.0773	43	-0.116	0.409
$T_p$	19	0.108	0.652	19	-0.325	0.171	19	0.353	0.135	19	0.281	0.239	19	0.149	0.536
SD $T_p$	19	0.287	0.227	19	0.119	0.620	19	0.237	0.323	19	0.194	0.418	19	0.529	<b>0.02</b>
CV $T_p$	19	0.286	0.23	19	0.088	0.715	19	0.252	0.294	19	0.21	0.381	19	0.515	<b>0.0236</b>
Biomes	55	-0.0434	0.752	54	-0.211	0.126	-	-	-	61	0.872	<b>≤ 0.001</b>	60	0.53	<b>≤ 0.001</b>
Macrohabitats	55	-0.109	0.425	54	-0.162	0.24	61	0.872	<b>≤ 0.001</b>	-	-	-	60	0.433	<b>≤ 0.001</b>
Microhabitats	54	0.0125	0.928	53	0.215	0.121	60	0.53	<b>≤ 0.001</b>	60	0.433	<b>≤ 0.001</b>	-	-	-
$T_{a \text{ max}}$	50	0.591	<b>≤ 0.001</b>	49	0.0956	0.512	53	-0.164	0.239	53	-0.256	0.0646	52	0.114	0.421
SD $T_{a \text{ max}}$	50	-0.713	<b>≤ 0.001</b>	49	-0.193	0.183	53	0.151	0.28	53	0.211	0.129	52	-0.0373	0.792
CV $T_{a \text{ max}}$	50	-0.689	<b>≤ 0.001</b>	49	-0.184	0.204	53	0.115	0.409	53	0.202	0.147	52	-0.121	0.392
$T_{a \text{ mean}}$	51	0.534	<b>≤ 0.001</b>	50	0.028	0.846	54	-0.0308	0.824	54	-0.133	0.336	53	0.0539	0.7
SD $T_{a \text{ mean}}$	51	-0.762	<b>≤ 0.001</b>	50	-0.253	0.076	54	0.19	0.169	54	0.207	0.133	53	-0.183	0.19
CV $T_{a \text{ mean}}$	51	-0.652	<b>≤ 0.001</b>	51	-0.349	<b>0.0124</b>	55	0.182	0.183	54	0.196	0.151	54	-0.207	0.132
$T_{a \text{ min}}$	53	0.675	<b>≤ 0.001</b>	52	0.325	<b>0.019</b>	56	-0.053	0.697	56	-0.0875	0.52	55	0.222	0.103
SD $T_{a \text{ min}}$	53	-0.683	<b>≤ 0.001</b>	52	-0.344	<b>0.0128</b>	56	0.108	0.427	56	0.126	0.354	55	-0.147	0.282
CV $T_{a \text{ min}}$	53	-0.592	<b>≤ 0.001</b>	52	-0.381	<b>0.006</b>	56	0.0429	0.753	56	0.079	0.561	55	-0.206	0.131



Table S18. Mean, standard deviation (SD), coefficient of variation (CV) and the mean of the CV of body temperature ( $T_b$ ), preferred body temperature ( $T_p$ ), and maximum, mean, and minimum environmental temperature ( $T_{a \text{ max}}$ ,  $T_{a \text{ mean}}$  and  $T_{a \text{ min}}$ ) for all populations separated by biomes, macro and microhabitats. Sample size is indicated in the  $N$  columns.

		$N$	$T_b$	SD	CV	$CV_{\text{mean}}$	$N$	$T_p$	SD	CV	$CV_{\text{mean}}$	$N$	$T_{a \text{ max}}$	SD	CV	$CV_{\text{mean}}$	$N$	$T_{a \text{ mean}}$	SD	CV	$CV_{\text{mean}}$	$N$	$T_{a \text{ min}}$	SD	CV	$CV_{\text{mean}}$
Biome	Cerrado	17	34.4	1.9	5.4		11	34.3	1.5	4.3		15	29.2	3.2	11.0		14	22.8	3.0	13.3		15	17.9	2.9	16.3	
	Caatinga	11	35.6	1.6	4.4		4	34.7	1.1	3.2		8	31.1	1.5	4.8		11	23.2	3.3	14.3		11	22.2	0.8	3.7	
	Rainforest	24	33.3	2.6	7.8		1	32.5	--	--		22	29.8	2.1	7.0		20	24.3	1.9	7.9		22	20.5	2.1	10.4	
	Coastal	4	35.2	1.1	3.2		3	36.1	0.5	1.4		4	25.3	4.3	17.1		4	21.3	3.4	15.7		4	18.2	3.0	16.3	
	Chaco	2	35.0	1.1	3.2		--	--	--	--		2	28.5	0.0	0.0		2	22.8	0.0	0.0		2	16.6	0.0	0.0	
	Overall	5	34.7	0.9	2.6	4.8	4	34.3	1.3	3.8	3.0	10.2	28.8	2.2	8.0	8.0	10	22.9	2.3	10.2	10.2	10.8	19.1	1.8	9.3	9.34
Macro-habitats	Cerrado	15	34.7	1.7	4.8		10	34.4	1.5	4.5		13	29.6	3.1	10.3		12	23.3	2.7	11.6		13	18.4	2.3	12.7	
	Caatinga	7	35.9	1.5	4.2		4	34.7	1.1	3.2		6	31.3	1.4	4.4		7	22.9	3.9	17.2		7	22.0	0.8	3.5	
	Rainforest	28	33.4	2.6	7.7		1	33.8	--	--		24	29.8	2.3	7.7		24	24.1	2.4	9.8		26	20.6	2.8	13.5	
	Chaco	2	35.0	1.1	3.2		--	--	--	--		2	28.5	0.0	0.0		2	22.8	0.0	0.0		2	16.6	0.0	0.0	
	Montane	2	34.4	0.4	1.2		--	--	--	--		2	27.1	0.0	0.0		2	21.8	0.0	0.0		2	17.6	0.0	0.0	
	Coast	4	35.2	1.1	3.2	4.1	3	35.7	0.8	1.8	3.2	4	25.3	4.3	17.1	6.6	4	21.3	3.4	15.7	9.1	4	18.2	3.0	16.3	7.7
Overall	6	34.8	0.8	2.3		4	34.6	0.7	2		6	28.6	1.8	6.6		6	22.7	2.1	9.1		6	18.9	1.5	7.7		
Micro-habitats	Generalist	9	35.6	1.1	3		7	34.6	0.8	<b>2.4</b>		8	29.7	3.1	10.5		8	23.3	2.6	11.0		8	18.5	2.3	12.3	
	Rock/Trunk	18	33.8	1.6	4.7		6	34.3	2	<b>6.4</b>		15	29.1	2.5	8.7		13	23.5	2.9	12.1		15	19.3	3.4	17.7	
	Soil/Trunk	5	35.2	1.1	3.1		3	35.5	1.5	<b>4.2</b>		5	26.4	5.1	19.1		5	21.4	3.5	16.2		5	17.2	2.5	14.7	
	Sand/Shrub	19	34.2	2.8	8.1		3	35.1	1	<b>2.8</b>		16	29.6	1.9	6.6		18	23.3	2.7	11.6		18	21.0	1.8	8.5	
	Trunk	6	32.9	3.1	9.3		--	--	--	--		5	31.3	1.6	5.1		6	24.8	2.0	7.9		6	20.7	2.4	11.3	
Overall	5	34.4	1.1	3.2	5.6	4	34.8	0.5	<b>1.4</b>	4.0	5	29.2	2.9	10.0	10.0	5	23.2	2.7	11.8	11.8	5	19.3	2.5	12.9	12.9	

Table S19. Relationship between the coefficient of variation (CV) of body ( $T_b$ ) and preferred body temperature ( $T_p$ ), and the CV of environmental temperature ( $T_{a \text{ min}}$ ,  $T_{a \text{ min}}$  and  $T_{a \text{ min}}$ ) for all populations separated by biomes, macro and microhabitats. Sample size is indicated in the  $n$  columns.

		CV $T_{a \text{ max}}$			CV $T_{a \text{ mean}}$			CV $T_{a \text{ min}}$		
		$n$	$S$	$P$	$n$	$S$	$P$	$n$	$S$	$P$
Biomes	CV $T_b$	5	-0.1	0.950	5	-0.4	0.517	5	-0.1	0.950
	CV $T_p$	3	-0.5	1.0	3	-1.0	0.333	3	-0.5	1.0
<i>Macrohabitats</i>	CV $T_b$	6	0.319	0.497	6	0.261	0.564	6	0.377	0.419
	CV $T_p$	3	-0.5	1.0	3	-0.5	1.0	3	-0.5	1.0
<i>Microhabitats</i>	CV $T_b$	5	-0.9	0.083	5	-0.4	0.517	5	-0.5	0.450
	CV $T_p$	4	0.0	1.0	4	0.8	0.333	4	0.8	0.333

## CHAPTER 3

Thermal sensitivity to global warming in populations of lizards of the *Tropidurus torquatus* species complex based on the variation in the locomotor performance

*(Co-authored with Nora R. Ibarzüengoytía, Carlos A. Navas and Donald Miles)*

## ABSTRACT

Climate change projections for Brazil foresee an increase in the mean air temperature of up to 6°C and a trend of decreasing rainfall by 5-20% by 2071-2100. Predicting the responses of organisms to climate change is one of the many urgent challenges faced by contemporary physiological ecologists. Climate warming is expected to overrun local adaptation; therefore, survival will rely on the plasticity and dispersal opportunities of each population. Ectothermic vertebrates are particularly sensitive to global warming, as temperature changes could shift behavioral and physiological performance to suboptimal levels, restricting time for activity. Although sensitivity of a species or individual depends not only on their thermal tolerance limits, but also on their behavior, and genetic diversity, most tropical ectotherms live close to their thermal limits for optimal metabolic performance and are considered thermal specialists which makes them more vulnerable to warmer environments. We test whether vulnerability to altered thermal niches through rising temperatures is influenced by the magnitude of variability in thermal physiology. We compare patterns of variability within populations (PVWP) with patterns of variation among populations and analyze the impact of PVWP in a warming scenario where ambient temperature ( $T_a$ ) increases by 3°C. We compare the physiological performance capacities for velocity and endurance for five populations of lizards from the *Tropidurus torquatus* species complex. TPCs were significantly different among and within populations, as shown by the different thermal breadths ( $B_{80}$ ) and safety margins (SM's). Both increased with climate variation and decreased with the variation in annual precipitation. We predict shifts in the fitness response with climate change as the impact of warming may be considerably high in the performance of these populations, particularly in the northern sites where lizards are currently coping with high  $T_a$ 's, and seem to be thermal specialists, thus, more vulnerable to thermal fluctuations. In addition, dispersal opportunities for the gallery forest population of *T. torquatus* are restricted, which worsens the scenario. The central populations also face local extinction risk as large proportions of registered operative temperatures ( $T_a$ 's) currently exceeds the upper limit of the  $B_{80}$  and thermal *preferenda* of the species.

**KEYWORDS.** Climate change, climate variability hypothesis, intra-specific variation, phenotypic plasticity, population differentiation.

## INTRODUCTION

The close relationship between ambient temperature ( $T_a$ ) and body temperatures ( $T_b$ ) in ectothermic vertebrates makes these lineages particularly sensitive to global warming, as environmental changes could shift behavioral and physiological performance to suboptimal levels, restricting time for activity (Huey, 1991; Dunham, 1993; Miles, 1994a; Angilletta, 2009; Kearney *et al.*, 2009; Moritz *et al.*, 2012; Seebacher and Franklin, 2012). The reasons and extent to which given taxa may be affected or not by warming are valid questions on their own. Along a continuum of effects climate warming may benefit some species (Chamaillé-Jammes *et al.*, 2006) and lead others to complete or partial extinction (Sinervo *et al.*, 2010). The differences among taxa may have a basis in the optimal temperature ( $T_o$ ) that best fit activity and the ability of individuals to compensate for thermal shifts. For example, in response to warming, some small heliothermic lizards can shift the timing for activity and basking (Bogert, 1949; Huey, 1982) or alter their phenotype in various manners, including acclimatization physiological responses (Corn, 1971; Spellerberg, 1972; Hertz, 1981; Somero, 2010). Therefore, the distribution of ectothermic tetrapods is shaped by two factors: the sensitivity of physiological performance to temperature (*e.g.* thermal tolerance) and the temperature dependent ecological effects of performance or fitness (Huey and Stevenson, 1979; Miles, 1994a).

One approach to infer the vulnerability of a given taxon to climate warming entails estimating its sensitivity and resilience to changes of  $T_a$  (Huey *et al.*, 2012), which takes into consideration the possibilities for phenotypic plasticity, as well as ecological (acclimatization) and evolutionary adaptation (Williams *et al.*, 2008). A fundamental premise is that the  $T_b$  experienced during a period of time determines the integrated performance and fitness of an individual (Kingsolver *et al.*, 2004; Angilletta, 2009). However, the ability to quantify the link between performance and fitness, particularly in free ranging animals, is rarely possible. Consequently, one approach is to seek approximate measurements that capture the association between performance and Darwinian fitness. Locomotor performance is a proxy variable routinely used, because of its presumed link with growth, survivorship, and reproduction (Miles, 1994a; 194b; Irschick and Losos, 1999; Kingsolver and Gomulkiewicz, 2003; Kohlsdorf *et al.*, 2004). In addition, locomotor performance is sensitive to changes in body temperature. Thus, quantifying the shift in performance with temperature provides a link between fitness and the thermal environment (Huey 1991). Thermal performance curves

capture the sensitivity of physiological performance in animals to body or environmental temperature (Huey and Stevenson, 1979; Huey 1982; Huey and Kingsolver, 1989). Thermal performance curves are described by the measuring the maximum and minimum thermal extremes compatible with any level of activity ( $CT_{\max}$  and  $CT_{\min}$ ), the range of temperatures characterizing the performance breadth ( $B_{80}$ ), and the optimal temperature for performance ( $T_o$ ). These thermal variables provide the information to assess adaptation to local environments and potential responses to climate change. Performance breadth should be narrower in species at tropical than temperate latitudes. Furthermore, the vulnerability of a population to rising ambient temperatures  $T_a$  can be determined comparing the difference between the thermal optimum at which performance reaches its maximum ( $T_o$ ) to  $T_b$  before and after the increase in ambient temperature (Huey *et al.*, 2012). The differences of  $T_o$  to the  $CT_{\max}$  and  $T_o$  to the maximum ambient ( $T_{a\max}$ ) or operative ( $T_{e\max}$ ;  $T_e$  as the "null" distribution of  $T_b$  that non-regulating animals would experience in their microhabitats; Heath, 1964) temperatures are equivalent to safety margins (hereinafter,  $SM_{ct}$ ,  $SM_{ta}$ , and  $SM_{te}$ ), or the magnitude of temperature increase before an individual's physiological performance is compromised.

Climatic factors most likely to impact a population are expected to be those leading to  $T_b$ 's higher than  $T_o$ 's (Huey *et al.*, 2012), particularly if  $T_o$  is rather inflexible, as may be the case for thermal specialists in stable environments (*e.g.* tropical forests; Ghalambor *et al.*, 2006; Deutsch *et al.*, 2008; McCain, 2009; Sunday *et al.*, 2011; Clusella-Trullas *et al.*, 2011). A given increase in  $T_b$  from warming will usually have a larger impact on a thermal specialist than on a thermal generalist, particularly for temperatures that exceed  $CT_{\max}$  (Huey *et al.*, 2012). Thus, tropical lizards are expected to be especially vulnerable to rapid changes (Huey *et al.*, 2009) and will probably suffer most of the extinctions (Sinervo *et al.*, 2010; Leal and Gunderson, 2012).

One challenge facing comparative and evolutionary physiologist is the need to control for the influence of phylogenetic relatedness among species when elucidating the potential responses to climate change. Whereas genetic variation may explain a large part of the morphological, behavioral and physiological differences among populations, latitudinal and altitudinal variation of life-history traits within and among taxa with wide geographic distributions has been commonly reported as a result of adaptive variation (Mayr, 1963). Thus, one approach is to investigate groups of closely related species or populations within a same species that

inhabit widely different habitat conditions. We selected five populations of the genus *Tropidurus* from the *torquatus* group that occupy a diverse spectrum of environments of the Brazilian Cerrado, including a gallery forest and open-urban areas. Although they are considered as heliothermic lizards, variation in the thermoregulatory behavior has been reported among populations. Previous studies on the thermal biology of populations from the Cerrado biome (Piantoni *et al.*, unpublished data) suggest that poor thermoregulation behavior and thermoconformity are mainly associated to populations from lower latitudes. Moreover, the larger proportion of  $T_b$  and  $T_e$  above  $T_{set}$  found at these studied sites is expected to augment the risk of overheating with an eventual raise of  $T_a$ , precluding time of activity and increasing these populations' vulnerability to extinction.

A main objective of this study is to test the hypothesis that vulnerability to altered thermal niches through rising temperatures is inversely related to latitude in species belonging to the widespread Brazilian *torquatus* lizard species complex (Family: Tropiduridae). A more specific hypothesis is that vulnerability may be influenced by the magnitude of variability in thermal physiology that exists within populations of this lizard. We focus on two locomotor performance traits, sprint speed and endurance. We capture the variation in performance induced by temperature by estimating and comparing the thermal performance curves of five populations of tropidurids of the *Tropidurus torquatus* group from the Cerrado Biome. We determine patterns of variability within populations (PVWP), compare them with patterns of variation among populations and analyze the impact of PVWP in the context of ecological climate change, to predict the response and vulnerability of the studied populations in a global warming scenario. In addition, we expect these curves to reflect PVWP with lower absolute values and increased variance in indicators of SM in populations exposed to more frequent extreme temperatures (*e.g.* southern and central populations - "generalist"). Conversely, we expect higher absolute values and decreased variance in indicators of SM's in populations exposed to a homogeneous thermal environment (*e.g.* northern populations - "specialist"; Bolnick *et al.*, 2003). Finally, we expect the differences in sprint speed and endurance among the populations to follow a latitudinal pattern (Sinervo, 1990; Sinervo and Huey, 1990): for example, populations inhabiting open environments (southern and central sites) will exhibit higher sprint speed, which give a larger SM in a climate change scenario.

## MATERIALS AND METHODS

### 1. Experiments and data collecting

Maximum speed and endurance experiments were carried out in 2012 and 2013 with lizards of five populations from three localities of the Brazilian Cerrado: 1) in the North, 18 females, and 14 males of *T. torquatus* (Clade B; hereinafter TOt) and one juveniles, 12 females, and 13 males of *T. oreadicus* (hereinafter TOo) from Formoso do Araguaia, Tocantins (11°47'S, 49°45'W, 192 m a.s.l.); 2) in the Centre, six juveniles, eight females and eight males of *T. torquatus* (Clade A) and one juveniles, seven females and six males of *T. etheridgei* from in Arinos, Minas Gerais (hereinafter MGt and MGe, respectively; 15°54'S, 46°06'W, 522 m a.s.l.); and 3) in the South, 23 juveniles, 26 females and 11 males of *T. catalanensis* (hereinafter SP) from Piracicaba, São Paulo (22°42'S, 47°38'W, 553 m a.s.l.). Ambient temperatures were measured in the field during the hours of activity (*sensu* Pough and Gans, 1982) using a Sper Scientific 4 Channel Datalogging thermometer (Mod. # 800024) and specific probes for surface ( $T_s$ ) and air ( $T_a$ ) (Sper Scientific Mod. # 800073 and # 800076, respectively). A catheter probe of 1.62 mm diameter (Sper Scientific Mod. # 800077) was used to measure each individual's body temperature ( $T_b$ ). Each individual was handled by their head to avoid heat transfer and the thermocouple was inserted 1 cm inside the cloaca.  $T_b$  was recorded within 10 s of handling. The snout-vent length (SVL; caliper Mitutoyo CD-6" CX  $\pm$  0.01 mm) and body mass (Pesola spring scale of 10 and 100  $\pm$  0.5 g) were registered for each lizard. Reproductive condition (juvenile or adult) was determined according to Wiedenhecker *et al.* (2002) and Meira *et al.* (2007), and sex by the presence of black scales in the ventral side of the hind legs as well as larger SVL in males (Rodrigues, 1987).

Lizards were captured by noose and transported to the lab where they were maintained on a 14 h: 10 h light:dark cycle at ambient temperature in terraria provided with a 60 W incandescent lamp, to allow behavioral thermoregulation. Lizards were fed three times a week with cockroaches and crickets, always after the performance experiments. The general condition of each lizard was monitored every week by measurements of body mass. The animals used in the experiments maintained original body mass while in captivity.

Experiments on locomotor performance were performed following Ibarguengoytía *et al.* (2007) and each experiment was recorded with a SONY PowerShot SD950 IS digital camera (15 frames per second). Individual lizards were raced down a 1 m racetrack three times and



then allowed to rest for a minimum of 3 h. We calculated the maximum speed ( $V_{\max}$ ) achieved by each lizard and the maximum endurance capacity ( $End_{\max}$ ) as individuals were raced in the same track until exhaustion (loss of righting response was used to assess exhaustion), following the methods of Huey and Stevenson (1979) and Angilletta *et al.* (2002). In 2012, a subsample of 21 specimens from SP was tested for endurance at three  $T_b$ 's (36°C, 30°C, and 40°C) and for velocity at five  $T_b$ 's (33°C, 23°C, 28°C, 39°C, and 37°C). In 2013, experiments were standardized at four  $T_b$ 's (35°C, 40°C, 25°C, and 30°C). The trials at different  $T_b$ 's were performed in a random sequence and data was obtained from the digital videos using Windows Live Movie Maker 6 software with a precision of  $\pm 0.04$  seconds.

The critical thermal maximum body temperature ( $CT_{\max}$ ) was estimated by placing an individual lizard in a closed container (10 x 10 x 15 cm<sup>3</sup>) submerged in a water bath at 50 °C.  $T_b$  was measured every 2 seconds using an ultra-thin (0.2 mm) catheter thermocouple fastened approximately 10 mm inside the cloaca (Sper Scientific 4 Channel Datalogging thermometer, Mod. # 800024).  $T_b$  heating rate was maintained at approximately 1°C per minute starting at 35 °C. Each lizard was observed as its body warmed and its behavior, such as vigorous movements of escape or panting was recorded. Lizards were removed from the heat source when they could not turn back when they were turned over. To determine the thermal critical minimum  $T_b$  ( $CT_{\min}$ ), lizards were placed individually in the same container in a refrigerator at 2 °C. Lizard  $T_b$  was measured every 15 s using the same thermocouple as for the  $CT_{\max}$  trials. The lizards were observed throughout the experiment and frequently placed on their back, especially after reaching  $T_b$  below 15 °C. The temperature at which the individual did not respond to intense stimulation was considered as the endpoint for  $CT_{\min}$ .

## 2. Thermal performance curves

Maximum endurance and velocity thermal curves were constructed for each individual of all five populations and for each population based on the individual curves using the modified Kumaraswamy Function written by Mike Sears and coded by Seema Sheth for R and the minpack.lm R 3.1.0 package.  $V_{\max}$  and  $End_{\max}$ , the thermal optimum ( $T_o$ ; as the  $T_b$  at  $V_{\max}$  and  $End_{\max}$ ), and the thermal performance breadths ( $B_{80}$ ; calculated as the range of  $T_b$  at which performance is greater than or equal to 80% of the  $V_{\max}$  and  $End_{\max}$  for all individuals) we obtained from each individual and population curves.

Due the striking sexual dimorphism of *Tropidurus* (Pinto *et al.*, 2005) SVL, the variation of

different parameters of the TPC's among the populations (patterns of variability within populations; PVWP) was analyzed using only adults' data.

Interpopulational comparisons were performed using one way analysis of variance (ANOVA), Student's t-test and all Pairwise Multiple Comparison Procedures (Holm-Sidak method). Normality and variance-homogeneity were tested with the one-sample Kolmogorov–Smirnov and Levene tests, respectively. When the assumptions were violated, non-parametric Kruskal–Wallis One Way ANOVA, Mann–Whitney Rank Sum test were used. The significance level used for all statistical tests was  $P = 0.05$  (Sokal and Rohlf, 1969; Norusis, 1986). Data with normal distributions are expressed as means  $\pm$  SD and the median and ranges.

### 3. Patterns of variation in the performance with latitude and climate variability

Operative temperatures ( $T_e$ ) were collected to better understand the daily thermal variation that lizards experience in their micro-environments. To do this, data logger connected to four plastic models were disposed in potential microenvironments of lizards at each site over one year between 2012 and 2013. Size and color of the models were determined based on the calibration against real specimens for previous studies of the same populations (Piantoni *et al.*, unpublished data).

Historical climate data on maximum ambient temperature ( $T_{a \text{ max}}$ ) and precipitation (mm) for the same period of time at the nearest (less than 50 km) weather stations for each population was obtained from the sites <http://www.inmet.gov.br/portal/index.php?r=bdmep/bdme> and <http://www.tutiempo.net>. Patterns of variation of the safety margins such as the distances between  $T_o$  and the  $CT_{\text{max}}$  ( $SM_{ct}$ ), the maximum  $T_a$  ( $T_{a \text{ max}}$ ;  $SM_{ta}$ ) and the maximum  $T_e$  ( $T_{e \text{ max}}$ ;  $SM_{te}$ ), and the thermal breadths ( $B_{80}$ ) were analyzed with respect to latitude, daily variation of  $T_e$ , and the variation of annual precipitation.

### 4. Estimate of the impact of warming on performance

Data on relative performance was estimated using the individual TPC and the lizards'  $T_b$ 's, for the time of the day when the lizards were captured and for the same hour in a warming scenario where  $T_a$  (and  $T_b$ ; assuming a positive increment of  $T_b$  with  $T_a$ ) is 3 °C higher. The relative performance was calculated with respect to the maximum value (1) of the population for the current and projected scenario. The effect of an increase of  $T_a$  was estimated as the daily variation in performance in the relation to the  $B_{80}$  of each population and as the

difference between the relative performance after warming and before warming.

## RESULTS

### 1. Variation in among the collected specimens and their habitats

Adults varied significantly in SVL and in mass among the populations ( $MGe \geq TOt \geq SP \geq MGt > TOo$ ; Tables 1, S1 & S2). Whereas juveniles were usually found in vegetated areas adults tended to occupy hard substrates in the sun (*e.g.*, basking on walls, trees, and concrete floors) with nearby shrubs and plants that could be used as retreat sites. In SP, lizards were found in urban areas as well as in the forests along the river Piracicaba. Only TOt was restricted to the gallery forest along the rivers 25 km from downtown Formoso do Araguaia, TO. The gallery forest was characterized by high humidity, exuberant and dense vegetation and lower temperatures compared to the town nearby occupied by TOo. Only one specimen of TOo was found in sympatry with TOt, basking on a termite mound by the highway. Its  $T_b$  (37.8 °C) was almost 2 °C higher than its congeners' at the same riverside (35.96 °C; range = 34.8 - 37.7 °C).

In the southern (SP) and central (MG) sites, lizards experienced the highest daily means of  $T_{a\max}$  (34.1 and 33.2 °C, respectively) whereas in TO it was 27.4 °C. Daily means of  $T_{e\max}$  were highest in MG 50.5 °C and lower in TO (38.4 °C) and SP (37.4 °C). The highest daily variation of  $T_e$  was found in MGt and MGe (15.9 °C). Daily variation of  $T_e$  for SP (19.95 °C) and TOt and TOo (10.2°C). Annual precipitation varied among sites being higher in SP and TO than in MG [mean and SD (mm), TO:  $119.9 \pm 30.9$ ; MG:  $93.7 \pm 27.4$ ; SP:  $130.5 \pm 29.7$ ; median (range; mm), TO: 115.7 (266.1); MG: 60.6 (259.6); SP: 96.1 (317.4)].

The highest  $T_b$ 's were collected in TOo and the lowest in SP ( $T_b$ :  $TOo > MGe > MGt > TOt > SP$ ; Table 1). Significant differences were found between the  $T_b$ 's of TOo and SP when juveniles were included in the analyses but adults shared similar  $T_b$ 's (Tables 1, S1 & S2).

### 2. Variation in the maximum performance among populations

Thermal performance curves for endurance and velocity varied among the populations (Figures 1 & 2).

Endurance increased with latitude ( $MGe > SP > MGt > TOo > TOt$ ) whereas  $T_o$  was lower in the MG and higher in SP and TO ( $TOo > SP > TOt > MGe > MGt$ ; Tables 1, S1 & S2). The

$B_{80}$  were similar among all populations (9.7-11.5 °C) but the lower- and upper- $TB_{80}$  differed following the pattern of  $T_o$  ( $TO_o > SP > TO_t > MGe > MGt$ ; Tables 1, S1 & S2).

Lizards were equally fast (109.3-129.3 cm/s) and reached the maximum velocity at a similar  $T_o$  (35.2-36.9 °C) in the five populations (Tables 1 & S1). The  $B_{80}$  differed among the populations, probably as a result of the difference among the lower- $TB_{80}$  as the upper- $TB_{80}$  did not vary ( $B_{80}$ :  $MGt > TO_o > MGe > TO_t > SP$ ;  $SP > MGe > TO_t > TO_o > MGt$ ; upper- $TB_{80}$ : 39.9-41 °C; Tables 1, S1 & S2).

### 3. Patterns of variation

Most of the observed patterns of variation contrasted with the expected results (Table 2). The safety margins with respect to  $CT_{max}$  ( $SM_{ct}$ ) for endurance were larger in the central site and smaller in the northern and southern sites whereas for velocity these increased progressively towards the North (Figure 3A). The  $SM_{ct}$  for endurance increased with the variation in daily  $T_e$  ( $TO > SP > MG$ ) but for velocity these were similar among the populations (Figure 3B). Finally, the  $SM_{ct}$  for overall performance (endurance and velocity) decreased with the increase of variation of annual precipitation which was lower in TO and MG and more significant in SP (Figure 3C).

The patterns of variation of the safety margins between  $T_o$  and the  $T_{e\ max}$  ( $SM_{te}$ ) with respect to latitude, and variation of daily  $T_e$  and annual precipitation were similar to the patterns of variation found for the endurance  $SM_{ct}$  (black symbols in Figure 3D-F). In contrast, the patterns of variation of the safety margins between  $T_o$  and the  $T_{a\ max}$  ( $SM_{ta}$ ) with respect to latitude, and variation of daily  $T_e$  and annual precipitation were similar to the patterns of variation found for the velocity  $SM_{ct}$  (white symbols in Figure 3D-F).

Thermal breadths ( $B_{80}$ ) varied with latitude similarly to the endurance  $SM_{ct}$  as the largest values correspond to the central site, MG, and the smaller to the southern and northern sites, SP and TO, respectively (Figure 3G). The  $B_{80}$ 's for endurance showed a slight positive relationship with the daily variation of  $T_e$ , whereas the  $B_{80}$ 's for velocity were considerable larger in the extremes, where daily variation of  $T_e$  was lowest (TO) and highest (MG; Figure 3H).  $B_{80}$  decreased with the variation of annual precipitation, particularly for velocity (Figure 3I).

#### 4. Impact of warming in the performance of *Tropidurus* species in the Cerrado

Lizards from the five populations had a similar endurance and speed capacity at the time of capture (Tables 1 & S1; Figures 4-6). In a warming scenario in which  $T_a$  would increase by 3 °C, endurance and speed capacity would drop, although significantly only in MGe (endurance) and TOo (velocity) considerably but will still be similar in the five populations (Tables 1, S1 & S3; Figures 4-6). The estimated increase of 3°C in  $T_a$  in a global warming scenario is expected to affect the performance of the lizards in all sites, particularly MG where the predicted  $T_b$ 's would exceed the  $T_{set}$ -range and consequently result in a significant decrease of the performance capacity.

Based on the field  $T_b$ 's when captured, lizards from TOo and MGt exhibited the maximum relative performance for endurance and speed, respectively (Table S4). In the predicted warming scenario, TOo would be the most affected as its endurance capacity would decay by 14.2% and its velocity by 21.4% (Table S4). Lizards in MGe would have their endurance and velocity capacity decreased by 13.8% and 8.8%, respectively, whereas in TOt lizards would suffer the lowest impact consisting in a decrease of 5% in their endurance and 5.7% in their velocity. On the other hand, warming may affect the velocity of MGt lowering it by 3.2% but make lizards' endurance capacity increase by 5.1. Similarly, in SP, lizards' endurance capacity would decrease by 15.3% but they are expected to be 4% faster (Table S4).

#### DISCUSSION

Our results suggests that vulnerability to altered thermal niches through rising ambient temperatures are mainly associated to gradients of environmental constraints and harshness as well as to the ecophysiological capacity of the lizards to adjust to changes. They reject the thermal conservatism hypothesis as they present variation among populations, within the genus and even within *T. torquatus*. The variation in locomotor performance with the variation of climate variables did not have a straightforward relationship and were contrary to our predictions. Moreover, indicators of variability (thermal breadths;  $B_{80}$ ) within populations and vulnerability ( margins,  $SM_{ct}$ ,  $SM_{te}$  and  $SM_{ta}$ ) were positively related to the daily thermal variation of  $T_e$  rather than to the daily thermal variation of  $T_a$ . The increase of the variation in annual precipitation had a direct relationship with  $T_o$  and inverse relationship with  $B_{80}$  and SM's in an inverse pattern. Predictions regarding the patterns of variation within the populations (PVWP) were partially corroborated as endurance  $B_{80}$  were higher at the sites

with more frequent extreme temperatures, whereas velocity  $B_{80}$  did not follow a defined climatic trend. Also as expected, the SD of maximum endurance and velocity decreased with latitude which may be directly associated to the lower thermal variation that lizards experienced during the year (Tsuji, 1988; Ghalambor *et al.*, 2006; Huey *et al.*, 2009). Finally, absolute values for endurance decreased with latitude which supports the hypothesis that this trait is mainly associated to open environments (Sinervo, 1990; Sinervo and Huey, 1990). On the other hand, maximum velocity was similar in all five populations, probably because sprint speed is commonly associated to escaping behavior (Blumstein, 2010; Stiller and McBrayer, 2013) and predation risk, both factors that may affect these populations in a similar manner.

Although theory suggests wider  $B_{80}$ 's with more variable or unpredictable environments (Stevens, 1989; Snyder and Weathers, 1975; Addo-Bediako *et al.*, 2000; Ghalambor *et al.*, 2006), various studies have obtained mixed results (Lynch and Gabriel, 1987; Angilletta, 2009). Our study reveal differences among the population TPC's, for both endurance and velocity and with respect not only to the  $B_{80}$  but the maximum performance values and optimum ( $T_o$ ). The observed flexibility may be the result of either phenotypic plasticity within the populations, local adaptation to the different environments or both, but further research is needed to explain the mechanisms underneath. In agreement with the theoretical perspective, the highest overall variation was found in the Central site, which coincided with the highest variation in the daily mean operative temperature ( $T_e$ ). The upper thermal limits ( $CT_{max}$  and the upper- $TB_{80}$ ) are considered highly conserved within lineages whereas thermal minima show little conservatism (Kearney *et al.*, 2009; Leal and Gunderson, 2012; Grigg and Buckley, 2013). Higher frequency or magnitude of environmental thermal variation may inflict selection on the lower limits of  $B_{80}$  (lower- $TB_{80}$ ; Levins, 1968; Watson and Hoffmann, 1996). The upper- $TB_{80}$  only differed when comparing endurance between *T. oreadicus* (highest:lowest thermal variation) and the species from MG (lowest:highest thermal variation), and the lower- $TB_{80}$  for both endurance and velocity differed among the studied populations following the same trend as the upper- $TB_{80}$  for endurance.

The effect of precipitation is also observed on  $B_{80}$  and  $T_o$ , but contradicts the results of previous reviews (Clusella-Trullas *et al.*, 2011) in which  $B_{80}$  and  $T_o$  have a positive relation with the variation of precipitation. Precipitation may have implications in the thermoregulatory opportunities of the lizards, which can be estimated by the range and frequency of  $T_e$ . In contrast with  $T_a$ ,  $T_e$  integrates the ambient thermal fluctuation with sun

radiation and convection (Gates, 1980) which may be affected by cloud covers and precipitation. In fact, the daily variation of  $T_e$  was a stronger predictor of the safety margins (SM's) than  $T_a$ . The truth of this observation may be specially expected in lizards that behave as thermoconformers, such as MGt, MGe and TOt (Piantoni *et al.*, unpublished data). These sites are the most extreme environments herein, where the risk of overheating (MG) or opportunities for thermoregulation are too few or absent (Hertz *et al.*, 1993) like in the gallery forest may constrain this behavior for temperature selection. Probably the contradiction between the literature and our results with respect to the positive relation between the variation of precipitation and  $T_o$  is related to the fact that the body temperatures ( $T_b$ 's) in warm and open areas where the risk of dehydration is high, are lower than the selected  $T_b$ 's in less harsh environments (Lorenzon *et al.*, 1999; Hertz, 1992). Overall, wider  $B_{80}$ ,  $SM_{ct}$ ,  $SM_{te}$  and  $SM_{ta}$ , as well as an enhanced endurance capacity may translate into a higher resilience of the populations in a climate change scenario. On the contrary, species like *T. oreadicus* and *T. torquatus* in the northern region of the Cerrado, show the lowest variation in numerous parameters of the TPC's and are currently exposed to high temperatures which also reduces the SM's. An increase in  $T_a$  may carry critical consequences, particularly to *T. torquatus* inhabiting the gallery forest as it behaves as a thermoconformer. At the central Cerrado site, despite the potential higher resilience to environmental changes, lizards are confined to thermoconformity while exposed more frequently to extreme  $T_a$ 's. This combination of factors may result detrimental with a slight increase in  $T_a$ .

In a global warming scenario, where  $T_a$  increases by 3 °C, lizards' initial activity time as well as the hours of activity are expected to change. Lizards may experience minimum  $T_b$ 's necessary to start thermoregulating (Cowles and Bogert, 1944) probably earlier in the morning and may stay active later in the evening. In all studied sites, midday  $T_a$ 's will exceed the thermal *preferenda* of the lizards (upper- $T_{set}$ ) and performance along the day is expected to decay in all populations. Performance may only improve with respect to the current performance in the late afternoon-evening (*e.g.* velocity of *T. torquatus* in the gallery forest and in MG; endurance of *T. catalanensis*). As mentioned before, activity may be shifted to earlier or later hours of the day but that would imply being active in the dark. Particularly at midday,  $T_a$ 's will exceed the upper- $T_{set}$  and a large proportion of the values may even exceed the  $B_{80}$ . Lizards may have to retreat in burrows to avoid dehydration and overheating, or be active at a considerably low performance. Thus, we predict shifts in fitness and a higher local

extinction risk at the northernmost and central sites where the current thermal environment already curtails lizards' performance and constrains the main buffer mechanisms to cope with warming, thermoregulation (Bogert, 1949; Huey *et al.*, 2003). Local adaptation in a warming scenario is incapable of happening for lizards (Angilletta, 2009), especially in the tropical regions (Tewksbury *et al.*, 2008; Huey *et al.*, 2009). Thus, survival of these populations will depend on the plasticity that even being low it may counteract the foreseen changes. We highlight the difficulty involved in predicting future impacts of global warming, particularly on species with flexible ecophysiology, for it has to include climatic and anthropogenic variables as well as consider the variation in the evolutionary responses of the organisms and the plasticity of traits that may buffer external fluctuations.

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Table 1. Data on snout-vent length (SVL) and mass, maximum endurance (A;  $End_{max}$ ; seconds) and velocity (B;  $V_{max}$ ; cm/seconds), optimal temperature ( $T_o$ ), and range ( $B_{80}$ ) and lower and upper values of thermal breaths (lower- and upper-TB<sub>80</sub>), for adults of *T. torquatus* (Clade B; TOt) and *T. oreadicus* (TOo) from Formoso do Araguaia, TO, *T. torquatus* (Clade A; MGt) and *T. etheridgei* (MGe) from Arinos, and MG, and *T. catalanensis* (SP) from Piracicaba, SP.

Population (N)	SVL (mm)	Mass (g)	Maximum performance	$T_o$ (°C)	$B_{80}$ (°C)	Lower-TB <sub>80</sub> (°C)	Upper-TB <sub>80</sub> (°C)	$T_b$ (°C)	Capture performance	Warming scenario performance
<i>(A) Endurance</i>										
TOt (32)	90.5 ± 13	28.7 ± 14.5	106.9 ± 36.5	34.2 ± 5	10.3 ± 4.8	28.6 ± 6.7	38.9 ± 3.6	36.2 ± 1.5	85.6 ± 36.4	80.2 ± 36.8
	90.3 (70-127)	26 (11.5-86.5)	102.1 (55-243)	35.5 (21.4-41.5)	9.9 (2.4-17.5)	28.8 (18.9-39.5)	39.3 (24-43.4)	36.3 (32.2-39.2)	86.1 (0-164)	81.6 (0-191)
TOo (25)	90.5 ± 13	28.7 ± 15	109.9 ± 40.2	37.5 ± 3.3	9.7 ± 3.8	31.7 ± 5	41.4 ± 1.8	37 ± 3.3	98 ± 39.8	82.5 ± 40.5
	90.3 (69.7-128)	26 (11.5-86.5)	105.2 (50.4-181.2)	38 (29-41.9)	10 (2.8-17)	31.7 (20.7-38.3)	41 (33.1-44.3)	38 (30.1-41.3)	95.2 (34.2-216.3)	83.9 (0-155.2)
MGt (16)	100.7 ± 11.2	37.3 ± 12.8	128.4 ± 40.9	31.3 ± 5	11.5 ± 4.7	25.3 ± 6.1	36.8 ± 4.2	35.6 ± 2.8	93.8 ± 39.8	100.4 ± 82.8
	101 (85.1-119)	34.5 (19-62)	112.5 (76-217.2)	28.4 (25-39.5)	13.8 (3.1-16.3)	23 (20-37.1)	36.3 (28.5-42.1)	36.4 (30.4-39.3)	94.7 (30.7-173.4)	86 (15.2-381.2)
MGe (13)	97.8 ± 9.2	32.3 ± 10.6	140 ± 41.6	32.1 ± 5.1	11.6 ± 6.9	25.6 ± 5.1	37.2 ± 6.5	36.2 ± 3.8	104.6 ± 31.8	85.3 ± 33.3
	97.1 (80.4-113)	31 (18-52)	134.5 (87.9-226.7)	32 (23.8-39.1)	12.6 (0-21)	24.8 (18.7-36.1)	39.7 (21.2-42)	37.4 (26.1-39.5)	105.8 (41.2-168.2)	89 (37.5-152.4)
SP (15)	86.9 ± 11.7	23.4 ± 10.4	147.4 ± 70.7	34.9 ± 5.5	10 ± 4.1	29.2 ± 6.6	39.2 ± 3.9	35.7 ± 2	102.5 ± 16.6	79.9 ± 34.2
	88.2 (67.3-116)	21.5 (10-57)	121 (84.9-341.1)	36.4 (27.5-42.2)	9.4 (2.6-16.6)	30.1 (20.3-39.2)	39.6 (32.2-43.7)	36 (31.8-39.3)	98 (76.3-137.2)	86.7 (0-120.9)
<i>(B) Velocity</i>										
TOt (32)	90.5 ± 13	28.7 ± 14.5	121.8 ± 22.5	35.2 ± 3.7	11 ± 4.1	28.9 ± 5.1	39.9 ± 2.9	36.2 ± 1.5	99.2 ± 33.4	92.2 ± 37.2
	90.3 (70-127)	26 (11.5-86.5)	119.6 (83.5-174.2)	35.4 (24.4-42.2)	11.4 (2-16.8)	28.1 (21.7-41.1)	40.2 (27-43.2)	36.3 (32.2-39.2)	103.4 (2.2-162.9)	89.1 (0-159.7)
TOo (25)	78.8 ± 8.9	18.6 ± 7.7	119.2 ± 23.9	35.5 ± 3.3	11.9 ± 4.1	28.7 ± 5.2	40.6 ± 1.6	37 ± 3.3	105.4 ± 23.4	82.2 ± 32.5
	78.1 (62-100.4)	17 (8-45)	118.6 (83.4-186.7)	35.3 (27.9-40.8)	12 (4.7-18.3)	27.5 (20.4-36.3)	40.7 (35.4-43.2)	38 (30.1-41.3)	103.1 (72.4-177.3)	86.1 (0-128.6)
MGt (16)	100.7 ± 11.2	37.3 ± 12.8	109.3 ± 30.1	35.6 ± 2.9	12.8 ± 3.2	28.2 ± 4.5	41 ± 1.3	35.6 ± 2.8	100.3 ± 26.9	96.2 ± 32.1
	101 (85.1-119)	34.5 (19-62)	109.9 (55-160.5)	35.2 (31.8-40.5)	13.1 (7.1-17.2)	27.8 (22.2-35.5)	40.8 (39.4-43.5)	36.4 (30.4-39.3)	102 (53.6-159)	104 (41.7-143)
MGe (13)	97.8 ± 9.2	32.3 ± 10.6	109.7 ± 31.6	36.2 ± 3.1	11.4 ± 4	29.5 ± 5.1	40.9 ± 1.4	36.2 ± 3.8	91.6 ± 34.2	81.9 ± 39.3
	97.1 (80.4-113)	31 (18-52)	103.2 (58.6-169.8)	36.9 (30.1-41.2)	10.8 (5.8-19.4)	30.4 (19-37.4)	40.9 (38.4-43.2)	37.4 (26.1-39.5)	96 (17.8-152.4)	63.7 (33.8-169.8)
SP (37)	87.1 ± 11.2	23.5 ± 9.9	129.3 ± 50.5	36.9 ± 3.6	8.6 ± 3.5	31.8 ± 4.8	40.4 ± 2.9	35.8 ± 2	98.7 ± 49.2	103.8 ± 59.2
	88.2 (67.3-116)	22 (10-57)	131 (58.6-272.8)	37.9 (27-42.1)	8.4 (2.6-15.2)	32.3 (21.9-40.2)	41.1 (30.1-43.7)	36 (31.8-39.3)	88.5 (4.3-205.7)	86.6 (0-244.3)

Table 2. Expected and observed patterns of variation of the safety margins between  $T_o$  and the  $CT_{\max}$  ( $SM_{ct}$ ), the maximum operative temperature ( $T_{e \max}$ ;  $SM_{te}$ ), and the maximum air temperature ( $T_{a \max}$ ;  $SM_{ta}$ ), and the thermal breadths ( $B_{80}$ ) for endurance and velocity with respect to latitude, daily variation of  $T_e$ , and the variation of annual precipitation.

	Expected patterns			Observed patterns					
	Latitude	Daily variation of $T_e$	Variation in annual precipitation	Latitude	Daily variation of $T_e$		Variation in annual precipitation		
	Endurance & velocity			Endurance	Velocity	Endurance	Velocity	Endurance	Velocity
$SM_{ct}$	decreases towards the Equator	increases with variation	increases with variation	MG > TO & SP	increases towards the Equator	<b>increases with variation (MG&gt;SP&gt;TO)</b>	similar, but TO > MG > SP		decreases with variation
$SM_{te}$	increases towards the Equator	increases with variation	increases with variation	MG > TO & SP		<b>increases with variation (MG&gt;SP&gt;TO)</b>	<b>increases with variation (MG&gt;SP&gt;TO)</b>		decreases with variation
$SM_{ta}$				slightly decreases towards the Equator	decreases towards the Equator	similar, but TO & MG > SP	similar, but TO & MG > SP		
$B_{80}$	decreases towards the Equator	increases with variation	increases with variation	similar, but MG > TO & SP	MG > TO & SP, decreases towards the Equator	similar, but MG > TO > SP	TO & MG > SP		decreases with variation, in velocity more accentuated

## FIGURE LEGENDS

Figure 1. Variation among the populations in the thermal performance curves for maximum endurance (s; solid lines) and the correspondent confident intervals (dashed lines) estimated using GAMM: (A) *Tropidurus torquatus* (Clade B) and (B) *T. oreadicus* from Formoso do Araguaia, TO; (C) *T. torquatus* (Clade A) and (D) *T. etheridgei* from Arinos, MG; and (E) *T. catalanensis* from Piracicaba, SP. The black and grey arrows indicate the means of field  $T_b$  and  $T_e$ , respectively. The grey areas specify the lower and upper set-points of the  $T_p$  ( $T_{set}$  range).

Figure 2. Variation among the populations in the thermal performance curves for maximum endurance ( $\text{cm}\cdot\text{s}^{-1}$ ; solid lines) and the correspondent confident intervals (dashed lines) estimated using GAMM: (A) *Tropidurus torquatus* (Clade B) and (B) *T. oreadicus* from Formoso do Araguaia, TO; (C) *T. torquatus* (Clade A) and (D) *T. etheridgei* from Arinos, MG; and (E) *T. catalanensis* from Piracicaba, SP. The black and grey arrows indicate the means of field  $T_b$  and  $T_e$ , respectively. The grey areas specify the lower and upper set-points of the  $T_p$  ( $T_{set}$  range).

Figure 3. Patterns of variation of the (A-C)  $SM_{ct}$ : the safety margins calculated as the difference between  $CT_{max}$  and the endurance  $T_o$  (black circles and solid lines) and the velocity  $T_o$  (white circles and dashed lines); (D-F)  $SM_{ta}$  &  $SM_{te}$ : the safety margins calculated as the interval between the maximum  $T_e$  (black symbols) and  $T_a$  (white symbols), and the endurance  $T_o$  (circles, and solid and dotted lines) and the velocity  $T_o$  (triangles, and dashed and dashed-dotted lines), and (G-I)  $B_{80}$ : the thermal breadths for the endurance (black circles and solid lines) and velocity (white circles and dashed lines) TPC's with respect to latitude (left graphs), daily variation of  $T_e$  (middle graphs), and the annual variation of the precipitation (right graphs) for *Tropidurus torquatus* (Clade B; TOt) and *T. oreadicus* (TOo) from Formoso do Araguaia, TO, *T. torquatus* (Clade A; MGt) and *T. etheridgei* (MGe) from Arinos, MG, and *T. catalanensis* (SP) from Piracicaba, SP.

Figure 4. Impact of climate warming on  $T_b$  and performance of *Tropidurus torquatus* (Clade B; TOt; A-D) and *T. oreadicus* (TOo; E-H) from Formoso do Araguaia, TO: (A-B) Estimated relative performance of TOt before (grey boxes, 2012) and after (white boxes) predicted ambient temperature increase of  $3^\circ\text{C}$ ; (C-D) body temperature of TOt before (2012) and after predicted warming; (E-F) estimated relative performance of TOo before (grey boxes, 2012)



and after (white boxes) predicted ambient temperature increase of 3°C; (C-D) body temperature of T<sub>Oo</sub> before and after predicted warming. In A-B and E-F, the shaded grey rectangle indicates the preferred temperature range of each species, the dashed lines delimit the thermal breadth ( $B_{80}$ ) and the grey solid line specifies the  $CT_{max}$ . Box plots depict the median, interquartile range and range.

Figure 5. Impact of climate warming on  $T_b$  and performance of *Tropidurus torquatus* (Clade A; MGt; A-D) and *T. etheridgei* (MGe; E-H) from Arinos, MG: (A-B) Estimated relative performance of MGt before (grey boxes, 2012) and after (white boxes) predicted ambient temperature increase of 3°C; (C-D) body temperature of MGt before (2012) and after predicted warming; (E-F) estimated relative performance of MGe before (grey boxes, 2012) and after (white boxes) predicted ambient temperature increase of 3°C; (C-D) body temperature of MGe before and after predicted warming. In A-B and E-F, the shaded grey rectangle indicates the preferred temperature range of each species, the dashed lines delimit the thermal breadth ( $B_{80}$ ) and the grey solid line specifies the  $CT_{max}$ . Box plots depict the median, interquartile range and range.

Figure 6. Impact of climate warming on  $T_b$  and performance of *Tropidurus catalanensis* (SP) from Piracicaba, SP: (A-B) Estimated relative performance of SP before (grey boxes, 2012) and after (white boxes) predicted ambient temperature increase of 3°C; and (C-D) body temperature of SP before (2012) and after predicted warming. In A-B, the shaded grey rectangle indicates the preferred temperature range of each species, the dashed lines delimit the thermal breadth ( $B_{80}$ ) and the grey solid line specifies the  $CT_{max}$ . Box plots depict the median, interquartile range and range.

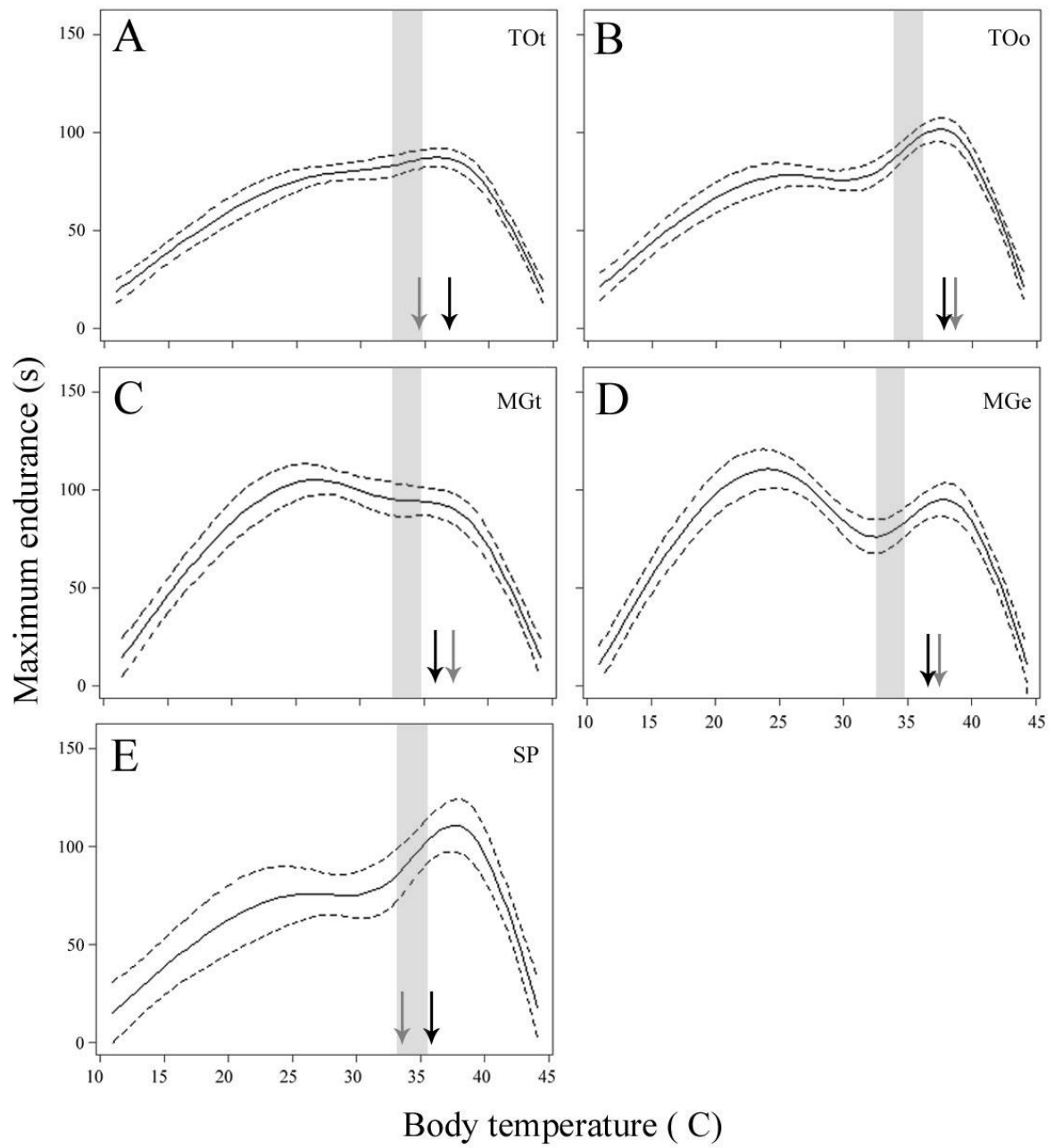


Figure 1.

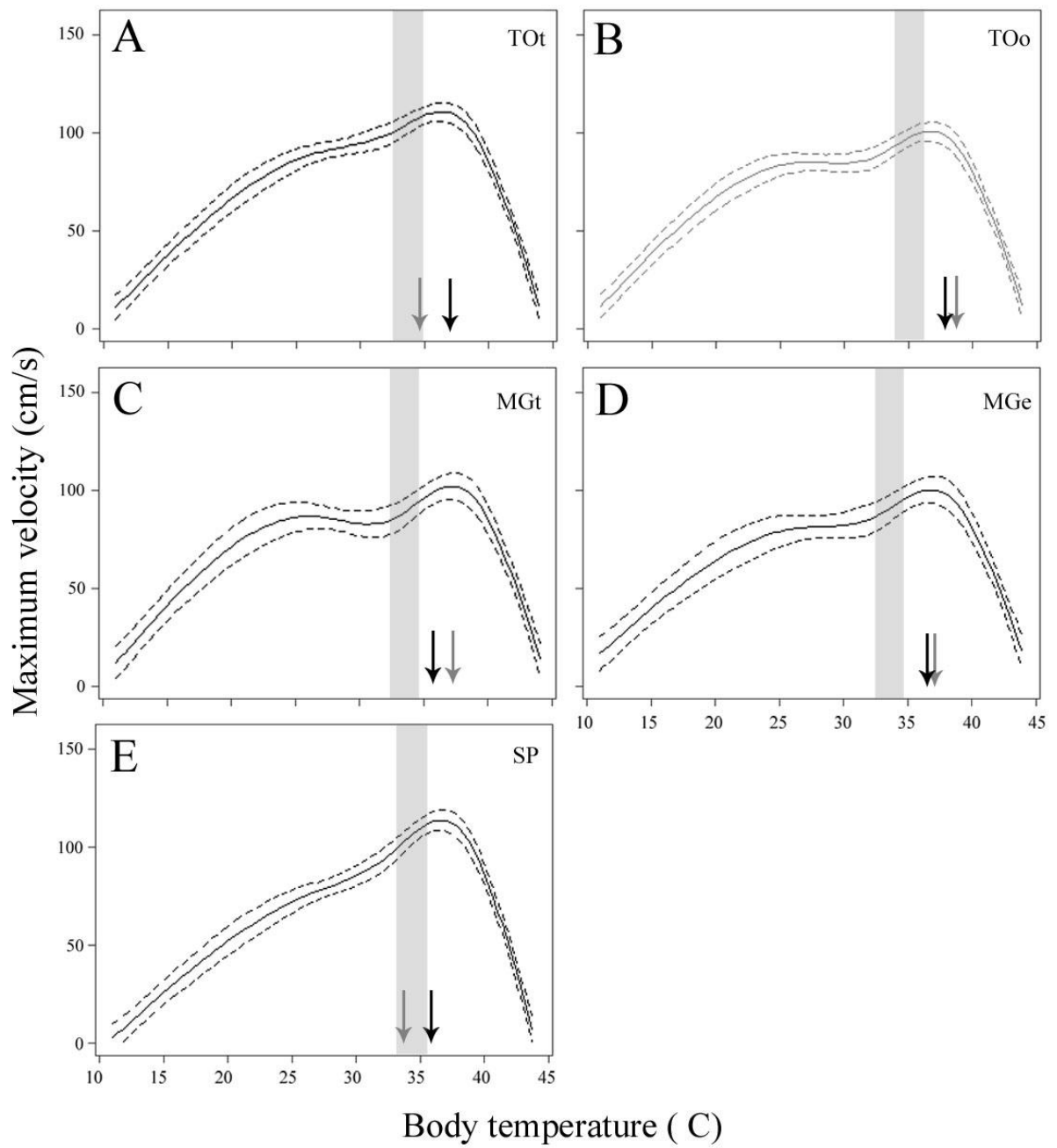


Figure 2.

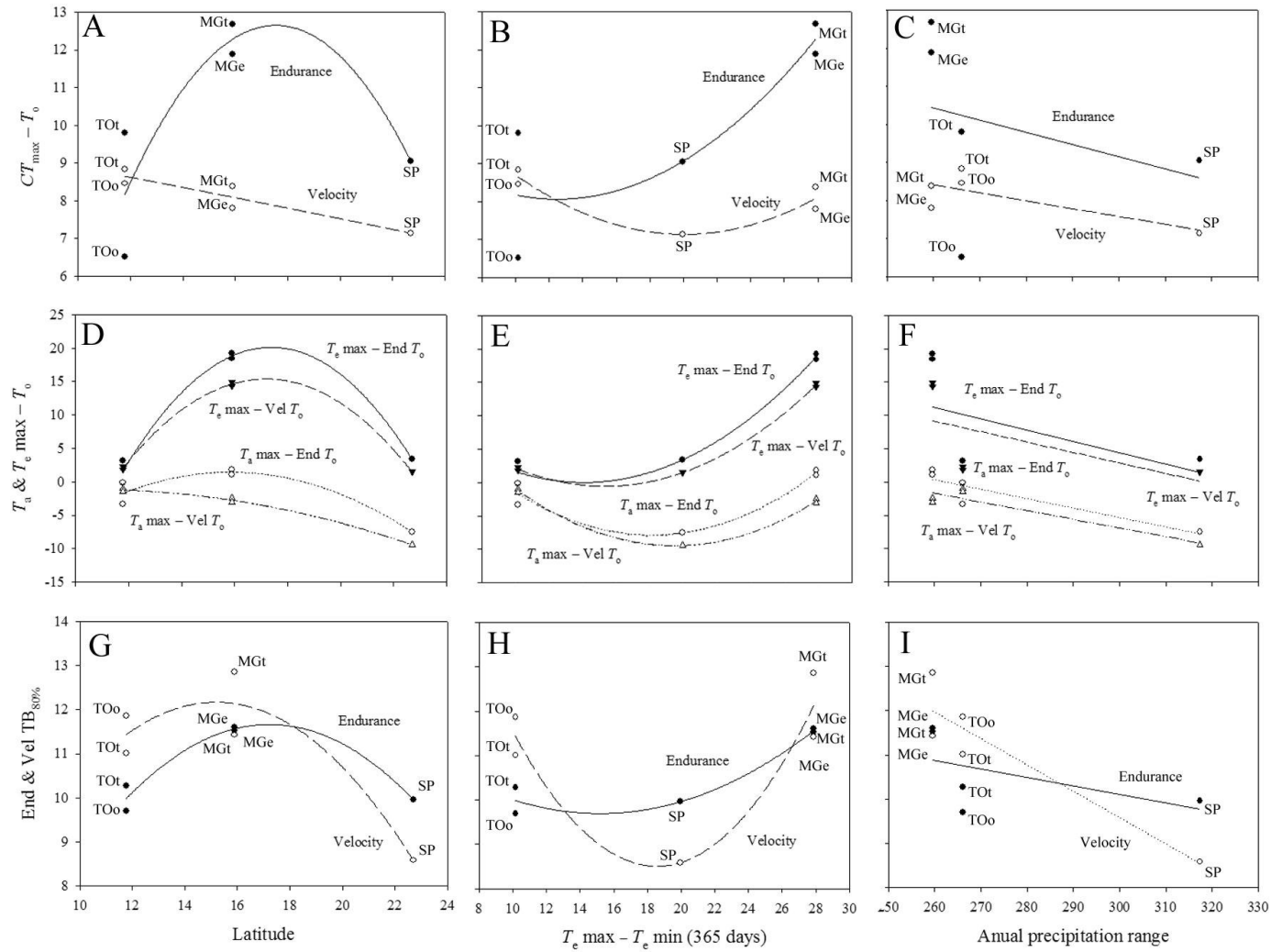


Figure 3.

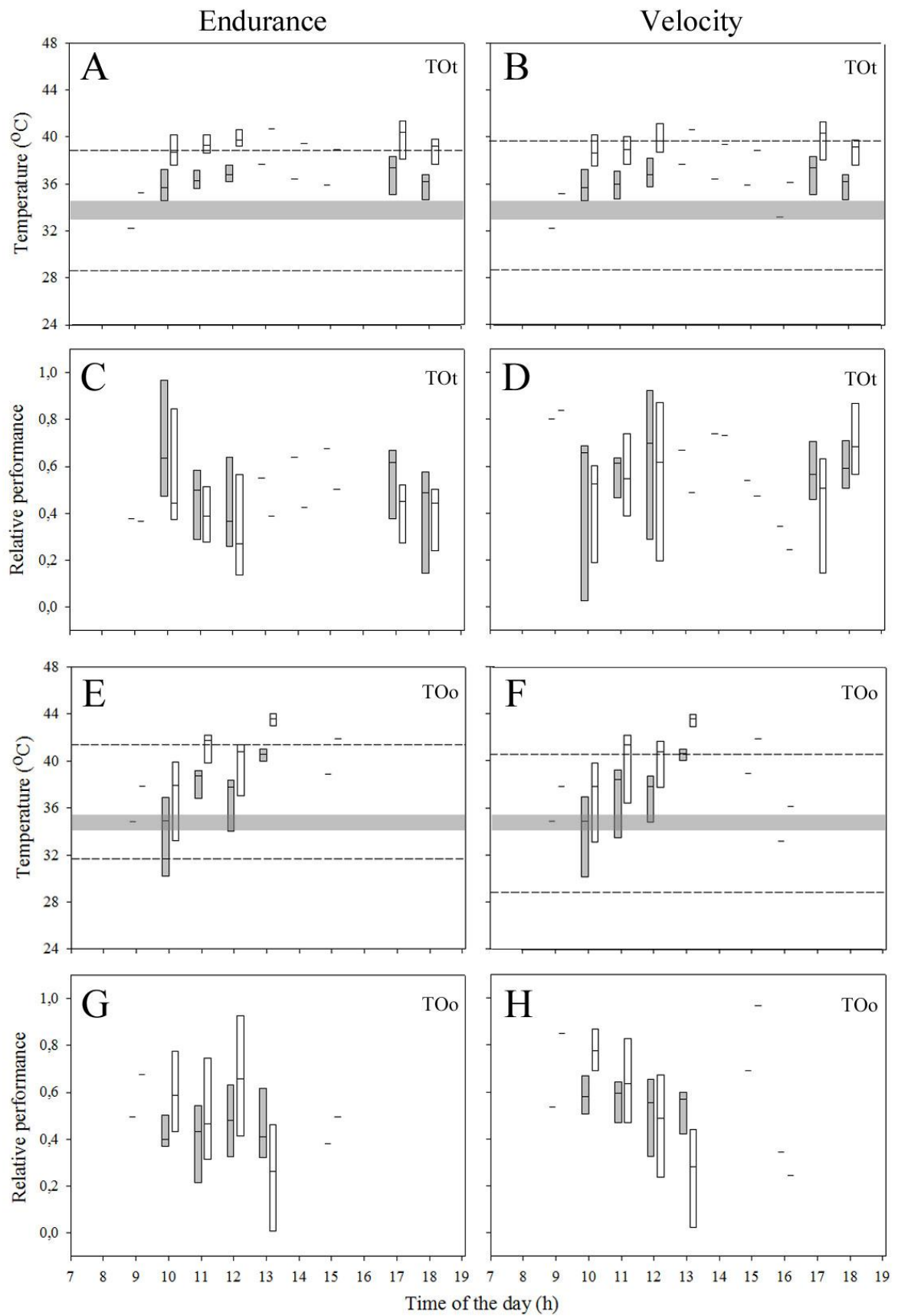


Figure 4.

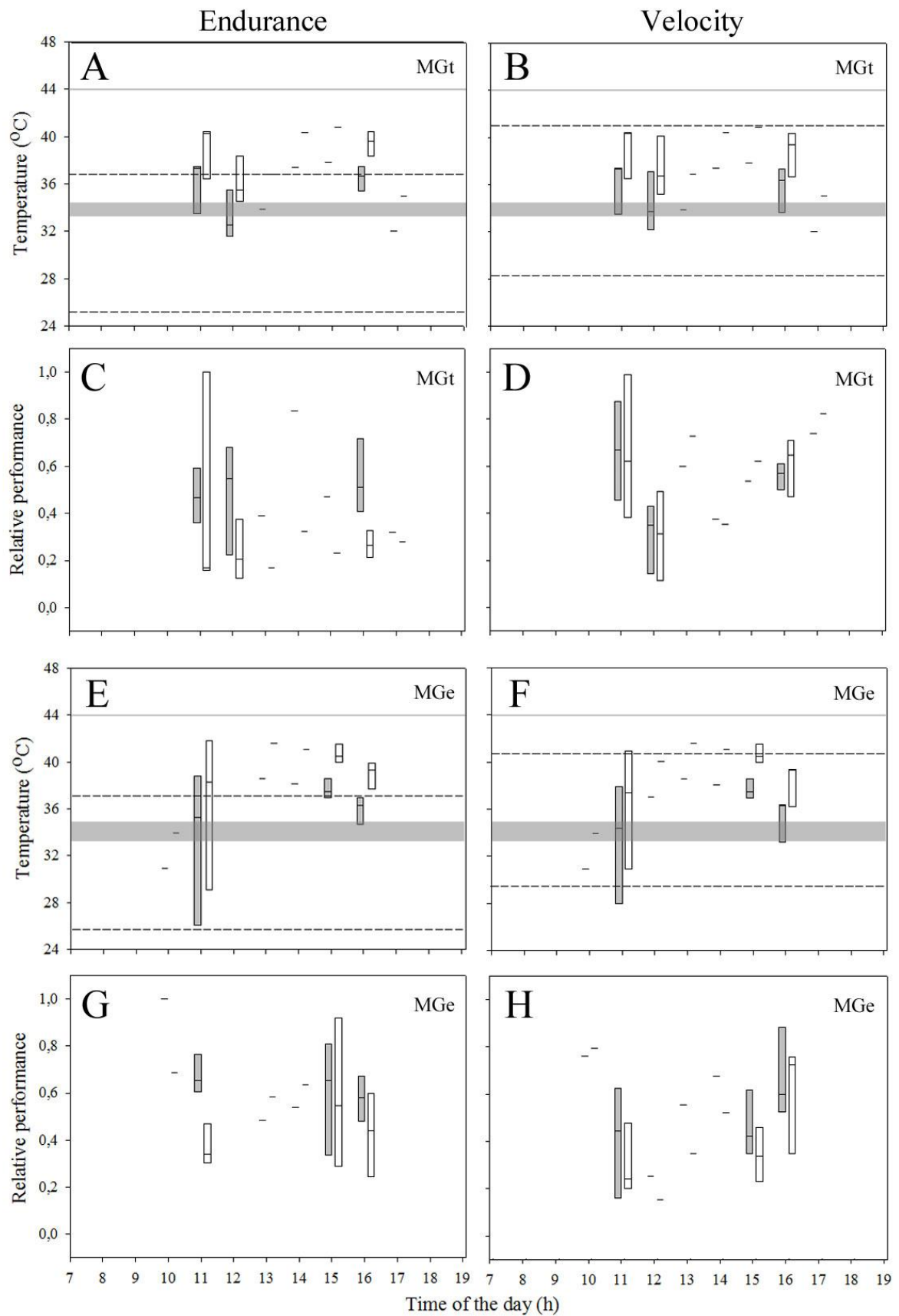


Figure 5.

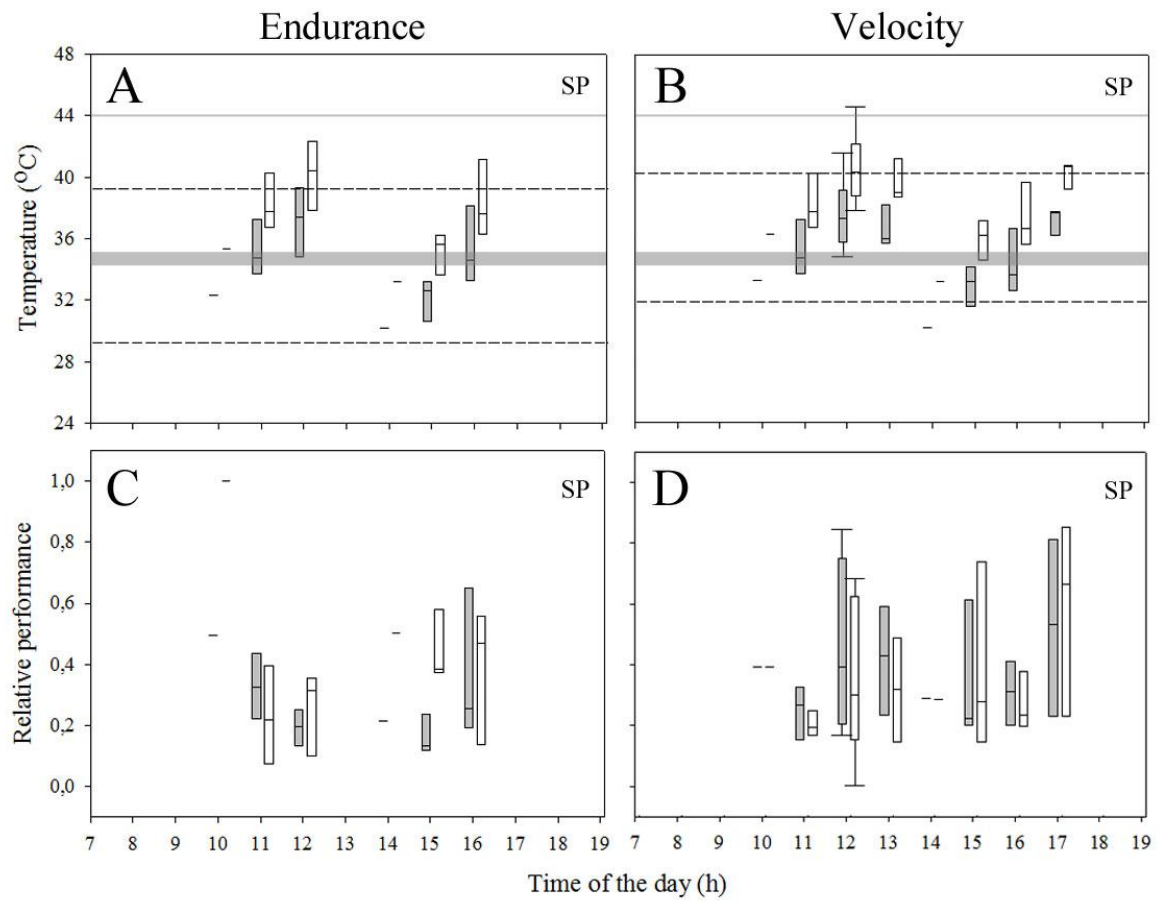


Figure 6.

## SUPPLEMENTAL MATERIAL

Table S1. Comparisons (One Way ANOVA,  $F$  statistic; Kruskal-Wallis One Way ANOVA on Ranks;  $H$  statistic) of snout-vent length (SVL), mass, field body temperature ( $T_b$ ), maximum performance, thermal optimum ( $T_o$ ), endurance thermal breadth range ( $B_{80}$ ) and lower- and upper-values (lower- and upper- $TB_{80}$ ), and the estimates of the capture and warming scenario endurance ( $End_{max}$ ) and speed ( $Vel_{max}$ ) capacity among adults of *Tropidurus torquatus* (TOt) and *T. oreadicus* (TOo) from Formoso do Araguaia, TO, *T. torquatus* (MGt) and *T. etheridgei* (MGe) from Arinos, MG, and *T. catalanensis* (SP) collected in Piracicaba, SP.

	Statistic	$P$ -values
SVL	$F_{4,118} = 12.141$	$\leq 0.001$
Mass	$H_4 = 33.708$	$\leq 0.001$
$T_b$	$H_4 = 9.118$	0.058
$End_{max}$	$H_4 = 13.717$	0.008
endurance $T_o$	$F_{4,100} = 5.146$	$\leq 0.001$
$B_{80}$	$F_{4,100} = 0.601$	0.662
lower- $TB_{80}$	$F_{4,100} = 3.673$	0.008
upper- $TB_{80}$	$H_4 = 17.939$	0.001
Capture endurance	$F_{4,100} = 1.386$	0.245
Warming scenario endurance	$H_4 = 1.017$	0.907
$Vel_{max}$	$H_4 = 3.296$	0.509
velocity $T_o$	$F_{4,122} = 1.211$	0.310
$B_{80}$	$F_{4,122} = 4.845$	0.001
lower- $TB_{80}$	$F_{4,122} = 2.583$	0.041
upper- $TB_{80}$	$H_4 = 3.131$	0.389
Capture velocity	$H_4 = 3.069$	0.546
Warming scenario velocity	$F_{4,118} = 0.556$	0.695



Table S2. Pair-wise multiple comparisons (Holm-Sidak and Dunn's methods;  $P$ -values or asterisk (\*) indicating significant differences,  $P \leq 0.05$ ) of (A) snout-vent length (SVL) and mass; (B) maximum endurance ( $End_{max}$ ) and endurance thermal optimum ( $T_o$ ); (C) lower- and upper- $TB_{80}$  of the TPC's of endurance; and (D) lower- and upper- $TB_{80}$  and the  $B_{80}$  of the TPC's of velocity among adults of *Tropidurus torquatus* (TOt) and *T. oreadicus* (TOo) from Formoso do Araguaia, TO, *T. torquatus* (MGt) and *T. etheridgei* (MGe) from Arinos, MG, and *T. catalanensis* (SP) collected in Piracicaba, SP.

	TOt	TOo	MGt	MGe	SP
(A) SVL and mass					
TOt		3.944*	2.995*	1.981; 0.04	1.304; 0.195
TOo	3.357*		6.153*	4.984*	2.851*
MGt	2.362	5.058*		0.711; 0.478	4.117*
MGe	1.411	3.977*	0.695		2.997*
SP	1.574	1.993	3.687*	2.617	
(B) $End_{max}$ and endurance $T_o$					
TOt		0.0917	1.721	2.664	2.578
TOo	2.59		1.569	2.49	2.395
MGt	1.983	4.056*		0.935	0.779
MGe	1.343	3.313*	0.444		0.183
SP	0.501	1.637	2.126	1.579	
(C) Lower- and upper- $TB_{80}$ (endurance TPC's)					
TOt		1.921	1.775	1.512	0.354
TOo	2.957		3.299*	2.954*	1.231
MGt	1.522	3.921*		0.124	1.82
MGe	0.35	2.646	0.94		1.604
SP	0.618	1.825	1.835	0.815	
(D) Lower- $TB_{80}$ and $B_{80}$ (velocity TPC's)					
TOt		0.113	0.460	0.374	2.484
TOo	0.838		0.346	0.448	2.433
MGt	1.576	0.808		0.706	2.475
MGe	0.332	0.335	0.999		1.479
SP	2.626	3.313*	3.731*	2.305	

\* The differences in the mean values among the treatment groups are greater than would be expected by chance; there is a statistically significant difference ( $P = 0.046$ ). Power of performed test with  $\alpha = 0.050$ : 0.425. Nevertheless, Pairwise Multiple Comparison Procedures (Holm-Sidak method) did not show significant differences among the populations.

Table S3. Results of the paired  $t$ -tests ( $t$  statistic) and the Wilcoxon signed rank tests ( $Z$  statistic) between the maximum endurance ( $End_{max}$ ; A) and velocity ( $Vel_{max}$ ; B) estimated for the time of capture and the expected performance in a warming scenario (with an increase of  $T_a$  by 3 °C), and the difference between mean values of  $End_{max}$  and  $Vel_{max}$  after warming.

Populations ( $N$ )	Statistic	$P$ -values	Max performance & performance before - after warming
<i>(A) <math>End_{max}</math></i>			
TOt (32)	$Z = -1.795$	0.074	102.1 & 86.1-81.6 s
TOo	$Z = -2.146$	0.033	105.2 & 92.1-80.3 s
MGt	$Z = -0.365$	0.728	112.5 & 99.8-95 s
MGe	$t_{13} = 2.668$	0.019	140 & 109.1-83.7 s
SP	$Z = -1.445$	0.151	121 & 73.9-57.2 s
<i>(B) <math>Vel_{max}</math></i>			
TOt	$t_{32} = 1.665$	0.019	121.8 & 99.2-92.2 cm/s
TOo	$t_{25} = 4.022$	$\leq 0.001$	119.2 & 105.3-79.2 cm/s
MGt	$t_{21} = 0.196$	0.019	109.3 & 91.4-90.8 cm/s
MGe	$t_{13} = 2.073$	0.059	109.7 & 88.7-78.5 cm/s
SP	$Z = 1.031$	0.305	131 & 58.1-59.2 cm/s

Table S4. Estimate endurance (A) and velocity (B) capacity at the moment of capture and in a warming scenario where  $T_a$  would increase by 3°C relative to each population's maximum performance (described in Table 1) for adults of *T. torquatus* (Clade B; TOt) and *T. oreadicus* (TOo) from Formoso do Araguaia, TO, *T. torquatus* (Clade A; MGt) and *T. etheridgei* (MGe) from Arinos, and MG, and *T. catalanensis* (SP) from Piracicaba, SP. The impact of warming corresponds to the difference between the after and before warming percentages.

Populations	Relative performance capacity before warming (%)	Relative performance capacity after warming (%)	Impact of warming on performance (%)
<i>(A) Endurance</i>			
TOt	80	75	5
TOo	89.2	75	14.2
MGt	73.1	78.2	-5.1
MGe	74.7	60.9	13.8
SP	69.5	54.2	15.3
<i>(B) Velocity</i>			
TOt	81.4	75.7	5.7
TOo	88.4	67	21.4
MGt	91.2	88	3.2
MGe	83.5	74.7	8.8
SP	76.3	80.3	-4

## CHAPTER 4

### Short-term benefits and long-term risks of becoming Godzilla

*To be submitted to PNAS*

*(Co-authored with Carlos A. Navas and Nora R. Ibarriengoytía)*

## ABSTRACT

For the last decades, climatic envelope models have predicted the extinction of populations to whole lineages with low dispersal abilities or options and with low physiological capabilities for adjustment to new environments. Very few studies on individual responses to climate change have been published though. Herein, we report on the geographic and temporal variation of growth of a South American lizard, *Tropidurus torquatus*, and results are analyzed considering the possible eco-physiological responses to the global warming scenario. We used skeletochronology to estimate individual age, growth rates, age at sexual maturity and longevity in specimens from five populations at different geographical and temporal scales: two populations from Tocantins, northern Cerrado (TO1966 and TO2012, from 1966 and 2012, respectively), and two populations from Minas Geras (MG1964-6 and MG2012, from 1964-6 and 2012). Populations displayed similar bone arrangement and the growth patterns fitted a sigmoid curve. The populations attained reproductive size at a minimum age of 3 yr in MG2012, and 5 yr in TO2012. The youngest adults within the 1966 populations were 5 yr old in MG1964-6 and 6-7 yr in TO1966. We found no differences in juvenile growth rates or in body size between juveniles of up to 3 yr of age in MG2012 and TO2012. However, juvenile growth rates were higher at MG2012 than at TO2012. Our results suggest that higher temperatures positively affect growth, denoting that global warming might shorten the number of hours that offer beneficial temperatures for metabolic processes to be complete. Long-term exposure to this scenario could affect the fitness of the species unable to cope with the rate of alteration of its habitat. Nevertheless, to achieve a better prediction of species persistence, one will probably need to combine both habitat and individual-based approaches.

KEY-WORDS: Growth, fitness, global warming, life-history trade-offs.

## INTRODUCTION

Global mean surface temperature (GMST) has increased about 0.89°C (0.69-1.08) since 1901 from which 0.72°C (0.49-0.89) rise occurred between 1951 and 2012 (IPCC, 2013), and most scenarios support further increase. Scenarios by 2071-2100 applied to the southern Amazonian region, and to the west central areas of Brazil are compatible with an increase in mean air temperature of 6°C and a decrease in rainfall by 5-20%, (Marengo *et al.*, 2009; IPCC, 2013). Elevated ambient temperature ( $T_a$ ) are associated to changes in the precipitation regimes and in season length (Meehl *et al.*, 2007; Adler *et al.*, 2008; Bradshaw and Holzapfel, 2008; Zhou *et al.*, 2009), and interact with stressors, like habitat modifications, destruction and fragmentation (Trenberth *et al.*, 2007; Brook *et al.*, 2008; Chown *et al.*, 2010; Harley, 2011; IPCC, 2013). The negative influence of an increase of  $T_a$  on biodiversity and the interactions between organisms and their competitors, predators, parasites, and mutualists (Buckley and Roughgarden, 2006; Gilman *et al.*, 2010; Huey *et al.*, 2012) may eventually affect food availability (Campero *et al.*, 2008), and have been linked to mechanisms acting at various levels of organization, but ultimately influencing individual behavioral and eco-physiological performance (Garland and Else, 1987; Andrews *et al.*, 2000; Adolph and Pickering, 2008). Nevertheless, climate warming is no necessarily deleterious, and exerts different impacts among taxa.

Many lineages of ectothermic vertebrates are sensitive to variation in  $T_a$  which, beyond certain ranges, may decrease their behaviors and physiological performance. Furthermore, in some lineages altered thermal regimes may change the whole expressed phenotype (Adolph and Porter, 1993). For example, lizards' reproductive phenology, longevity, and growth rates are considered *labile* and change in response to variations of  $T_a$  (Adolph and Porter, 1993; 1996; Angilletta, 2009).

Whereas some lineages such as *Lacerta vivipara* and *Homonota darwini* may benefit from a short-term increase of  $T_a$  (Chamaillé-Jammes *et al.*, 2006; Kubisch *et al.*, 2012) others are being lead towards partial or complete extinction by climate warming, particularly in the tropics (Huey *et al.*, 2009; Sinervo *et al.*, 2010). Studies on the effects of global warming on life-history traits, mainly on phenology, have demonstrated the species and populations often respond in a nonlinear way which depends not only from intrinsic characteristics of the organisms but also the environment that may buffer or strengthen the effects (Chamaillé-

Jammes *et al.*, 2006; Kubisch *et al.*, 2012; Gutierrez *et al.*, 2013). Higher  $T_a$ 's could also shift behavioral and physiological performance to suboptimal levels, restricting time for activity (*e.g.* for foraging and digesting to allocate energy into growth and reproduction; Huey, 1991; Dunham, 1993; Miles, 1994; Angilletta, 2009; Kearney *et al.*, 2009; Moritz *et al.*, 2012; Seebacher and Franklin, 2012). The differences among populations or species may have basis on the absolute temperature that best fit activity and the ability of individuals to compensate thermal shifts.

Active thermoregulating lizards can maintain their  $T_b$  within narrow ranges despite the temperature shifts and changes in thermal regime associated with temporal and geographic variation (Bogert, 1949). Yet, the  $T_b$  during inactivity and the time possibly allocated to activity at preferred  $T_b$  can vary due to thermal constrains (Adolph and Porter, 1993). Despite the unambiguous impact of sub- and supra-optimal  $T_a$ 's on performance, a whole family of additional impacts are possible for thermal regime influences metabolic trade-offs. For example, co-specific lizards that occupy and are active in different thermal environments can exhibit the same  $T_b$  but differ in the total time of exposure to predators and solar radiation, time of activity for foraging and mating, and hence, show variations in growth patterns (Grant and Dunham, 1990). Metabolic costs like pursuing prey and mating should increase with daily activity time together with an increase in energy assimilation that is maximized at or near the activity  $T_b$  (Porter and Tracy, 1983; Sinervo and Adolph, 1989). The assimilated energy that is not expended will be allocated to reproduction, growth and storage (Adolph and Porter, 1993). For that reason, longer activity seasons and appropriate  $T_a$ 's for processing the food while inactive would allow lizards to grow faster and attain sexual maturity at a younger age (Tinkle and Ballinger, 1972; Ballinger 1983; Grant and Dunham, 1990). On that account, an increase in  $T_a$  can constrain the activity time of a lizard, especially in tropical warm environments, and consequently affect growth and reproduction (Sinervo *et al.*, 2010). Therefore, hours of restriction and energy balance are interdependent variables, so that, as hours of restriction increase due to high temperatures, the metabolic cost of inactivity increases, whereas energy input decreases. We need to consider that the life history of an organism is not fixed and can adjust along with the changing habitat (Radder, 2006). The rate in which the organism can respond to these changes will determine its survival (Huey *et al.*, 2012).

Herein we aim to determine the direction and magnitude of change in key life history traits associated to growth with the geographical and temporal variation of  $T_a$  in the widespread tropical lizards *T. torquatus*, and whether plasticity in phenology allows the species to adjust warming as a consequence of climate change. Based on the increment in  $T_a$  recorded over the last decades in the chosen localities, the latter extent of variation provides an estimate of the sensitivity of the populations to environmental change as well as an indication of the potential evolutionary response of a population to adjust to novel environmental conditions. A more specific hypothesis is that rising temperatures and changing precipitation patterns over the last decades have constrained time of activity and consequently affect individual growth. The variation along the latitudinal gradient is expected to mimic the expected temporal change. We take two broad approaches to test this hypothesis. Firstly, we estimate spatial variation of growth rates, age at sexual maturity, longevity, and bone growth during ontogeny between two populations from northern and Central Brazilian Cerrado. Second, we estimate the temporal variation of growth rates, age at sexual maturity, longevity, and bone growth during ontogeny at each site over a 40-year period.

In *Tropidurus torquatus* (Wied-Neuwied, 1820), body size and other life-history traits, like clutch size and the length of the reproductive season, were found to be geographically variable and dependent on climatic conditions (Rodrigues, 1987; Kiefer *et al.*, 2005; Wiedenhecker *et al.*, 2002). The variability in these traits apparently involves phenotypic plasticity. This plasticity may be evolved, and be part of an adaptive trend related to environmental variability. Thus, this species a good model for investigating plasticity as a buffering mechanism to global warming.

## MATERIALS AND METHODS

### *1. The species and its characteristics in the Brazilian Cerrado*

*Tropidurus torquatus* has been described as the species with the broadest geographic distribution of the genus which ranges throughout the Cerrado and Atlantic Forest biomes of Brazil (Rodrigues, 1987), and includes populations that differ in various aspects of their ecology (Wiedenhecker *et al.*, 2002; Kiefer *et al.*, 2005, 2008; Gomides *et al.*, 2006; Ribeiro *et al.*, 2008), and behavior (Kiefer *et al.*, 2007). A recent study on its phylogeny (Sena, unpublished data) has separated the populations of the Cerrado from the Atlantic Forest which coincides with the observations of ecophysiologicalists'. The Cerrado is a mosaic of



physiognomies that range from open grass fields to forested formations (wooded savannas and gallery forests along the rivers) which seasonal climate is determined by dry winters and wet summers (Wiederhecker *et al.*, 2002). In the southern and central parts of the biome, the species is commonly found in urban areas, while in the North, it seeks cooler microhabitats in gallery forests along the rivers (personal observation).

Continental specimens present larger body size than in the littoral populations (Rodrigues, 1987). Newborns emerge at a snout–vent length (SVL) of around 30 mm. Females reached sexual maturity at about 65 mm SVL, whereas males became sexually mature at 70 mm SVL (Wiedenhecker *et al.*, 2002). Males are usually larger and heavier than females (Vitt and Goldberg, 1983; Giaretta, 1996; Wiedenhecker *et al.*, 2002) and are highly territorial (Wiedenhecker *et al.*, 2002). In the Cerrado biome, females lay clutches of six eggs on average up to three times per reproductive season (August-February, Wiedenhecker *et al.*, 2002).

Although *T. torquatus* is clearly a visually oriented sit-and-wait predator (Arruda *et al.*, 2007) and its diet includes plant material (Siqueira *et al.*, 2012). The species' diet varies between the dry and rainy seasons, similarly to the diet of the lizards inhabiting the coastal *restingas* that is influenced by seasonal rainfall variations (Van Sluys, 1995; Rocha, 1996; Gadsden and Palacios-Orona 1997; Fialho *et al.*, 2000).

## 2. Study sites and specimens

We chose two sites separated by 590 km in the Brazilian Cerrado biome: Arinos, Minas Gerais (hereafter referred as MG: central site, 15°54'36" S, 46°06'0" W; 519 m a.s.l.), and Formoso do Araguaia, Tocantins (hereafter referred as TO: northern site, 11°48'39.11" S, 49°31'29.27" W; 230 m a.s.l.). We collected 34 specimens in MG (March, 2012), and 30 specimens in TO (September, 2012) by hand or by noose. We registered body temperature ( $T_b$ ) 30 sec. after capture using a Sper Scientific data logging thermometer and probes. In the laboratory we recorded the snout-vent length (SVL; caliper Mitutoyo CD-6" CX  $\pm$  0.01 mm) and the body mass (Pesola spring scale of 10 and 100  $\pm$  0.5 g) for each lizard. We included 19 juveniles that were born at the laboratory soon after capturing the females MG2012 ( $n = 6$ ) and TO2012 ( $n = 5$ ). The newborns belonging to MG2012 and TO2012 did not reach the sixth months of life.

For the temporal comparisons we selected museum specimens captured in the 1960s from localities that were not more than 120 km from the collecting sites. Museum samples were loaned by the Herpetological Collection of the Museum of Zoology of the University of São Paulo (MZUSP) and consisted in eleven specimens captured in 1964 in Arinos, Buritis (15°37'33" S, 46°25'28" W; 556 m a.s.l.; 40 km NW from MG2012) and Unaí (16°07'54.91" S, 46°54'21.996" W; 684 m a.s.l.; 64 km SW from MG2012), Minas Gerais (MG1964-6), and 21 specimens collected in 1964 and 1966 in Barra do Tapirapes, Tocantins (TO1966; 11°20'19" S, 50°40'28" W; 200 m a.s.l.; 120 km W from TO2012). Sample sizes were determined by the availability of specimens at the museums, which was a limiting factor when choosing the site for study. Although apparently small, the sample size for the central site collected in 1960s explain the growth pattern and is representative of the population, as the size gradient for females and males is wide and varied.

### 3. Climatic data

Data was obtained from Instituto Nacional de Meteorologia (INMET - <http://www.inmet.gov.br/portal/index.php?r=bdmep/bdmep>) for the nearest national weather stations for each collecting site located in Arinos, Minas Gerais (15°54'36" S, 46°06'0" W; 519 m a.s.l.) at MG, and Peixe, Tocantins (11°50'28.89" S, 48°33'31.77" W; 242 m a.s.l.), approximately 100 km from TO. To determine the climatic differences between sites we compared monthly means of daily mean, maximum and minimum  $T_a$ , cloud cover and precipitation registered over the 1995-2012 period, which corresponds to the years of life of the oldest specimen collected for this study.

For the geographical comparison and in order to analyze the lizards' thermal microenvironment and the thermoregulation opportunities we used daily means of maximum  $T_a$  as the best descriptor of temperature variation (Huey, 1982) and we collected operative temperatures ( $T_e$ ) that represent the "null" distribution of  $T_b$  that non-regulating animals would experience in their microhabitats (Heath, 1964; Grant and Dunham, 1988; Bakken, 1992; Hertz, 1992; Dzialowski, 2005; Angilletta, 2009). Data logger connected to four plastic models were disposed in potential microenvironments that lizards might occupy at each locality over one year (from March, 2012 to March, 2013 in MG, and September, 2012 to October, 2013 in TO). Size and color of the models were determined based on the calibration (following Medina *et al.*, 2009) against real specimens simultaneously to register the

temperatures of both the models and the lizards.  $T_e$  may characterize more accurately the thermal environment of the lizards but, no specific data can be obtained retrospectively as this may be speculative. Thus,  $T_e$  was only used in the geographical comparisons.

For temporal comparisons within the sites we analyze warming trends in MG and TO using historical records for the 1976-2014 period, as 1976 was the oldest data available registered by the INMET. This year was also reported as the start-point of the sharp increase of global temperature by Intergovernmental Panel on Climate Change (IPCC, 2001).

#### *4. Histology, bone measurements, and age determination*

We anesthetized and killed the specimens with an intraperitoneal injection of 0.5 mL of hypnol. We dissected one leg of each animal and removed the femur without damaging the tissues. We processed the pieces using the skeletochronological technique as suggested by Leclair and Castanet (1987): 1) decalcification of the samples in a 4% EDTA solution for approximately 3 days, depending on size; 2) dehydration using increasing ethanol concentrated solutions and clearing with xylene; 3) embedding in paraffin during 24 h in a heater at 60°C; 4) cross-sectioning at mid-diaphyseal level (5 to 8  $\mu\text{m}$ ); and 5) staining with hematoxylin and eosin.

Bone sections were analyzed under an optic microscope (TIM-2008-CCD, Opton, DF, Brazil) equipped with a High Performance CCD Camera. We took digital pictures at different magnifications (x40, x100, and x400) and used the software TSVIEW 7 to measure the variables proposed by Leclair and Castanet (1987): (1) minimum and maximum radius from the center of the medullar cavity, (2) minimum and maximum diaphyseal diameter, (3) estival-layers or ring thickness, and (4) the number of lines of arrested growth (LAGs) which corresponds to the winter growth. The average of the minimum and maximum radius of each variable was calculated to minimize the asymmetry of the bone sections and medullar cavity.

When endosteal resorption had taken place, estimated age was calculated using the size of the first growth marks of juveniles in order to back-calculate the number of rings removed following Piantoni *et al.* (2006). In those cases the number of reabsorbed rings was added to the number of observed rings.

### 5. Body size, individual age and growth curves

We determine the growth curve for each population as the best fitted curve (highest  $r^2$  and lowest AIC) that described individual SVL *vs.* age using the Table Curve 2D v5.01 software. We calculated growth rates as the derivatives of the curve of SVL *vs.* age. Then, we obtained specific growth rates dividing the growth rates by the SVL of each estimated age group.

### 6. Statistical analyses

We used Sigma Stat 3.5<sup>®</sup>, and Sigma Plot 10.0<sup>®</sup> (Systat Software Inc., USA/Canada) to analyze the data. We analyzed the differences between the mean values of two samples using unpaired and paired *t*-tests and the nonparametric equivalents Mann-Whitney and Wilcoxon Signed Rank tests. For more than two samples we used one-way ANOVA, and Holm-Sidak method as a post hoc test. The correlation between  $T_a$  and  $T_e$  was tested Spearman's method. The assumptions of normality and homogeneity of variance for parametric procedures were tested using Kolmogorov-Smirnov and Levene's tests, respectively.

## RESULTS

### 1. Study sites and climatic data

In MG, *Tropidurus torquatus* is commonly found in urban areas whereas in TO, it occupies the gallery forests along the rivers. We observed a clear difference among the climatic data for each locality. Monthly means of number of days with precipitation, total precipitation, maximum, mean and minimum environmental temperatures ( $T_a$ ) registered since 1995 were lower in MG than in TO (Tables S1 & S2; Figures 1 & 2).

Monthly means of the operative temperature ( $T_e$ ) collected during 2012 and 2013 were higher in MG than in TO (Tables S2 & S3; Figure 1D). Mean  $T_e$  was correlated to the monthly means of daily maximum, mean and minimum  $T_a$ 's in both sites, except for the maximum  $T_a$  in TO (Table S4). Mean values of  $T_e$  resulted lower than the maximum  $T_a$ 's but higher than the mean and minimum  $T_a$ 's (Tables S3 & S5). Mean  $T_e$  significantly predicted maximum, mean and minimum  $T_a$ 's (Table S6D; Figure 3).

Since 1976, monthly means of maximum, mean and minimum  $T_a$  increased between 0.9 to 1.7 °C in both MG and TO (Spearman rank order correlations: MG, maximum  $T_a$ :  $r_{(380)} = 0.21$ , mean  $T_a$ :  $r_{(232)} = 0.19$ , minimum  $T_a$ :  $r_{(367)} = 0.16$ ; and TO, maximum  $T_a$ :  $r_{(449)} = 0.27$ , mean  $T_a$ :

$r_{(450)} = 0.22$ , minimum  $T_a$ :  $r_{(451)} = 0.27$ ;  $P \leq 0.001$ ; Table S6A; Figure 4A-C). Mean precipitation did not vary significantly (Spearman rank order correlations: MG,  $r_{(405)} = -0.05$ ; and TO,  $r_{(451)} = -0.05$ ;  $P \geq 0.247$ ) although the absolute values decreased between 13.2 to 26.2 mL in both sites (Table S6A; Figure 4D).

## 2. Histology, bone measurements, and age determination

We observed a similar bone pattern in the four samples that consisted in lamellar bone with very low density of blood vessels (Figure 5A-B). Lines of arrested growth (LAGs), which in *T. torquatus* correspond to the dry season, were strongly stained by hematoxylin in 92% of the sample and appeared between lighter and thicker growth rings that corresponded to summer growth periods (Figure 5A-B).

In newborns hatching lines divided the cortex in two different growth zones: the embryonic bone next to the marrow and the first growth ring that corresponded to the first activity season (Figure 5A-B). LAGs were present in animals born in captivity ( $n = 4$ ) that spent one dry season in terraria under an artificial photoperiod of LD 12:12, light from 07:00 till 19:00 h and constantly provided with water and food *ad libitum* and a heating source for thermoregulation. In young animals the distance between LAGs were larger than in adults and became narrower after sexual maturity.

Medullar radius increased with SVL in femurs of all four samples (Table S6B). Soon after birth, medullar resorption starts removing up to two rings in juveniles, from two to five rings in females and from one to seven rings in males (Table 1; Figure 6). Thus, we back calculated the number of absent LAGs in order to estimate the age by adding the number of reabsorbed rings to the number of observed rings (Table 1). Sexual maturity was achieved earlier in MG2012 at the age of three, and in TO2012 at the age of five. The museum samples had only one juvenile of three years from MG1964-6. The youngest adults from MG1964-6 were two years older than the young adults from MG2012. Also, in TO1966, the youngest adults were one to two years older than in TO2012 sample (Table 1). Based on these results, sexual maturity would be reached during the third year in MG2012, the fifth year in TO2012 and MG1964-6 and the sixth-seventh year in TO1966.

## 3. Body size

Only one juvenile of MG1964-6 could be included in the analyses and none from TO1966

was found in the collections, which hampered the comparisons. Nevertheless, they presented a consistent size range (Table 1). Adults, females and males were larger in MG2012 than in MG1964-6 but no differences in SVL of adults, females and males between TO2012 and TO1966 (Tables 1, S7 & S8). Overall, males were larger than females although the difference was not significant in MG1964-6 (Tables 1 & S7).

#### 4. Individual age

With respect to estimated body size at each age, females between the fifth and seventh year were smaller in TO2012 than in MG2012 (Table 2). Between the fifth and tenth year males were smaller in TO2012 than in MG2012 (Table 2). Females and males between five and eight years old were larger in MG2012 than in MG1964-6, although the difference between males was not significant (Table S7). Females and males between six and ten, and between nine and 17 years, respectively, were larger in TO2012 than in TO1966 (Table S7).

#### 5. Growth curves

The relationship between estimated age and SVL in all four samples fitted a sigmoid regression (Table S6C; Figure 7). Between the first and the eleventh year, growth curves indicated differences in body size at each age among MG2012 ( $89.2 \pm 26.9$  mm) and TO2012 ( $75.1 \pm 23.2$  mm; Tables 2 & S7D). Although, specific growth rates during those years did not differ among populations absolute values they suggested that lizards in TO2012 grew slightly faster [median = 0.0981 (mm/year)/mm] than in MG2012 [median = 0.0685 (mm/year)/mm]; Tables 2 & S7D; Figure 8).

The specific growth rates indicated that juveniles grew faster than adults in both sites (Tables 2 & S7D). Estimated growth rates in juveniles younger than 4 years were higher in MG2012 than in TO2012; Tables 2 & S7E; Figure 8). Adults of five to eleven years old showed a similar specific growth rate in MG2012 and TO2012 (Tables 2 & S7D; Figure 8). MG2012 and MG1964-6 shared similar estimated and specific growth rates between the years of one and nine (Table S7D-E; Figure 8). Estimated and specific growth rates in TO2012 between the ages of one and 17 were significantly higher than in TO1966 (Table S7D-E; Figure 8).

Regarding sex and reproductive states among populations, females' estimated and specific growth rates were higher in MG2012 than in TO2012 (Tables 2 & S7D-E). Estimated and specific growth rates in males of MG2012 and TO2012 were similar (Tables 2 & S7D-E).

Females from MG2012 and MG1964-6 also presented similar estimated and specific growth rates although the absolute values were higher in MG2012 than in MG1964-6 (Tables 2 & S7D-E). Males from MG2012 and MG1964-6 presented no difference as well (Tables 2 & S7D-E). In TO2012, estimated and specific growth rates in females and males were higher than in TO1966 (Tables 2 & S7D-E).

## DISCUSSION

Our results confirm warming may not only accelerates growth but also anticipates sexual maturity and curtails longevity. Moreover, the number of reproductive years seem to decrease with climate warming having a direct effect on the long-term survival of these populations. Differences among populations may reflect genetic variability, plasticity plays an important role in coping with climatic variation (Adolph and Porter, 1993; Sorci *et al.*, 1996; Lorenzon *et al.*, 1999; 2001). Manifold life-history traits in lizards are highly geographically variable and may occur within and across populations (Sears and Angilletta, 2004) where ambient temperature ( $T_a$ ) is considered to be one of the main factors affecting these traits and altering the relationship between physiological and chronological time (Niewiarosky and Roosenburg, 1993; Sinervo and Adolph, 1994).

The link between the variation in  $T_a$  and the geographical and temporal differences in growth patterns agrees with previous finding on other species. Lizards in cold climates present metabolic arrest and reduced growth (Castanet and Baez, 1991; Martori *et al.*, 1998; Andreone and Guarino, 2003), whereas lizards with longer activity seasons spend more time at high body temperature ( $T_b$ ), grow faster and reach reproductive maturity at a younger age (Pianka, 1970; James and Shine, 1988). Herein, the differences in  $T_a$  between the northern and southern site is comparable to the variation of  $T_a$  experienced by the lizards at both localities over the last 40 years, and the temporal and geographical variation of the growth patterns follow the same trend. In fact, numerous phenological traits respond to global warming (Beebee, 1995; Peñuelas *et al.*, 2002; Réale *et al.*, 2003; Visser *et al.*, 2003). Moreover, previous studies also suggest that adults at both sites behave as constraint thermoconformers (Piantoni *et al.*, unpublished data), thus, a major influence of  $T_a$  on the physiology of the lizards is expected. The mean and variation of the  $T_e$  were significantly higher in MG2012 than in TO2012 ( $29.3 \pm 2.7$  and  $27.2 \pm 1.7$  °C, respectively). This difference between the distributions of  $T_e$  between the sites explains the higher specific growth rates in MG2012

when compared to the ones in TO2012. The correlation between  $T_e$  and  $T_a$  suggests that both temperatures increased during the last decades. Thus, lizards in the 1960s are suspected to have experienced lower  $T_e$ 's at both sites, which coincides with the lower growth rates observed in the estimated growth curves.

Higher growth rates due to warmer temperatures result in early sexual maturity. As in most lizards, *T. torquatus* displayed indeterminate growth represented by the sigmoid curve, also observed in the co-genders *T. catalanensis* from Piracicaba, SP (Piantoni *et al.*, unpublished data; Figure S1). The higher growth rate in juveniles (steep slope) reflects an allocation of energy towards growth until it is re-allocated to reproduction after attaining sexual maturity (asymptote slope; Wapstra *et al.*, 2001; Bruce *et al.*, 2002; Piantoni *et al.*, 2006a, 2006b). Some parameters of this curve such as sexual maturity may be affected by variation in  $T_a$ . Earlier reproduction is especially relevant in harsh (*e.g.* too hot) environment (Ibargüengoytía and Casalins, 2007). For example, in cooler sites in southern Cerrado, *T. catalanensis* attains sexual maturity at similar ages as *T. torquatus* in the gallery forest of Tocantins, which means much later than in Central Cerrado where lizards experience the highest temperatures (Table 1). Similar results were found in the Patagonian species *Homonota darwini* that shows a limited growth (a late onset of sexual maturity and the lowest estimated body size at each age) in the colder sites whereas, at warmer temperatures, it reaches sexual maturity earlier and shows a higher reproductive output (Kubisch *et al.*, 2012). In Tasmania, the skink *Niveoscincus ocellatus* matures at the age of 3 at a warmer site and delays maturity one year at a colder site (Wapstra *et al.*, 2001). An early sexual maturation may benefit a population or species in a short-term as lizards' reproductive years may increase. Nevertheless, longevity also varies with the thermal environment and not necessarily in a lineal relationship with sexual maturity.

Life history models predict that populations that experience high adult mortality also have high early maturity in comparison to populations that exhibit low mortality (Roff, 1992; Stearns, 1992), and in fact, adult survival rate is positively correlated with age at maturity in lizards and snake (Shine and Charnov, 1992). *T. torquatus* follows this trend with early maturity and mortality at the warmest sites, but the two traits in a non-linear manner. With respect to the maximum life-span in a temporal context, a reduction in the absolute number of reproductive years is clearly observed at the northern site, where it decreased from 6 to 5 yrs in females and from 14 to 12 yrs in males. However, the warmer sites houses the larger



females (larger estimated SVL at each age; MG2012 > MG1964-6 and TO2012 > TO1966; MG2012 > TO2012). Like in *Lacerta vivipara*, females' SVL increases with  $T_a$  (Chammaillé-Jammes *et al.*, 2006), which may compensate for the limited reproductive years and potentially enhance the populations' reproductive output with warming.

The field-active body temperature ( $T_b$ ) of *T. torquatus* in both sites is higher than the interquartile range of preferred body temperature in the lab ( $T_{set}$ -range; 33-34.8 °C; Piantoni *et al.*, unpublished data). However, lizards'  $T_b$ 's were closer to their optimal temperature ( $T_o$ ; ~ 35 °C; Piantoni *et al.*, unpublished data) suggesting that performance is not being affected by climate warming, at least momentarily. In a warming scenario, as  $T_a$  continues rising and  $T_b$  exceeds  $T_o$ , lizards are expected to retreat in burrows more frequently reducing the hours of activity, thus, infringing on the performance and overall fitness of the populations. Multiple field studies support these predictions demonstrating that hours of activity are positively correlated to growth rates (Davis, 1967; Tinkle, 1972; Ballinger, 1983; Grant and Dunham, 1990) and early maturation (Tinkle and Ballinger, 1972; Goldberg, 1974; Grant and Dunham, 1990). In addition, laboratorial studies on *L. vivipara*, *Sceloporus occidentalis*, and *S. graciosus* confirmed that juvenile growth rates increase with activity time (Avery, 1984; Sinervo and Adolph, 1989; Sinervo, 1990). Therefore, a decrease in the activity time may have a sublethal effect on *T. torquatus*, while not being lethal in the short-run, it may considerably affect the lizards' performance in such vital processes as locomotion, growth, and reproduction. Whereas the sublethal threats associated to warming may lead to local extinctions (Somero, 2011), phenotypic plasticity may potentially enhance resistance and resilience in a changing climate (Prober *et al.*, 2011). In a warming scenario, a shortage of hours of activity will probably be the main difficulty for *T. torquatus*, but plasticity may significantly contribute to the species' adaptive capacity and allow the survival of the populations.

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Table 1. Mean and range of snout-vent length (SVL; mm), medullar resorption (number of rings) and age range (years) of juveniles, females and males of lizards of the species *Tropidurus catalanensis* from Piracicaba, SP (SP), and *T. torquatus* from Arinos, MG, collected in 2010s (MG2012) and in 1960s (MG1964-6), and from Formoso do Araguaia, TO collected in 2010s (TO2012) and in 1960s (TO1966).

	Mean SVL (range; n; mm)			Medullar resorption (rings)			Age range (yrs)		
	Juveniles	♀	♂	Juveniles	♀	♂	Juveniles	♀	♂
SP	41.7 ± 12; 37 (27.2-67.7; 26)	81.2 ± 9.6; 81.1 (67.1-97.1; 17)	103.8 ± 9.5; 102.1 (87.4-118.4; 20)	0-3	3-5	5	0-5	4-7	5-10
MG2012	39.3 ± 10; 37.4 (29-63.4; 15)	91.9 ± 5.3; 92.4 (83.3-101; 11)	103.4 ± 7.4; 103.8 (88.5-113.1; 12)	0-2	2-3	2-4	0-3	3-7	3-11
MG1964-6	53.2 (1)	79.7 ± 12; 76.5 (69.2-96.5; 4)	84.1 ± 7.5; 84 (75.2-93; 4)	2	2-4	2-4	3	5-9	5-8
TO2012	36 ± 15.4; 30.3 (28.1-67.3; 6)	85 ± 7; 84.7 (76.2-102; 17)	98.3 ± 13.1; 94.7 (72.4-124.1; 12)	0-2	2-4	1-5	0-4	5-10	5-17
TO1966	-	83.2 ± 6.7; 83.7 (75.5-93.6; 8)	98.3 ± 10.1; 95 (83.6-115; 13)	-	3-5	4-7	-	6-12	7-20

Table 2. Estimated SVL [Mean  $\pm$  SD (*n*); mm] for juveniles, females and males of specific age ranges, and estimated growth rate [Mean  $\pm$  SD (*n*); median (range); mm/years] and specific Growth Rate {Mean  $\pm$  SD (*n*); median (range); [(mm/years)/mm]} of juveniles, adults, females and males of *T. torquatus* from Arinos, MG, collected in 2010s (MG2012) and in 1960s (MG1964-6), and from Formoso do Araguaia, TO collected in 2010s (TO2012) and in 1960s (TO1966).

		MG2012	MG1964-6	TO2012	TO1966
Estimated SVL [Mean $\pm$ SD ( <i>n</i> ); mm]	Juveniles (0-3 yrs)	40.8 $\pm$ 6	-	44.1 $\pm$ 6.1	-
	♀ (5-7 yrs)	94.5 $\pm$ 2.1	79.7 $\pm$ 5.7	78.8 $\pm$ 4.6	75.5 $\pm$ 2.5
	♂ (5-10 yrs)	106.7 $\pm$ 5.5	85.2 $\pm$ 5.9	90.2 $\pm$ 7.9	85.7 $\pm$ 2.1
	♀ (MG: 5-8 yrs. TO: 6-10 yrs)	94.5 $\pm$ 2.1	82.6 $\pm$ 7.3	88 $\pm$ 7.2	80.7 $\pm$ 5.5
	♂ (MG: 5-8 yrs. TO: 9-17 yrs)	103.7 $\pm$ 3.8	85.2 $\pm$ 5.9	113.1 $\pm$ 11.4	96.2 $\pm$ 8.2
Estimated growth rate [Mean $\pm$ SD ( <i>n</i> ); median (range); mm/years]	Juveniles	13.2 $\pm$ 1.4; 13.3 (11.4-15.1; 15)	10.5 (1)	6.3 $\pm$ 0.8; 6 (6-7.9; 6)	-
	Adults	7.4 $\pm$ 3.3; 8.1 (1-12.2; 23)	7.9 $\pm$ 1.8; 8.4 (4.8-9.9; 8)	6.2 $\pm$ 1.5; 6.6 (1.2-7.7; 29)	3.12 $\pm$ 2; 3.5 (-1.3-5.6; 21)
	♀	9.6 $\pm$ 1.7; 9.5 (6.6-12.2; 11)	8.2 $\pm$ 2.3; 9 (4.8-9.9; 4)	6.8 $\pm$ 0.7; 7 (4.8-7.5; 17)	4.6 $\pm$ 0.9; 4.7 (3.2-5.6; 8)
	♂	5.3 $\pm$ 3; 5.4 (1-10.8; 12)	7.6 $\pm$ 1.4; 7.8 (5.8-9.2; 4)	5.2 $\pm$ 1.8; 5.9 (1.2-7.7; 12)	2.2 $\pm$ 1.9; 3 (-1.3-4.8; 13)
	Juveniles	0.35 $\pm$ 0.04; 0.36 (0.24-0.4; 15)	0.2 (1)	0.19 $\pm$ 0.04; 0.2 (0.12-0.22; 6)	-
Specific Growth Rate {Mean $\pm$ SD ( <i>n</i> ); median (range); [(mm/years)/mm]}	Adults	0.08 $\pm$ 0.04; 0.08 (0.01-0.15; 23)	0.1 $\pm$ 0.03; 0.1 (0.05-0.14; 8)	0.07 $\pm$ 0.02; 0.07 (0.01-0.11; 29)	0.04 $\pm$ 0.02; 0.04 (-0.01-0.07; 21)
	♀	0.11 $\pm$ 0.02; 0.1 (0.07-0.15; 11)	0.11 $\pm$ 0.04; 0.12 (0.05-0.14; 4)	0.08 $\pm$ 0.01; 0.08 (0.05-0.1; 17)	0.06 $\pm$ 0.01; 0.06 (0.03-0.07; 8)
	♂	0.05 $\pm$ 0.03; 0.05 (0.01-0.12; 12)	0.09 $\pm$ 0.02; 0.09 (0.06-0.12; 4)	0.06 $\pm$ 0.03; 0.06 (0.01-0.11; 12)	0.02 $\pm$ 0.02; 0.03 (-0.01-0.06; 13)

## FIGURE LEGENDS

Figure 1. Monthly variation of maximum (A), mean (B), minimum (C) environmental temperatures ( $T_a$ ; °C) based on data gathered from the nearest weather stations and pooled across the period 1995-2012, and (D) operative temperatures ( $T_e$ ; °C) collected during 2013 in Arinos, MG (solid triangles and lines) and Formoso do Araguaia, TO (empty triangles and dashed lines). Dashed horizontal lines and grey area indicate the range of preferred temperatures ( $T_{set-range}$ ).

Figure 2. Monthly variation of cloud cover (A; tenths of sky), and total precipitation (B; mm) based on data gathered from the nearest weather stations and pooled across the period 1995-2012 for Arinos, MG (solid triangles and lines, and grey bars) and Formoso do Araguaia, TO (empty triangles, dashed lines and bars).

Figure 3. Relationship between the daily means of maximum ( $T_{a\ max}$ ; solid triangles and dashed lines), mean ( $T_{a\ mean}$ ; empty circles and dotted lines), and minimum ( $T_{a\ min}$ ; solid circles and solid lines) ambient temperatures (°C), and the operative temperatures ( $T_e$ ; °C) corresponding to one year period in 2012-2013 in Arinos, MG (A) and Formoso do Araguaia, TO (B).

Figure 4. Variation of the monthly mean of maximum ( $T_{a\ max}$ ; A), mean ( $T_{a\ mean}$ ; B), minimum ( $T_{a\ min}$ ; C) temperatures (°C; circles), and mean precipitation (mm; triangles; D) based on data gathered from the nearest weather stations and pooled across the period 1995-2012 for Arinos, MG (solid symbols and lines) and Formoso do Araguaia, TO (empty symbols and dashed lines).

Figure 5A-B. Diaphyseal cross-sections of femur of 14 lizards of the species *Tropidurus torquatus*: A-B) new-borns; (C) 1-yr-old juvenile; (D) 2-yr-old juvenile; (E) 2-yr-old juvenile; (F) 3-yr-old juvenile; (G-H) 4-yr-old juveniles; (I-J) 5-yr-old females; (K-M) 6-yr-old females; (N) 5-yr-old male. LAGs are indicated by arrows. EnB = endosteal bone; MC = medullar cavity.

Figure 6. Estimation of the medullar resorption. Linear relationship between mean medullar radius (first bottom line of each graph) and mean radius of each growth ring, and snout-vent length in *Tropidurus torquatus* collected in Arinos, MG, in 1960s (A) and 2010s (B); and in Formoso do Araguaia, TO, in 1960s (C) and 2010s (D). The number of reabsorbed rings at a certain SVL (indicated by the vertical dashed line) corresponds to the number of regression

lines (rings) that are between the medullar radius at that SVL and the horizontal dashed line that intersects the horizontal and medullar radius regression line [*e.g.* specimens larger than 33.7 (A), 41.3 (B), 73.7 (C), and 82.2 (D) mm SVL suffered a resorption of 1, 2, 3, and 4 rings, respectively].

Figure 7. Sigmoid relationship [the fitted line ( $r^2 = 0.82-0.97$ ) and 95% confidence intervals are indicated] between snout-vent length (SVL; mm) and age (yrs) in *Tropidurus torquatus* collected in Arinos, MG (A), and in Formoso do Araguaia, TO (B), in 1960s (solid lines) and in 2010s (dashed lines).

Figure 8. Specific growth rates (triangles and squares) and sigmoid relationship [circles and diamonds; lines indicate the fitted line ( $r^2 = 0.94-0.99$ ) and 95% confidence intervals] between snout-vent length (SVL; mm) and age (yrs) in *Tropidurus torquatus* collected in Arinos, MG (A), and in Formoso do Araguaia, TO (B), in 1960s (empty symbols and dashed lines) and 2010s (solid symbols and lines).

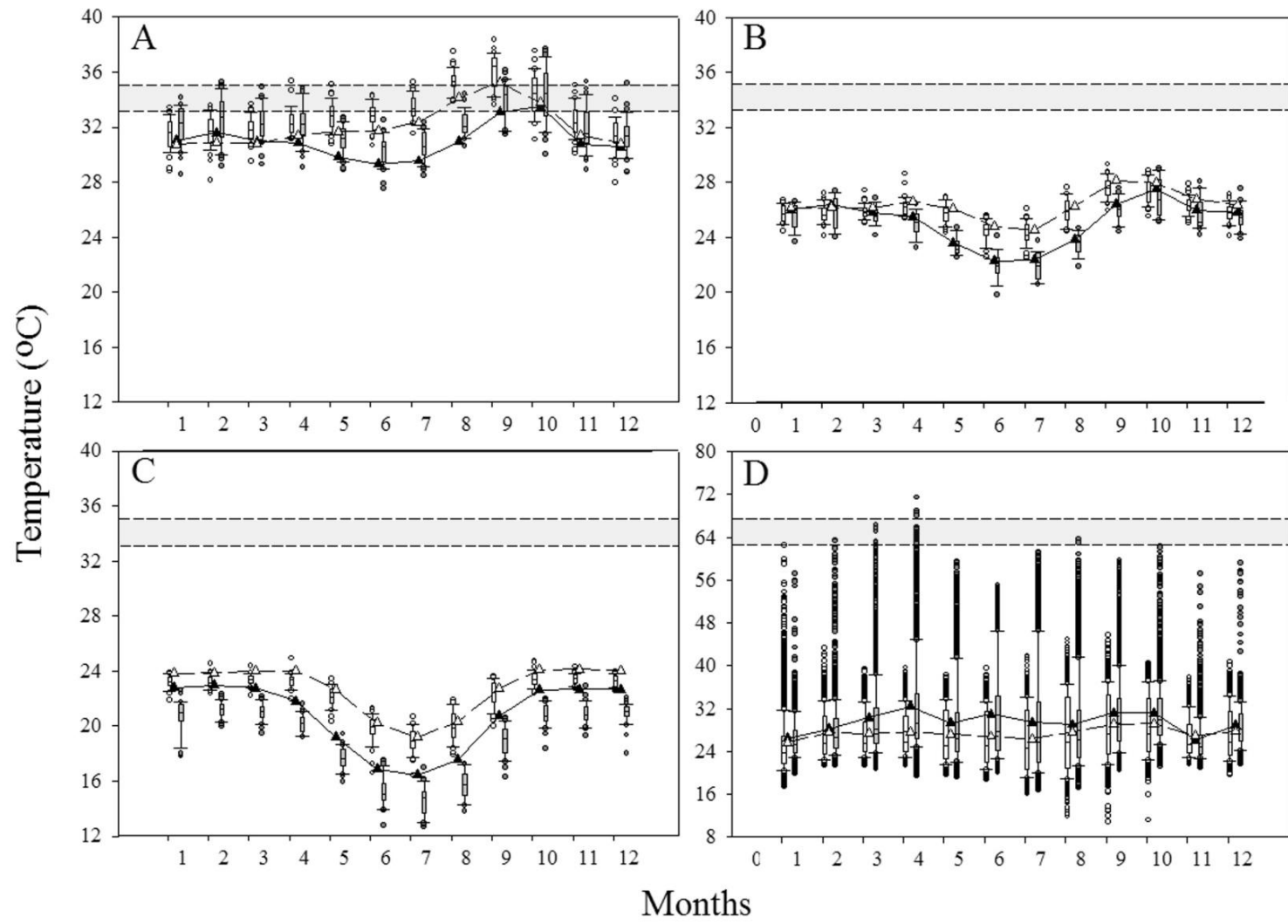


Figure 1.

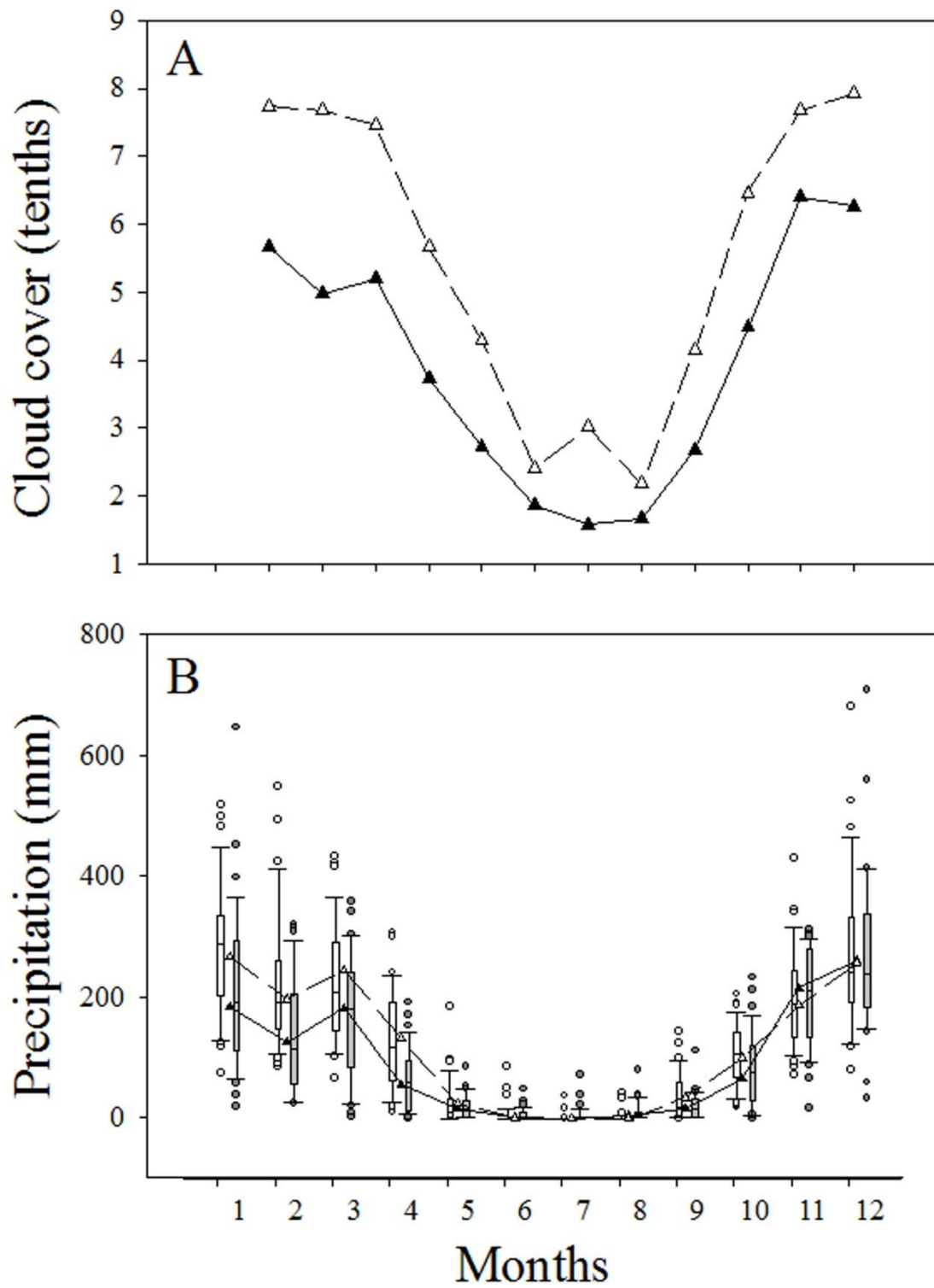


Figure 2.



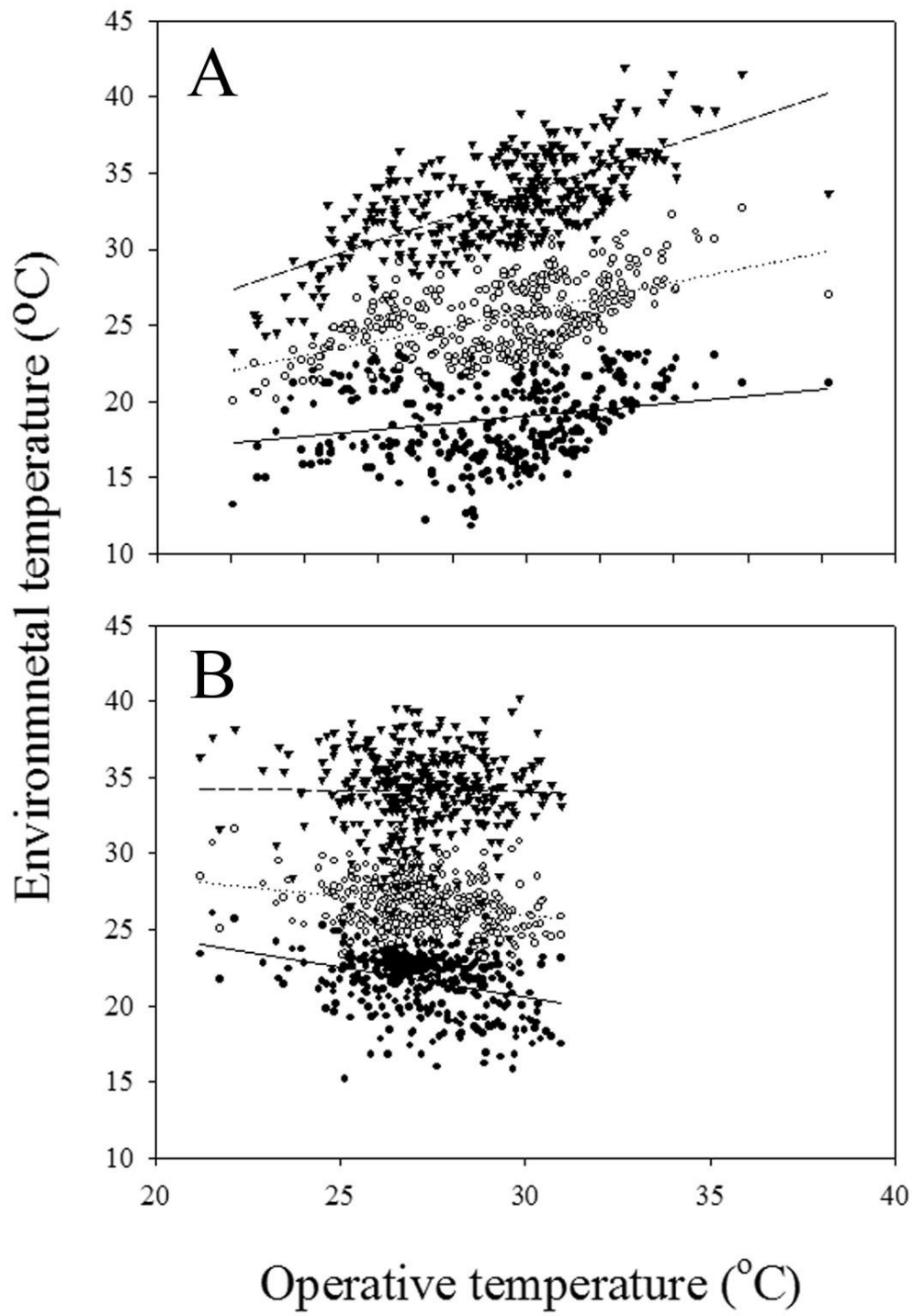


Figure 3.

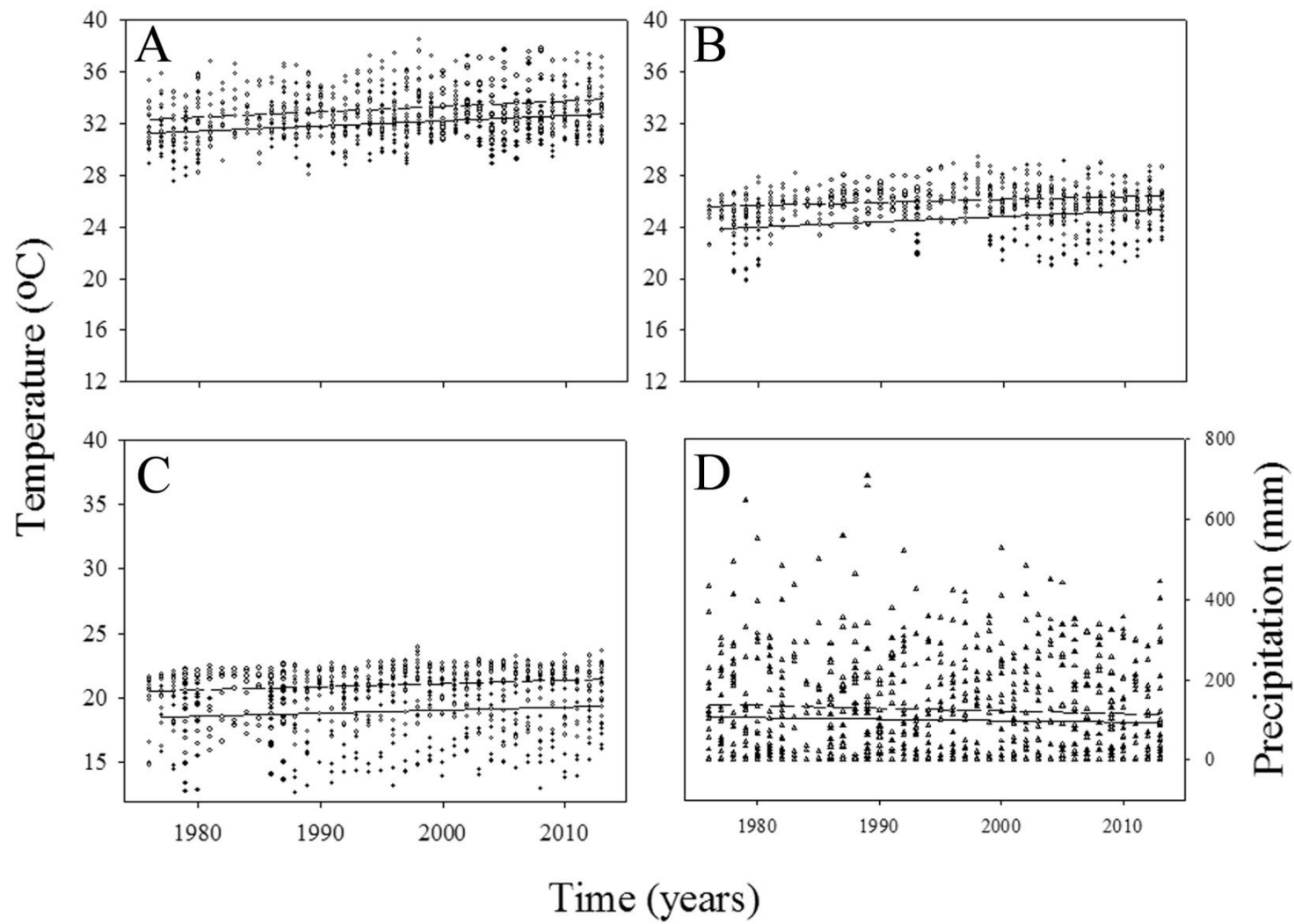


Figure 4.

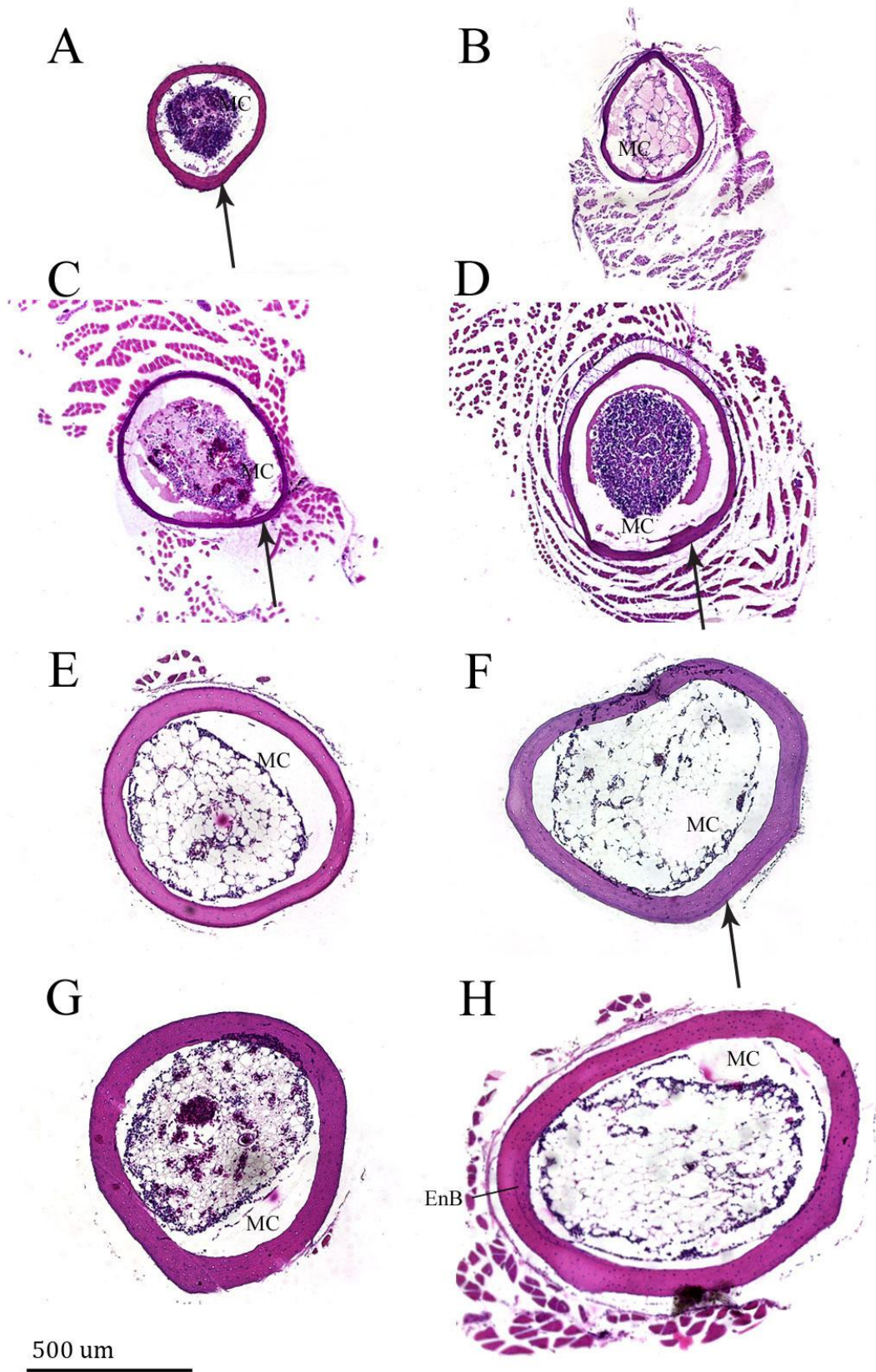


Figure 5A.



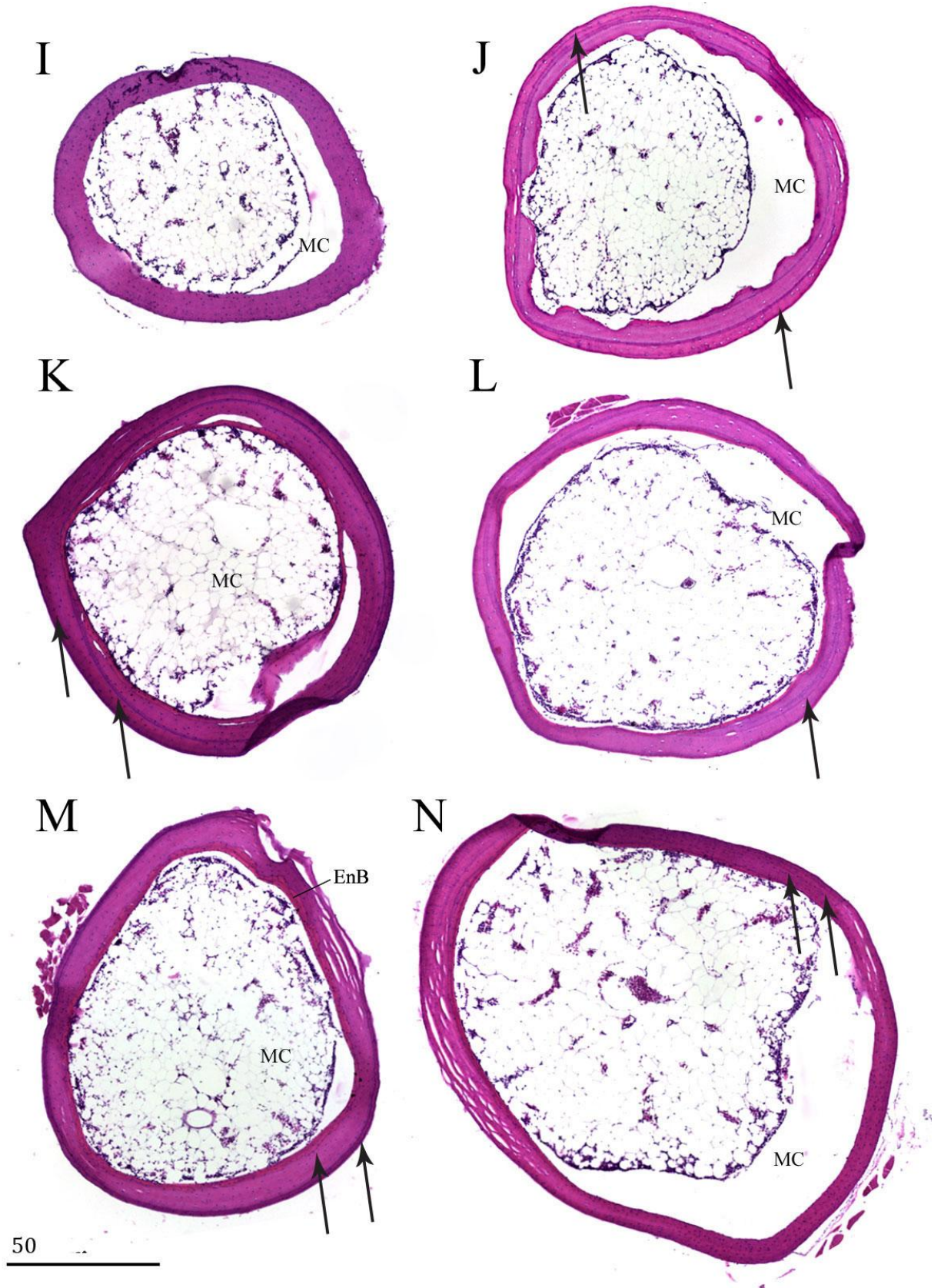


Figure 5B.

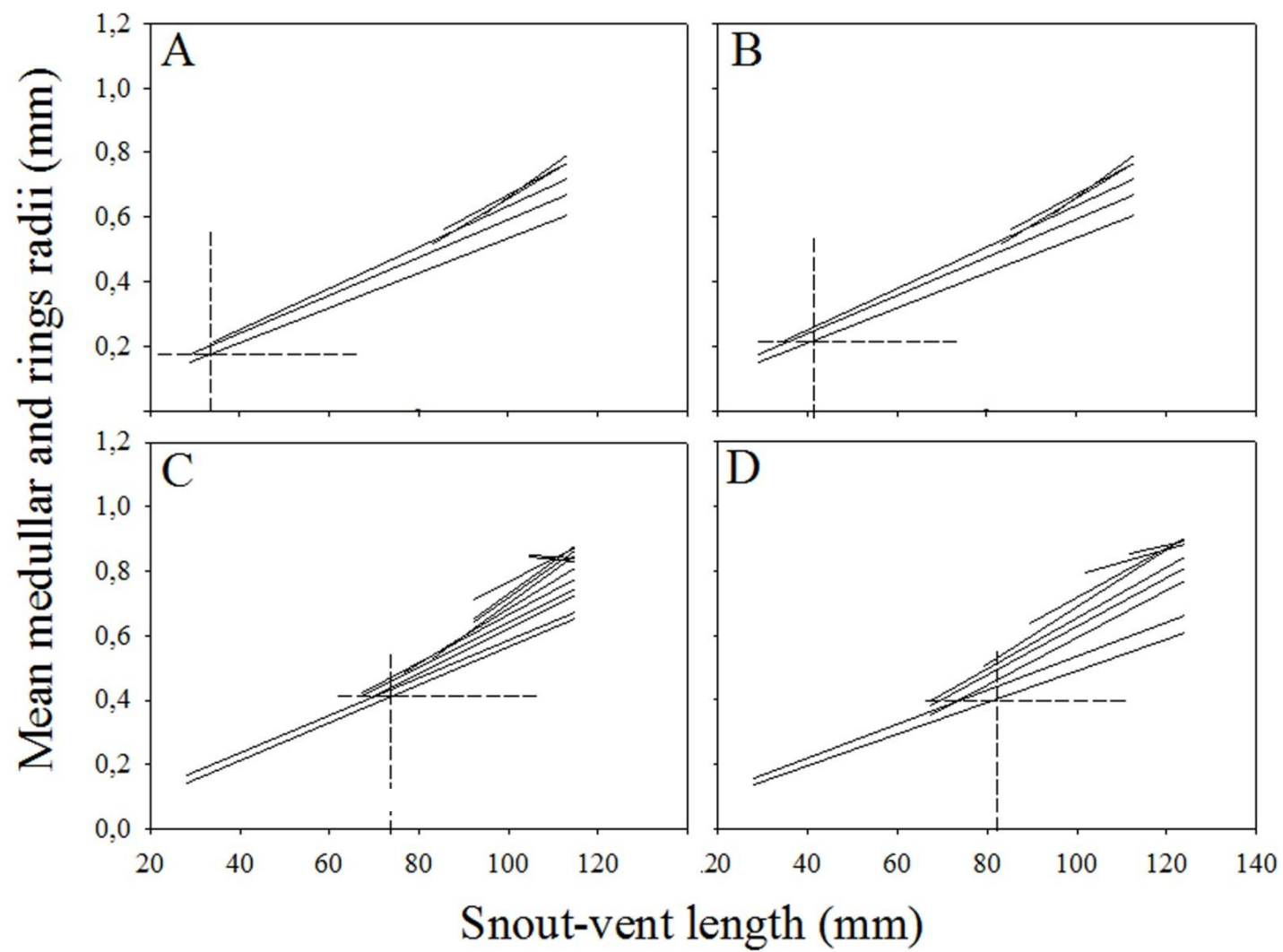


Figure 6.

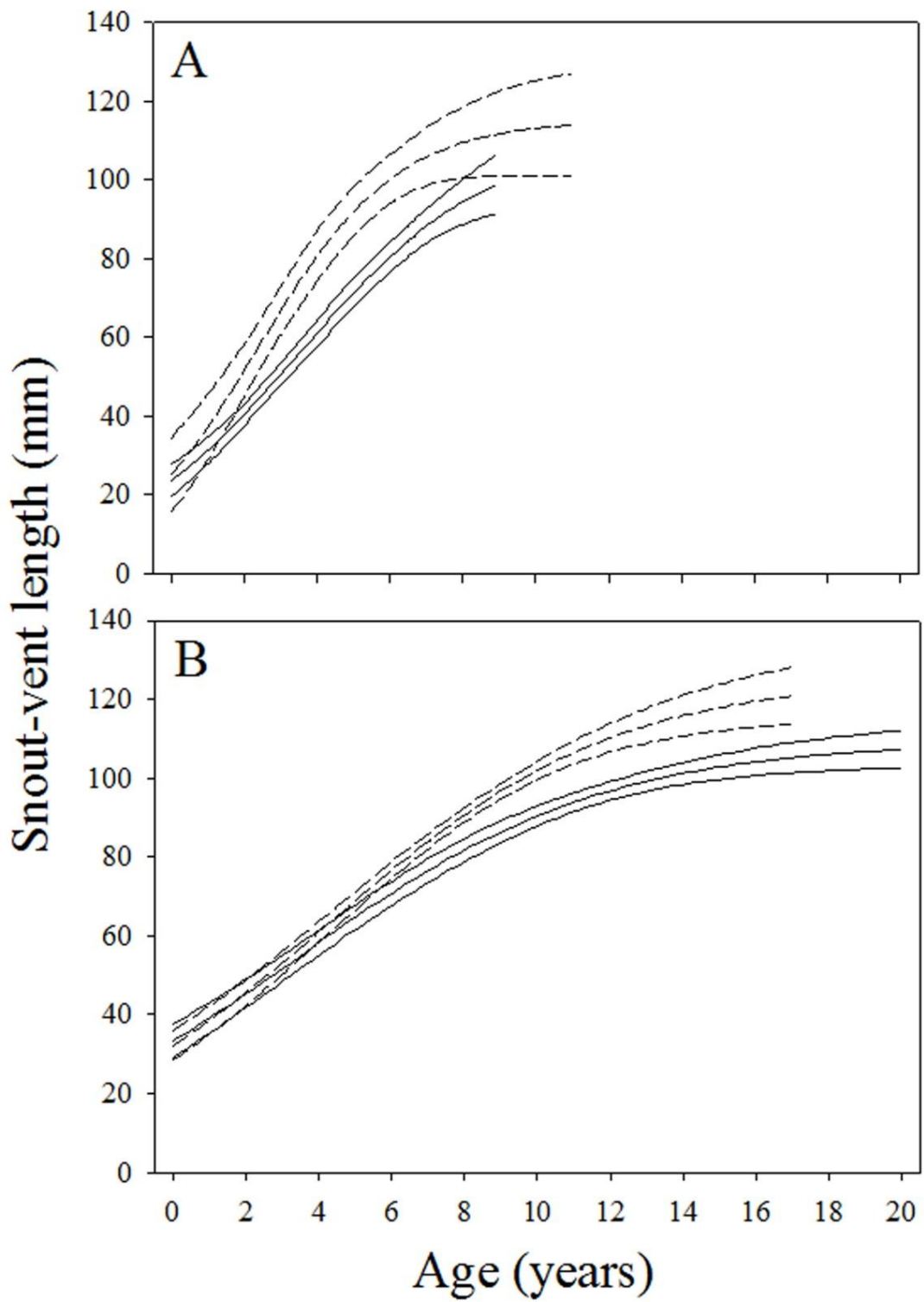


Figure 7.

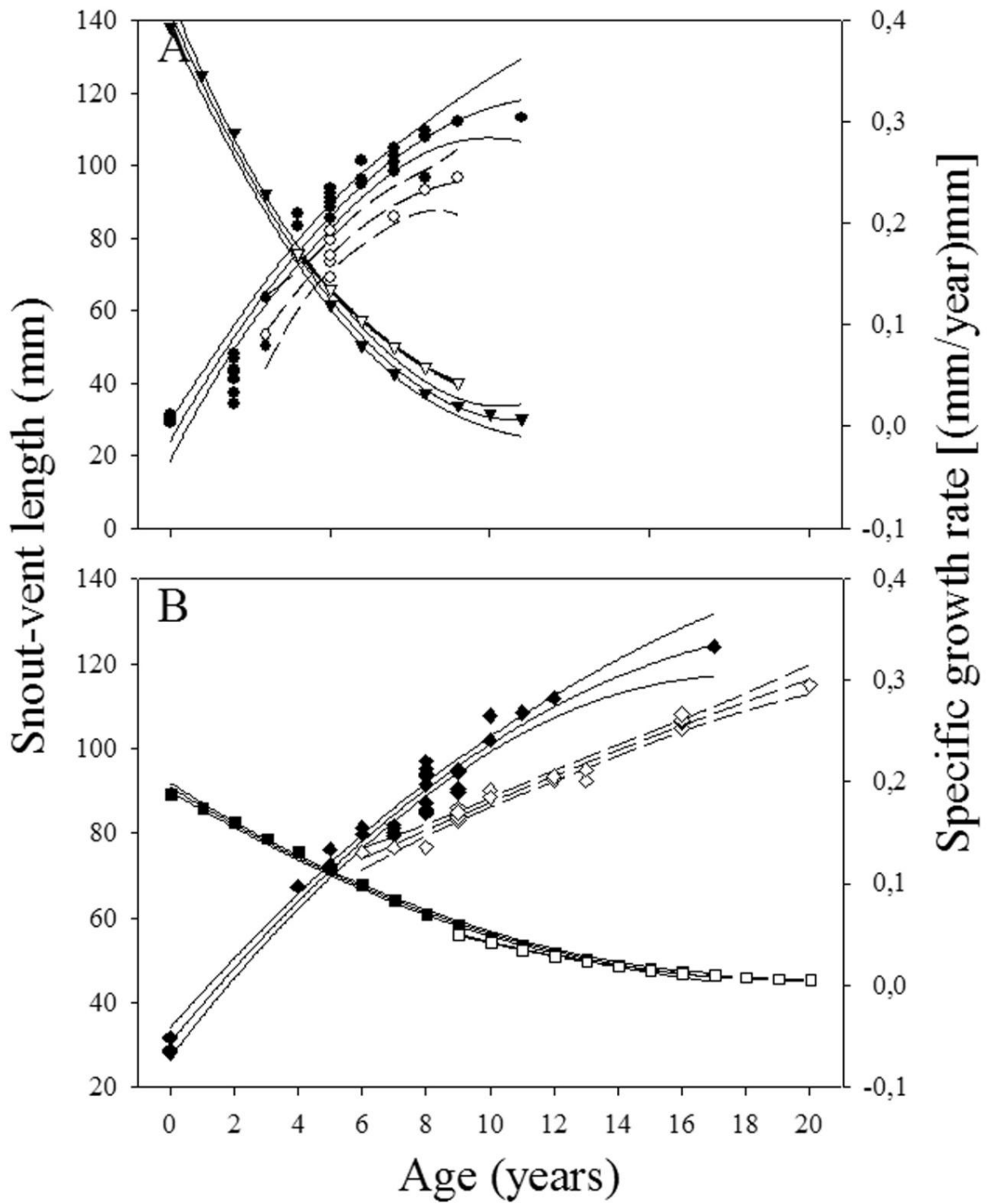


Figure 8.

## SUPPLEMENTAL MATERIAL

Table S1. Differences in the number of days with precipitation, total precipitation (mm), maximum, mean and minimum environmental temperature ( $T_a$ ; °C) in the period 1995-2013 between Arinos, MG and Formoso do Araguaia, TO. Data belong to the nearest weather stations to both sites.

	MG		TO	
	Mean $\pm$ SD (N)	Median (range; interquartile)	Mean $\pm$ SD (N)	Median (range; interquartile)
Number of Days with Precipitation	8.5 $\pm$ 7.7 (170)	6.5 (0-2; 1-16)	12.1 $\pm$ 8.2 (170)	14 (0-26; 3-19)
Total Precipitation (mm)	95.6 $\pm$ 112 (224)	40.6 (0-451; 0.6-170.4)	120.9 $\pm$ 124.2 (228)	94.7 (0-527.5; 0.7-204.1)
Maximum $T_a$ (°C)	32.3 $\pm$ 1.7 (224)	32.1 (28.9-37.7; 31.1-33.4)	33.6 $\pm$ 1.9 (207)	33.2 (29.5-38.5; 32.2-35)
Mean $T_a$ (°C)	25 $\pm$ 1.8 (183)	25.4 (21-29; 23.8-26.3)	26.2 $\pm$ 1.2 (227)	26.2 (22.9-29.4; 25.5-26.9)
Minimum $T_a$ (°C)	19.3 $\pm$ 2.6 (224)	20.4 (13-22.9; 17.1-21.3)	21.2 $\pm$ 1.9 (228)	22.1 (16.1-23.9; 19.9-22.5)



Table S2. Inter-site comparisons of the number of days with precipitation, total precipitation (mm), maximum, mean and minimum environmental temperature ( $T_a$ ; °C), and the operative temperature ( $T_e$ ; °C) for Arinos, MG and Formoso do Araguaia, TO. Precipitation and  $T_a$  data were gathered at the nearest weather stations to both sites in the period 1995-2013, and the  $T_e$  were collected by data-loggers during one year between 2012 and 2013. All differences are significant;  $P$ -values  $\leq 0.001$ .

Variables	Inter-site comparisons (Wilcoxon Signed Rank Test and Paired $t$ -test)
Number of Days with Precipitation	$Z = 6.387$
Total Precipitation	$Z = 5.152$
Maximum $T_a$	$Z = 8.449$
Mean $T_a$	$t_{181} = -13.658$
Minimum $T_a$	$Z = 12.963$
$T_e$	$t_{363} = 16.058$

Table S3. Mean ( $\pm$  SD) and median (range; interquartile) values for the maximum, mean and minimum of operative ( $T_e$ ; °C) and environmental temperature ( $T_a$ ; °C), and the for Arinos, MG and Formoso do Araguaia, TO.  $T_a$  data were gathered at the nearest weather stations to both sites in the same period during which the  $T_e$  were collected (2012-2013).

	MG		TO	
	Mean $\pm$ SD ( <i>N</i> )	Median (range; interquartile)	Mean $\pm$ SD ( <i>N</i> )	Median (range; interquartile)
Maximum $T_e$	50.5 $\pm$ 10 (365)	53.6 (25.1-71.4; 44.4-57.8)	37.4 $\pm$ 4.8 (365)	36.8 (22.4-62.7; 34.9-39.6)
Mean $T_e$	29.3 $\pm$ 2.7 (365)	29.7 (22.1-38.2; 27.4-31.1)	27.2 $\pm$ 1.7 (365)	27.1 (20.2-30.8; 26.2-28.3)
Minimum $T_e$	22.6 $\pm$ 2.1 (365)	22.8 (16.8-28.9; 21.3-24)	21 $\pm$ 2.5 (365)	21.8 (8.7-24.9; 19.9-22.7)
Maximum $T_a$	33.1 $\pm$ 3.1 (365)	33.1 (23.3-41.9; 31.1-35.5)	34.1 $\pm$ 2.7 (362)	34.4 (24.4-40.2; 32.8-36)
Mean $T_a$	25.5 $\pm$ 2.3 (365)	25.5 (20-32.7; 23.7-27.2)	26.6 $\pm$ 1.5 (360)	26.5 (22.6-31.6; 25.5-27.6)
Minimum $T_a$	18.8 $\pm$ 2.5 (360)	18.8 (11.8-24.4; 16.8-21)	21.7 $\pm$ 2 (357)	22.2 (15.2-26.1; 20.6-23.1)

Table S4. Correlations [Pearson's  $r$ ;  $P$ -value ( $N$ )] between maximum, mean and minimum environmental temperature ( $T_a$ ; °C), and the maximum, mean and minimum of the operative temperature ( $T_e$ ; °C) for Arinos, MG, and Formoso do Araguaia, TO, during one year period between 2012-13.

	MG			TO		
	Maximum $T_e$	Mean $T_e$	Minimum $T_e$	Maximum $T_e$	Mean $T_e$	Minimum $T_e$
Maximum $T_a$	0.536; 1.477E-28 (365)	0.696; 3.608E- 54 (365)	0.525; 3.219E-27 (365)	<b>0.0415;</b> <b>0.432 (361)</b>	<b>-0.0108;</b> <b>0.837 (361)</b>	<b>0.0207;</b> <b>0.695 (361)</b>
Mean $T_a$	0.311; 1.25E-10 (365)	0.565; 3.74E-32 (365)	0.779; 1.67E-75	<b>-0.00159;</b> <b>0.976 (359)</b>	-0.259; 6.57E-7 (359)	0.108; 0.0412 (359)
Minimum $T_a$	<b>0.0163;</b> <b>0.758 (360)</b>	0.231; 9.48E-6	0.730; 3.05E-61 (360)	<b>-0.0544;</b> <b>0.305 (357)</b>	-0.328; 2.2E-10	<b>0.0535;</b> <b>0.314 (357)</b>

Table S5. Comparisons (Wilcoxon Signed Rank Test and  $Z$  statistic; Paired  $t$ -test and  $t$  statistic) between the maximum, mean and minimum environmental ( $T_a$ ; °C) and the mean operative ( $T_e$ ; °C) temperatures in Arinos, MG (MG) and in Formoso do Araguaia, TO (TO), for the period 2012-2013.

	Mean $T_e$ MG		Mean $T_e$ TO	
Maximum $T_a$	$Z = 16.416, P \leq 0.001$	$\max T_a > T_e$	$t_{358} = -41.494, P \leq 0.001$	$\max T_a > T_e$
Mean $T_a$	$Z = -16.256, P \leq 0.001$	$\text{mean } T_a < T_e$	$t_{358} = 4.281, P \leq 0.001$	$\text{mean } T_a < T_e$
Minimum $T_a$	$Z = -16.443, P \leq 0.001$	$\min T_a < T_e$	$Z = -16.231, P \leq 0.001$	$\min T_a < T_e$

Table S6. Results ( $b$  coefficient,  $t$ -test and analysis of variance statistics and equation) of: (A) the linear regression of the monthly means of maximum, mean and minimum environmental temperature ( $T_a$ ) and precipitation vs. time for the period 1976 until 2013 for Arinos, MG (MG) and Formoso do Araguaia, TO (TO); (B) the bone resorption vs. snout-vent length (SVL); (C) the sigmoid non-linear regression between estimated age and SVL for lizards from Arinos, MG, collected in 2010s (MG2012) and in 1960s (MG1964-6), and from Formoso do Araguaia, TO collected in 2010s (TO2012) and in 1960s (TO1966); and (D) relationship between the maximum, mean and minimum  $T_a$  and the operative temperature ( $T_e$ ) collected during one year (2012 and 2013) at each site.

Populations	Variables	$b$	$t$ -test	$r^2$	$F$	$P$	Equation
<i>(A) Variation of <math>T_a</math> since 1976 until 2013</i>							
MG	Maximum $T_a$	0.04	$t_{379} = 5.012$	0.0623	$F_{1,378} = 25.124$	$\leq 0.001$	Max $T_a = -50.661 + (0.0414 * \text{Time})$
	Mean $T_a$	0.04	$t_{231} = 3.803$	0.0592	$F_{1,230} = 14.461$	$\leq 0.001$	Mean $T_a = -54.931 + (0.0398 * \text{Time})$
	Minimum $T_a$	0.02	$t_{366} = 1.823$	0.009	$F_{1,365} = 3.322$	0.069	Min $T_a = -29.314 + (0.00902 * \text{Time})$
	Precipitation	-0.35	$t_{404} = -0.649$	0.00104	$F_{1,403} = 0.421$	0.517	Prec. = $791.999 - (0.347 * \text{Time})$
TO	Maximum $T_a$	0.04	$t_{448} = 5.828$	0.0706	$F_{1,447} = 33.968$	$\leq 0.001$	Max $T_a = -53.883 + (0.0436 * \text{Time})$
	Mean $T_a$	0.02	$t_{449} = 4.797$	0.0489	$F_{1,448} = 23.009$	$\leq 0.001$	Mean $T_a = -20.467 + (0.0233 * \text{Time})$
	Minimum $T_a$	0.03	$t_{450} = 3.124$	0.0213	$F_{1,449} = 9.761$	0.002	Min $T_a = -27.827 + (0.0245 * \text{Time})$
	Precipitation	-0.69	$t_{450} = -1.251$	0.00348	$F_{1,449} = 1.566$	0.211	Prec. = $1502.15 - (0.69 * \text{Time})$
<i>(B) Variation of medullar radius with SVL</i>							
MG2012		0.0054	$t_{37} = 32.081$	0.97	$F_{1,36} = 1029.168$	$\leq 0.001$	Resorption = $-0.00569 + (0.0054 * \text{SVL})$
MG1964-6		0.0054	$t_{22} = 18.77$	0.94	$F_{1,21} = 352.3.589$	$\leq 0.001$	Resorption = $-0.00693 + (0.0054 * \text{SVL})$
TO2012		0.0049	$t_{34} = 249.34$	0.88	$F_{1,33} = 249.339$	$\leq 0.001$	Resorption = $-0.00242 + (0.0049 * \text{SVL})$
TO1966		0.0059	$t_{28} = 13.37$	0.87	$F_{1,27} = 178.749$	$\leq 0.001$	Resorption = $-0.0246 + (0.0059 * \text{SVL})$
<i>(C) Estimated age vs. SVL</i>							
MG2012		2.4		0.82	$F_{3,35} = 82.49906$	$\leq 0.001$	
MG1964-6		3.47		0.96	$F_{3,20} = 212.3931$	$\leq 0.001$	
TO2012		4.23		0.97	$F_{3,32} = 468.7614$	$\leq 0.001$	
TO1966		3.4525		0.97	$F_{3,26} = 377.0710$	$\leq 0.001$	
<i>(D) Relation between maximum, mean and minimum <math>T_a</math> and <math>T_e</math> at each site</i>							
MG $T_e$	Maximum $T_a$	0.798	$t_{364} = 18.468$	0.484	$F_{1,363} = 25.124$	$\leq 0.001$	Max $T_a = 9.811 + (0.798 * T_e)$
	Mean $T_a$	0.483	$t_{364} = 13.043$	0.319	$F_{1,363} = 170.111$	$\leq 0.001$	Mean $T_a = 11.397 + (0.483 * T_e)$
	Minimum $T_a$	0.219	$t_{364} = 4.493$	0.0534	$F_{1,363} = 20.189$	$\leq 0.001$	Min $T_a = 12.448 + (0.219 * T_e)$
TO $T_e$	Maximum $T_a$	0.018	$t_{360} = -0.206$	0.0001	$F_{1,359} = 0.0423$	0.837	Max $T_a = 34.608 + (0.0180 * T_e)$
	Mean $T_a$	-0.243	$t_{364} = -5.065$	-0.243	$F_{1,357} = 25.653$	$\leq 0.001$	Mean $T_a = 33.26 - (0.243 * T_e)$
	Minimum $T_a$	-0.397	$t_{356} = -6.536$	0.107	$F_{1,355} = 42.715$	$\leq 0.001$	Min $T_a = 32.473 - (0.397 * T_e)$

Table S7. Comparisons (One Way ANOVA,  $F$  statistic; Student  $t$ -test,  $t$  statistic; Mann-Whitney Rank Sum Test,  $U$  statistic; and Wilcoxon Signed Rank Test,  $Z$  statistic) of; (A) Snout-vent length (SVL) among adults, females and males of *T. torquatus* from Arinos, MG, collected in 2010s (MG2012) and in 1960s (MG1964-6), and from Formoso do Araguaia, TO collected in 2010s (TO2012) and in 1960s (TO1966); (B) SVL between females and males within MG2012, MG1964-6, TO2012 and TO1966; (C) SVL within females and males of same age ranges within MG and TO; (D) specific growth rates [(mm/yr)/mm] between and within sites and samples; and (E) estimated growth rates (mm/yr) between and within sites and samples.

Comparisons when different			Statistic	P-values
<b>(A) SVL among MG2012, MG1964-6, TO2012, TO1966</b>				
Adults	MG2012 > TO1960 > TO2012 > MG1964-6		$F_{3,80} = 4.883$	0.004*
♀	G2012 > TO2012 > TO1960 > MG1964-6		$F_{3,36} = 4.128$	0.013*
♂	MG2012 > TO2012 > TO1960 > MG1964-6		$F_{3,40} = 3.576$	0.023*
<b>(B) SVL within samples</b>				
♀ MG2012	♂ MG2012	♀ < ♂	$t_{21} = -4.235$	≤ 0.001*
♀ MG1964-6	♂ MG1964-6		$t_{12} = -0.62$	0.558
♀ TO2012	♂ TO2012	♀ < ♂	$U = 33, n = 12, n = 17$	0.002*
♀ TO1960	♂ TO1960	♀ < ♂	$t_{11} = -3.742$	0.001*
<b>(C) SVL within females and males of same age</b>				
♀ MG2012 (5-8 yrs)	♀ MG1964-6 (5-8 yrs)		$t_3 = 5.775$	0.010
♂ MG2012 (5-8 yrs)	♂ MG1964-6 (5-8 yrs)		$Z = -10.000$	0.125
♀ TO2012 (6-10 yrs)	♀ TO1960 (6-10 yrs)	TO2012 > TO1960	$t_4 = 9.342$	≤ 0.001*
♂ TO2012 (9-17 yrs)	♂ TO1960 (9-17 yrs)	TO2012 > TO1960	$t_8 = 15.196$	≤ 0.001*
MG2012 (1-11 yrs)	TO2012 (1-11 yrs)	MG2012 > TO2012	$t_{10} = 5.769$	≤ 0.001*
<b>(D) Specific growth rates</b>				
MG2012 (1-11 yrs)	TO2012 (1-11 yrs)		$Z = 0.0889$	0.966
Juveniles MG2012	Juveniles TO2012	MG2012 > TO2012	$t_{19} = 7.62$	≤ 0.001*
Adults MG2012 (5-11 yrs)	Adults TO2012 (5-11 yrs)		$t_{12} = -1.929$	0.078
Juveniles MG2012	Adults MG2012	Juv > Ad	$t_{36} = 19.324$	≤ 0.001*
Juveniles TO2012	Adults TO2012	Juv > Ad	$t_{33} = 8.263$	≤ 0.001*
MG2012 (1-9 yrs)	MG1964-6 (1-9 yrs)		$t_9 = 0.572$	0.582
TO2012 (1-17 yrs)	TO1960 (1-17 yrs)	TO2012 > TO1960	$Z = -3.724$	≤ 0.001*
♀ MG2012	♀ TO2012	MG2012 > TO2012	$U = 36, n = 11, n = 17$	0.007

Comparisons when different			Statistic	P-values
♂ MG2012	♂ TO2012		$t_{22} = -0.202$	0.842
♀ MG2012	♀ MG1964-6		$t_{13} = -0.0838$	0.935
♂ MG2012	♂ MG1964-6		$t_{14} = -2.115$	0.053
♀ TO2012	♀ TO1960	TO2012 > TO1960	$t_{23} = 4.101$	$\leq 0.001^*$
♂ TO2012	♂ TO1960	TO2012 > TO1960	$U = 25, n = 12, n = 13$	$\leq 0.001^*$
<i>(E) Estimated growth rates</i>				
Juveniles MG2012	Juveniles TO2012	Juv > Ad	$U = 90, n = 6, n = 15$	$\leq 0.001^*$
Juveniles MG2012	Adults MG2012	Juv > Ad	$U = 10, n = 15, n = 23$	$\leq 0.001^*$
Juveniles TO2012	Adults TO2012		$U = 95, n = 6, n = 29$	0.742
MG2012 (1-9 yrs)	MG1964-6 (1-9 yrs)		$t_9 = 1.084$	0.307
TO2012 (1-17 yrs)	TO1960 (1-17 yrs)	TO2012 > TO1960	$t_{17} = 8.366$	$\leq 0.001^*$
♀ MG2012	♀ TO2012	MG2012 > TO2012	$U = 13, n = 11, n = 17$	$\leq 0.001^*$
♂ MG2012	♂ TO2012		$t_{22} = 0.0984$	0.923
♀ MG2012	♀ MG1964-6		$t_{13} = 1.322$	0.209
♂ MG2012	♂ MG1964-6		$t_{14} = -1.515$	0.152
♀ TO2012	♀ TO1960	TO2012 > TO1960	$U = 133, n = 8, n = 17$	$\leq 0.001^*$
♂ TO2012	♂ TO1960	TO2012 > TO1960	$U = 19, n = 12, n = 13$	$\leq 0.001^*$

Table S8. Pairwise multiple comparisons (Holm-Sidak method;  $t$  statistics;  $P$ -values or \* indicating significant differences; Overall significance level = 0,05) of snout-vent length (SVL) among: (A) adults (above the diagonal) and females (below the diagonal); and (B) males of *T. torquatus* from Arinos, MG, collected in 2010s (MG2012) and in 1960s (MG1964-6), and from Formoso do Araguaia, TO collected in 2010s (TO2012) and in 1960s (TO1966).

	MG2012	MG1964-6	TO2012	TO1966
<i>(A) Adults' and females' SVL</i>				
MG2012		3.641*	2.466	1.654
MG1964-6	2.953*		2.019	2.396
TO2012	2.525	1.344		0.660
TO1966	2.635	0.816	0.577	
<i>(B) Males' SVL</i>				
MG2012		3.275*	1.205	1.248
MG1964-6			2.423	2.433
TO2012				0.0191



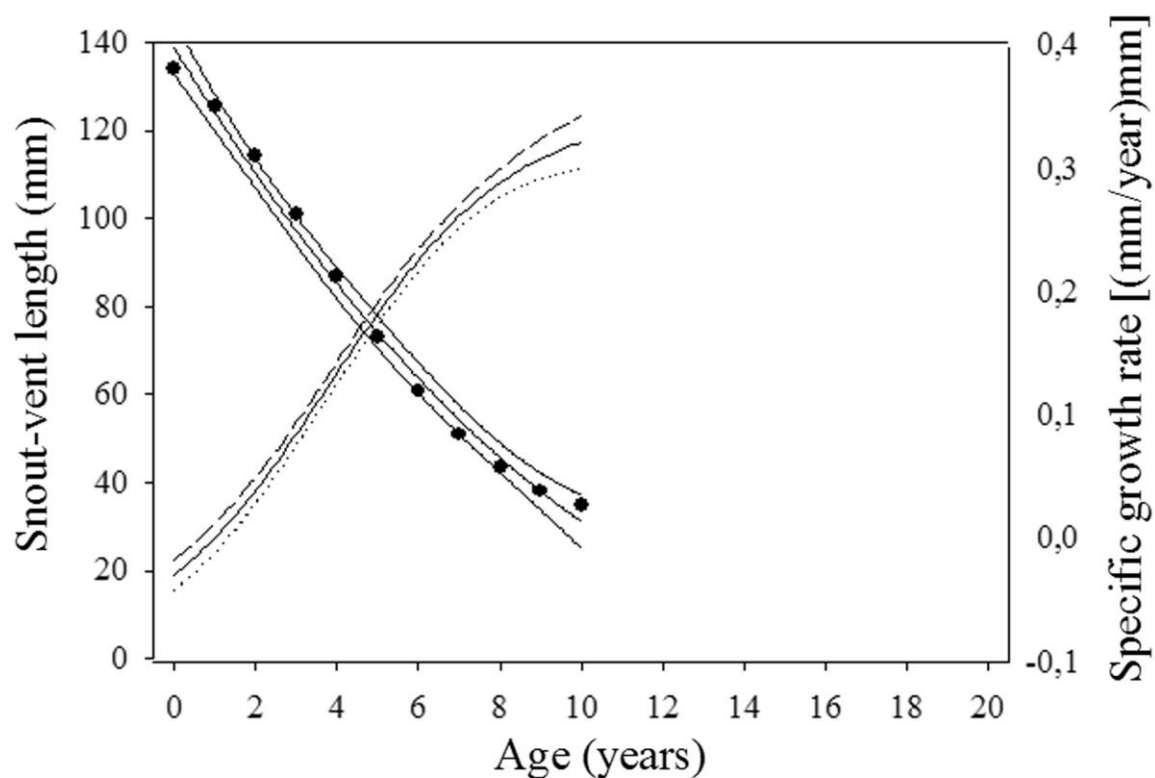


Figure S1. Specific growth rates (solid circles,  $r^2 = 0.99$ ) and sigmoid relationship between snout-vent length (SVL; mm) and age (years; dashed lines;  $r^2 = 0.95$ ) in *Tropidurus catalanensis* collected in Piracicaba, SP, in 2010s. The fitted line and 95% confidence intervals are indicated.

## CONCLUSIONS

- (1) A general pattern suggests that thermoregulatory behavior in iguanians increases with latitude and altitude (except for two southernmost liolaemids), and that tropical and lowland lizards tend to behave as thermoconformers.
- (2) A large proportion of the field body ( $T_b$ ) and operative ( $T_e$ ) temperatures of tropical and lowland populations exceed the thermal *preferenda* ( $T_{set}$  range) of the lizards. This combined with the thermoconformity that characterizes these populations may curtail the activity hours and augment the risk of overheating of the animals.
- (3) Tropical populations, especially the ones inhabiting open and low elevation sites, are the most susceptible to rising temperatures suggesting priorities in the conservation of these environments.
- (4) Patagonia and montane environments seem to represent future thermal refuges for many northern or lowland lizards that would eventually be forced to retreat to these environments.
- (5) The decrease of thermoregulatory behavior towards the Equator may be associated to the decrease of environmental variation and the increase of the thermal constrains.
- (6) In most tropidurids,  $T_b$  and the preferred temperature ( $T_p$ ) are similar and higher than the air temperature ( $T_a$ ) pointing to a plesiomorphic condition, probably related to earlier forested environments.
- (7) Variation in the thermal performance curves was significant among and within the populations of the *Tropidurus torquatus* group from the Cerrado.
- (8) Thermal breadths ( $B_{80}$ ) and safety margins (SM's) increased with climate variation and decreased with the variation of annual precipitation. Thus, both were broader in the Central Cerrado and narrower towards the margins of the biome.
- (9) Predictions on the shifts in the fitness response with climate change suggest that the impact of warming will be considerably high in the performance of all populations, particularly in the northern sites where lizards are currently coping with high  $T_a$ 's, and seem to

be thermal specialists, thus, more vulnerable to thermal fluctuations.

(10) The central populations of *T. torquatus* and *T. etheridgei* face local extinction risks as large proportions of the  $T_e$ 's currently exceeds the upper limit of the  $B_{80}$  and  $T_{set}$ -range of the species. In a warming scenario, performance and overall activity will decay during most of the day and be precluded in certain hours, particularly at midday.

(11) The histological analyses of the lizards' humeri of *T. torquatus* from Arinos, MG [collected in 1964-6 (MG1964-6), and in 2012 (MG2012)], and Formoso do Araguaia, TO [collected in 1966 (TO1966), and in 2012 (TO2012)] enabled the assessment of individual age, based on the number lines of arrested growth (LAG's; that correspond to the dry seasons), and the back calculation of the reabsorbed growth rings (which correspond to the wet seasons).

(12) Results confirmed that higher temperatures accelerate growth rates, anticipate sexual maturity and shorten the life-span in lizards. Although short-term effects of an increasing  $T_a$ 's may seem beneficial with respect to growth and reproduction, we predict an overall decay in the fitness in all populations in the long-term.

(13) Long-term exposure to warming, particularly at the northernmost and Central regions of the Cerrado, may lead lizards' performance to suboptimal levels, restricting time for activity and affecting foraging and reproduction, which consequently may affect the species fitness and unable them to cope with the rate of alteration of its habitat. Nevertheless, to achieve a better prediction of species persistence, one will probably need to combine both habitat and individual-based approaches.

(14) Species' or individuals' sensitivity depends not only on their thermal tolerance limits, but also on their behavior, and genetic diversity. Whereas thermoregulation may be considered as a buffer mechanism in the face of warming, northernmost and Central populations live close to their thermal limits for optimal metabolic performance and are considered constraint thermoconformers, which makes them more vulnerable to the raise of  $T_a$ .

(15) High variation in performance and growth traits may compensate for the impact of climate warming in the Central region of the Cerrado. On the contrary, in the gallery forest at the northernmost site, the low variation in performance traits, probably low physiological

capabilities for adjustment, narrow safety margins and no dispersal options enhance the extinction risk of *T. torquatus*.

(16) We highlight the importance of adding to climatic envelope models parameters that take into consideration plasticity and variation of ecophysiological traits to predict extinction of populations with more accuracy to whole lineages with low dispersal abilities or options and with.

## RESUMO

Nos próximos 85, no Brasil, espera-se um aumento real de até 6 °C na temperatura média do ar, além de uma queda de 5–20% nas taxas de precipitação. Neste sentido, o aquecimento do clima deve sobrepujar adaptações locais, e a sobrevivência dependerá da plasticidade fisiológica das espécies, além de sua capacidade de dispersão. Atualmente, a previsão das respostas ecológicas e fisiológicas dos organismos a estas alterações compreende um dos principais desafios dos ecofisiologistas. Os lagartos são particularmente sensíveis ao aquecimento global, uma vez que alterações de temperatura podem alterar sua performance para níveis sub-ótimos, restringindo os períodos de atividade com impacto direto em sua história natural. Em lagartos de regiões com baixa variabilidade climática (próximas ao Equador), a baixa resiliência às alterações ambientais, associada a opções restritas de dispersão e habitats cuja temperatura do ar ( $T_a$ ) seja superior aos seus ótimos termais, entre outros fatores, fazem destas populações as mais vulneráveis ao aquecimento. Neste estudo, foram realizadas análises espaciais e temporais no intuito de avaliar a vulnerabilidade de populações de lagartos do complexo *Tropidurus torquatus* no Cerrado brasileiro, e se a resiliência é influenciada pela magnitude da flexibilidade intrapopulacional de fisiologia termal e de performance. O estudo consta de três abordagens principais: (1) comparações de dados de temperatura corporal ( $T_b$ ) e temperatura operativa ( $T_e$ , temperaturas hipotéticas para termoconformadores); temperaturas corporais preferenciais ( $T_p$  média e amplitude dos valores de  $T_{set}$ ), e índices quantitativos de regulação de temperatura e de qualidade do ambiente termal ( $d_b$ ,  $d_e$  e  $E$ ) de *Tropidurus* com dados de literatura para espécies dos gêneros *Anolis*, *Liolaemus* e *Sceloporus*, bem como de 60 populações pertencentes a 21 espécies de tropidurídeos dos domínios da Caatinga, Amazônia, Cerrado e Chaco, e outras regiões como a costa do Peru e as ilhas Galápagos; (2) análises dos padrões intra e interespecíficos de variabilidade das capacidades de performance para velocidade e resistência em populações de *T. torquatus*, *T. oreadicus*, *T. etheridgei* e *T. catalanensis*, e estimativa do impacto de um aumento da  $T_a$  em 3 °C sobre a performance e a atividade destes lagartos num cenário de aquecimento, e (3) examinar as variações temporais e geográficas de idade, taxas de crescimento, maturidade sexual e longevidade em espécimes de *T. torquatus* em duas regiões a distintas latitudes; a variação temporal foi estimada através do estudo de amostras coletadas em cada uma das regiões em épocas distintas (década de 1960 e 2012), enquanto as comparações geográficas foram feitas apenas com base nas amostras recentes destas regiões (2012). Os resultados confirmam as hipóteses sugerindo que o comportamento termorregulatório aumenta acompanhando os

parâmetros de latitude e altitude e que os lagartos tropicais e de áreas situadas a baixas altitudes tendem a se comportar como termoconformadores. Estima-se que populações tropicais com pouco ou nenhum comportamento termorregulatório presentes em ambientes com restrições termais impostas por parâmetros altitudinais (de baixas ou elevadas altitudes) são os mais vulneráveis ao aquecimento do clima. Em contraste, as estepes e montanhas da Patagônia, bem como outras áreas montanhosas, representam refúgios termais para populações de lagartos que serão progressivamente forçados a se deslocar para estes ambientes. Dentre os tropidurídeos, um padrão geral sugere que o comportamento termorregulatório ambiental diminui na direção do Equador, particularmente devido à menor variabilidade ambiental. Na maioria das linhagens, valores similares e mais elevados de  $T_b$  e  $T_p$  em relação a valores de  $T_a$  apontam para uma condição plesiomórfica, provavelmente relacionada à ocorrência em ambientes florestais. O comportamento termorregulatório limitado ou ausente, combinado com grandes proporções de  $T_b$  e  $T_e$  acima dos ótimos termais aumentam os riscos de superaquecimento e limitam o tempo de atividade especialmente nas regiões central e setentrional do Cerrado. As curvas de performance demonstram que os intervalos termais de desempenho ( $B_{80}$ 's) e as margens de segurança aumentaram com a variação de temperatura, mas diminuíram com a variação anual de precipitação. Os resultados das comparações entre os padrões de variação temporal e regional do crescimento das populações de *T. torquatus* sugerem que o aquecimento do clima afeta o crescimento dos indivíduos, que tendem a ser maiores em regiões de clima mais quente. O aumento nos valores de  $T_a$  das últimas décadas aceleraram as taxas de crescimento, anteciparam a maturação sexual e encurtaram a expectativa de vida nas duas regiões estudadas. Embora em curto prazo os efeitos do aumento nos valores de  $T_a$  possam parecer vantajosos no que tange o crescimento e a reprodução, é plausível estimar uma queda geral no desempenho de todas as populações a longo prazo. Devido às grandes proporções de valores de  $T_e$  atualmente superando o limite superior de  $B_{80}$  e das preferências termais de *T. torquatus* e *T. etheridgei* na região Central, à capacidade de dispersão restrita e à baixa variabilidade na biologia termal de *T. torquatus* nas matas quentes de galeria, espera-se que os maiores impactos devam se concentrar sobre as populações das regiões central e setentrional.

**PALAVRAS-CHAVE:** Alterações climáticas, crescimento, desempenho, diferenciação populacional, ecologia termal, flexibilidade, eficiência termorregulatória, padrões geográficos, padrões temporais, plasticidade fenotípica, variação ambiental, vulnerabilidade.

## ABSTRACT

In Brazil, an increase in the mean air temperature ( $T_a$ ) of up to 6 °C and a trend of decreasing rainfall by 5–20% are expected within 85 years. Climate warming is expected to overrun local adaptation and survival will depend on the plasticity and dispersal options and abilities. Predicting how organisms will respond these changes is one of the most critical challenges for contemporary ecophysiologicalists. Lizards are particularly sensitive to global warming, as temperature changes could shift overall performance to suboptimal levels, restricting time for activity. The low resilience to environmental changes of lineages from regions of low climatic variability (close to the Equator) combined with low dispersal options and current habitats'  $T_a$  that exceeds their thermal optima, among other factors, make these populations the most vulnerable to warming. We conducted spatial and temporal analyses to assess the vulnerability of populations of the *Tropidurus torquatus* species complex in the Brazilian Cerrado and whether resilience is influenced by the magnitude of flexibility in thermal physiology and performance that exists within populations using three different approaches: (1) we compare data on body ( $T_b$ ) and operative temperatures ( $T_e$ , "null temperatures" for nonregulating animals), preferred body temperatures (mean  $T_p$  and  $T_{set}$  range), and quantitative indices of temperature regulation and quality of the thermal environment ( $d_b$ ,  $d_e$  and  $E$ ) for *Tropidurus* with data from the literature for *Anolis*, *Liolaemus*, and *Sceloporus*, and for 60 populations of 21 species of tropidurids from the Caatingas, Amazonia, Cerrado, Chaco, and other regions as the coast of Peru and Galapagos Islands; (2) We analyze patterns of variability in the performance capacities for velocity and endurance within and among populations of *T. torquatus*, *T. oreadicus*, *T. etheridgei* and *T. catalanensis*, and estimate the impact of a  $T_a$  increase by 3 °C on performance and activity of these lizards in a warming scenario; and (3) we examine the geographic and temporal variation of individual age, growth rates, age at sexual maturity and longevity in specimens of *T. torquatus* at two sites at different latitudes; temporal variation was estimated studying subsamples at each site collected in 1960s and 2012, whereas the geographical comparisons were performed between the two subsamples collected in 2012 both at the two sites. Our results confirm the hypotheses by suggesting that thermoregulatory behavior increases with latitude and altitude and that tropical and lowland lizards behave as thermoconformers. We estimate that tropical populations with poor or no thermoregulatory behavior that inhabit stressful environments

(open and low elevation sites) are the most vulnerable to rising temperatures. In contrast, Patagonia steppe and mountains as well as other montane environments represent future thermal refuges for lizards that would eventually be forced to retreat to these environments. Within tropidurids, a general pattern suggests that the thermoregulatory behavior decreases towards the Equator, particularly due to environmental constraints and probably to the low environmental variation. In most lineages, similar and higher  $T_b$  and  $T_p$  with respect to  $T_a$  point to a plesiomorphic condition, probably related to earlier forested environments. Constraint or no thermoregulation combined with the large proportions of  $T_b$  and  $T_e$  above the thermal optima augment the risk of overheating and preclude time of activity particularly in the central and northernmost regions of the Cerrado. Based on the thermal performance curves, thermal breadths ( $B_{80}$ 's) and safety margins increased with the thermal variation and decreased with the variation of annual precipitation. The results on the temporal variation and between sites differences on the growth patterns suggest that warming positively affect growth in *T. torquatus*. The increase of  $T_a$  of the last decades accelerated growth rates, anticipated sexual maturity and shortened the life-span at both sites. Although short-term effects of an increasing  $T_a$ 's may seem beneficial with respect to growth and reproduction, we predict an overall decay in the fitness response in all populations in the long term. Due to the large proportions of  $T_e$ 's currently exceeding the upper limit of the  $B_{80}$  and thermal *preferenda* of *T. torquatus* and *T. etheridgei* at the Central site and the limited dispersal capacity and low variability on the thermal biology of *T. torquatus* in the warm gallery forest, the northernmost and Central populations are expected to experience the highest impact.

**KEY-WORDS:** Climate change, fitness, flexibility, geographical patterns, growth, environmental variation, phenotypic plasticity, population differentiation, temporal patterns, thermal ecology, thermoregulatory efficiency, vulnerability.



## ABBREVIATIONS

CB	sample of <i>T. torquatus</i> collected in 2014 at the western site, Cuiaba, MT (15°55'01" S, 46°06'21" W; 211 m a.s.l.)
CT <sub>max</sub>	critical thermal maximum
CT <sub>min</sub>	critical thermal minimum
CV	coefficient of variation; $SD \times mean^{-1} \times 100$
B <sub>80</sub>	thermal tolerance breadths; range of $T_b$ at which performance is greater than or equal to 80% of the performance
$d_b$	average of the absolute distance of $T_b$ from the set-point range of each individual
$d_e$	is the deviations between $T_e$ and $T_{set}$ which specifies the average thermal quality of a microenvironment from the organism's standpoint
$E$	thermoregulatory efficiency; calculated as $E = 1 - (\text{mean } d_b / \text{mean } d_e)$
End <sub>max</sub>	maximum endurance
lower- $T_{B80}$	first interquartile of the distribution of B80
lower- $T_{set}$	first interquartile of the distribution of $T_p$
M	body mass
MG	central site, Arinos, MG (15°54'36" S, 46°06'0" W; 519 m a.s.l.)
MG1964	museum sample of <i>T. torquatus</i> at MG collected in 1964
MG2012	sample of <i>T. torquatus</i> at MG collected in 2012
MGe	sample of <i>T. etheridgei</i> at MG collected in 2012
MGt	sample of <i>T. torquatus</i> at MG collected in 2012
SM <sub>ct</sub>	safety margin: $CT_{max} - T_o$
SM <sub>ta</sub>	safety margin: $T_{a\ max} - T_o$
SM <sub>te</sub>	safety margin: $T_{e\ max} - T_o$
SP	southern site, Piracicaba, SP (, 15°54'36" S, 46°06'0" W; 519 m a.s.l.)
SPnr	sample of <i>T. catalanensis</i> at SP collected in 2011, in the non-reproductive season
SPr	sample of <i>T. catalanensis</i> at SP collected in 2013, in the reproductive season
SVL	snout-vent length
$T_a$	air or environmental temperature
$T_b$	field body temperature, in activity
$T_e$	operative temperature; "null temperatures" for non-thermoregulatory lizards
$T_o$	optimum temperature
TO	northern site, Formoso do Araguaia (11°48'39.11" S, 49°31'29.27" W; 230 m a.s.l.)
TO1964-6	museum sample of <i>T. torquatus</i> at TO collected between 1964 and 1966
TO2012	sample of <i>T. torquatus</i> at TO collected in 2012
TOo	sample of <i>T. oreadicus</i> at TO collected in 2012
$T_p$	preferred body temperature
TOt	sample of <i>T. torquatus</i> at TO collected in 2012
$T_s$	substrate temperature
$T_{set}$ -range	range between the first and third interquartile of the distribution of $T_p$
upper- $T_{B80}$	third interquartile of the distribution of B80
upper- $T_{set}$	third interquartile of the distribution of $T_p$
Vel <sub>max</sub>	maximum velocity