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Tese apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção de Título de Doutor em Ciências, na Área de Fisiologia Geral.

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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.

INTRODUCTION

The term “climate change” was firstly used in a scientific publication in 1950s (Plass, 1956). The author explained how the extra, mainly industrial, CO₂ 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 21st 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).

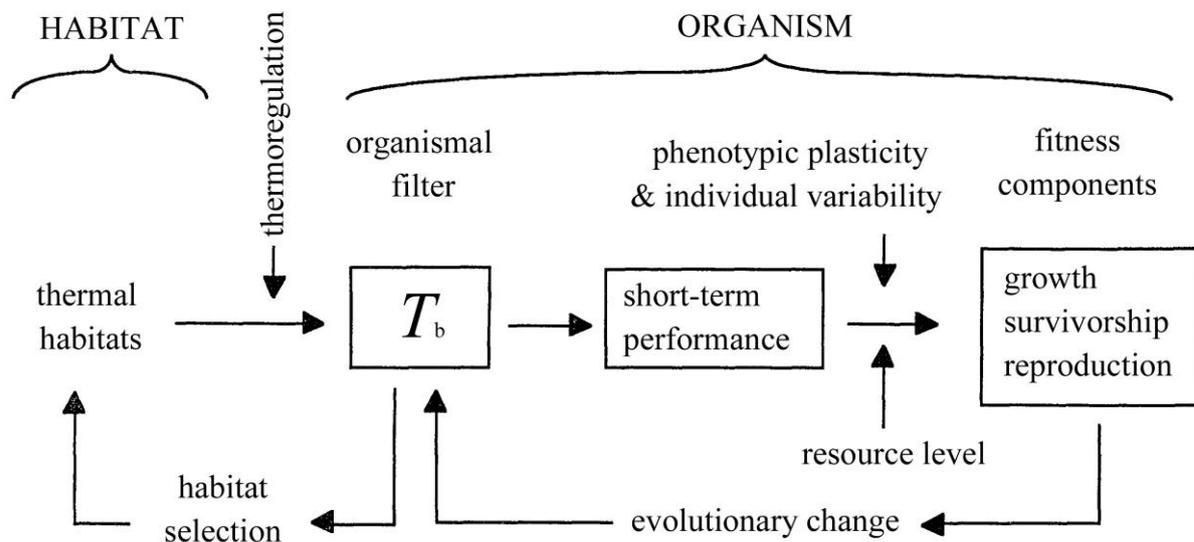


Figure 1. Conceptual summary of how habitat selection influences an organism's fitness by affecting the body temperature (T_b) and, thus, performance. Buffer mechanisms such as thermoregulation become beneficial when coping with changes of T_a and phenotypic plasticity and individual variability, in 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 (Chamaillé-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;

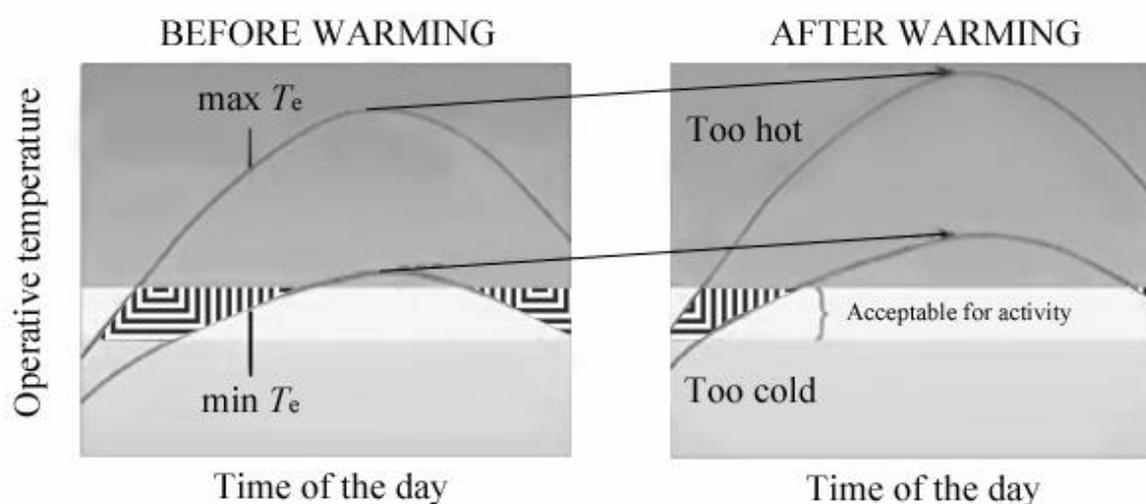


Figure 3. Hypothetical scenario of the effects of warming on the activity times of lizards. A shorten of the hours of activity are expected to reduce energy gains affecting reproduction and consequently causing extinction. (A) The maximum (upper curve) and minimum (bottom curve) operative temperatures (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

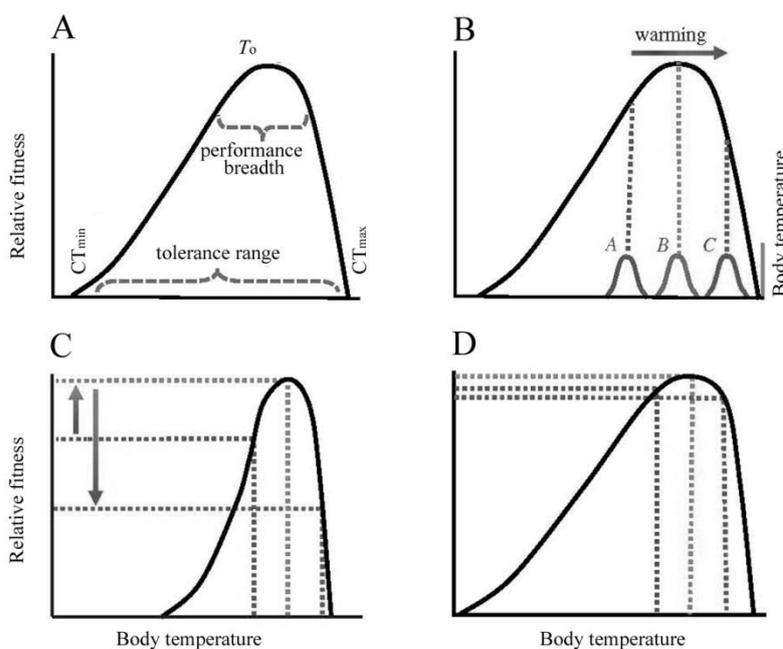


Figure 4. (A) Theoretical performance curve of a hypothetical ectotherm as a function of body temperature (e.g. maximum velocity or endurance vs. T_b). CT_{min} : minimum or lower critical temperature; CT_{max} : maximum or upper critical temperature; T_o : optimal temperature (modified from Huey and 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),

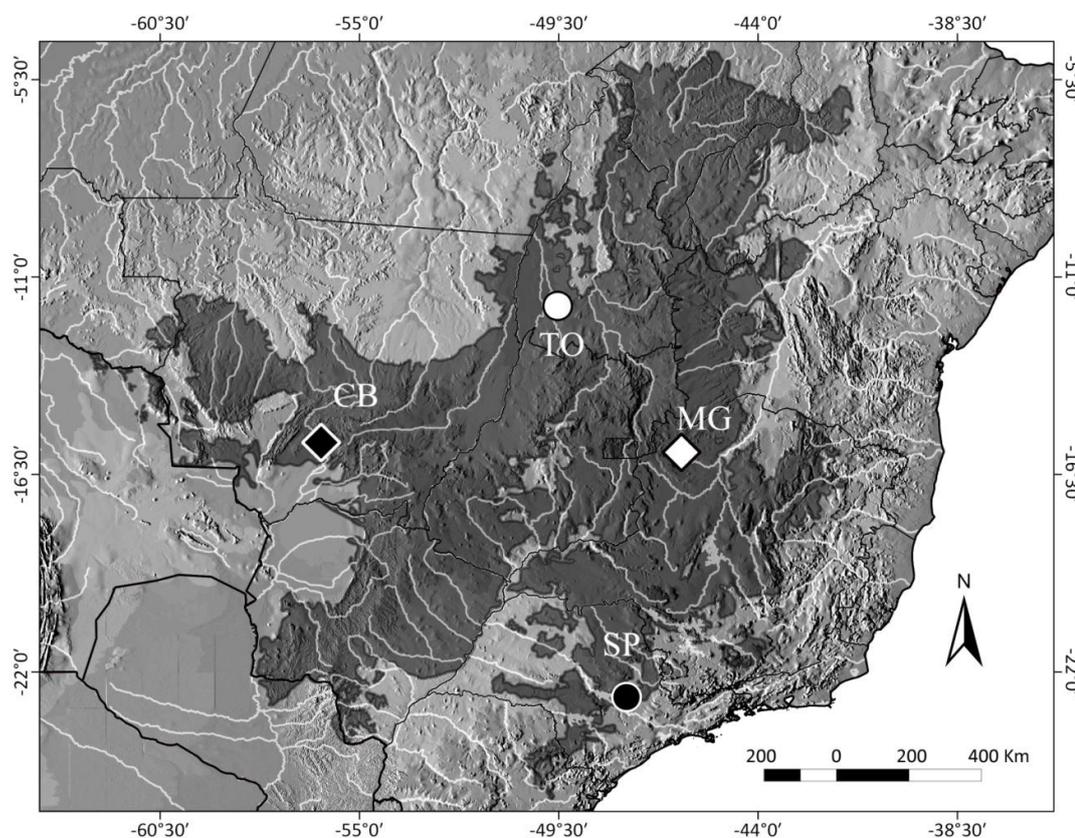


Figure 5. Study sites for *Tropidurus torquatus* (TOt) and *T. oreadicus* (TOo) from Formoso do Araguaia, Tocantins (TO, white circle), *T. torquatus* (MGt) and *T. etheridgei* (MGe) from Arinos, Minas Gerais (MG, white diamond), *T. torquatus* from Cuiaba, Mato Grosso (CB, black diamond), and *T. catalanensis* (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.

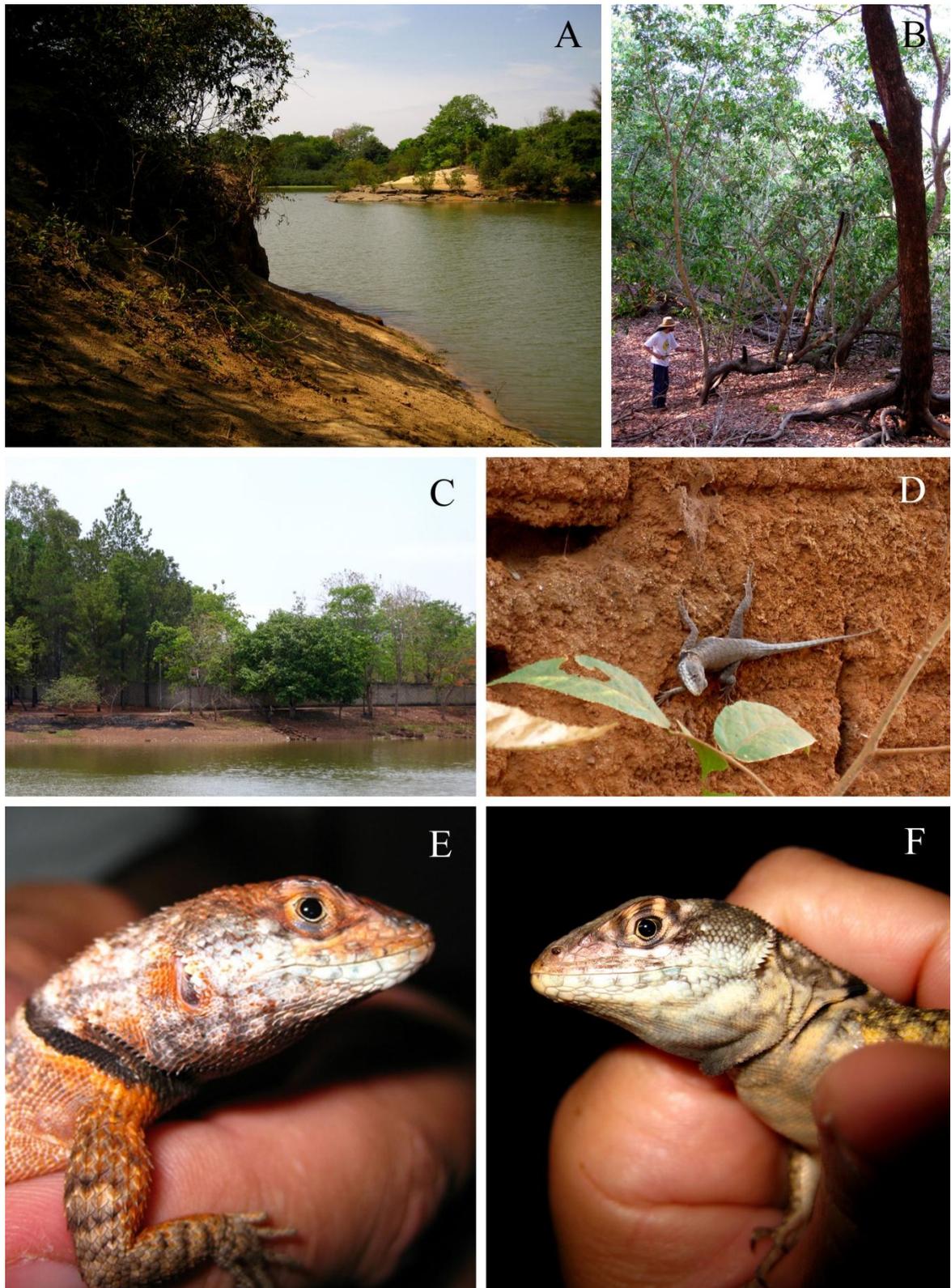


Figure 6. Gallery forests and urban Formoso do Araguaia, Tocantins, inhabited by *T. torquatus* (TOT) and *T. oreadicus* (TOO): (A) Formoso do Araguaia river (TOT's habitat); (B) gallery forest along the Córrego Papagaio (TOT's habitat); (C) downtown Formoso do Araguaia (TOO's habitat); (D) adult of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

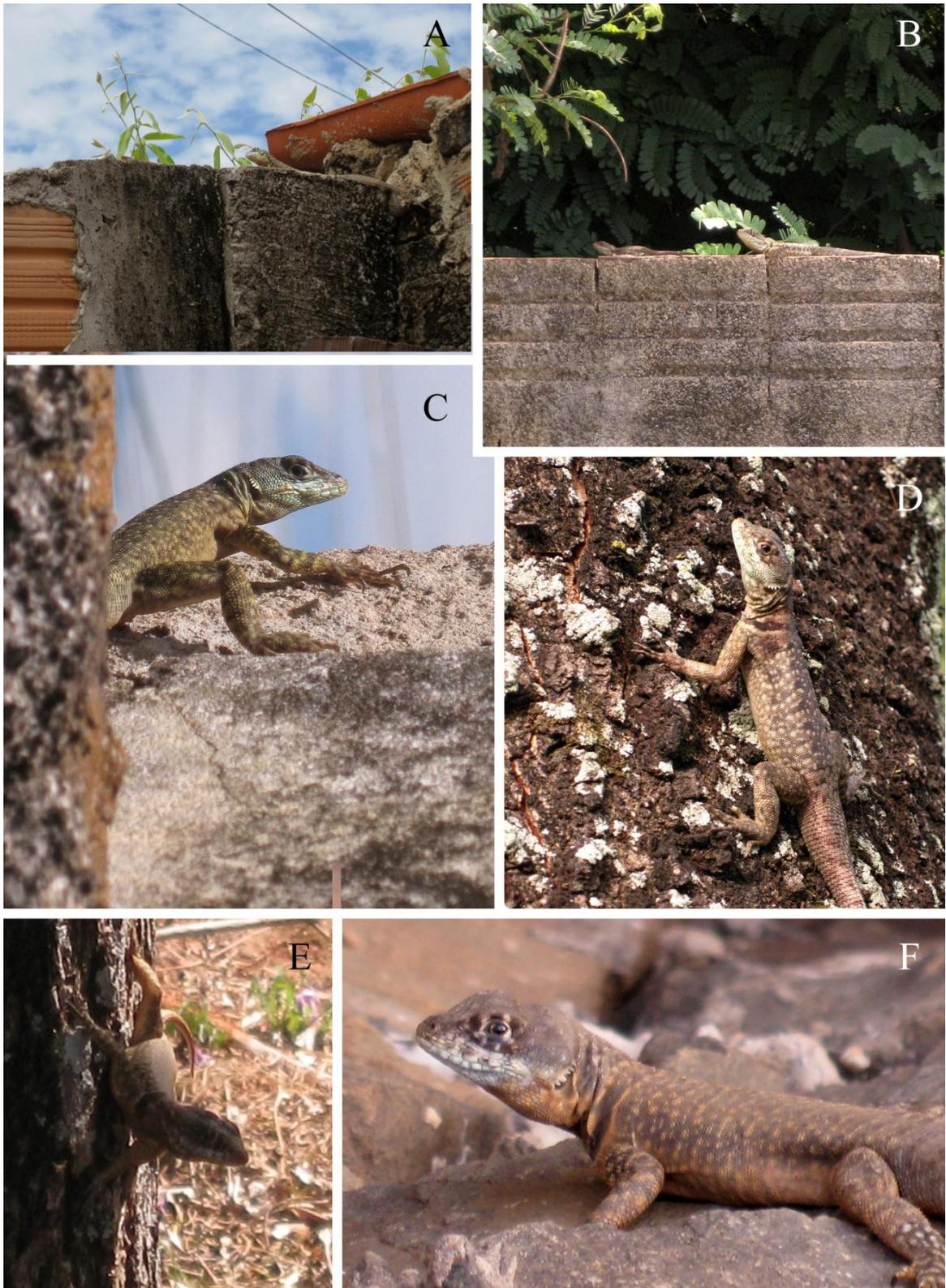
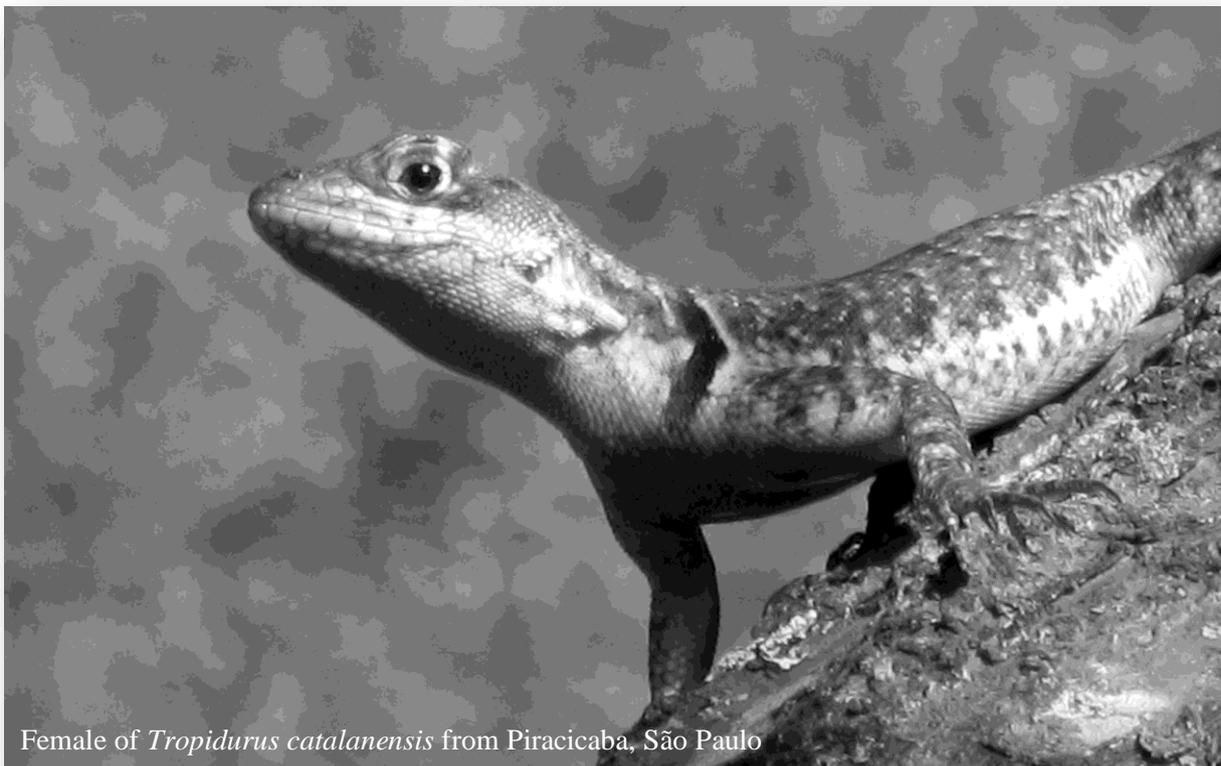


Figure 7. Specimens collected at the Central and southern sites in their typical environments or substrates: (A-B) Adults of *T. etheridgei* (MGe) and *T. torquatus* (MGt) from Arinos, Minas Gerais; (C-D) adults of *T. torquatus* (CB) from Cuiaba, Mato Grosso; (E-F) specimens of *T. catalanensis* (SP)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

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.

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