



Thermal ecology and microhabitat use of an arboreal lizard in two different Pantanal wetland phytophysionomies (Brazil)

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ABSTRACT

Temperature is one of the main environmental variables shaping the evolution and biology of terrestrial ectotherms. The Pantanal is the largest continuous wetland in the World. However, a lack of knowledge still exists on the thermal ecology of terrestrial ectotherms from this wetland. In this context, the thermal ecology of the lizard *Tropidurus lagunablanca* Carvalho, 2016 (Squamata, Tropiduridae) was investigated in the Brazilian Pantanal. The thermal ecology and microhabitat use of lizards from a riparian forest was compared to lizards from a park savanna. At both studied areas, air and body temperatures of lizards did not differ between sexes. Mean *T. lagunablanca* body temperatures were higher at the savanna compared to the forest, while air temperatures were similar in both habitats. The main substrates were tree trunks, with a frequency of approximately 90% of the observations. Lizards from the savanna used higher perches than those from the forest despite -in average- trees were higher at the forest. Lizard sun and shade exposure was similar for both areas. Lizards from both habitats showed similar strong linear relationships between body and air temperatures. However, lizard behaviour of using tree trunk perches differently under different sunlight situations suggests that these lizards actively thermoregulate. Further research on the thermoregulation abilities of this species, with a null hypothesis and behavioral observations will shed light on lizard thermal biology. Studies on the ecophysiological aspects of these lizards should be a priority to understand how they will react to climate change and which conservation measures will be more effective concerning their preservation.

1. Introduction

The biology and evolution of ectotherms is highly conditioned by the temperature of their habitats, being one of the most important traits affecting their lives (Angilletta, 2009; Pörtner, 2002). Most ectothermic vertebrates display the ability to behaviorally regulate their body temperatures to some extent. There is a gradient of behavioral thermoregulation, from thermoconformists, which do not display any behaviour to regulate their body temperatures -that passively change with environmental temperatures- to perfect thermoregulators, which exhibit a set of active behaviors to acquire or dissipate environmental heat -so that their body temperatures remain narrowly around their optimum (Angilletta, 2009; Hertz et al., 1993). The main mechanisms that lizards, as ectotherms, use for thermoregulation are adjusting their activity periods (Adolph and Porter, 1993; Gunderson and Leal, 2016; Hertz, 1992), shuttling between different thermal microhabitats (Bauwens et al., 1996; Heath, 1970; Sears et al., 2016), and adjusting

their body posture (Bauwens et al., 1996; De Lanuza et al., 2016). Lizards combine these thermoregulation strategies in a cost-benefit model, depending on their habitat characteristics (Basson et al., 2016; Blouin-Demers and Nadeau, 2005; Huey and Slatkin, 1976; Vickers et al., 2011). Dense forests have been traditionally considered to exhibit little thermal heterogeneity, and, thus, being scarcely suitable habitats for lizard thermoregulation (Fitzgerald et al., 2003; Hertz, 1974) compared to open areas, such as park savannas or arid habitats (Kiefer et al., 2007; Vitt et al., 1997). However, a recent comparative study demonstrates that tropical forests are highly thermally heterogeneous at a scale relevant to lizards (Scheffers et al., 2016).

Several studies have addressed the thermal ecology of tropidurid lizards from different neotropical habitats, such as rain forests (Rocha and Bergallo, 1990; Vitt and Zani et al., 1996; Vitt et al., 1997), dry forests (Jordán and Pérez, 2012; Martoni and Aun, 1994; Olivera, 2015), xeromorphic savanna's woodlands (Colli et al., 1992), dry forests of arid shrubby regions (Vitt, 1995), coastal sand dunes (Bergallo and

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Rocha, 1993; Kiefer et al., 2007), rocky outcrops (Meira et al., 2007; Ribeiro and Freire, 2010; Ribeiro et al., 2007; Rocha and Bergallo, 1990; Vitt et al., 1996), dry montane forest and shrubland areas (Andrango et al., 2016), and coastal deserts (Báez and Cortés, 1990; Sepúlveda et al., 2008, 2014). A comparative study on lizards (Tropidurinae) verified that other ecological parameters related to these organisms evolved in a different way than their thermoregulatory behaviour during the colonization of different Brazilian habitats (Kohlsdorf and Navas, 2006). Important research is currently being conducted in order to understand the thermal ecology of neotropical lizards and their vulnerability to climate change (e.g. Diele-Viegas et al., 2018; Pontes-da-Silva et al., 2018). In this scenario, the thermal ecology of lizards from the Pantanal is still poorly understood, despite the high abundance of individuals in this habitat (Alho, 2011; Strüssmann et al., 2011).

In this context, the aim of the present study was to investigate the thermal ecology and microhabitat use of *Tropidurus lagunablanca* Carvalho (2016) in two different Pantanal habitats (Mato Grosso do Sul, Brazil), namely a closed habitat (a riparian forest) and an open area (a park savanna). We aimed to answer the following questions: (1) which body temperatures does this species achieve in the field and to which extent is it related to air temperatures?, (2) which types of microhabitats does *T. lagunablanca* use at the Pantanal? and (3) does thermal ecology and microhabitat use of *T. lagunablanca* vary between the study areas (forest vs savanna)?

2. Material and methods

2.1. Study species

Tropiduridae is one of the richest families of neotropical lizards, with 42 species occurring in Brazil (Costa and Bérnils, 2018), broadly distributed throughout rain forests, Cerrado, arid habitats and coastal dunes (Bergallo and Rocha, 1993; Rodrigues, 1987). The *Tropidurus spinulosus* (Cope, 1862) species group was delimited by Frost et al. (2001), Carvalho (2016) and Cacciali and Köhler (2018), comprising five species. Among these species, *T. spinulosus* (= *T. guarani*) is restricted to central and southern Bolivia, some areas in western Brazil, the Paraguayan Chaco (west of Paraguay River), and a narrow area in the Argentinean Dry Chaco, while *T. lagunablanca* (= *T. tarara* and *T. tejumirim*) is broadly distributed throughout Mato Grosso and Mato Grosso do Sul (Brazil), narrowing its distribution southwards, with the Paraguari Department (Paraguay) as the southernmost record for the species (Cacciali and Köhler, 2018).

Tropidurus lagunablanca inhabits Cerrado and Pantanal areas and Chaco domains (Cacciali and Köhler, 2018; Carvalho, 2013; Ferreira et al., 2017; Frost et al., 1998; Souza et al., 2010). Within the Tropiduridae from the Pantanal area, *T. lagunablanca* is noteworthy due to its abundance. However, little information is available regarding the ecology of this medium-sized insectivorous lizard (Ávila et al., 2010; Colli et al., 1992). *Tropidurus lagunablanca* lizards from two habitats, a park savanna and a riparian forest, were investigated. Lizards from both areas exhibited sexual dimorphism regarding body size, with males larger than females. In addition, lizards from the forest (mean \pm sd [range]: males: 110 ± 17.16 [80–140] mm, females: 95 ± 5.84 [85–105] mm) were larger than lizards from the open area (males: 100 ± 16.71 [70–125] mm, females: 85 ± 4.89 [78–95] mm).

2.2. Study area

The Pantanal, the largest continuous wetland in the World, is dominated by water flux overflow and retraction, which changes between years (Junk et al., 1989; Junk, 1999). The Pantanal comprises approximately 160,000 km² and exhibits a mosaic of different types of vegetation (Junk and Cunha, 2005). This study took place at the Pantanal sub-region of Miranda (Mato Grosso do Sul, Brazil; 19°34'24.64"S 57° 0'58.27"W), at about 110 m of altitude. This area exhibits a hot

tropical climate (Kottek et al., 2006) with high seasonality, characterized by wet (October to March) and dry (April to September) seasons (Tarifa, 1986). Mean monthly rainfall is of 200 mm during the wet season and 30 mm during the dry season, and environmental temperatures range from 23° to 34 °C in the wet season and 8–23 °C in the dry season (Tarifa, 1986).

Two areas were compared: a riparian forest along the Miranda River (hereafter named 'forest') and a park savanna (hereafter named 'savanna'). The forest usually floods between January and March -depending on rainfall intensity-, and exhibits a dense canopy comprising many tree species varying from 8 to 13 m in height (Ragusa-Netto, 2002). The savanna is a monodominant stand of *Tabebuia aurea* (Silva Manso) Benth. & Hook. f. ex S. Moore, trees that can reach up to 12 m in height, alternated with shrubs -forming an open habitat- and distributed in small hills, that do not flood during the wet season (Por, 1995; Ribeiro and Brown, 2006; Soares and Oliveira, 2009). Both areas were selected due to their high abundance of *T. lagunablanca* lizards and because they are close to each other (< 2 km), preventing atmospheric condition variations that could affect the study results.

2.3. Data collection

The forest was sampled from September 2007 to July of 2008 and the savanna, from September 2008 to July of 2009. Five linear transects of approximately 500 m each were established in each habitat, visited six consecutive days per month (four transects per day), from 07:00–17:00 h (local Brasilia time: GMT – 4). After the observation of each *T. lagunablanca* individual, the substrate (main trunk of the tree, branch, or on the ground), sun or shade conditions, and sex were reported. As the juvenile observations were less frequent, only adult individuals were considered in the present study, in order to reduce possible confounding factors. In addition, a total of 92 adult lizards were captured by noosing, totaling 26 males and 18 females at the forest and 24 males and 14 females at the savanna. Their cloacal temperature (T_b) and the capture area air temperature (T_a) were recorded, with a Miller and Webber® quick-reading mercury thermometer (precision 0.2 °C) within 15 s of capturing and shadowing the probe. The snout-vent lengths (SVL) and body mass of each captured lizard were also determined, the former with a measuring tape (precision 0.1 cm) and the latter with a Pesola® spring scale (precision 0.1 g). Finally, the height and diameter of the tree on which each lizard was observed and the height at which lizards were registered were also determined. Tree diameter was determined as diameter at breast height, DBH, always measured by the same researcher at 130 cm in height, with a measuring tape, with a 0.1 cm precision. All procedures were carried out under Brazilian government IBAMA (#029/04) and SISBIO (#10604) authorizations.

2.4. Data analyses

The frequencies of the substrates and sunlight situations of lizards between sexes and habitats (forest vs savanna) were compared applying chi-square tests. The mean T_b , T_a , height (of the tree and of the lizard) and DBH values of trees used by lizards were compared between sexes and/or habitats with a one-way ANOVA. When residuals were not normally distributed, we computed bootstrap of the ANOVA. When variances were homogeneous, we used the Welch correction of ANOVA. The T_b of lizards from both areas was compared by ANCOVA, using T_a as covariable. Correlations between T_a and T_b were evaluated by Spearman's rank correlation, as data present some outliers. The relation between T_a and T_b were assessed by simple linear regressions (Crawley, 2012; Sokal and Rohlf, 1995). All analyses were carried out on the R software, version 3.4.0 (R Core Team, 2017). The mean values of the variables are reported, accompanied by their respective standard errors. The significance level for all analyses was set at $\alpha = 0.05$.

Table 1

Mean ± SE (n) of the investigated *Tropidurus lagunablanca* variables in the Pantanal wetland (Brazil): height of the animal on the tree (height), height of the tree on which the lizard was observed (tree), diameter at breast height of the tree on which the lizard was observed (DBH), cloacal body temperature (T_b), and air temperature of the observation place (T_a). For comparisons between sexes, the one-way ANOVA was applied.

	Habitat	Males	Females	Comparison
T _b (°C)	Forest	28.67 ± 0.70 (26)	27.79 ± 0.86 (14)	F = 0.627, p = 0.434
	Savanna	29.54 ± 0.65 (24)	29.65 ± 0.73 (14)	F = 0.012, p = 0.903 ^a
T _a (°C)	Forest	30.45 ± 0.39 (61)	30.25 ± 0.35 (63)	F = 0.152, p = 0.697
	Savanna	30.68 ± 0.47 (65)	29.89 ± 0.44 (69)	F = 1.493, p = 0.224
Height (cm)	Forest	220.76 ± 15.49 (82)	207.70 ± 13.87 (78)	F = 0.392, p = 0.532
	Savanna	282.90 ± 16.62 (69)	272.29 ± 14.66 (81)	F = 0.231, p = 0.631
Tree (cm)	Forest	1133.55 ± 36.91 (76)	1085.33 ± 41.01 (75)	F = 0.765, p = 0.383
	Savanna	844 ± 20 ± 21.34 (69)	865.66 ± 19.47 (83)	F = 0.552, p = 0.459
DBH (cm)	Forest	41.05 ± 2.36 (71)	45.61 ± 2.73 (72)	F = 1.587, p = 0.210
	Savanna	35.02 ± 1.23 (69)	36.59 ± 1.08 (83)	F = 0.937, p = 0.335

^a Since residuals were not normally distributed, we performed 1000 bootstraps of this analysis, resulting that the bootstrapped p-value is 0.903 and the original was 0.912.

3. Results

Most lizards were observed on tree trunks (84.7% at the forest and 96.1% at the savanna). The T_b and T_a were similar for males and females both in the forest and in the savanna (Table 1). The microhabitat traits where lizards were observed (height of the first observation, height and diameter of the tree) were also similar for both sexes in both study areas (Table 1). In addition, the frequencies of lizards observed in sun or shade conditions were also similar for males and females at the forest (Chi² = 0.129, df = 1, p = 0.720) and the savanna (Chi² = 3.752, df = 1, p = 0.053). Hence, the data for both sexes was pooled for further analyses concerning comparisons between lizards of both studied areas.

The amount of lizards using the different substrates varied significantly between the forest and the savanna (Chi² = 14.944, df = 3, p = 0.002; Fig. 1). However, the share of lizards in sun and shade was similar for both habitats (Chi² = 2.946, df = 1, p = 0.086). Trees used by lizards were significantly taller (Welch one-way ANOVA; F_{1, 226.04} = 66.677, p < 0.0001) and thicker (DBH; Welch one-way ANOVA, F_{1, 197.11} = 14.168, p < 0.0001) in the forest compared to the savanna (Table 2). However, lizards were found at lower heights in the forest compared to the open area (One-way ANOVA; F_{1, 308} = 17.249, p < 0.0001). In the sun, lizards were found at similar heights in both

Table 2

Mean ± SE (n) values for *Tropidurus lagunablanca* of the two studied habitats at the Pantanal (Mato Grosso do Sul, Brazil): a forested area (riparian forest along Miranda River) and an open area (park savanna). Variables comprised cloacal body temperature (T_b), air temperature of the observation place (T_a), height of the animal on the tree (height) height of the tree on which the lizard was observed (tree), and diameter at breast height of the tree on which the lizard was observed (DBH).

	Forest	Savanna
T _b (°C)	28.31 ± 0.54 (35)	29.58 ± 0.48 (38)
T _a (°C)	30.35 ± 0.26 (124)	30.27 ± 0.32 (134)
Height (cm)	217.40 ± 10.41 (160)	277.17 ± 10.97 (150)
Tree (cm)	1109.60 ± 27.55 (151)	855.92 ± 14.36 (152)
DBH (cm)	43.35 ± 1.81 (143)	35.88 ± 0.81 (152)

areas (F_{1, 106} = 1.718, p = 0.193), while lizards using shaded microhabitats perched significantly higher in the savanna (One-way ANOVA; F_{1, 200} = 15.476, p < 0.0001).

Lizards exhibited a significantly lower T_b in the forest than at the savanna, even when removing the effect of T_a (ANCOVA, F_{1, 70} = 8.595, p = 0.005), and T_a were similar for both habitats (One-way ANOVA; F_{1, 256} = 0.035, p = 0.852). A significant linear relationship was observed between T_b and T_a in the forest (Spearman's rank correlation: r_s = 0.709, p < 0.0001, n = 35) as well as in the open area (r_s = 0.782, p < 0.0001, n = 38). The regression for T_a on T_b was significant and slopes were similar for both lizards of both areas (ANCOVA slope test, F_{1, 70} = 0.280, p = 0.599; T_b = 6.69 + 0.76 *T_a, R² = 0.553; Fig. 2).

4. Discussion

Tropidurus lagunablanca is mainly arboreal in the Pantanal wetland, both in the forest and savanna areas, observed only sporadically on the ground. Individuals found on the ground (less than 2%) were always close to the trees, mainly foraging between their roots, or climbing up. Some lizards were also observed moving from one tree to another, perhaps searching for food, mates or more thermally suitable or safe conditions. *Tropidurus spinulosus* from the Argentinean Chaco was also found to use trees in more than the 90% of the observations (Cruz, 1998). Nonetheless, it is worthy noticing that the southernmost population of *T. lagunablanca* uses rock surfaces for basking and seeks shelter underneath rock blocks and crevices (Cacciari and Köhler, 2018; Carvalho, 2016). Many *Tropidurus* species are generalist regarding microhabitat use, such as *T. etheridgei*, *T. hispidus*, *T. itambere*, *T. montanus*, *T. oreadicus* and *T. torquatus*, while others, like *T. cocorobensis*, *T. erythrocephalus*, *T. macujensis*, *T. psammonastes* and *T. spinulosus* (a population currently known as *T. lagunablanca*) are specialists (Colli et al.,

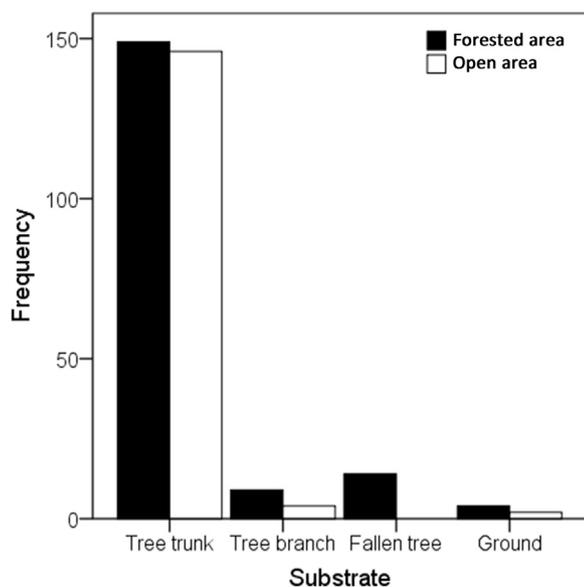


Fig. 1. Frequency of adult *Tropidurus lagunablanca* observations at forested (n = 152) and an savanna (n = 176) areas in the Pantanal (Brazil).

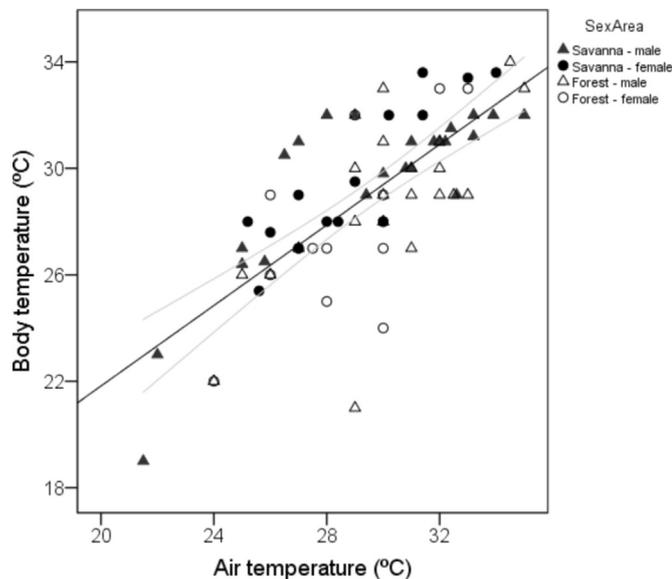


Fig. 2. Linear regression models of air temperatures (T_a) on body temperatures (T_b) of *Tropidurus lagunablanca* lizards from two habitats of the Pantanal (Mato Grosso do Sul, Brasil). Air and substrate temperatures were registered in °C at the individual capture places.

1992; Rodrigues, 1987; Rodrigues et al., 1988; Vitt, 1991a). Several examples of other arboreal lizards exist among the Tropiduridae family (Howland et al., 1989; Vitt, 1991b; Vitt and Zani, 1996; Vitt et al., 1997).

Tropidurus lagunablanca selects trees with thick trunks in both study areas. Thicker trunks could hold more prey and/or present a higher diversity of microhabitats for thermoregulation (Hanula et al., 2000; Neves et al., 2013). Lizards perched higher on tree trunks in the savanna, despite trees being -on average- higher in the forest. Between 40% and 60% of observed lizards were exposed to the sun, with similar ratios for the forested vs open area. In the riparian forest, comprising a dense canopy, lizards would easily find shaded perches along the trunk. Meanwhile, shadows would be sparse in the tree trunks of the savanna area, mainly concentrated below the tree crown. Lizards in sunny microhabitats perched at similar heights in both areas, while those at shaded microhabitats perched significantly higher in the savanna. This finding suggests that lizards search for specific microhabitats aiming at thermoregulation. However, there is still a need for studies concerning microhabitat availability, in order to clearly understand how lizards select each type of microhabitat for thermoregulation or other functions.

Mean body temperature of adult *T. lagunablanca* was higher in the savanna (29.58 °C) than at the forest (28.31 °C). Moreover, the body temperatures of Pantanal lizards of both studied habitats are quite lower compared with other species displaying similar habitats belonging to the *Tropidurus* genus. Studied *Tropidurus* species in open areas exhibit mean body temperatures between 29.2 and 37.8 °C (Cruz, 1998; Cruz et al., 1998; Bergallo and Rocha, 1993; Hatano et al., 2001; Kiefer et al., 2007; review in Rocha et al., 2009; Vitt, 1995; Vitt and Zani, 1996;), with the exception of a *T. spinulosus* population in a temperate open area in Argentina, that exhibited mean body temperature of 30.3 °C (Martoni and Aun, 1994). On the contrary, the *T. lagunablanca* body temperatures from both investigated habitats are in accordance to those reported for other *Tropidurus* species living in forest areas, which range between 26 and 33 °C (Vitt and Zani, 1996; Vitt et al., 1997). Due to logistic constraints, we sampled the forest and the savanna in different years, which could bias our results.

Arboreal lizards have been traditionally considered as exhibiting more limited thermoregulation abilities than lizards living in open areas, or even to be thermoconformers (Huey and Webster, 1976; Huey

et al., 2009; Piantoni et al., 2016). This is attributed to the lower availability of thermally heterogeneous microhabitats for thermo-regulation, mainly due to the scarcity of sunny patches (but see Scheffers et al., 2016). Thus, the body temperature of lizards living in dense forests use to be more dependent on air temperatures (Huey and Slatkin, 1976; Kiefer et al., 2005; Van Sluys et al., 2004). We observed significant linear relationships between air and lizards' body temperature for *T. lagunablanca* of both studied areas, with a correlation coefficient of approximately 0.7–0.8. Although this high correlation may indicate thermoconformism, it may be misleading. In a revision carried out on Lacertidae thermal ecology for a meta-analytic study (unpublished data), we found that 37.5% of the studied lacertids show correlation coefficients close to or even higher than those determined herein for *T. lagunablanca*, although they inhabit open areas and are highly effective thermoregulators (e.g. Carretero and Llorente, 1995; Maragou et al., 1997; Ortega and Pérez-Mellado, 2016; Ortega et al., 2016). In fact, *T. lagunablanca* lizard behaviour, of using different trunk heights in the different study areas depending on the sunlight situation suggests active thermoregulation. Thus, despite most literature and the correlations found here could indicate thermoconformism of the study species, the behaviour of *T. lagunablanca* regarding use of sun/shade patches suggest behavioral thermoregulation, as recently found for *T. spinulosus* in laboratory conditions (López-Juri et al., 2018). In any case, temperature data should be compared with behavioral observations and a null thermoregulation hypothesis (Hertz et al., 1993), in order to be able to assess *T. lagunablanca* thermoregulation abilities.

Lizards are among the most vulnerable animals to climate change (Gibbons et al., 2000). Sinervo et al. (2010) predicted that the 20% of all lizard species can become extinct in 2080 due to these changes, and this scenario could be even worse for tropical lizards living in forests, mainly those exhibiting more frequent thermoconformer habits, specialized in high temperatures and with lower acclimation capacities (Huey et al., 2009, 2012; Tewksbury et al., 2008; Piantoni et al., 2016). In addition, the habitat specialism of these tropical species would be an important factor contributing to their vulnerability to climate change (Brusch et al., 2016). A recent study on Amazonian lizards supported the extinction scenarios reported by Sinervo et al. (2010) but found hope for their persistence in local adaptations that could derive from populational thermo-physiological differences (Pontes-da-Silva et al., 2018). Besides temperature increases, the Pantanal wetland is predicted to suffer hydrology changes related to climate change (Junk et al., 2013), which could also modify lizard habitats, such as the evaluated riparian forests and park savannas. The consequences of anthropogenic climate change on terrestrial Pantanal ectotherms subjected to special climatic conditions that significantly depend on rains and flood cycles are still difficult to predict. *Tropidurus lagunablanca* is reported herein as a habitat specialist mainly inhabiting tree trunks, that exhibit different body temperatures in different habitats (open vs closed) and seems to display behavioral thermoregulation to some extent. Thus, it is possible that populations of this species may also be highly vulnerable to climate change -being habitat specialists- but they do not seem to be thermoconformers and could perhaps adapt to new thermal conditions. To the best of our knowledge, no predictions regarding the consequences of climate change on ectotherms from the Pantanal wetland are available. Further studies on the ecophysiology of this and other terrestrial Pantanal ectotherms will shed light on the consequences of climate change, and the possible differences to the tropical animals studied to date.

In conclusion, this arboreal Pantanal lizard presents higher body temperatures in an open area -a park savanna- compared to a closed one -a riparian forest- while air temperatures were similar for both habitats. Body and air temperatures were strongly correlated, which would, at first, suggest thermoconformity. However, some evidence for behavioral thermoregulation was observed. Despite the trees being taller in the forest, lizards were found at higher perches on the park savanna tree trunks when lizards were in shaded microhabitats, while they were at similar heights in sunny microhabitats. Shadows are abundant in the

riparian forest, due to the dense vegetation, while they are scarce in the savanna, mostly below the treetops. Thus, it is probable that lizards are selecting higher perches in the savanna to cool themselves. The next step would be to deepen insights on the thermoregulation abilities of this species in different habitats, and the potential of different Pantanal habitats for temperature regulation of other small ectotherms.

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