Microhabitat selection of the poorly known lizard *Tropidurus lagunablanca* (Squamata: Tropiduridae) in the Pantanal, Brazil

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Abstract. Understanding how different environmental factors influence species occurrence is a key issue to address the study of natural populations. However, there is a lack of knowledge on how local traits influence the microhabitat use of tropical arboreal lizards. Here, we investigated the microhabitat selection of the poorly known lizard *Tropidurus lagunablanca* (Squamata: Tropiduridae) and evaluated how environmental microhabitat features influence animal’s presence. We used a Resource Selection Function approach, in a case/control design where we analyzed the effect of substrate temperature and tree’s diameter at breast height (DBH) in the probability of presence of lizards using mixed Conditional Logistic Regression. We found that *T. lagunablanca* uses trees with DBH from 0.40 m to 4 m and substrate temperatures ranging from 25.9°C to 42°C. Moreover, we showed that thickness of the trees and substrate temperatures significantly increased the probability of presence of *T. lagunablanca* individuals, being the probability of presence higher than 50% for trees up to 1.5 m DBH and temperature of substrate up to 37.5°C. Our study probed that *T. lagunablanca* individuals choose trees non-randomly, selecting thicker and warmer tree trunks. This information advances the knowledge of the spatial ecology of Neotropical arboreal lizards and is relevant for conservation, putting an emphasis on preserving native vegetation in the Pantanal.

Keywords. Microhabitat use; Thermal biology; Activity patterns; Substrate temperature; Thermoregulation; Lizards; Wetlands.

INTRODUCTION

Understanding how different environmental variables affect species’ occurrence is of great importance for the study of natural populations and a central topic of organismal biology (Schwenk et al., 2009; Ehrlén & Morris, 2015). Although other mechanisms can also influence the occurrence of species (e.g., competition, coexistence, predation; Chesson, 2000; HilleRisLambers et al., 2012; Cadotte & Tucker, 2017), locally, environmental filters can determine the presence of individuals. In this context, one of the most important factors for the spatial organization of population is how individuals select the resources in the environment (Pianka, 1973; Nogueira et al., 2005; Rocha & Anjos, 2007; Gonçalves-Sousa et al., 2019; Peixoto et al., 2020). However, within their habitats, animals deal with many environmental constraints that directly influence their activity patterns and microhabitat selection (Rutherford & Gregory, 2003; Domenici et al., 2007; Ariano-Sánchez et al., 2020; Ortega et al., 2019).

Lizards exhibit a diverse set of lifestyles and inhabit a variety of habitats, ranging from tropical forests to sandy deserts (Vitt & Pianka, 1994). In Brazil, there are high levels of species richness and endemism (Costa & Bérnils, 2018), and a high diversity of forms with striking adaptations, as psammophilous and fossorial species (e.g., Calypptomma, Notobachia and Ophiole), with vestigial legs or even limbless (Rodrigues, 1996; Recoder & Rodrigues, 2020). Because lizards are ectotherms, body temperature regulation is essential for the development of all activities such as foraging, anti-predatory behaviors, and mating.
strategies (Adolph, 1990; Angilletta, 2009). Microhabitat selection is, with some contribution of changes in body posture and adjustment of activity periods, the main thermoregulatory strategy of small lizards (Adolph & Porter, 1993; Bauwens et al., 1996; Ortega et al., 2019), including in species from deserts (e.g., Phrynosoma platyrhinos; Newbold & MacMahon, 2014), temperate areas (e.g., Podarcis guadarramae; Ortega & Pérez-Mellado, 2016), as well as in Neotropical region (Ameivula aff. ocellifera and Tropidurus oreaticus; Ortega et al., 2019).

In general, lizards are abundant, occur in almost all types of environments, and respond strongly to local variables, thus being good models for studies focusing on habitat selection and its ecophysiological consequences in different spatial scales (Smith & Ballinger, 2001; de Andrade, 2020). A growing body of knowledge about microhabitat use and the understanding of their relations with local environmental variables has recently been produced (e.g., Cosendey et al., 2019; Franzini et al., 2019; Xavier et al., 2019). However, there is still a lack of knowledge about microhabitat selection for various lizard species and habitats, as is the case of the Pantanal (Brazil), where organisms experience complex climatic changes and flood dynamics (Alho et al., 2001). Until now, and recently, only three studies evaluated the microhabitat use and/or selection of lizards in the Pantanal (i.e., Terra et al., 2018; Benício et al., 2019; Ortega et al., 2019). In this particular biome, the dynamic of organisms is primarily driven by flood and dry cycles that are quite variable in terms of recurrence and duration (Gonçalves et al., 2011; Mercante et al., 2011; Souza et al., 2017). Thus, both flooding extension and extended droughts may limit the occurrence of species and shape local patterns of microhabitat use, reinforcing the necessity to better understand the habitat selection processes in this environment.

Here, we characterize the microhabitat use of the poorly known lizard Tropidurus lagunablanca (Squamata: Tropiduridae) and test hypotheses on the influence of environmental traits on microhabitat selection of this arboreal species. Tropidurus lagunablanca (Fig. 1) is a recently described lizard, medium-sized (SLV = 101.22 mm), diurnal, heliothermic and arboreal, sit-and-wait forager, that occurs predominantly in open formations (Carvalho, 2016). Although T. lagunablanca has not been yet evaluated by any red list, Carvalho (2016) suggests that, according to the rules proposed by IUCN (2001), the species could be classified as “critically endangered”, mainly because of the conversion of its natural habitat into agricultural areas. Furthermore, little information is available regarding the ecology of this species (Colli et al., 1992; Ávila et al., 2010; Terra et al., 2018).

Our specific aims were to describe microhabitat use and investigate microhabitat selection by T. lagunablanca in the Pantanal (Brazil), assessing the influence of environmental traits on the probability of presence of the individual lizards in the available microhabitats. Since different trees can provide different opportunities for thermoregulation, feeding, defense and mating, we formulated two major hypotheses about microhabitat selection of this species (Fig. 2): (i) T. lagunablanca individuals would select their microhabitats depending on their thermal properties, which would enhance thermoregulation (H1); and (ii) T. lagunablanca individuals would choose thicker trees, since they would offer more food and shelter, and, consequently more mating opportunities (H2).

**MATERIAL AND METHODS**

We conducted the study in the Pantanal region of Miranda-Abrobal, near the Base de Estudos do Pantanal (19°34 37”S, 57°00’42”W) of the Federal University of Mato Grosso do Sul (Corumbá, Mato Grosso do Sul, Brazil), in September 2017 (dry season). This article is the result of a research project of the 20th course Pantanal Ecology Course (EcoPan2017) of the Universidade Federal of Mato Grosso do Sul. The Pantanal is located in one of the most distinct macroregions formed from relief variations: the
floodplain (Prado et al., 1992; Lourival et al., 2000). The Pantanal occupies an area of approximately 195,000 km², which makes it one of the largest wetlands of the world (Ferreira et al., 2017).

We sampled lizards along three consecutive days through active visual search (Crump & Scott Jr., 1994) from 07:00 h to 17:00 h (local time) on two transects of 1 km each, both close to Base de Estudos do Pantanal. To avoid pseudoreplicates, we divided each transect into parts, sampling each of them sequentially each day. In this way, each part of the transect was sampled only once. To avoid the effect of the observer’s perception capacity, only one researcher sampled the individuals during the three days. The active visual search is effective in habitats with good visibility (such as the Pantanal), useful for presence/absence data and appropriate for monitoring populational trends, while the sampling bias is consistent over space and time (Crump & Scott Jr., 1994).

When a lizard was observed, we registered the hour (local time) and the substrate temperature (Tₛ in °C) of its exact location, with a laser infrared thermometer (Benetech® Model Number GS320; Distance-to-spot ratio: 12:1; Resolution: 0.1°C) from 1 m (maintaining a constant distance in order to maximize the accuracy of the measurement). In addition, we measured the height of the point where the individual was observed and the diameter at breast height (DBH, in cm, measured always by the same observer at 1.20 m height) of the tree. We established a case/control design in order to assess the influence of these habitat traits on microhabitat selection. Thus, we simultaneously measured the environmental variables (Tₛ and DBH) in the four (unused) closer trees to the tree where the individual was observed. In order to understand microhabitat selection, it is important to consider unused points that could be poten- tially used by the target species (keep in mind its ecology and behavior), at the temporal and spatial scale of the study. Thus, while sampling the unused trees, we excluded those trees with DBH < 7 cm, that are out of the range used by the species (see details in Terra et al., 2018). Thus, for each observed lizard we gathered data of one used microhabitat VS four available (unused) ones. The study was purely observational, so we did not capture any individual, minimizing animal stress. However, many specimens of T. lagunablanca from the studied area are available at the Coleção Zoológica da Universidade Federal de Mato Grosso do Sul (Brazil).

To test the hypotheses of microhabitat selection, we used a Resource Selection Function (RSF) approach (Manly et al., 2007). Resource Selection Functions calculate, by fitting a function on the probability of presence of the individual, the odds ratio of an individual to use a certain resource relative to its availability in the environment. We solved the RSF through a mixed Conditional Logistic Regression (mixed-CLR) analysis. The mixed-CLR was conditioned by the identity of each individual lizard, to guarantee that values of the explicative variables of each used microhabitat were paired with those available to a given individual (Duchesne et al., 2010; Liedke et al., 2018). In this way, the RSF allows comparing the availability of the environmental variables for each individual simultaneously to the moment when the animal is observed in the used point. This method provides a more mechanistic and powerful approach to understand microhabitat selection than considering the general availability for all individuals of a population (Liedke et al., 2018). We used Generalized Linear Mixed Models (GLMM) to fit the mixed-CLR, built with a binomial distribution, a logit link function, and the ID of individuals as a random factor (i.e., random intercepts). The predictor variables were substrate temperature (Tₛ in °C) and diameter at breast height (DBH, in cm), and the response variable was the presence of the individual (binomial: 0 = absence, 1 = presence). Thus, the model is as follows: Presence ~ DBH + Tₛ + (1|ID). We performed all analyses in the software R, version 3.5.2 (R Core Team, 2020) using the “lme4” package (Bates et al., 2015).

RESULTS

We gathered data on 26 adult individuals of T. lagunablanca. The first active individual of T. lagunablanca was observed at approximately 07:30 h, and the last one was observed at approximately 17:00 h (Fig. 3). The pattern of Tₛ at which T. lagunablanca were observed varied widely throughout the day (Fig. 3), being that the average temperature of the used places was 32.06°C (ranging from 25.9°C to 42°C, SD = 4.26). Individuals of T. lagunablanca occurred in trees with mean DBH of 40.50 cm (ranging from 12.73 cm to 68.44 cm, SD = 15.14).

The mixed-CLR analysis showed that both Tₛ and DBH of the trees significantly influenced the presence of T. lagunablanca individuals (P = 0.002 and P < 0.001, respectively; Table 1). The probability of presence of T. lagunablanca was conditioned by the identity of each individual (GLMM) to fit the mixed-CLR, built with a binomial distribution, a logit link function, and the ID of individuals as a random factor. AIC = 588.5; log likelihood = -290.3; df residual = 496.

Table 1. Results of the mixed Conditional Logistic Regression analysis on substrate temperature (Tₛ in °C) and diameter at breast height (DBH, in cm) of the trees on the probability of presence of Tropidurus lagunablanca individuals, including the individual identity as a random factor. AIC = 588.5; log likelihood = -290.3; df residual = 496.

| Estimate | Std. Error | Z value | P value |
|----------|------------|---------|---------|
| Tₛ       | 0.25371    | 0.08163 | 3.108   | P = 0.002 |
| DBH      | 0.07239    | 0.01094 | 6.619   | P < 0.001 |

Figure 3. Substrate temperatures (Tₛ) of the sites where Tropidurus lagunablanca were observed along daily activity period (local time) at the Base de Estudos do Pantanal, Corumbá, Mato Grosso do Sul, Brazil.
Tropidurus oreadicus and T. lagunablanca, the presence of these lizards is determined by substrate temperature. Using a Resource Selection Function approach, we also demonstrated that the probability of presence increases in ~1.3 times for each 1°C increase of substrate temperature (Ts) above 34°C, within the studied limits. The probability of a lizard to be recorded is higher than the 50% for Ts above 34°C. The probability of presence of T. lagunablanca is 1.08 times higher for each cm that the DBH increases, is higher than the 50% for the mean DBH (40.50 cm) of the trees (B). The probability of presence depending on environmental temperature and amount of sunlight. A recent study disentangling the effect of heat sources and structural components of the habitat found that microhabitat selection of other two Neotropical lizard species (Tropidurus oreadicus and Ameiva aff. ocellifera) is independent of substrate temperature, but are strongly dependent on solar radiation (Ortega et al., 2019). In addition, neither substrate temperature nor sun exposure affect the microhabitat selection by Ameiva ameiva at the same location of this study (Benicio et al., 2019). However, it is important to remember that A. ameiva is a ground-dwelling active forager that moves constantly through space (Rocha et al., 2009), whilst T. lagunablanca is an arboreal ambush forager.

Our results on T. lagunablanca showed a clear influence of substrate temperature on microhabitat selection. This finding suggests thermoregulation, although further studies comparing the preferred thermal range of the species with operative and body temperatures can provide details on the accuracy and effectiveness of thermoregulation in T. lagunablanca (Hertz et al., 1993; Vickers et al., 2011). Despite environmental temperature is high at the Pantanal, forests act as thermal buffers (De Frenne et al., 2019). Thus, thermal ecology of tropical arboreal lizards may differ from that of species inhabiting open areas. It is possible that T. lagunablanca lizards search for warmer substrates on their surroundings to raise their body temperatures and enhance performance. A similar pattern, of an increasing presence of lizards with increasing air temperature, has been found in another arboreal tropidurid, Uracentron azureum (formerly Tropidurus azureus) in the Amazon forest of Venezuela (Ellinger et al., 2001). Thus, we suggest that microhabitat selection can be a relevant driver for thermoregulation of tropical arboreal lizards.

Adult T. lagunablanca actively select trees that are thicker than available. This may be due to the larger area that those trunks provide for thermoregulation, foraging and shelter. An increase in the trunk area would be related to a higher availability of arthropods (e.g., Gonçalves et al., 2005; Horak, 2013), resulting in better quality home ranges. This pattern of selection for thicker trees is in tune with the

**DISCUSSION**

We showed that the poorly known lizard T. lagunablanca uses trees with a mean temperature of 32.06°C and a mean thickness of 40.5 cm in the Pantanal of Brazil. By assessing microhabitat selection using a Resource Selection Function approach, we also demonstrated that lizard’s presence is determined by substrate temperature and thickness of the tree. Particularly, T. lagunablanca lizards are selecting thicker trees than randomly available on their habitats and, within those trees, select slightly warmer places than randomly available on their surroundings. Our results evidence that T. lagunablanca is a thermoregulator species, since they are choosing microhabitats non-randomly regarding substrate temperature. Besides, these findings are relevant for conservation, indicating the importance of preserving thicker trees for the conservation of this species. Finally, our results also have a practical component for field biologists, providing data on where the chances of finding these arboreal lizards are maximized, helping to save time and money in sampling efforts.

The choice for a particular warmer location in the tree in relation to the others, confirm the information suggested by Carvalho (2016) that the species is heliophilius and the frequency of specimens encountered apparently depends on environmental temperature and amount of sunlight. A study disentangling the effect of heat sources and structural components of the habitat found that microhabitat selection of other two Neotropical lizard species (Tropidurus oreadicus and Ameiva aff. ocellifera) is independent of substrate temperature, but are strongly dependent on solar radiation (Ortega et al., 2019). In addition, neither substrate temperature nor sun exposure affect the microhabitat selection by Ameiva ameiva at the same location of this study (Benicio et al., 2019). However, it is important to remember that A. ameiva is a ground-dwelling active forager that moves constantly through space (Rocha et al., 2009), whilst T. lagunablanca is an arboreal ambush forager.

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**Figure 4.** Result of the mixed Conditional Logistic Regression model for the presence of Tropidurus lagunablanca as a function of predictor variables: substrate temperature, in °C (A) and diameter at breast height (DBH, in cm) of the trees (B). The solid line represents the probability predicted by the model and the dashed lines represent the respective confidence intervals. The circles are the observed values measured in the points of presence (used microhabitats) and availability (the four respective unused microhabitats paired to each used one). As we included the ID of the observation (one ID for one used site, plus the correspondent four available microhabitats) in the model as a random factor, we colored the circles in the plot by ID, so one can have an idea of what used value corresponds to each available value. Please note that the location of the circles was vertically jitterted to enhance visualization, but all points of availability correspond to the exact same probability of 0 and all points of presence correspond to the exact same probability of 1.

**gunablanca** is less than 30% for the mean temperature (32.06°C) (Fig. 4A) and higher than 50% for the mean DBH (40.50 m) of the trees (Fig. 4B). The probability of presence of **T. lagunablanca** is higher than the 50% for trees up to 40 cm DBH (an increase of 1 cm in DBH is associated with an increase of 0.07 units in the expected log odds of presence; that is, the probability of presence is 1.08 times higher for each cm that the DBH increases, within the studied limits). The probability of a lizard to be recorded is higher than the 50% for Ts above 34°C (an increase of 1°C implies 0.25 higher log odds of presence; that is, the probability of presence increases in ~1.3 times for each 1°C, within the studied limits).
typical foraging pattern observed for several other species (e.g., *Christinus marmoratus*, *Enyalioides laticeps*, *Polychrus marmoratus*, *Uracentron flaviceps*; Garda et al., 2013; Taylor et al., 2016). The clear selection of trees with a higher DBH has important implications for conservation, since the removal of these trees can compromise the structure of the habitat and consequently the survival of the species.

We found a well-defined pattern of microhabitat selection by *T. lagunablanca* which may be related to its foraging, defensive, and mating strategies. Some Tropiduridae lizards (e.g., *Tropidurus hispidus*), due to their ambush foraging behavior, do not need to travel large areas to find food and mates, resulting in a relative restricted home range size (Melo et al., 2017). In this sense, the selection of *T. lagunablanca* for higher substrate temperature and thicker trees may also indicate, besides microhabitat selection, a possible site fidelity. However, behavioral studies on spatial and social organization are needed to better understand this issue. In any case, conservation efforts should be focused on preserving thicker trees in order to keep a suitable habitat for this species. The Pantanal is suffering from unprecedented bushfires in 2020, and the predictions estimate that bushfires will get worse in future years by climate change. Recent studies estimated a loss of more than 14,000 km² of native vegetation for 2,050 related to bushfires in the Pantanal (Guerra et al., 2020). Therefore, this might constitute a great threat to *T. lagunablanca*, given its arboreal habits and selection for thicker trees.

In short, our results on microhabitat selection of *T. lagunablanca* showed how this species selects for microhabitats with higher substrate temperatures and thicker trees than randomly available in its habitat. This information provides knowledge on the habitat selection process of Neotropical arboreal lizards and can be used to maximize sampling efforts for the studied species. Finally, we reinforce the necessity to preserve the native vegetation in the Pantanal.

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**AUTHORS' CONTRIBUTIONS**

R.A.B.: Conceptualization, Methodology, Formal analysis, Writing – original draft. D.C.P.: Formal analysis, Writing – review & editing. A.M.: Methodology, Formal analysis, Writing – review & editing. Z.O.: Methodology, Formal analysis, Supervision, Writing – review & editing. All the authors actively participated in the discussion of the results, they reviewed and approved the final version of the paper.

**REFERENCES**

Adolph, S.C. 1990. Influence of behavioral thermoregulation on microhabitat use by two Sceloporus lizards. *Ecology*, 71(1): 315-327. DOI

Adolph, S.C. & Porter, W.P. 1993. Temperature, activity, and lizard life histories. *The American Naturalist*, 142(2): 273-295. DOI

Alho, C.J.R.; Strüssmann, C. & Vasconcellos, L.A.S. 2001. Indicadores da magnitude da diversidade e abundância de vertebrados silvestres do Pantanal num mosaico de hábitats sazonais. In: do III Simpósio sobre Recursos Naturais e Sócio-Econômicos do Pantanal, 3ª. Anais. 2000. Corumbá, EMBRAPA – Empresa Brasileira de Agropecuária (Ed.). p. 1-54. (CD-ROM)

de Andrade, A.C. 2020. Metropolitan lizards? Urbanization gradient and the density of lagartixas (*Tropidurus hispidus*) in a tropical city. *Ecology and Evolution*, 10(4): 1740-1750. DOI

Angilletta, M.J. 2009. Thermal adaptation: A theoretical and empirical synthesis. Oxford, Oxford University Press.

Ariano-Sánchez, D.; Mortensen, R.M.; Reinhards, S. & Rosell, F. 2020. Escaping drought: Seasonality effects on home range, movement patterns and habitat selection of the Guatemalan Beaded Lizard. *Global Ecology and Conservation*, 23: e01178. DOI

Ávila, R.W.; Souza, F.L. & Da Silva, R.J. 2010. Helminths from seven species of lizards (Reptilia: Squamata) at the Cerrado of Mato Grosso do Sul State, Brazil. *Comparative Parasitology*, 77(1): 67-71. DOI

Bates, D.; Maechler, M.; Bolker, B. & Walker, S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67: 1-48. DOI

Bauwens, D.; Hertz, P.E. & Castilla, A.M. 1996. Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. *Ecology*, 77(6): 1818-1830. DOI

Benício, R.A.; Ortega, Z.; Mencia, A. & Passos, D.C. 2019. Microhabitat selection of *Ameiva ameiva* (Linnaeus, 1758), in the Brazilian Pantanal. *Herpetozoa*, 31(3-4): 211-218. DOI

Cadotte, M.W. & Tucker, C.M. 2017. Should environmental filtering be abandoned? *Trends in Ecology & Evolution*, 32(6): 429-437. DOI

Carvalho, A.L.G. 2016. Three New Species of the *Tropidurus spinulosus* Group (*Squamata: Tropiduridae*) from Eastern Paraguay. *American Museum Novitates*, 3853: 1-44. DOI

Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31: 343-366. DOI

Colli, G.R.; Araújo, A.F.B.; Silveira, R. & Roma, F. 1992. Niche partitioning and habitat selection by two syntopic lizards (*Reptilia: Squamata*) at the Cerrado of Mato Grosso, Brazil. *Brazilian Journal of Herpetology*, 26(1): 66-69. DOI

Cosendey, B.N.; Rocha, C.F.D. & Menezes, V.A. 2019. Habitat structure and their influence in lizard’s presence. *Papéis Avulsos de Zoologia*, 59(59): 1-10, e20195959. DOI

Costa, H.C. & Bérnils, R.S. 2018. Répteis do Brasil e suas Unidades Federativas: Lista de espécies. *Herpetologia Brasileira*, 7(1): 11-57. DOI

Crump, M.A. & Scott Jr., N.J. 1994. Visual Encounter Surveys. In: Heyer, W.R.; Donnelly, M.A.; Mcdiarmid, R.W.L.; Hayek, A.C. & Foster, M.S. (Eds.). *Measuring and monitoring biological diversity: standard methods for amphibians*. Washington, Smithsonian Institution Press. p. 84-92.

De Frenne, P.; Zeller, F.; Rodrigues-Sánchez, F.; Scheffers, B.R.; Hylander, K.; Luoto, M.; Vellend, M.; Verheyen, K. & Lenoir, J. 2019. Global buffering...
of temperatures under forest canopies. *Nature Ecology & Evolution*, 3(5): 744-749. DOI

Domenici, P.; Claireaux, G. & McKenzie, D.J. 2007. Environmental constraints upon locomotion and predator-prey interactions in aquatic organisms: an introduction. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1487): 1929-1936. DOI

Duchesne, T.; Fortin, D. & Courbin, N. 2010. Mixed conditional logistic regression for habitat selection studies. *Journal of Animal Ecology*, 79(3): 548-555. DOI

Ehrén, J. & Morris, W.F. 2015. Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters*, 18(3): 303-314. DOI

Ellinger, N.; Schlatter, G.; Jerome, N. & Hödl, W. 2001. Habitat use and activity of the neotropical arboreal lizard *Tropidurus (= Uracentron) azureus wernerii* (Tropiduridae). *Journal of Herpetology*, 35(3): 395-402. DOI

Ferreira, V.L.; Terra, J.S.; Piatti, L.; Delatorre, M.; Strüssmann, C.; Bêda, A.F.; Kawashita-Ribeiro, R.A.; Landgref-Filho, P.; Aoki, C.; Campos, Z.; Souza, F.L.; Ávila, R.W.; Duleba, S.; Martins, K.S.; Ritz, P.H.S. & Albuquerque, N.R. 2017. Répites do Mato Grosso do Sul, Brasil. *Iheringia, Série Zoológica*, 107(Supl.): 1-13, e2017153. DOI

Franzini, L.D.; Teixeira, A.A.M.; Tavares-Bastos, L.; Vitt, L.J. & Mesquita, D.O. 2020. Auteoclogia of *Kentropyx calcarata* (Squamata: Teiidae) in a Remnant of Atlantic Forest in Eastern South America. *Journal of Herpetology*, 53(3): 209-217. DOI

Garda, A.A.; Wiederhecker, H.C.; Gainsbury, A.M.; Costa, G.C.; Pyron, R.A.; Vieira, G.H.C.; Werneck, F.P. & Colli, G.R. 2013. Microhabitat variation explains local-scale distribution of terrestrial Amazonian lizards in Rondônia, Western Brazil. *Biotropica*, 45(2): 245-252. DOI

Gonçalves, H.C.; Mercante, M.A. & Santos, E.T. 2011. Hydrological cycle. *Brazilian Journal of Biology*, 71(1): 241-253. DOI

Gonçalves, T.T.; Souza, O.F.F.D.; Reis-Júnior, R. & Ribeiro, S.P. 2005. Effect of tree size and growth form on the presence and activity of arboreal termites (*Insecta: Isoptera*) in the Atlantic Rain Forest. *Sociobiology*, 46(2): 421-431. DOI

Gonçalves-Sousa, J.G.; Mesquita, D.O. & Ávila, R.W. 2019. Structure of a lizard assemblage in a semiarid habitat of the Brazilian Caatinga. *Herpetologica*, 75(4): 301-314. DOI

Guerra, A.; de Oliveira Roque, F.; Garcia, L.C.; Ochoa-Quintero, J.M.; de Oliveira, P.T.S.; Guarietno, R.D. & Rosa, I.M. 2020. Drivers and projections of vegetation loss in the Pantanal and surrounding ecosystems. *Land Use Policy*, 91: 104388. DOI

Hertz, P.E.; Huey, R.B. & Stevenson, R.D. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate regression for habitat selection studies. *Journal of Herpetology*, 17(1): 241-253. DOI

HilleRisLambers, J.; Adler, P.B.; Harpole, W.S.; Levine, J.M. & Mayfield, M.M. 2007. Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics*, 38(4): 227-248. DOI

Horak, J. 2013. Effect of Site Level Environmental Variables, Spatial Autocorrelation and Sampling Intensity on Arthropod Communities in an Ancient Temperate Lowland Woodland Area. *PLoS ONE*, 8(12): e81541. DOI

International Union for Conservation of Nature and Natural Resources (IUCN). 2001. *IUCN Red List Categories and Criteria: Version 3.1*. IUCN Species Survival Commission. Gland, Switzerland, IUCN.

Liedke, A.M.; Bonadona, R.M.; Segal, B.; Ferreira, C.E.; Nunes, L.T.; Burigo, A.P.; Buck, S.; Oliveira-Santos, L.G.R. & Floeter, S.R. 2018. Resource partitioning by two sympatric sister species of butterflyfish (*Chaetodontidae*). *Journal of the Marine Biological Association of the United Kingdom*, 98(7): 1767-1773. DOI

Lourival, R.; Harris, M. & Montambault, J.R. 2000. Introdução ao Pantanal, Mato Grosso do Sul, Brasil. In: Willink, P.W.; Chernoff, B.; Alonso, L.E.; Montambault, J.R. & Lourival, R. (Eds.). *A biological assessment of the aquatic ecosystems of the Pantanal, Mato Grosso do Sul, Brasil*. Washington, D.C., Conservation International. p. 146-151. (RAP Bulletin of Biological Assessment, NP 18)

Manly, B.F.; McDonald, L.; Thomas, D.L.; McDonald, T.L. & Erickson, W.P. 2007. Resource selection by animals: statistical design and analysis for field studies. *Springer Science & Business Media*. DOI

Melo, G.C.; Pinheiro, L.T.; Passos, D.C. & Galdino, C.A.B. 2017. Spatial organisation of the Neotropical lizard *Tropidurus hispidus* (Squamata: Tropiduridae). *Salamandra*, 53(3): 435-438.

Mercante, M.A.; Rodrigues, S.C. & Ross, J.L.S. 2011. Geomorphology and habitat diversity in the Pantanal. *Brazilian Journal of Biology*, 71(1): 233-240. DOI

Newbold, T.S. & MacMahon, J.A. 2014. Determinants of habitat selection by desert horned lizards (*Phrynosoma platyrhinos*): the importance of abiotic factors associated with vegetation structure. *Journal of Herpetology*, 48(3): 306-316. DOI

Nogueira, C.; Valdujo, P.H. & França, F.G. 2005. Habitat variation and lizard diversity in a Cerrado area of Central Brazil. *Studies on Neotropical Fauna and Environment*, 40(2): 105-112. DOI

Ortega, Z. & Pérez-Mellado, V. 2016. Seasonal patterns of body temperature and microhabitat selection in a lacertid lizard. *Acta Oecologica*, 77: 201-206. DOI

Ortega, Z.; Mencia, A.; Martins, K.; Soares, P.; Ferreira, V.L. & Oliveira-Santos, L.G. 2019. Disentangling the role of heat sources on microhabitat selection of two Neotropical lizard species. *Journal of Tropical Ecology*, 35(4): 149-156. DOI

Peixoto, M.G.; de Fraga, R.; Araújo, M.C.; Kaefler, I.L. & Lima, A.P. 2020. Hierarchical effects of historical and environmental factors on lizard assemblages in the upper Madeira River, Brazilian Amazonia. *PLoS ONE*, 15(6): e0238881. DOI

Pianka, E.R. 1973. The structure of lizard communities. *Annual Review of Ecology, Evolution, and Systematics*, 4: 53-74. DOI

Prado, D.E.; Gibbs, P.E.; Pott, A. & Pott, V.J. 1992. The Chaco-Pantanal transition in southern Mato Grosso, Brazil. In: Furley, P.A.; Proctor, J. & Ratter, J.A. (Eds.). *Nature and dynamics of forest-savanna boundaries*. London, Chapman and Hall. p. 451-470.

R Core Team. 2020. *R: A language and environment for statistical computing*. Vienna, R Foundation for Statistical Computing. Disponível em: https://www.R-project.org

Recoder, R.S. & Rodrigues, M.T. 2020. Diversification processes in lizards and snakes from the middle São Francisco river dune region, Brazil. In: Rull, V. & Carnaval, A. (Eds.). *Neotropical diversification: patterns and processes*. Cham, Springer. p. 713-740. DOI

Rocha, C.F.; Van Sluys, M.; Vicribadig, D.; Kiefer, M.C.; de Menezes, V.A. & da Costa Siqueira, C. 2009. Comportamento de termorregulação em lagartos brasileiros. *Oecologia brasiliensis*, 13(1): 115-131.

Rocha, C.F.D. & Anjos, L.A. 2007. Feeding ecology of a nocturnal invasive alien lizard species, *Hemidactylus mabouia* (Gekkonidae), living in an outcrop rocky area in southeastern Brazil. *Brazilian Journal of Biology*, 67(3): 485-491. DOI

Rodrigues, M.T. 1996. Lizards, snakes, and amphibians from the quaternary sand dunes of the middle Rio São Francisco, Bahia, Brazil. *Journal of Herpetology*, 30(4): 513-523.

Rutherford, P.L. & Gregory, P.T. 2003. Habitat Use and Movement Patterns of Northern Alligator Lizards (*Elgaria coerulea*) and Western Skinks (*Eumeus skiltonianus*) in Southeastern British Columbia. *Journal of Herpetology*, 37(1): 98-106. DOI
Schwenk, K.; Padilla, D.K.; Bakken, G.S. & Full, R.J. 2009. Grand challenges in organismal biology. *Integrative and Comparative Biology*, 49(1): 7-14. DOI

Smith, G.R. & Ballinger, R.E. 2001. The ecological consequences of habitat and microhabitat use in lizards: a review. *Contemporary Herpetology*, 3: 1-37. DOI

Souza, F.L.; Prado, C.P.A.; Sugai, J.M.M.; Ferreira, V.L.; Aoki, C.; Landgref-Filho, P.; Strüssmann, C.; Ávila, R.W.; Rodrigues, D.I.; Albuquerque, N.R.; Terra, J.; Uetanabaro, M.; Béda, A.F.; Piatti, L.; Kawashita-Ribeiro, R.A.; Delatorre, M.; Faggioni, G.P.; Demczuk, S.D.B. & Duleba, S. 2017. Diversidade de anfíbios do Estado de Mato Grosso do Sul, Brasil. *Iheringia, Série Zoologia*, 107(Suppl.): 1-10, e2017152. DOI

Taylor, D.; Daniels, C.B. & Johnston, G. 2016. Habitat selection by an arboreal lizard in an urban parkland: not just any tree will do. *Urban Ecosystems*, 19(1): 243-255. DOI

Terra, J.S.; Ortega, Z. & Ferreira, V.L. 2018. Thermal ecology and microhabitat use of an arboreal lizard in two different Pantanal wetland phytosystems (Brazil). *Journal of Thermal Biology*, 75: 81-87. DOI

Vickers, M.; Manicom, C. & Schwarzkopf, L. 2011. Extending the cost-benefit model of thermodregulation: high-temperature environments. *The American Naturalist*, 177(4): 452-461. DOI

Vitt, L.I. & Pianka, E.R. 1994. *Lizard ecology, historical and experimental perspectives*. New Jersey, Princeton University Press.

Xavier, M.A.; da Silva, T.L. & Dias, E.J.D.R. 2019. Habitat use and diet of the endemic lizard *Ameivula nigrigula* (Squamata: Teiidae) in Caatinga domain, Northeastern Brazil. *Journal of Natural History*, 53(29-30): 1787-1797. DOI

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