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Microhabitat selection of *Ameiva ameiva* (LINNAEUS, 1758), in the Brazilian Pantanal
(Squamata: Sauria: Teiidae)

Mikrohabitatwahl von *Ameiva ameiva* (LINNAEUS, 1758) im brasilianischen Pantanal
(Squamata: Sauria: Teiidae)

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KURZFASSUNG

Die Autoren untersuchten den Einfluß einiger Umweltparameter auf die Mikrohabitatwahl von *Ameiva ameiva* (LINNAEUS, 1758) im brasilianischen Pantanal, einem Lebensraum mit markantem Wechsel von Überflutung und Trockenfallen. Die Analyse der Mikrohabitatwahl erfolgte im September mittels Ressourcenauswahlfunktion (RSF) und Bedingter Logistischer Regression (CLR) an neunundzwanzig adulten Individuen von of *A. ameiva*. Die mittlere Temperatur an den Aufenthaltsorten betrug 36 °C (Spannweite: 27 °C – 51 °C; Standardabweichung: 6,8 °C). Im Verlauf der Tagesaktivität waren die Temperaturen des Substrats auf dem *A. ameiva* beobachtet wurde, abwechselnd sowohl bei sehr hohen als auch deutlich niedrigeren Werten gehäuft. Das CLR Modell zeigte, daß keiner der untersuchten Umweltparameter Substrattemperatur, Substrattyp und Sonnenexposition die Wahrscheinlichkeit des Vorkommens von *A. ameiva* an einem bestimmten Aufenthaltsort signifikant beeinflußte (zugehörige *P*-Werte: 0,11; 0,69 und 0,87), wobei bei der Sonnenexposition die Qualitäten volle Besonnung, Schatten und Halbschatten und beim Substrattyp Gras, Laubstreu und blanker Boden unterschieden wurden. Die Ergebnisse legen nahe, daß *A. ameiva* zumindest während der Trockenzeit im brasilianischen Pantanal kein Mikrohabitat-Spezialist ist.

ABSTRACT

The authors studied the influence of three environmental traits on the microhabitat selection of *Ameiva ameiva* (LINNAEUS, 1758), in the Brazilian Pantanal, an environment with a marked effect of seasonality, i.e., alternating periods of flooding and falling dry. Microhabitat selection was assessed in the dry season using a Resource Selection Function (RSF) and Conditional Logistic Regression (CLR) analysis. Twenty-nine adult individuals of *A. ameiva* were observed. The average temperature in places where individuals occurred was 36 °C (ranging from 27 °C to 51 °C; SD = 6.8 °C). The pattern of the temperature of the substrate on which *A. ameiva* was observed showed peaks, occurring alternatively either at very high but also milder temperatures along its daily activity period. The CLR model revealed that none of the studied environmental variables (substrate temperature, type of substrate or sun exposure) significantly affected the probability of occurrence of *Ameiva* lizards at a particular point ($P = 0.11$, $P = 0.69$, $P = 0.87$, respectively). Regarding the sun exposure situation the qualities full sun, shade and filtered sun were distinguished, the substrate type comprised the parameter values grass, leaflitter and exposed soil. The results suggest that *A. ameiva* is not a microhabitat specialist, at least during the dry season in the Pantanal of Brazil.

KEY WORDS

Reptilia: Squamata: Sauria: Teiidae; *Ameiva ameiva*; ecology, behavior; foraging activity, microhabitat use, occurrence, substrate, wetlands, Pantanal, Brazil

INTRODUCTION

Ameiva ameiva (LINNAEUS, 1758), is a medium-sized (snout-vent length up to 174 mm after VITT & COLLI 1994; Fig. 1) ground-dwelling lizard that spends a large amount of its activity period moving, a typical pattern of wide/ active foragers (ROCHA et al. 2009). It has a vast geographical distribution, living mainly in open areas of South America (VANZOLINI et al. 1980) and occurring in almost all Brazilian territory (AVILA-PIRES 1995). Across its distribution, this species inhabits a variety of environments (VITT & COLLI 1994), such as forest edges and open areas within rainforests (CRUZ-NETO & GORDO 1996; LIMA et al. 2001), seasonally dry forests (VITT 1995; SALES et al. 2011a), savannas (Colli 1991) and coastal shrublands (Zaluar & Rocha 2000) as well as human disturbed areas (Sartorius et al. 1999). *Ameiva ameiva* mainly feeds on invertebrates (Vitt & Colli 1994; Zaluar & Rocha 2000, Sales et al. 2011b, Freitas et al. 2012), despite sporadically including some vertebrates and plant material in the diet (Rocha & Vrcibradic 1998; Sales et al. 2010; Moraes & Santos 2012; Silva et al. 2013). These lizards are mainly diurnal and concentrate their activity within the warmer hours of the day, usually between 10:00 h and 14:00 h (Vitt & Colli 1994; Sartorius et al. 1999; Zaluar & Rocha 2000; Sales et al. 2011a). Their life-history traits vary along the broad geographical range, but reproduction begins and tends to be more intense during the wet period (Vitt 1982; Colli 1991; Vitt & Colli 1994; Rocha 2008).

Microhabitat use of several populations of *A. ameiva* was studied at different Brazilian biomes (Sartorius et al. 1999; Zaluar & Rocha 2000; Sales et al. 2011a). However, there is still a lack of knowledge about *A. ameiva* lizards from the Pantanal, an area of flooded grasslands from western Brazil (Junk & De Cunha 2005). Widely distributed species often vary geographically in the microhabitat use, and it is important to study this intraspecific variability since it is related to niche specialization, evolution and adaptability to environmental changes (Borzee et al. 2016; Bars-Closel et al. 2017). Thus, the authors' present study aimed to evaluate which environmental traits influence the occurrence of *A. ameiva* in the Pantanal, an environment with a marked effect of seasonality, i.e., alternating periods of flooding and falling dry (Mercante et al. 2011).

MATERIALS AND METHODS

The study was conducted in the Pantanal region of Miranda-Abrobal, near the Base de Estudos do Pantanal (BEP) of the Federal University of Mato Grosso do Sul (Corumbá, Mato Groso do Sul, Brazil) at 19°34'37" S, 57°00'42" W, in the dry season, September 2017. The Pantanal domain is embedded in one of the most distinct ecoregions concerning orography: the flooded grasslands and savannas (Prado et al. 1992; Lourival et al. 2000). Located in the western portion of the state of Mato Grosso do Sul, the Pantanal occupies approximately 71.500 km^2 of the state territory (Ferreira et al. 2017).

The *Ameiva* lizards were sampled within three consecutive days (September 26-28) through active visual search (Crump & Scott 1994) in the period from 07:00 h to 17:00 h (local time) on two transects of one kilometer each, both in the surroundings of the BEP. To avoid pseudoreplication, each transect was divided into parts, sampled sequentially in different days. In this way, each part of the transect was sampled only once. The study was purely observational, without capture of any individual, to avoid animal stress. Upon observation of a lizard, the time of the day (hour in local time) and the substrate temperature (T_S) of its exact location were registered, measured with a laser infrared thermometer (Benetech® GS320, precision 0.1 °C) from one meter maintaining a constant distance, to maximize the comparability of the measurements. In addition, the authors recorded the type of substrate ('grass', 'leaflitter' and 'exposed soil') and the sun exposure ('full sun', 'shade' and 'filtered sun') of the microhabitat where the individual was observed (= used point). To assess microhabitat selection, the same variables (T_S, type of substrate and sun exposure) were registered at four unused points related to each used point. Unused points were defined one meter north, south, west and east from each used point as an objective criterion to standardize their location. These unused points represented the available microhabitats for each lizard in a given moment. Comparing environmental variables of the used and unused points would allow for the study of the influence of the registered variables in the microhabitat selection of *A. ameiva*.

Microhabitat selection was assessed using a Resource Selection Function (RSF) (Manly et al. 2007). Resource Selection Functions calculate the odds ratio of an individual to use a certain resource relative to its availability in the environment. In the pres-

Fig. 1: Adult individual of *Ameiva ameiva* (LINNAEUS, 1758), at the Base de Estudos do Pantanal, Federal University of Mato Grosso do Sul, Corumbá, Mato Grosso do Sul, Brazil.

Abb. 1: Adulte *Ameiva ameiva* (LINNAEUS, 1758) in der Base de Estudos do Pantanal der Universität von Mato Grosso do Sul, Corumbá, Mato Grosso do Sul, Brasilien.

ent case, the resources are the microhabitat explicative variables of interest: T_S, type of substrate and sun exposure. Solving RSFs by means of Generalized Linear Models (GLMs) allows modeling the probability of occurrence of the lizard, given several explicative variables and their interactions. In addition, this approach can calculate the effect of each explicative variable in the same probabilistic selection process (LIEDKE et al. 2018). Finally, the RSF allows determining 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, thus, needing fewer individuals to obtain representative results than with traditional approaches (LIEDKE et al. 2018).

The authors assessed the RSF through a Conditional Logistic Regression (CLR) analysis. The response variable was the presence of the lizard in a certain microhabitat (recorded as 1 for the used points and 0 for the four associated unused points). The 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 such individual (DUCHESNE et al. 2010; LIEDKE et al. 2018). Hence, values of the explicative variables of the microhabitat used by one lizard are compared with the simultaneously available values of these variables at its surroundings. An analogous approach, Paired Logistic Regression (PLR), has been used for many years to study habitat selection of reptiles (COMPTON et al. 2002; ORTEGA & PÉREZ-MELLADO 2017). Conditional Logistic Regression has the advantage of having more than one unused point paired to each used point, so the availability of microhabitats is better represented for each individual. All analyses were performed in the software R, version 3.4 (R CORE TEAM 2018) using the 'lme4' package (BATES et al. 2015).

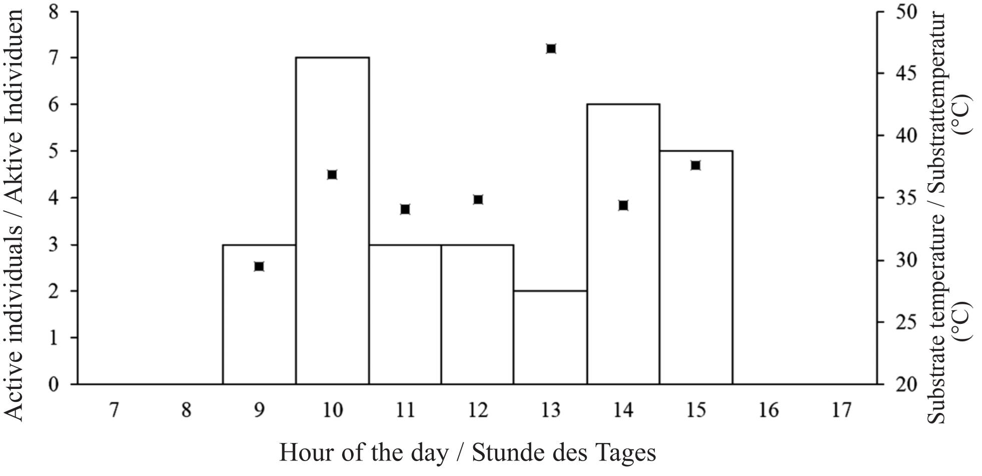

Fig. 2: Absolute frequency during the hours of the day of 29 active adult individuals of *Ameiva ameiva* (Linnaeus, 1758), including the mean substrate temperature (■) at the respective observation points. Study site: Base de Estudos do Pantanal of the Federal University of Mato Grosso do Sul, Corumbá, Mato Grosso do Sul, Brazil.

Abb. 2: Absolute Häufigkeit der 29 beobachteten aktiven Adulten von *Ameiva ameiva* (Linnaeus, 1758) und die mittlere Substrattemperatur (°C) an deren jeweiligem Aufenthaltsort (■) im Tagesverlauf auf dem Untersuchungsgelände (Base de Estudos do Pantanal der Universität von Mato Grosso do Sul, Corumbá, Mato Grosso do Sul, Brasilien).

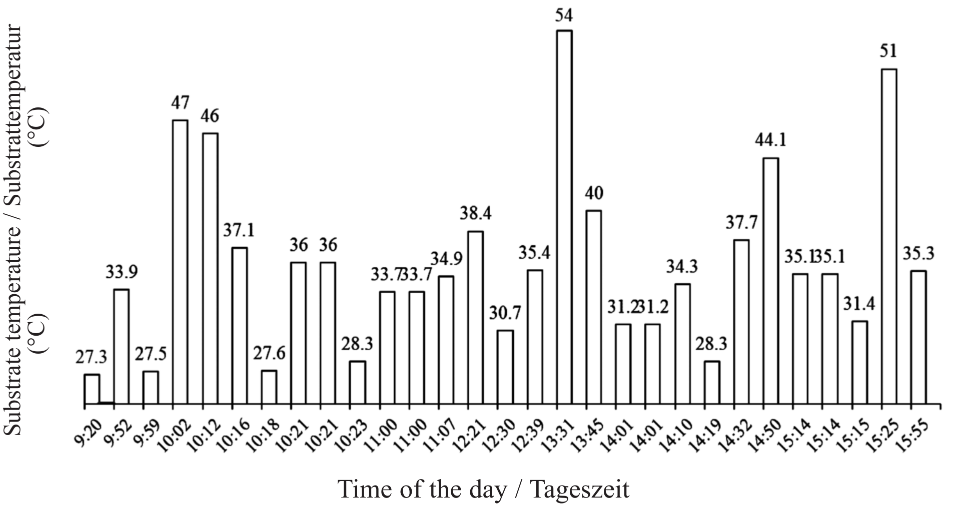

Fig. 3: Substrate temperatures (°C) of the 29 sites where active *Ameiva ameiva* (Linnaeus, 1758), were observed, sorted by the time of observation (local time). Study site: Base de Estudos do Pantanal of the Federal University of Mato Grosso do Sul, Corumbá, Mato Grosso do Sul, Brazil.

Abb. 3: Substrattemperaturen (°C) an jenen Stellen, an denen *Ameiva ameiva* (Linnaeus, 1758) beobachtet wurde, geordnet nach der Beobachtungszeit. Untersuchungsgelände: Base de Estudos do Pantanal der Universität von Mato Grosso do Sul, Corumbá, Mato Grosso do Sul, Brasilien.

Table 1: Microhabitat descriptive data [substrate temperature (°C), exposure to sun [1)] and type of substrate [2)]] of the 29 points (Pt.), where the 29 individuals of *Ameiva ameiva* (LINNAEUS, 1758), were observed (= main points) and of four comparative points, one meter north, south, west and east (N, S, W, E), respectively, of each main point. [1)] full sun (sun), shade (shade) and filtered sun (filtered); [2)] grass (grass), leaflitter (leaflitter) and exposed soil (exp. soil).

Tab. 1: Beschreibende Angaben zum Mikrohabitat [Substrattemperatur (°C), Sonnenexposition [1)] und Substrattyp [2)]] an den 29 Stellen, an denen die 29 Individuen von *Ameiva ameiva* (LINNAEUS, 1758) beobachtet wurden (= Fundpunkt), sowie zu vier Vergleichspunkten (Pkt.), die jeweils einen Meter nördlich, südlich, westlich und östlich (N, S, W, E) der Funktpunkte lagen. [1)] volle Sonne (sun), Schatten (shade), Halbschatten (filtered); [2)] Gras (gras), Laubstreu (leaflitter), blanker Boden (exp. soil).

Ind.	Substrate temperature / Substrattemperatur					Exposure to sun / Sonnenexposition					Type of substrate / Substrattyp				
	Main point Fundpunkt	Pt. 1 m N	Pt. 1 m S	Pt.. 1 m W	Pt.. 1 m E	Main point Fundpunkt	Pt.. 1 m N	Pt. 1 m S	Pt. 1 m W	Pt. 1 m E	Main point Fundpunkt	Pt. 1 m N	Pt. 1 m S	Pt. 1 m W	Pt. 1 m E
A1	27.3	27.8	27.5	27.8	28.2	filtered	filtered	filtered	filtered	filtered	leaflitter	leaflitter	leaflitter	leaflitter	leaflitter
A2	33.9	35.8	30.8	36.1	40	full sun	full sun	full sun	full sun	full sun	grass	grass	grass	grass	exp. soil
A3	27.5	27.1	26.7	29	27	filtered	filtered	filtered	filtered	filtered	leaflitter	leaflitter	leaflitter	leaflitter	leaflitter
A4	47	31.8	38	28.9	37.3	sun	full sun	full sun	full sun	full sun	leaflitter	leaflitter	leaflitter	leaflitter	exp. soil
A5	46	45.8	48.9	41.1	41.8	sun	full sun	full sun	full sun	full sun	exp. soil	exp. soil	exp. soil	exp. soil	exp. soil
A6	37.1	35.9	32.9	49	29	filtered	full sun	full sun	full sun	full sun	exp. soil	leaflitter	leaflitter	exp. soil	leaflitter
A7	27.6	28.4	27.7	26.6	29.9	shade	filtered	filtered	filtered	filtered	leaflitter	leaflitter	leaflitter	leaflitter	leaflitter
A8	36	27	26.1	25.3	31.1	filtered	filtered	filtered	filtered	filtered	exp. soil	leaflitter	leaflitter	leaflitter	leaflitter
A9	36	27	26.1	25.3	31.1	filtered	filtered	filtered	filtered	filtered	exp. soil	leaflitter	leaflitter	leaflitter	leaflitter
A10	28.3	28.1	28.5	28.4	28.7	shade	shade	shade	shade	shade	exp. soil	leaflitter	leaflitter	leaflitter	leaflitter
A11	40	33	33.2	34.3	33.7	sun	filtered	filtered	filtered	filtered	leaflitter	leaflitter	leaflitter	leaflitter	leaflitter
A12	37.7	36.2	33.5	36.3	33.5	filtered	filtered	filtered	filtered	shade	leaflitter	leaflitter	leaflitter	leaflitter	leaflitter
A13	44.1	44.2	44.2	37.5	47.2	sun	sun	sun	shade	sun	exp. soil	exp. soil	exp. soil	grass	exp. soil
A14	31.4	31.7	30.7	31.6	30.8	shade	shade	shade	shade	shade	exp. soil	grass	grass	grass	grass
A15	51	48.1	46.8	40.8	43.8	sun	sun	sun	shade	sun	exp. soil	exp. soil	exp. soil	grass	exp. soil
A16	35.3	33.8	34.9	40	32.2	filtered	filtered	filtered	sun	shade	leaflitter	leaflitter	leaflitter	leaflitter	leaflitter
A17	33.7	31.3	32.6	31.2	33.3	filtered	filtered	filtered	filtered	filtered	leaflitter	leaflitter	leaflitter	leaflitter	leaflitter
A18	33.7	31.3	32.6	31.2	33.3	filtered	filtered	filtered	filtered	filtered	leaflitter	leaflitter	leaflitter	leaflitter	leaflitter
A19	34.9	35.7	54.7	35.1	33.1	shade	shade	sun	shade	shade	grass	grass	exp. soil	grass	grass
A20	38.4	36.9	37.2	37.2	30.1	sun	sun	sun	sun	shade	exp. soil	exp. soil	exp. soil	exp. soil	leaflitter
A21	30.7	30	29	30.7	29.5	filtered	sun	sun	sun	sun	grass	grass	grass	grass	grass
A22	35.4	38.4	34	36	34	filtered	filtered	filtered	filtered	filtered	leaflitter	leaflitter	leaflitter	leaflitter	leaflitter
A23	54	48.3	47	45.7	32.8	sun	sun	sun	sun	shade	exp. soil	exp. soil	exp. soil	exp. soil	leaflitter
A24	31.2	31.4	31.1	35.6	32	filtered	filtered	filtered	filtered	filtered	leaflitter	leaflitter	leaflitter	leaflitter	leaflitter
A25	31.2	31.4	31.1	35.6	32	filtered	filtered	filtered	filtered	filtered	leaflitter	leaflitter	leaflitter	leaflitter	leaflitter
A26	34.3	31.3	34.1	36.9	29.2	sun	sun	sun	sun	shade	leaflitter	leaflitter	leaflitter	exp. soil	leaflitter
A27	28.3	28.6	28.2	36.2	27.9	shade	shade	shade	sun	shade	leaflitter	leaflitter	leaflitter	exp. soil	leaflitter
A28	35.1	35	32.1	36.2	29.5	sun	sun	sun	sun	shade	exp. soil	exp. soil	exp. soil	exp. soil	grass
A29	35.1	35	32.1	36.2	29.5	sun	sun	sun	sun	shade	exp. soil	exp. soil	exp. soil	exp. soil	grass

Table 2: Results of the Generalized Linear Models analysis of substrate temperature (°C), type of substrate (categories: grass, leaflitter and exposed soil) and exposure to the sun (categories: full sun, shade and filtered sun) in 145 points on the probability of representing a habitation of an *Ameiva ameiva* (Linnaeus, 1758), individual.

Tab. 2: Ergebnisse der Analyse des verallgemeinerten linearen Modells. Untersucht wurden Substrattemperatur (°C), Substrattyp (Kategorien: Gras, Laubstreu und blanker Boden) und Sonnenexposition (Kategorien: volle Besonnung, Schatten, Halbschatten) an 145 Meßpunkten hinsichtlich der Wahrscheinlichkeit, ein Aufenthaltsort eines Individuums von *Ameiva ameiva* (Linnaeus, 1758) zu sein.

	Estimate Schätzwert	Std. Error Standardfehler	*Z* value *Z*-Wert	*P* value *P*-Wert
Substrate temperature / Substrattemperatur	0.04892	0.03130	1.563	0.11
Type of substrate / Substrattyp	0.28925	0.73933	0.391	0.69
Exposure to sun / Sonnenexposition	-0.10989	0.68181	-0.161	0.87

RESULTS AND DISCUSSION

Twenty-nine adult individuals of *A. ameiva* (116 unused points, see the complete dataset in Table 1) were observed. The average temperature at the used points was 36 °C (ranging from 27 °C to 51 °C; SD = 6.8 °C). The first individual was observed around 09:00 h, foraging, and the last one ended its activity at approximately 16:00 h (Fig. 2). The pattern of the temperature of the substrate (T_S) on which *A. ameiva* was observed showed peaks, occurring alternatively either at very high but also milder temperatures along its daily activity period (Fig. 3). The CLR model revealed that none of the environmental variables (T_S, type of substrate or sun exposure) significantly affected the probability of occurrence of *Ameiva* lizards ($P = 0.11$, $P = 0.69$, $P = 0.87$, respectively; Table 2).

Previous studies found that *A. ameiva* maintained high and stable body temperatures in thermally and spatially heterogeneous habitats, and that they stopped activity when environmental temperatures were low (Sartorius et al. 1999). The studied lizards started their activity later in the morning and finished it sooner in the evening than other saurian species living in the same habitat (e.g., *Tropidurus lagunablanca* Carvalho, 2016, was active between 07:30 h and 17:00 h during the same days and in the same habitat; the authors' personal observations). Thus, the studied population seemed to follow the same strategy reported for several other populations of *A. ameiva*: remaining inactive under unsuitable environmental temperatures (e.g., temperatures prevailing before 09:00 h and after 17:00 h; Sartorius et al. 1999; Zaluar & Rocha 2000; Sales et al. 2011a).

The selected study design revealed that neither the sun exposure condition (full sun, shade or filtered sun), the type of substrate (grass, leaflitter or exposed soil) nor substrate temperature, affected the probability of occurrence at a particular point of *A. ameiva* in the Pantanal. The present results showed that the studied environmental variables did not affect the microhabitat selection of *A. ameiva*, at least during in the dry season (September).

Ameiva ameiva lizards show a relatively high plasticity in microhabitat use depending on the habitat in which they occur. For instance, while a population of *A. ameiva* from the Amazonian savanna showed the narrowest niche breadth within its lizard community regarding microhabitat use (Mesquita et al. 2006), another population from a *sensu stricto* Caatinga habitat showed one of the broadest microhabitat niche breadths within its lizard community (Vitt 1995). In fact, even among open habitats, *A. ameiva* is reported to use different types of microhabitats. In seasonally dry forests from northeastern Brazil, this species was found virtually on all types of substrate at the ground level, except for rocky ones (Sales et al. 2011a). Nonetheless, in a sand dune habitat form southeastern Brazil, *A. ameiva* only used three kinds of microhabitats, in a similar pattern as found for a Pantanal population in the present study. However, it is important to remember that *A. ameiva* lizards are active foragers that move constantly through space

(ROCHA et al. 2009), and which maintain their preferential body temperature throughout their wide geographic distribution, despite the thermal differences between ecosystems (VITT & COLLI 1994).

In this sense, the present results and the existing literature show that *A. ameiva* is not a microhabitat specialist, as other coexisting neotropical lizards are (see, e.g., VITT 1991). Nonetheless, it is possible that other variables that were not considered in the present study, such as food availability or predation risk can map the microhabitat choice of these lizards. In addition, it is possible that substrate temperature, type of substrate or sun exposure are important in determining microhabitat selection of *A. ameiva* in other periods of its annual activity. The results of the selected approach show that neither the *in situ* type or temperature of the substrate nor the sun exposure influenced the microhabitat use of *A. ameiva* during the dry season (September) in the Pantanal of Brazil.

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