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The Flood or the Woods: Natural History of the Red-tailed Vanzosaur in Seasonal Floodplains

Leonardo F.B. Moreira[1,4], *Natália P. Smaniotto*[1], *Vanda L. Ferreira*[2], *and Christine Strüssmann*[3]

[1]*Instituto Nacional de Pesquisa do Pantanal (INPP), Museu Paraense Emílio Goeldi, Avenida Fernando Corrêa da Costa, 2367, Boa Esperança, 78060-900, Cuiabá, Mato Grosso, Brazil*

[2]*Instituto de Biociências, Universidade Federal de Mato Grosso do Sul (UFMS), Avenida Costa e Silva, sem número, Cidade Universitária, 79070-900, Campo Grande, Mato Grosso do Sul, Brazil*

[3]*Faculdade de Medicina Veterinária, Universidade Federal de Mato Grosso (UFMT), Avenida Fernando Corrêa da Costa, 2367, Boa Esperança, 78060-900, Cuiabá, Mato Grosso, Brazil*

[4]*Corresponding author, e-mail: leonardobm@gmail.com*

Abstract.—**In floodplains, habitat mosaics are subject to seasonal changes that may shape the behavior and life history of many organisms. To determine whether ground-dwelling lizards show trait differences associated with vegetation types (a proxy for flood duration), we surveyed individuals of Red-tailed Vanzosaur (*Vanzosaura rubricauda*) inhabiting a mosaic of seasonally flooded grassland patches and dense arboreal savannas in the southern Pantanal ecoregion. We captured lizards in 20 sites using sets of pitfall traps with drift fences. We sampled each site four times in the dry season and four times in the rainy season. Contrary to our expectations, individuals from grassland patches seem able to take advantage from environmental shifts associated to flood pulse. Overall, adults from grasslands were larger and heavier than individuals from arboreal savanna. Vegetation type and season were important to explain variation in morphometric traits of *V. rubricauda*; however, responses differed by sex and age classes. Adult movement rate was higher during the dry season, and we captured juveniles more often in the dense arboreal savanna. The reproductive activity was not constrained by annual flooding. Our findings highlight the role of vegetation types on morphological traits and space use of a small lizard inhabiting seasonally flooded environments. Long-term studies focusing on natural history questions will help elucidate effects associated with changes in the intensity of the flood regime, one of the most likely consequences of global warming.**

Key Words.—Gymnophthalmidae; morphometric traits; Pantanal; savanna; *Vanzosaura rubricauda*

Introduction

Knowledge about animal movement, habitat use, and behavior provides essential insights into patterns of biodiversity and ecosystem functioning, being fundamental to accurate ecological forecasting (e.g., Tewksbury et al. 2014; Kays et al. 2015). Despite the exponential increase in data volumes about biodiversity, there are several knowledge gaps (i.e., Linnean and Wallacean shortfalls, geographic variation in traits, population trends, and major threats), especially in megadiverse countries (Tingley et al. 2016; Oliveira et al. 2017). The situation is not different in the natural history of non-avian reptiles from tropical ecosystems. These systems exhibit a high diversity and reptile species are important ecologically, acting as gene transporters, ecological engineers, and nutrient transporters (Miranda 2017).

Tropical lizard richness patterns are a complex interplay of local environmental heterogeneity and species habitat specialization (Nogueira et al. 2009; Kutt et al. 2011). In floodplains, habitats are subject to flood pulses that affect individual life-history and behavior of surface-dwelling reptiles and may even limit their persistence (Piatti et al. 2019; Treilibs et al. 2019). Thus, opportunistic strategies would favor persistence in such high-risk environments, rather than specialized resource use (i.e., feeding specialization, low vagility, or narrow thermal tolerance). For example, it would be expected that lizards in areas subject to floods have the ability to occasionally live in trees, semi-aquatic habits, or have high vagility to be able to disperse. Otherwise, persistence in seasonally flooded areas will rely on recruitment occurring from adjacent upland areas (McDonald et al. 2012).

It is well known that flood pulse is a key factor in structural stability and productivity of wetlands and is responsible for the variation of habitat availability (i.e., brackish and freshwater ponds, extensive flooded grasslands, and savannas) between dry and rainy season (Junk et al. 2011). The Pantanal ecoregion is a large lowland alluvial plain in South America, with recurrent flood and drought events. Currently, 47 lizard species are known in the region (Ferreira et al. 2017; Dorado-

Rodrigues et al. 2018), and most of them are widespread along neighboring regions not subject to periodic floods: the Cerrado, Caatinga, and Chaco. Many lizard species in these areas have scansorial/arboreal microhabitats (e.g., Iguanidade, Mabuyidae, and Tropiduridae), can occasionally dive under water (e.g., Iguanidae, Mabuyidae, Teiidae), or are widely foraging lizards of relatively large size (Teiidae). Small lizards belonging to the Gymnophthalmidae represent almost 20% of known lizard species from the Pantanal (Ferreira et al. 2017). Like other species that make up the family, Pantanal gymnophthalmids show limb reduction (or even atrophy) and other characters that favor secretive or burrowing habits (Pellegrino et al. 2001). So, an interesting question is how low vagility lizards that are strictly terrestrial cope with flood-related changes? Among these lizards, the Red-tailed Vanzosaur (*Vanzosaura rubricauda*) is a species distributed along the Dry Chaco and savannas of western Brazil (Avila et al. 2013; Recoder et al. 2014). Until recently, it represented a species complex (*V. multiscutata*, *V. rubricauda*, and *V. savanicola*) usually associated with leaf litter and sandy soils (Recoder et al. 2014). Despite the large geographic coverage by Recoder et al. (2014), there are few data about Pantanal populations and most of these data are from borders within the Cerrado ecoregion. Lizards in open areas of South America show a high number of cryptic species (Fenker et al. 2020), and the lack of species-specific data may obscure ecological and behavioral patterns.

Here we provide information on the natural history of *V. rubricauda* from an interfluvial region in the southern portion of the Pantanal ecoregion. We investigated whether morphometric traits change according temporal and environmental factors. In the Pantanal, vegetation physiognomies show a gradient associated with maximum flooding patterns and water level (Salis et al. 2014). We expected that *V. rubricauda* would show trait differences associated with vegetation because individuals from grassland patches are more often subject to flood effects than individuals from higher areas such as dense arboreal savannas, which only flood in extreme rainfall events. Individuals from arboreal savanna live in a more stable habitat, allowing them to reach larger sizes. We also present data about sexual dimorphism, space use, and reproductive activity.

Materials and Methods

Study area.—The study area was located in the southern part of the Taquari River Megafan, a region locally known as *Nhecolândia*, whose main feature is the high number of lagoons (for more details see Oliveira et al. 2018). We conducted field sampling at the Nhumirim Ranch (18°58'59"S; 56°39'00"W; 103 m elevation; datum WGS84), an experimental station belonging to the Empresa Brasileira de Pesquisa Agropecuária (Fig. 1). The site comprises about 4,300 ha and is located in the municipality of Corumbá, Mato

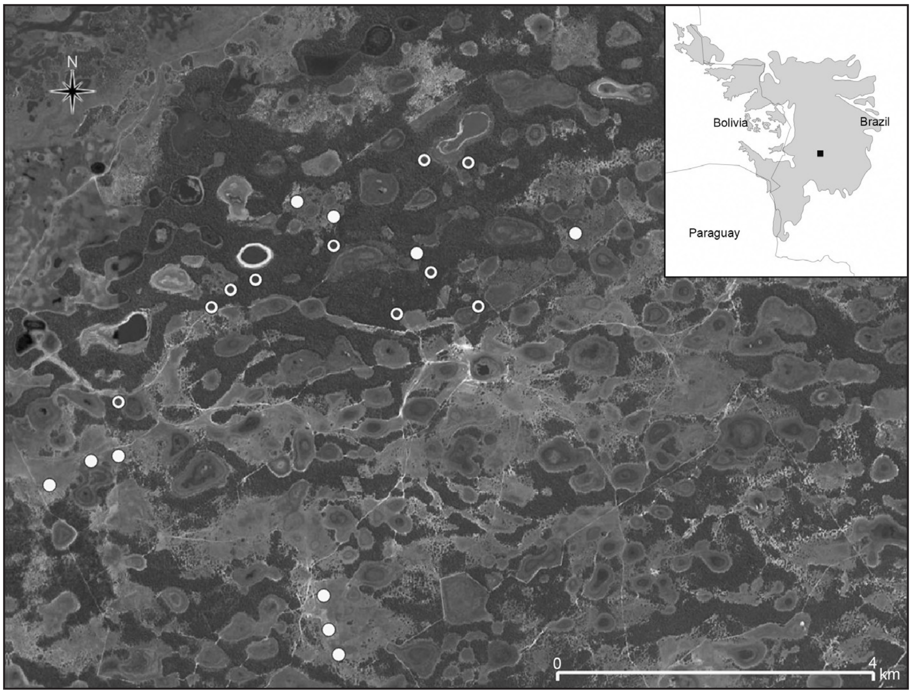

Figure 1. Location of the Pantanal ecoregion (grey) and the study area (dark square) in South America (inset map). Circles in the main image represent sampled sites at Nhumirim Ranch experimental station in Brazil. Filled circles represent pitfall traps surround by grasslands and open circles represent pitfall traps surround by arboreal savannas.

Grosso do Sul, Brazil, with 20% of its area preserved as a Natural Heritage Private Reserve (Nunes et al. 2021). Annual rainfall in the region is highly seasonal, being concentrated from December to March (see Appendix Figure). Air temperature is also seasonal with lower values in the beginning of the dry season. Floods are common in the region because of rainfall-runoff with a limited influence of overflow water from rivers. Although inter-annual variations may occur, the flood often begins in mid-December and persists through March, with a water drawdown period until June (Delatorre et al. 2015).

In Nhumirim Ranch, the topography is basically flat with low-level terrain, and the predominant landscapes included a mosaic of dry and seasonally flooded grasslands of native and exotic species, open savannas, and arboreal savannas on ancient levees locally called *cordilheiras* (Pott et al. 2011). The soil comprises fluvial and lacustrine sands with high aluminum saturation (Junk et al. 2011). Woody and grassy formations did not show a clear distinction at small scales, grassland patches were common in areas subject to long flood duration (5–6 mo), and woody types were established in areas that become flooded only for a few days or weeks. Grasslands comprised a mosaic of native and exotic grasses, such as Purpus' Carpetgrass (*Axonopus purpusii*) and Koronivia Grass (*Urochloa humidicola*), respectively. In contrast, areas dominated by Wire Lemongrass (*Elionurus muticus*), locally known as *caronal*, are rarely flooded. Dense arboreal savannas comprised a mix of trees and dense woodlands where there was little grass cover. These areas are characterized by species such as the shrubs Canjiqueira (*Byrsonima cydoniifolia*) and Araticum (*Annona dioica*), and the trees Sambaíba (*Curatella americana*), Urucuri Palm (*Attalea phalerata*), and Wild Guava (*Cordiera sessilis*; Salis et al. 2006).

Sampling procedures.—Between 2005 and 2006, we captured lizards at 20 sites using a pitfall trap system with drift fences (Fig. 1). We installed 10 trap systems in grasslands and 10 in dense arboreal savannas, and all trap systems were surrounded by similar vegetation up to 100 m. During the rainy season, the area was almost completely covered by surface water, except for patches at higher elevation (i.e., about 1 m above the flood level). Thus, trap systems were constrained by logistic issues and established in sites above the mean flood level.

We sampled each site four times in the dry season (May, June, August, and October 2005) and four times in the rainy season (February and March 2005, January and March 2006). We located trap systems 0.3–8 km apart and they were composed of four plastic buckets (100 L) each, 10 m apart from each other, and arranged in Y pattern with plastic fences (100 cm tall) connecting them. During each field sampling, all buckets remained open for nine consecutive days, and we examined them daily for lizards. We transported each captured *V. rubricauda* to the field laboratory, and we marked individuals by toe clipping (Waichman 1992; Plummer and Ferner 2012). We released lizards in their original capture location the next day. Toe clipping followed approved protocols and was provided for in the field permit. We also recorded sex, body mass, snout-vent length (SVL), tail length (TaL), and additional information on color pattern, evidence of regenerated or broken tails, the presence/absence of eggs, and natural marks. We considered individuals < 24.5 mm SVL juveniles (Recoder et al. 2014) and we did not determine their sex. We anesthetized voucher specimens and we killed them with an overdose of thiopental. We preserved lizards in 10% formalin. Vouchers are housed in the zoological collection of the Universidade Federal de Mato Grosso do Sul (ZUFMS).

Data analyses.—We used a Chi-square Test to determine if the sex ratio of captured lizards deviated from the 1:1 ratio. We used a Two-way Analysis of Variance (ANOVA) to investigate the influence of vegetation cover and season on the number of captures. We tested the normality of capture data prior to ANOVA with Shapiro-Wilk test, and the data were normally distributed ($P = 0.397$). We did not include marked individuals that we recaptured in the same sampling event in the analysis. There is evidence that *V. rubricauda* is sexually dimorphic for body size and shape (Recoder et al. 2014). We tested for dimorphism in body mass, SVL, and TaL with the Mann-Whitney U test. For traits where sexual dimorphism was identified, we analyzed the sexes separately in subsequent analysis to avoid additional noise related to dimorphism.

Because tail autotomy can vary markedly with age and across lizard taxa (Bateman and Fleming 2009), we included only individuals with intact tails in the morphometric analysis. We used Generalized Linear Models with Gamma distribution and log-link function to assess factors affecting morphometric traits because lizard morphometric data were skewed and had a non-normal distribution. In the analyses, the categorical explanatory variables were vegetation cover (grassland or savanna) and season (dry or rainy). The dependent variables were body mass, SVL and TaL. We analyzed adults and juveniles separately. We used the statistical software R version 4.0.0 for all analyses (R Core Team 2020) and we visualized data using the R package gglot2 (Wickham 2016). For all tests, $\alpha = 0.05$.

Results

We registered 344 *V. rubricauda* (Table 1), and the sex-ratio was slightly male-biased 1.31 M: 1.00 F,

Table 1. The number of male, female, and juvenile Red-tailed Vanzosaurs (*Vanzosaura rubricauda*) we collected with pitfall traps at the Nhumirim Ranch experimental station, southern Pantanal, Brazil, between 2005 and 2006.

	Grassland		Savanna	
	Dry	Rainy	Dry	Rainy
Females	40	28	36	13
Males	62	27	46	19
Juveniles	12	14	25	22

although not significantly different than 1:1 (X^2 = 2.81, df = 1, *P* = 0.090). We recaptured five males only, which we caught at the same sites and between 2–6 mo apart. Males with nuptial coloration (i.e., reddish gular region) were more often captured in mid dry season (August-October; n = 37); however, some males also exhibited nuptial coloration in the middle of the rainy season (January-February; n = 15). In the same way, we captured 10 females with eggs in the dry season (October), but we also captured four gravid females in the rainy season (January). While captures of gravid females were higher in grasslands (n = 10) than in savannas (n = 4), we captured 26 males with nuptial coloration in equal numbers in both vegetation types. Overall, adult lizard captures were significantly higher in the dry season than in the rainy season ($F_{1,157}$ = 6.97, *P* = 0.009) and did not differ significantly between vegetation types ($F_{1,157}$ = 1.981, *P* = 0.161); however, juvenile captures follow a different pattern (Table 1). While season did not affect their captures significantly ($F_{1,157}$ = 0.054, *P* = 0.817), we captured significantly more juvenile lizards in the dense savanna pitfalls than in the grasslands ($F_{1,157}$ = 5.358, *P* = 0.022).

Although females were significantly larger than males (*W* = 11586, *P* < 0.001), sexes were not dimorphic for body mass (*W* = 9140, *P* = 0.836) or tail length (*W* = 2282, *P* = 0.777). Both vegetation type and season were important to explain variation in morphometric traits of *V. rubricauda*; however, responses differed by sex and age classes (Table 2). Females in grassland areas were significantly larger than in arboreal savannas (Table 2), but female SVL did not differ significantly between dry and rainy seasons (Table 2, Fig. 2). Males were also significantly larger in grassland areas than in the savanna (Table 2), and we caught significantly larger males in the rainy season than in the dry season (Table 2, Fig. 2). Juveniles that we caught in the dry season were significantly larger than those we caught in the rainy season, but they did not show significant differences associated with vegetation type (Table 2, Fig. 2). Adult tail length (Fig. 3) and body mass (Fig. 4) showed significantly higher values in grassland areas than in savannas (Table 2), but season did not significantly affect TaL or body mass (Table 2). In contrast, mass and TaL of juveniles we caught in the rainy season were

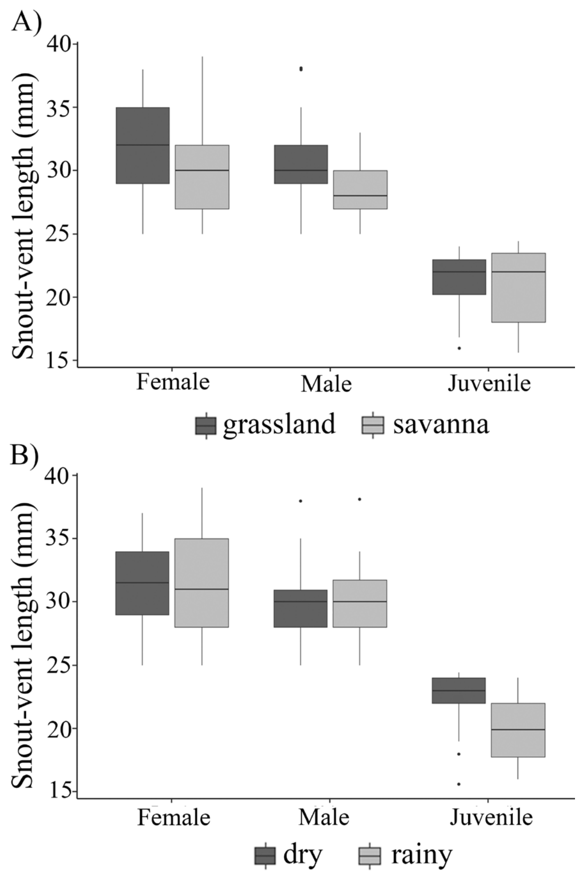

Figure 2. Median (horizontal lines), quartiles (boxes), and range of values (vertical lines) of snout-vent lengths (mm) in male, female, and juvenile Red-tailed Vanzosaurs (*Vanzosaura rubricauda*) at the Nhumirim Ranch experimental station, southern Pantanal, Brazil, across (A) grassland and savanna vegetation and (B) dry and rainy seasons. Data points above and below vertical lines are outlier values.

significantly lower than in the dry season (Table 2) but did not show significant differences associated with vegetation (Table 2, Fig. 3 and 4).

Discussion

We found that life-history traits of *Vanzosaura rubricauda* were associated with vegetation types in flooded areas of southern Pantanal. Overall, our data indicated that adult individuals from grassland patches are larger and heavier than individuals from dense arboreal savannas. Juvenile traits, though, were more closely tied to seasonal changes. Our results also pointed to an inter-dependence of flood and drought on space use of *V. rubricauda*. Reproductive activity (i.e., gravid females and males with nuptial coloration) was not constrained by annual flooding, but there seems to be a reproductive gap at the beginning of the dry season (i.e., coldest months). Such results are in accordance with

Table 2. Effects of temporal and environmental factors on the morphometric traits of Red-tailed Vanzosaurs (*Vanzosaura rubricauda*) at the Nhumirim Ranch experimental station, southern Pantanal, Brazil, using Generalized Linear Models. Individuals did not show sexual dimorphism for tail length and body mass, so female and male data were analyzed together.

Response variable	Class	Explanatory variable	Estimate	SE	*t*	*P*
Snout-vent length	Female	Vegetation	-0.06	0.02	-3.04	0.003
		Season	-0.01	0.02	-0.60	0.557
	Male	Vegetation	-0.05	0.01	-4.40	< 0.001
		Season	0.03	0.01	2.03	0.040
	Juvenile	Vegetation	-0.03	0.03	-1.01	0.317
		Season	-0.117	0.03	-4.36	< 0.001
Tail length	Adult	Vegetation	-0.19	0.04	-4.37	< 0.001
		Season	-0.08	0.04	-1.77	0.080
	Juvenile	Vegetation	-0.02	0.07	-0.302	0.764
		Season	-0.162	0.07	-2.325	0.020
Body mass	Adult	Vegetation	-0.144	0.04	-3.301	0.001
		Season	0.03	0.05	0.720	0.472
	Juvenile	Vegetation	-0.185	0.10	-1.81	0.080
		Season	-0.543	0.10	-5.09	< 0.001

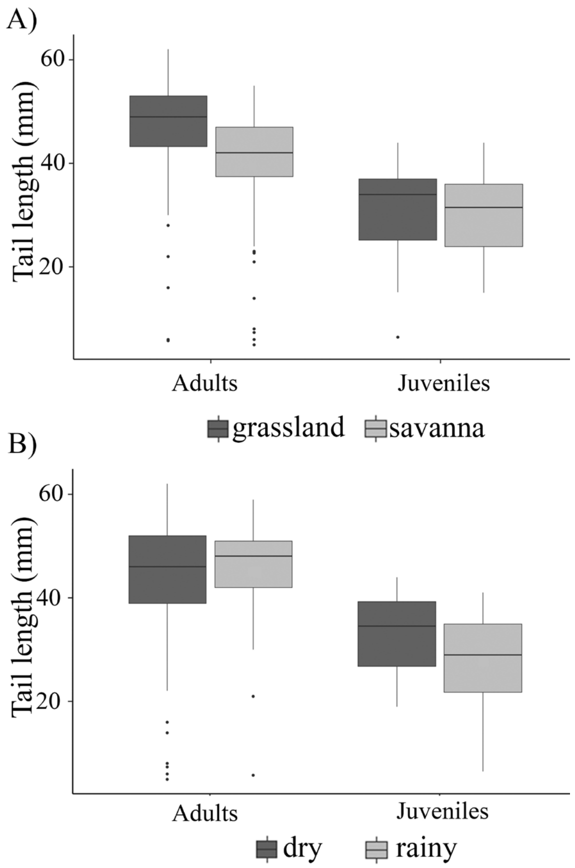

Figure 3. Median (horizontal lines), quartiles (boxes), and range of values (vertical lines) of tail lengths (mm) in male, female, and juvenile Red-tailed Vanzosaurs (*Vanzosaura rubricauda*) at the Nhumirim Ranch experimental station, southern Pantanal, Brazil, across (A) grassland and savanna vegetation and (B) dry and rainy seasons. Data points above and below vertical lines are outlier values.

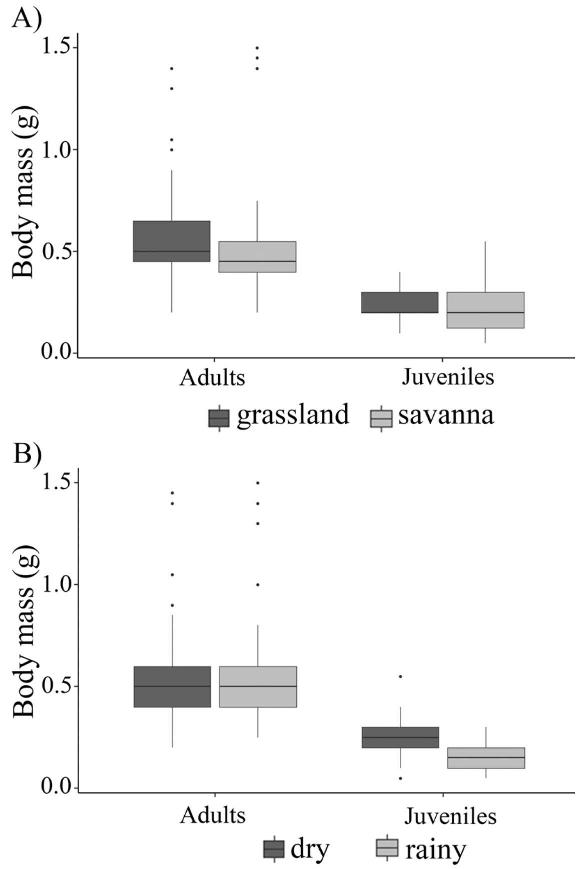

Figure 4. Median (horizontal lines), quartiles (boxes), and range of values (vertical lines) of body mass (g) in male, female, and juvenile Red-tailed Vanzosaurs (*Vanzosaura rubricauda*) at the Nhumirim Ranch experimental station, southern Pantanal, Brazil, across (A) grassland and savanna vegetation and (B) dry and rainy seasons. Data points above and below vertical lines are outlier values.

patterns observed in the Chaco region of Argentina (Cruz 1994). Adult movement rate seems to be higher during the dry season, as reflected by the number of captures. In addition, juveniles were not evenly distributed across vegetation types, and we captured most individuals in shaded areas of dense arboreal savannas. Even at a steady flood period, the water surface profile is not level in the Pantanal areas (Fernandes 2007; Girard et al. 2010; Oliveira et al. 2018) and ancient levee occurrence is an important factor for local flooding patterns. In this sense, we posit that *V. rubricauda* may combine a high fidelity to suitable refuges by juveniles with a propensity of adults to move between different vegetation patches.

Although we expected that *V. rubricauda* could be constrained by seasonal floods, especially in areas subjected to long-duration floods, our data showed that individuals from grassland patches are able to take advantage of environmental shifts associated with flood pulse. Evidence in the literature highlights that a high degree of plasticity (namely, some ability to climb trees in species mainly found on the ground) would be important to withstand the seasonal flooding period (Mesquita et al. 2015). In regions subject to extreme seasonal fluctuations, lizard abundance and body condition appear to be more related to indirect pathways (biotic mechanisms and shifting species interactions) than direct effects of seasonal climate (Deguines et al. 2017; Grimm-Seyfarth et al. 2019). The Pale-rumped Ctenotus (*Ctenotus regius*) and the South-eastern Morethia Skink (*Morethia boulengeri*), both small skinks inhabit arid floodplains in Australia, have body conditions mainly driven by herb-layer biomass and predation, while occupancy is positively impacted by flood parameters (Grimm-Seyfarth et al. 2019). Because we did not assess prey availability and potential predators, we can only speculate about which factors in the grassland patches would favor *V. rubricauda*. Flooding might be a disturbance that reduces terrestrial habitat availability, but the rainy season also leads to an increase in herbaceous cover (Ivory et al. 2019), which in turn might increase lizard prey abundance and decrease attack rates by visually oriented predators.

As *V. rubricauda* prey upon a wide variety of litter arthropods, the smaller size and body mass of savanna individuals may reflect the fact that they spend little time active rather than the constraints of prey availability. Small leaf-litter lizards are vulnerable to a wide range of predators, including litter species (e.g., spiders, frogs, other reptiles; Shepard 2007; Do Couto and Menin 2014; Reyes-Olivares et al. 2020) and species that also forage at other microhabitats (e.g., birds and mammals; Shepard 2007; Gomes et al. 2012; Smaniotto et al. 2017). In the Brazilian Cerrado, the attack rate to clay-covered plastic model lizards, including one representing *Vanzosaura*, was twice as high in more structurally complex habitats than in grassland habitats (Shepard 2007). A positive association between habitat heterogeneity and species diversity, including lizard predators, is a recurrent pattern in savanna-like ecosystems (Figueira et al. 2006; Thoresen et al. 2021). One reasonable explanation for our results is that individual *V. rubricauda* in savanna patches would be less active, because of higher predation risk, than in grasslands. In our study area, grasslands are apparently simple habitats in relation to savanna patches that exhibit higher canopy cover and vertical stratification (Rodela et al. 2008). In addition, the flood season may cluster some potential predators (large lizards, birds, and mammals) in higher patches, which include dense arboreal savannas (Alho et al. 2011; De Lázari et al. 2013). During flood season, most grassland areas became flooded, with exception of some small mounds, such as termite nests. So, small lizards occupying grassland areas close to such non-flooded mounds could face a relatively small predation risk during the rainy season when compared with dense arboreal savannas.

Intriguingly, we captured juveniles more often in the dense arboreal savannas, and juveniles had lower body mass and SVLs in the rainy season than in the dry season. This indicates that habitat preferences can differ between cohorts in longitudinal studies (i.e., following adults and juveniles). While high capture rates indicate an overall great abundance of individuals, they are also an indirect proxy to quantify natural animal movement. Information on home range and movement patterns remain limited for many lizard species, but studies have indicated that juvenile dispersal contributes more than adult dispersal to regional persistence (Warner and Shine 2008; Dubey and Shine 2010; Schofield et al. 2012). We posit that environmental conditions in the grassland areas may encourage juveniles to explore savanna patches. Adults and juveniles have different physiology and behaviors (thermoregulation, foraging, activity time; Angilletta Jr 2001; Liwanag et al. 2018). These differences seem to influence the microhabitat used by individuals of different cohorts. The movement of juvenile lizards of some species through the environment is more frequent than in adults (Eifler et al. 2007). Juveniles appear to choose environments where the temperature is lower, move more often to detect prey and predators, and prefer more elevated habitat spots (Eifler et al. 2007; Zhu et al. 2015; Garrison et al. 2017; Eifler and Eifler 2019). For *V. rubricauda*, such specific characteristics of juveniles can make them explore different vegetation types, but the dense arboreal savanna environment seems to present the best age-related conditions (shade, perch, and camouflage).

To conclude, we showed the role of vegetation types on morphological traits of a small lizard in seasonally flooded environments of South America. Dynamic conditions of the floodplain also influenced habitat preference of different cohorts and the reproduction of *V. rubricauda*. A focus of further research should include a more detailed investigation of the response of *V. rubricauda* and other small secretive lizards to seasonal flood pulse. Research into the dynamics of vertical migrations and laboratory experiments about swimming performance would also be relevant. Our results contribute to the understanding of how ground-dwelling organisms behave in floodplains. A better understanding of the natural history of this species will help elucidate possible effects associated with present and predicted climate changes (i.e., changes in the intensity and duration of the flood regime).

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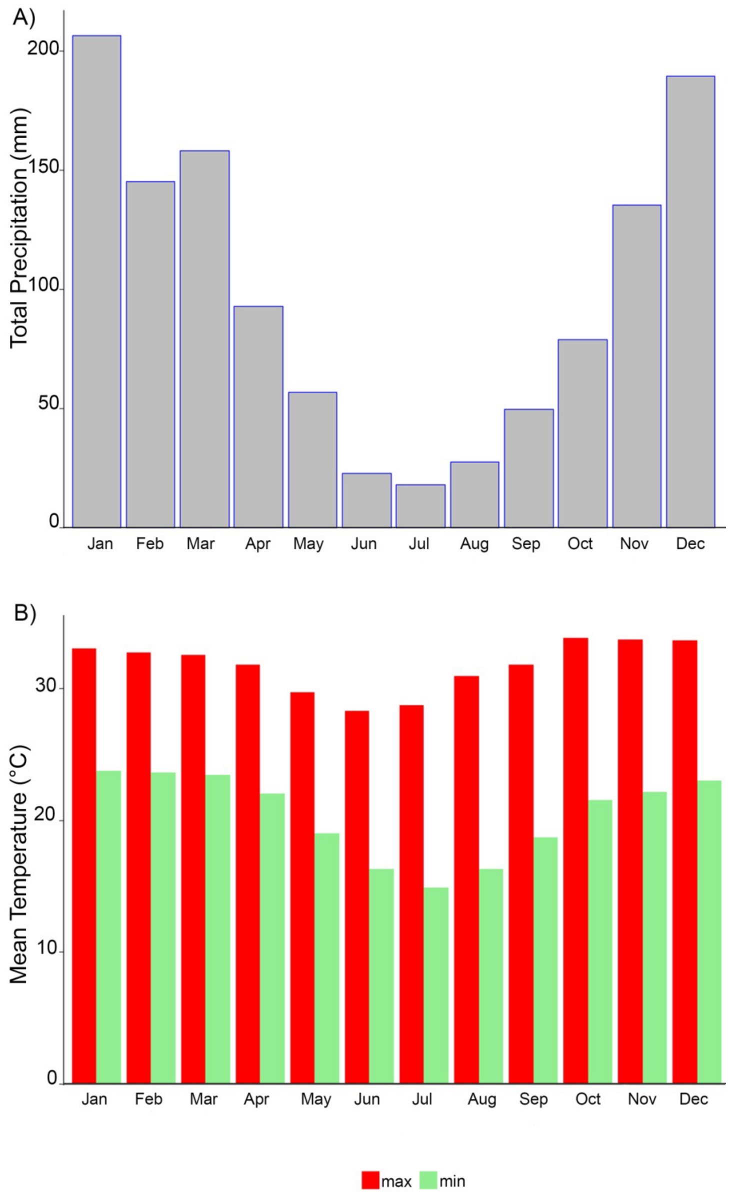
Leonardo F.B. Moreira received a Ph.D. in Biology (2013) from the Universidade do Vale do Rio dos Sinos, São Leopoldo, Brazil. He is interested in community ecology, mainly in freshwater environments. His research has focused on the mechanisms structuring communities of amphibians and reptiles and effects of the habitat conversion. (Photographed by Marcos Ardevino).

Natália P. Smaniotto earned her M.S. in Ecology and Biodiversity Conservation in 2017 from the Universidade Federal de Mato Grosso, Cuiabá, Brazil. Her thesis focused on the movement patterns and home range of Yellow Anacondas (*Eunectes notaeus*). Currently, Natália is involved in a project about the effects of climate change in the Pantanal ecoregion. Her research interest involved mainly natural history of amphibians and reptiles, but also other groups of the Pantanal fauna. (Photographed by Natália P. Smaniotto).

Vanda L. Ferreira is a Professor in the Universidade Federal de Mato Grosso do Sul, Campo Grande, Brazil. She received her Ph.D. in Biosciences from the Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil (2001). Vanda has expertise in zoology and ecology, with an emphasis on amphibians and reptiles from the Cerrado and Pantanal ecoregions. (Photographed by Vanda Ferreira).

Christine Strüssmann is an Associated Professor in the Universidade Federal de Mato Grosso, Cuiabá, Brazil. She received her Ph.D. in Biosciences from the Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil (2003). Her research interests lie in taxonomy, systematics, and ecology of amphibians and reptiles. (Photographed by Christine Strüssmann).



Appendix Figure. Climatic variation for Nhecolândia region, Mato Grosso do Sul, Brazil. Measures correspond to mean values between 1971 and 2001. (A) Monthly total precipitation. (B) Mean temperatures. (Source: Soriano and Alves 2005)