

Bromeliad rosettes as shelters for hylid treefrogs during a heat wave in the Brazilian Pantanal

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ABSTRACT – During a heat wave in November 2023, we assessed the use of bromeliad rosettes as shelters for hylid treefrogs in the Brazilian Pantanal (area of Nhecolândia). During the day time, four hylid species (genera *Boana*, *Scinax*, *Trachycephalus*) were detected sheltering in 40 rosettes of the terrestrial bromeliad *Bromelia balansae*; this was a different species complex from when observations were made in October 2019 when the temperature conditions corresponded to long-term averages. The internal and external day time temperature of each shelter was measured. The mean daytime temperature inside the shelters was 36.1 °C (range 24.0–43.5 °C), this varied depending on the microhabitat conditions, and was 1.1 °C lower than the mean temperature of the leaves of the upper part of the rosettes; the difference was statistically significant. We suggest that during this very dry and hot period the main advantage provided by the bromeliad shelters was to enable frogs to have behavioural control of overheating so that they could avoid excessive evaporative water loss.

INTRODUCTION

The Pantanal is an ecological sub-region of the Cerrado formed by flat plains of Quaternary sediments covered by seasonally flooded grassland and Cerrado vegetation (Griffith et al., 1998). The climate of the Pantanal is characterised by humid and hot summer months (December to January) and dry and colder winters (June to August) with mean monthly temperatures in the range of 19.9–27.4 °C (Tarifa, 1986; Uetanabaro et al., 2008). However, in recent years due to climatic change, the Pantanal is experiencing prolonged periods of drought accompanied by extreme heatwaves (Campos et al., 2020; Marengo et al., 2021).

The Pantanal is well known for the diversity and abundance of its wildlife, in particular a very rich amphibian fauna comprising more than 50 anuran species (Strüssmann et al., 2007; 2010; Uetanabaro et al., 2008; Valério et al., 2016). Amphibians generally play an important role in ecosystem food webs and contribute significantly to various ecosystem services (Hocking & Babbitt, 2014). However, they are experiencing a global crisis of decline and current climate change is one important contributing factor (Beebee & Griffiths, 2005; Corn, 2005). It has been predicted that increased temperature, increased length of dry season, decreased soil moisture and increased inter-annual rainfall variability will negatively affect amphibian populations (Donnelly & Crump, 1998; McMenamin et al., 2008; Walls et al., 2013). Drought and drastic environmental changes have also recently been reported from the Pantanal (Campos et al., 2020; Campos & Mourão, 2020; 2021). Therefore, from the perspective of the conservation of the Pantanal herpetofauna, it is important to know how local amphibian populations are responding to these changes.

In general, the appropriate choice of retreat sites and good timing of retreat appears to be fundamental for survival under hot and dehydrating conditions (Navas et al., 2004). In the area of Nhecolândia (sub-region of the Brazilian Pantanal) an important source of anuran retreats is the terrestrial bromeliad *Bromelia balansae* Mez, 1891 (Bromeliaceae) and at least two hylid treefrogs, *Dendropsophus nanus* and *Scinax nasicus*, frequently use the rosettes of *B. balansae* as diurnal shelters (Moravec & Campos, 2020). In the current study, we evaluate the role of bromeliad rosettes as shelters for treefrogs during a heatwave in Nhecolândia.

MATERIALS & METHODS

From 1–12 November 2023, we surveyed bromeliad rosettes for the presence of treefrogs in the territory of the Fazenda Nhumirim and nearby Fazenda Campo Dora, in the Brazilian Pantanal (Nhecolândia, state Mato Grosso do Sul). Anuran species were identified using Uetanabaro et al. (2008). The research coincided with unusually hot, dry weather in the first half of November (maximum daily air temperatures ranged 40–42.5 °C) which lasted until the beginning of December 2023. Average maximum October and November air temperatures for the Corumbá area (period 1991–2020) located ca. 150 km west of Nhumirim, are 34.1 and 33.8 °C (World climate guide, 2024). Average air temperature recorded in Fazenda Nhumirim in October 2019 was 29.1 °C (B. Soriano, personal communication, 24 April 2024).

The area of Nhecolândia is covered by a mosaic of three major habitats: seasonally flooded grassland (floodplains), permanent or temporary lagoons and pockets of forest. The marginal understory of the forest ‘islands’ is often formed by dense growths of the terrestrial bromeliad *B. balansae*

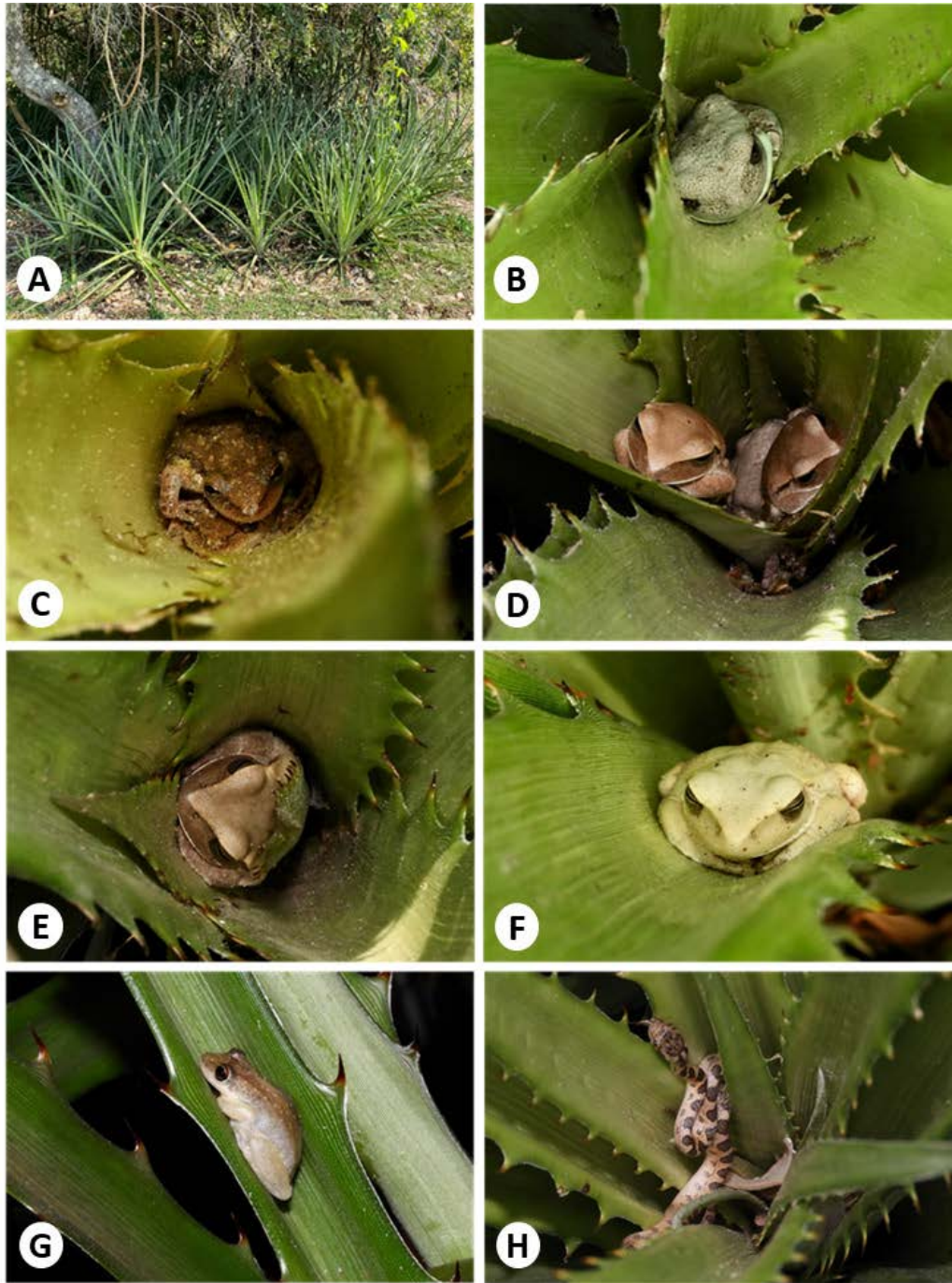


Figure 1. Hylid treefrogs sheltering in the terrestrial bromeliad *Bromelia balansae* in the Brazilian Pantanal (area of Nhecolândia)- **A.** Patch of *B. balansae* at the Lagoon B, **B.** Diurnal shelter of *Trachycephalus cf. typhoni* in the centre of the bromeliad rosette, **C.** Two individuals of *Scinax nasicus* in the mutual contact in the bromeliad centre, **D.** Two individuals of *Boana raniceps* and one individual of *T. cf. typhoni* sharing the same shelter, **E.** *B. raniceps* having their ventral and dorsal surfaces pressed against the bromeliad leaves, **F.** *B. raniceps* with light body colour in the leaf axil (at 41 °C), **G.** *S. nasicus* adopting water-conserving posture on the bromeliad leaf during the night, **H.** Subadult individual of *Leptodeira pulchriceps* exploring the bromeliad centre

(Fig. 1A). These sharply delimit the forest margin from the grassland lying between the forest pockets and the lagoons (Moravec & Campos, 2020). The stiff leaves of *B. balansae* form dense rosettes, which do not accumulate rainwater and lack phytotelmata (Romero, 2006). Nevertheless, a small amount of water can be present in the deepest part of the rosettes after rainfall (Moravec & Campos, 2020). In the surveyed localities, the rigid thorny leaves of the individual

rosettes usually reached the height of 700–1,500 mm (maximally 3,000 mm) and were 25–60 mm wide (up to 90 mm at the rosette base). Due to the heatwave, no traces of water were detected in any of those bromeliad rosettes that were inspected.

The study areas were three bromeliad patches growing at the forest margins in the vicinity of three permanent lagoons: Lagoon A (Fazenda Campo Dora, 18° 53'34" S, 56°

43°49' W), Lagoon B (Fazenda Campo Dora, 18° 57'24" S, 56° 44'48" W) and Lagoon C (Fazenda Campo Dora, 18° 58'43" S, 56° 43'36" W). The straight distance between the Lagoons A and B was ca. 7.2 km and between Lagoons A and C ca. 9.3 km. Additional diurnal and night observations were made in bromeliad patches at a fourth permanent lagoon in Fazenda Nhumirim (Lagoon D, 18° 59'03" S, 56° 36'58" W) lying ca. 16.0 km straight from the Lagoon A. The distances of bromeliad patches from the nearest water margins of the respective lagoons ranged between 20–40 m. In total, more than 800 rosettes of *B. balansae* were inspected around Lagoons A–D during the 12 days of the investigation.

On 6–9 November 2023 between 08:00–14:00 h, rosettes being used as hylid shelters were documented in detail at the bromeliad patches of Lagoons A–C (150 bromeliad rosettes inspected). For each bromeliad containing a hidden hylid we measured (i) the surface temperature of the shaded leaves of the open upper part of the bromeliad rosette ca. 30 cm above the hidden hylid, and (ii) the inner temperature of the funnel-shaped central part of the rosette containing the hidden hylid. The temperatures were measured with a Benetech non-contact infrared digital thermometer (temperature extent -50 to 420 °C) from the distance 50–100 mm. Control measurements of air temperature inside and outside the bromeliad rosette were made with a digital thermometer EMOS RS8471 with an external sensor. Each measurement was repeated three times, and the mean value was rounded to the nearest 0.5 °C. In addition, maximum temperatures of the sunlit surface of the ground at the edges of the bromeliad patches and the maximum surface temperature of the bromeliad leaves exposed to the sun were measured to document temperature conditions at the study area.

Paired t-test was used to evaluate the possible difference between average temperatures of the upper open part of the bromeliad rosette and the inner central part of the rosette containing the hidden hylids.

RESULTS

From 6–9 November 2023, around the Lagoons A–C, 150 rosettes of *B. balansae* were inspected during the daytime, of which 40 (26.7%) were occupied by 53 hylids of four species. We observed 18 *Boana raniceps*, 7 *Trachycephalus cf. typhonius*, 1 *Scinax acuminatus* and 27 *Scinax nasicus*. The local occupancy on the outer edges of the bromeliad growths facing the lagoons reached up to 56.0% (n = 25 inspected rosettes). Usually only one individual hylid occupied a bromeliad centre (Fig. 1B). However, in eight cases, 2–4 individuals shared the same shelter (Fig. 1C). In three cases, two different species (*B. raniceps* and *T. cf. typhonius* or *B. raniceps* and *S. acuminatus*) were hidden in the same shelter with bodies in mutual contact (Fig. 1D). The hylids were hidden in the deepest parts of the centres of the rosettes (exceptionally also in the near leaf axils). Their ventral and dorsal surfaces were usually pressed against the leaves (Fig. 1E).

The highest temperatures of the sunlit surface of the ground at the edge of the bromeliad growths reached 50–54 °C and the maximum surface temperature of the bromeliad leaves exposed to the sun reached 50–56 °C. The mean

temperature of the shaded leaves of the upper part of the rosette was 37.2 °C (range 28.0–45.0, SD = 4.06, n = 40), while the mean temperature of inner occupied central part of the rosettes was 36.1 °C (range 24.0–43.5 °C, SD = 4.23, n = 40), i.e. 1.1 °C lower. This difference was statistically significant $t = -4.119$, $df = 39$, $p < 0.001$.

The distribution of treefrogs was not even, as they were more numerous on the outer edges of the bromeliad growths, which were closer to the lagoons, but they were less numerous in bromeliads that were exposed to the sun for longer parts of the day (e.g. whole morning). In such sunlit shelters the temperature reached 40–43.5 °C and the hylids lightened their colour to reflect the light energy (Fig. 1F). The hylids were not found in bromeliads covered with a layer of leaf litter, which filled the centres of rosettes. The same was true for bromeliads growing under trees frequented by herons and other water birds, as the rosettes of these bromeliads were thickly covered with bird droppings.

At the time of the investigation, the hylids using bromeliad shelters were not breeding or vocalising. After dark when the air temperature was still 30–31 °C, some individuals remained hidden in bromeliad shelters. Others were observed perching on leaves outside the bromeliad centre, some adopting a water-conserving posture (limbs tucked in close to the body and the chin resting against the substrate; sensu Heatwole et al., 1969) to control evaporative water loss (Fig. 1G). The expected nocturnal movement of hylids into the lagoons to replenish water was not observed, but insufficient effort was made to confirm this movement.

During night inspections of the control bromeliad patches at the Lagoon D, three individuals of the frog-eating colubrid snake *Leptodeira pulchriceps* were observed exploring the bromeliad rosettes (Fig. 1H).

DISCUSSION

Bromeliad rosettes are commonly used by Neotropical frogs as diurnal shelters (Peixoto, 1995; Silva et al., 2011; Sabagh et al., 2017). However, the present data indicate that, depending on climatic conditions, the species spectrum of treefrogs using bromeliad shelters may vary. In October 2019, the bromeliad rosettes were frequently occupied by subadult and adult *D. nanus* and *S. nasicus* (Moravec & Campos, 2020). However, during the heatwave of November 2023, the same bromeliad growths also served as diurnal shelters for three physically larger hylid species - *B. raniceps*, *S. acuminatus* and *T. cf. typhonius*. Interestingly, the physically smallest species, *D. nanus*, which is more sensitive to desiccation than the other species, did not shelter in bromeliads in November 2023 but survived the hot days in the moist littoral vegetation on the shores of the lagoons.

We originally assumed that the observed hylids could profit by occupying the rosettes of *B. balansae* in three ways: (i) the thorny leaves of rosette centres protect the frogs from larger predators, (ii) the diverse groups of arthropods associated with bromeliads provide food, and (iii) the deep basal parts of rosette centres provide shady and humid shelters (Moravec & Campos, 2020) and certainly in the semi-arid Brazilian Caatinga, wetter and cooler conditions

have been recorded inside the bromeliad *Aechmea aquilega* (species with phytotelmata) and inside the plots of the rupicolous bromeliad *Encholirium spectabile* (species lacking phytotelmata) (Protázio et al., 2013; Jorge et al., 2020). Our findings from November 2023 show that rosettes of *B. balansae* are completely dry at high ambient temperatures. On the other hand, the average temperature inside the shelters was statistically significantly lower than outside the bromeliad rosettes. Therefore, the question is what is the actual role of the bromeliad shelters?

The temperature in bromeliad shelters varied considerably depending on the microhabitat conditions – from 24.0 °C (deeply shaded rosette at 08:20 h) to 43.5 °C (rosette fully exposed to the sun at 10:00 h). Some bromeliads were exposed to varying lengths of partial or even full sunlight during the day. Consequently, the temperature inside the shelters could be the same or even higher than outside the bromeliad. When compared with the results of other studies on terrestrial bromeliads in semi-arid Brazilian Caatinga (Protázio et al., 2013; Jorge et al., 2020), the difference between the average temperatures inside and outside bromeliad rosettes was 0.5–2.9 °C lower for *B. balansae* in the Pantanal. The fact that in *B. balansae* a small but statistically significant difference (1.1 °C) was detected despite changing microhabitat conditions indicates that evaporative cooling from the skin of the hidden frogs likely contributes to maintaining a lower temperature in the shelter. Evaporative cooling has been reported for different anuran species including the African genera *Chiromantis* and *Hyperolius* and South American genera *Phyllomedusa* and *Pithecopus* (Geise & Linsenmair, 1986; Shoemaker et al., 1987; 1989).

It appears that none of the five hylid species seeking out *B. balansae* as diurnal shelters has any specialisations that enables them to withstand hot and desiccating conditions. They are all bromeliculous species that breed and develop in stagnant water and use the bromeliads as shelters and foraging places (Peixoto, 1995; Gordo & Campos, 2003; Uetanabaro et al., 2008; Jorge et al., 2020). Further, they do not hide in holes and bar access to the shelter with their heads (phragmotic behaviour) as reported in the hylid *Corythomantis greeningi* in the Brazilian Caatinga (Navas et al., 2004; Jared et al., 2005) nor do they wipe cutaneous lipid secretions over the body to reduce evaporative water loss as do the species of the neotropical genera *Phyllomedusa* and *Pithecopus* (Brattstrom, 1979; Shoemaker et al., 1987; Gomez et al., 2006). Nevertheless, despite the absence of such specialisations, the bromeliad shelters enabled four of the observed species to overcome unusually hot and dry daily conditions. Therefore, the following observations suggest that the bromeliads provided to these treefrogs shelters suitable for behavioural control of overheating and excessive evaporative water loss: (i) The species in question were able to tolerate high temperatures (up to 43.5 °C in the case of *S. nasicus*), which reach or even exceed the maximum body temperatures reported for some other South American or African anurans inhabiting seasonally dry and hot ecoregions – e.g. around 40 °C in *Chiromantis xerampelina*, *Phyllomedusa sauvagii* and *Pithecopus azureus*, 43–44 °C in *Hyperolius nitidulus*, 45 °C in *Rhinella granulosa* (Geise

& Linsenmair, 1986; Shoemaker et al., 1987; 1989; Navas et al., 2004); (ii) They use colour change, probably to reduce radiation absorption; (iii) Observed crowding in the shelter can contribute to the evaporative water loss reduction; (iv) Individuals staying in the tight centres of bromeliads or in the limited space of the leaf axils can reduce evaporative water loss by pressing their dorsal and ventral surfaces against the leaves. Although evaporative cooling is limited in such situations, an individual can easily increase it by changing its position.

Longer-term and more thorough research will be needed to understand all aspects of the association of frogs with bromeliads in the Pantanal. For example, it would be appropriate to focus in detail on the changes in humidity conditions in bromeliad shelters during different climatic conditions. Also, repeated night observations of *L. pulchriceps* and others anuran predators exploring the bromeliad rosettes (e.g. Sabagh et al., 2020) raise the interesting question of the extent to which closer association of anuran with bromeliads during hot periods may increase snake predation pressure.

The importance of *B. balansae* for maintaining the high biodiversity of the Pantanal is already well established in a number of groups of vertebrate and invertebrate species (e.g. Campos, 1993; Medri & Mourão, 2005; Romero, 2006; Campos & Mourão, 2015; Antunes et al., 2016; Paulino-Neto et al., 2016; Menezes et al., 2018) and the results of the current study suggest that this is also the case for hylid treefrogs.

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