

Anuran life histories remain consistent across contrasting precipitation regimes in Northeastern Brazilian forests

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Abstract. Amphibians are inherently dependent on water, and many species characteristics are influenced by this resource, particularly in ecoregions with contrasting precipitation regimes, such as the dry Caatinga and the moist Atlantic Forests of Northeastern Brazil. We compared these environments and hypothesized that anurans, regardless of the species, would be smaller in the Caatinga due to unpredictable duration of the rainy season, which accelerates metamorphosis, and the resulting fluctuations of resources, which limit energy reserves for growth. Furthermore, we anticipated that female reproductive strategies in the Caatinga would be more focused on quality rather than quantity, with small clutches and large oocytes. To test these hypotheses, we sampled areas of Caatinga and Atlantic Forest (two of each) in northeastern Brazil through 15-day consecutive campaigns conducted during the dry and rainy seasons. We combined active searches and pitfall traps to collect the anurans. We performed intraspecific comparisons using morphometric measurements and number and volume of oocytes. Contrary to our expectations, body size did not differ between forests for either sex. In moist environments, the extended reproductive period and the associated energetic demands may constrain growth, imposing costs similar to those in the semiarid environment, resulting in comparable body sizes. Similarly, few differences were observed in oocyte numbers and volumes. *Leptodactylus macrosternum* and *Rhinella diptycha* showed fewer and smaller oocytes, respectively, in the Caatinga. Biological factors such as lifespan and body size, and environmental factors such as the duration of the hydroperiod, predation, and insolation can influence oocyte size and numbers in different conditions. However, they likely interact in minimizing energy expenditure, resulting in similar reproductive strategies in contrasting environments.

Keywords. Frogs, local adaptation, abiotic conditions, selective pressures, Ecophysiology, life history, precipitation seasonality.

INTRODUCTION

Understanding how abiotic factors shape species' life histories is a central question in ecology (Blaustein et

al., 1999; Saenz et al., 2006; Pavón-Vázquez et al., 2022). This issue is particularly relevant for amphibians, given their critical dependence on water for essential biological functions (Pough et al., 1983; Dayton and Fitzgerald,

2006; Brandão et al., 2020). Consequently, life history of these organisms can be directly affected by hydrological dynamics and precipitation regimes (Sullivan and Fernandez, 1999; Navas et al., 2004; Li et al., 2023).

External morphology evolves under selective pressures tied to specific ecological demands, such as increased efficiency in competitive interactions or survival in environments with fluctuating resource availability (Demetrius, 2000; Schauble, 2004). Consequently, marked morphological variation may arise across populations subject to the selective pressures of different environments. These modifications in life history traits (e.g. body size, clutch size) can result from phenotypic plasticity or local evolutionary adaptation (Pfennig and Murphy, 2002; García et al., 2021; Tiar-Saadi et al., 2022). Howard (1981) suggested that adult body size in amphibians is directly related to reproductive effort, responding to ecological constraints that influence development trajectories of each sex.

In stable environments, with limited resource fluctuations, body size of both sexes increases with the rise in resource acquisition, and sexual selection favors larger individuals, even though dimorphism is preserved (Howard, 1981). Additionally, physiological performance during the larval phase directly influences adult body size (Werner, 1986). Conversely, in unstable environments with high resource fluctuations, anurans encounter sharp increases in prey availability, mainly invertebrates, during the brief and irregular rainy season (Bento et al., 2016; Silva et al., 2021). As a result, post-metamorphic individuals may endure extended periods of reduced resource availability, limiting energy intake for growth and ultimately leading to smaller adults.

Harsh environments can also compromise reproductive output, affecting reproductive investment by imposing significant losses on clutches due to high temperature, solar radiation rates or irregular water availability (Blaustein et al., 1995; Neckel-Oliveira, 2004; Kissel et al., 2019). Life history theory posits that in unstable environments investing in larger oocytes reduces clutch sizes but increases chances of survival of both reproductive females and juveniles (Roff, 1992; Roff, 2002). For example, clutch size in *Bufo andrewsi* increases with female body size in seasons that favor growth, making them more enduring (Liao et al., 2016). Meanwhile, oocyte size increases during shorter, less favorable periods for resource acquisition regardless of body size (Liao et al., 2016).

In the Neotropical realm, the dry Caatinga and the moist Atlantic Forest of Brazil are ecoregions with contrasting abiotic conditions. While the former experiences an extended dry season, semiarid climate, reduced and irregular precipitation regimes, and predominance

of temporary aquatic environments (Nimer, 1989; Ab'Saber, 1999; Silva et al., 2017), the latter has a humid tropical climate with high and evenly distributed precipitation throughout the year and greater predominance of permanent aquatic environments, due to its proximity to the coast (Ab'Saber, 1977; Tonhasca-Júnior, 2005; Joly et al., 2014). Anurans occurring in these contrasting environments exhibit shorter reproductive periods in the Caatinga, as a result of the reduced spatial and temporal availability of water (Caldas et al., 2016; Caldas et al., 2019). Given the contrasting conditions occupied by frogs in these quite different environments, we hypothesized that: 1) Anuran males and females are smaller in the Caatinga compared to the Atlantic Forest, as water irregularity and the predominance of temporary aquatic environments would accelerate metamorphosis, and marked seasonal fluctuations in resources availability in the post-metamorphic period would reduce the energy stock necessary for growth; 2) Females in the Caatinga are expected to prioritize reproductive quality over quantity, producing fewer but larger oocytes compared to their counterparts in the Atlantic Forest. These strategies could ensure higher chances of survival for larvae in harsh and unstable environments.

To test the hypotheses, we measured morphometric traits of reproductive males and females of species occurring both in Caatinga and Atlantic Forest and counted the mature oocytes of females from both ecoregions. Four species were selected for the morphometric analysis: *Boana raniceps* (Chaco tree frog), *Leptodactylus vastus* (Northeastern Pepper Frog), *Scinax x-signatus* (Venezuela snouted treefrog), and *Leptodactylus troglodytes* (Pernambuco white-lipped frog). Three species were selected for the reproductive analysis [*B. raniceps*, *Leptodactylus macrosternum* (Miranda's White-lipped Frog) and *Rhinella diptycha* (cururu toad)]. All species have aquatic reproductive modes and the entire larval period occurs in the water (Nunes-de-Almeida et al., 2021) making them interesting models to evaluate both questions tested in this paper.

MATERIAL AND METHODS

Study areas

The study was conducted with anuran specimens from four protected areas in the Northeast region of Brazil: the Benjamin Maranhão Botanical Garden Permanent Preservation Area, the Seridó and Aiuaba Ecological Stations and the Guaribas Biological Reserve (Fig. 1). The Seridó and Aiuaba Ecological Stations are situated in the Northern Sertaneja Depression, located in the Caatinga ecoregion, part of the biome "Tropical & Subtropical Dry

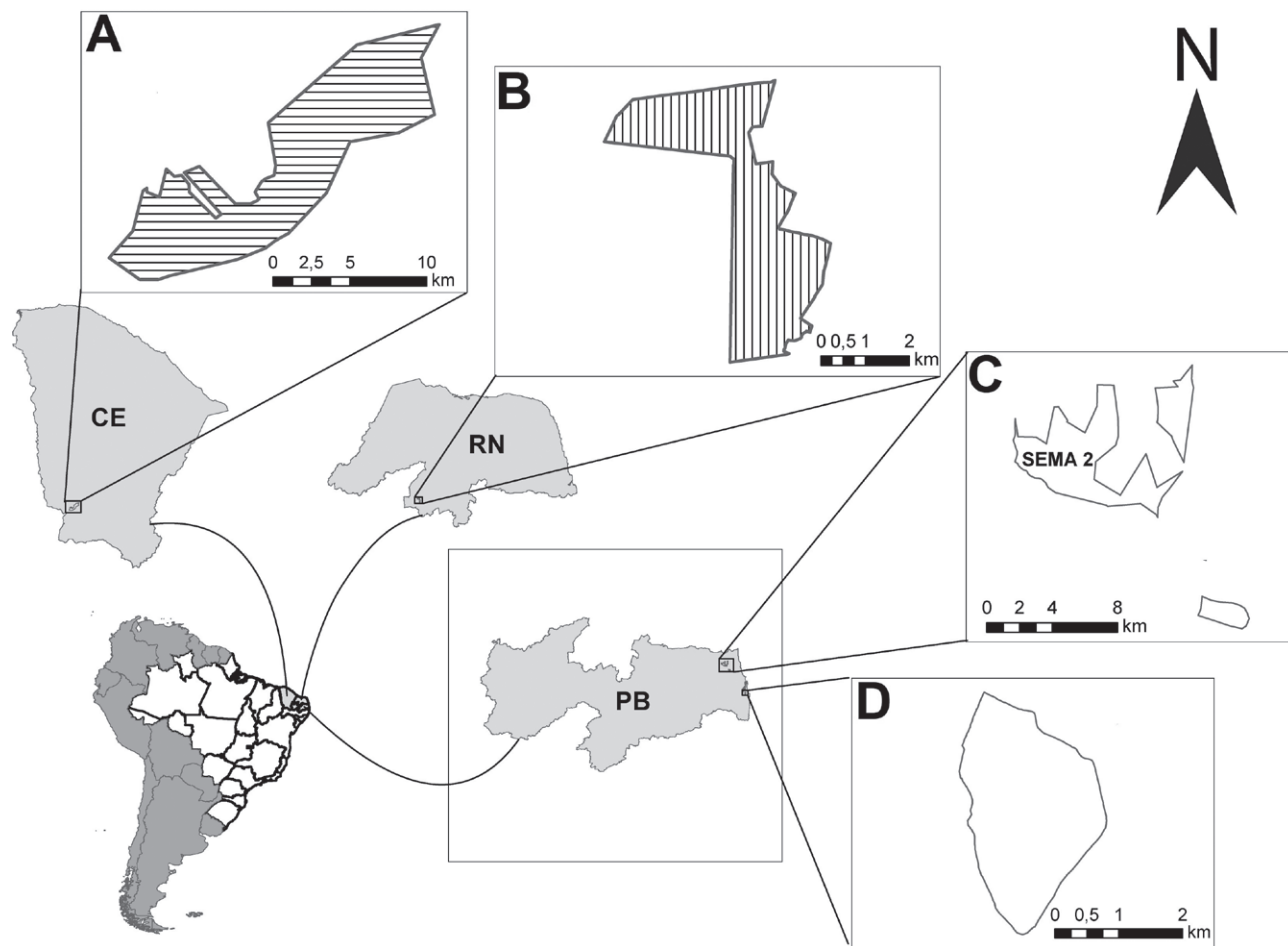


Fig. 1. Study areas: Aiuaba Ecological Station – CE (A), Seridó Ecological Station – RN (B), Guaribas Biological Reserve – PB (C), and Benjamin Maranhão Botanical Garden – PB (D). Caatinga are filled with lines, and Atlantic Forest areas are without lines.

Broadleaf Forests” (Dinerstein et al., 2017). The climate is hot and semi-arid, and the average precipitation is below 800 mm (Velloso et al., 2002). The Guaribas Biological Reserve and the Benjamin Maranhão Botanical Garden are located in the Atlantic Forest ecoregion, part of the biome “Tropical & Subtropical Moist Broadleaf Forests” (Dinerstein et al., 2017) with a tropical rainy climate and a short dry season (Köppen type Am) and have average precipitation above 1500 mm (Nimer, 1979).

The Seridó Ecological Station (Fig. 1) is located in the state of Rio Grande do Norte (06°35' to 06°40'S, 37°20' to 37°39'W), in the municipality of Serra Negra do Norte, totaling an area of approximately 1,166 ha, mainly composed of herbs and shrubs, predominating genus such as *Amburana* (Fabaceae), *Mimosa* (Fabaceae), among others, and an endemic species, *Gossypium mustelinum* (Malvaceae) (Velloso et al., 2002). The Aiuaba Ecological Station (Fig. 1) located in the state of Ceará (06°36'01" to 06°44'35" S and 40°07'15" to 40°19'19" W), in the muni-

pality of Aiuaba, totaling an area of 11,525 ha (Velloso et al., 2002). It includes an arboreal Caatinga remnant with predominantly open vegetation formations with *Cnidoscolus-Bursera-Caesalpinia* (Andrade-Lima, 1981).

The Guaribas Biological Reserve and Benjamin Maranhão Botanical Garden (Fig. 1) are located in Paraíba state. The former is located in the municipalities of Mamanguape (91.59%) and Rio Tinto (8.41%), encompassing areas termed SEMA 01, 02, and 03. We sampled SEMA 2 (06°40'40" a 06°44'59" S e 41°12'47" a 41°07'11" O) which has an area of approximately 3,378 ha (Barbosa et al., 2011). This protected area is highly heterogeneous, comprising tree formations, typical coastal restingas savannas, and an arboreal formation of semi-deciduous seasonal forest (Oliveira-Filho and Carvalho, 1993). In turn, the Botanic Garden is a remnant of forest located in the urban area of the municipality of João Pessoa (07°06'S and 34°52'W). The area is divided by the BR-230 highway, resulting in a larger continuous por-

tion of 471 ha (sampling site) and 11 small fragments located within Campus I of the Federal University of Paraíba. This environment is typical of the Northeast coastal moist forest, featuring secondary growth and a flora of trees, shrubs, and herbaceous plants, with a low sub-canopy layer and few lianas (Dias et al., 2006).

Data collection

Sampling for this study was conducted in 2013 across the four protected areas. We conducted surveys during the dry season in January (Guaribas), September (Aiuaba), and December (Seridó), while rainy season surveys were made in May (Seridó), April (Aiuaba), and June (Guaribas). For the Benjamin Maranhão Botanical Garden, sampling took place between 2011 and 2012. These data were obtained using the same collection methods as the other sites over a period of 12 months. Since it was possible to filter data covering a similar range of days as the other areas in a seasonal approach, no inconsistencies were caused in the sampling. We selected May, June and July (three of the rainiest months) and October, November, and December (three of the driest months). These intervals showed rainfall averages similar to those of the Guaribas REBIO in 2013 (see National Institute of Meteorology, INMET, 2012). These months were chosen based on seasonal definitions established by Lima and Heckendorff (1985), Aguiar and Martins (2002) and Velloso et al. (2002): in the Benjamin Maranhão Botanic Garden, the period of highest rainfall concentration typically occurs between March and August, in the Guaribas Biological Reserve between April and October, and in the Northern Sertaneja Depression, rainfall occurs from October to April. These patterns have been corroborated by 2013 monthly precipitation averages for each site (data from the Brazilian National Institute of Meteorology, INMET, 2012; INMET, 2013).

Each survey site was sampled for 15 consecutive days per season, resulting in 30 sampling days per site and a total of 90 days across sites. Two methodologies were used for field sampling. The main survey approach involved systematic visual and auditory inspection of the environments for anurans following standard methods (Crump and Scott, 1994), conducted between 18:00 and 22:00 hours. The active search has always been performed by two scientists, totaling 360 hours per person, and after being located, the specimens were manually collected. We tried to survey as many aquatic environments of aquatic environments based on the availability of each site: Guaribas Biological Reserve – five temporary ponds, one perennial stream and one perennial lake; Benjamin Maranhão Botanic Garden – a dammed section of the Jaguaribe River (7°08'42" S and 34°51'54" W); Seridó Ecological

Station – three temporary ponds, one intermittent stream, and one perennial lake; Aiuaba Ecological Station – four temporary ponds and one perennial lake. We believe the surveyed environments were adequate to record the species used in the comparisons. Their structural variation among sites was not considered problematic, as the species do not have riparian habits, and all but one (*Corythomantis greeningi*) reproduce in lentic habitats (Arzabe, 1999; Vieira et al., 2007; Santana et al., 2008).

The complementary survey approach involved the use of pitfall traps. We selected two aquatic environments with distinct conditions (temporary and perennial) in each survey site and install three trapping systems at the margins of each (except at the Botanical Garden, where two areas on the banks of the Jaguaribe River were used). The system consisted of four 30-L buckets buried in the ground and connected by 5-m plastic drift fences arranged in a Y pattern (Cechin and Martins, 2000; Enge, 2001). The traps were checked twice daily for 15 days to prevent animal mortality.

Morphometry

We selected four anuran species, *B. raniceps*, *L. vastus*, *S. x-signatus*, and *L. troglodytes*. The collected specimens were transported to the laboratory, euthanized with 2% lidocaine, fixed in 10% formalin, and then preserved in 70% ethanol (Caldas et al., 2016; Caldas et al., 2019), with each specimen assigned an identification number. After fixation, we measured 11 morphometric traits for each individual using a digital caliper (precision of 0.01 mm): snout-vent length (SVL), head length, head width, inter-eye distance, eye-nostril distance, inter-nostril distance, thigh length, tibia length, foot length, eye diameter, and inter-orbital distance (Napoli and Pimenta, 2009).

Next, we dissected the sampled individuals to determine their sex through direct observation of the gonads. The reproductive condition was assessed by examining the reproductive organs in females and the vocal sacs in males. Females were considered reproductive and suitable for comparison if they had highly convoluted oviducts and developed ovaries, while males were considered reproductive if they displayed fully evident vocal sacs (Mesquita et al., 2004). Individuals lacking these characteristics were classified as non-reproductive and excluded from the analyses.

Reproduction

We selected three species for these analyses: *B. raniceps*, *L. macrosternum*, and *R. diptycha*. They were the

only ones that had females with oocytes and occurred in both of the compared ecoregions. We obtained large samples for each species (*B. raniceps*, $n = 73$; *L. macrosternum*, $n = 210$; *R. diptycha*, $n = 86$). However, the proportions of females were low [*B. raniceps* = 25 (34%); *L. macrosternum* = 81 (39%); *R. diptycha* = 24 (28%)], a situation that commonly occur in some anurans (Braun and Braun, 1977; Wiens et al., 2011). Few of these cataloged females contained oocytes (*B. raniceps*, $n = 8$ (32%); *L. macrosternum*, $n = 31$ (38%); *R. diptycha*, $n = 9$ (37%)). Due to the smaller number of females and the occasional presence of oocytes in them, it was not possible to obtain information for the last two species at one of the Atlantic Forest sites (APP JBBM). In the laboratory, we dissected the specimens and removed the mature ovarian oocytes (post-vitellogenic) from females. These oocytes were identified by their well-differentiated hemispheres, with the animal pole displaying a dark brown coloration and the vegetative pole appearing milky and ivory in color (Melchior et al., 2004). The material was then preserved in 70% ethanol.

We counted oocytes using a graduated cylinder filled with water up to a fixed measurement (properly recorded). We submerged the entire mass of oocytes into the container and recorded the displacement of the water column. Subsequently, we removed the mass and reintroduced only enough to displace 1.5 mm³. Next, the oocytes present in this small mass were dissociated by immersing them in a 10% sodium hypochlorite solution for 20 minutes (Melchior et al., 2004). The dissociation allowed for the individual counting of the oocytes using a stereoscopic magnifying glass. With the total volume of the oocyte mass and the number of oocytes present in 1.5 mm³, it was possible to estimate each oocyte's total number and average volume through a simple proportion. After completing the procedures, we layed all specimens and oocytes in the Coleção Herpetológica da Universidade Federal da Paraíba.

Data analysis

We initially assessed the normality of the data using the Shapiro-Wilk test to determine whether parametric or nonparametric analyses would be appropriate. Body size was treated as an isometric variable (Rohlf and Bookstein, 1987), following the protocol described by Somers (1986). An isometric eigenvector was calculated with predefined values of $p=0.5$, where “p” represents the number of variables (Jolicoeur, 1963). The scores for this eigenvector, referred to as “composite body size,” were obtained by multiplying the $n \times p$ matrix of log10-transformed data, where “n” is the number of observations. To evaluate differences in composite body size between individuals of the same species across ecoregions, we conducted separate analyses of variance (ANOVA) for males and females.

For the oocyte masses, we calculated the average number of oocytes for species from both the Caatinga and Atlantic Forests. To test whether the total number and average individual volume of oocytes differed significantly between specimens from the two ecoregions, we performed an analysis of variance (ANOVA) (Shapiro-Wilk, $p > 0.05$) or Mann-Whitney test (Shapiro-Wilk, $p < 0.05$), depending on the normality of the data. All analyses were conducted using the R program for Windows (R Development Core Team, 2018): package Rcmdr version 2.9-5 for Shapiro-Wilk, ANOVA, and Mann-Whitney (Fox et al., 2020).

RESULTS

We did not find significant differences in body size in the four species between the two ecoregions, regardless of sex. Males and females exhibit similar body sizes in both forests: males of *B. raniceps* (ANOVA, $F_{1,46}$: 0.60; $P = 0.44$), females of *B. raniceps* (ANOVA, $F_{1,23}$: 0.01; $P = 0.91$), and other males: *S. x-signatus* (ANOVA, $F_{1,47}$: 0.41; $P = 0.52$), *L. vastus* (ANOVA, $F_{1,33}$: 2.70; $P = 0.11$), and *L. troglodytes* (ANOVA, $F_{1,18}$: 2.10; $P = 0.16$) (Table 1).

Table 1. Descriptive statistics and body size comparisons for amphibians from the Caatinga (within parentheses) and the Atlantic Forest. NS = not significant.

Variables	<i>B. raniceps</i> n = 24 (49)		<i>S. x-signatus</i> n = 22 (27)	<i>L. vastus</i> n = 15 (20)	<i>L. troglodytes</i> n = 6 (15)
	males n = 15 (33)	females n = 9 (16)	males n = 22 (27)	males n = 15 (20)	males n = 6 (15)
SVL	68.66 ± 3.42 (63.00 ± 10.35)	72.57 ± 11.15 (68.91 ± 7.82)	34.89 ± 2.78 (33.19 ± 4.12)	135.25 ± 31.87 (153.30 ± 20.37)	48.33 ± 1.59 (43.42 ± 6.74)
Composite Body Size	4.15 ± 0.08 (4.08 ± 0.30)	4.23 ± 0.30 (4.24 ± 0.14)	3.07 ± 0.17 (3.10 ± 0.16)	5.11 ± 0.61 (5.34 ± 0.14)	3.65 ± 0.09 (3.55 ± 0.15)
	$F_{1,46} = 0.60$ NS	$F_{1,23} = 0.01$ NS	$F_{1,47} = 0.41$ NS	$F_{1,33} = 2.70$ NS	$F_{1,18} = 2.10$ NS

Table 2. Descriptive statistics and comparisons of reproductive traits for amphibians from the Caatinga (within parentheses) and the Atlantic Forest. * $P < 0.05$; NS = not significant.

Variables	<i>B. raniceps</i> n = 4 (4)	<i>L. macrosternum</i> n = 10 (21)	<i>R. diptycha</i> n = 4 (5)
Average number of oocytes	4,765 $\pm$ 4,634 (3,728 $\pm$ 2,487) $F_{1,6} = 0.15^{NS}$	5,255 $\pm$ 2,051 (2,877 $\pm$ 1,723) $F_{1,29} = 11.41^*$	24,818 $\pm$ 10,013 (18,024 $\pm$ 17,440) $U_{1,7} = 0.97^{NS}$
Average volume of oocytes	0.0029 $\pm$ 0.0017 mm ³ (0.0013 $\pm$ 0.0002 mm ³) $F_{1,6} = 3.55^{NS}$	0.0018 $\pm$ 0.0005 mm ³ (0.0019 $\pm$ 0.0010 mm ³) $F_{1,29} = 0.20^{NS}$	0.0036 $\pm$ 0.0013 mm ³ (0.0015 $\pm$ 0.0008 mm ³) $F_{1,7} = 7.77^*$

Similarly, the number of oocytes did not differ between ecoregions for *B. raniceps* and *R. diptycha* (Table 2). However, we observed differences in the number of oocytes for *L. macrosternum*, which was lower in the Caatinga (mean = 2,877 $\pm$ 1,723) and higher in the Atlantic Forest (mean = 5,255 $\pm$ 2,051); (ANOVA, $F_{1,29}$: 11.41; $p = 0.02$) (Table 2). The other species did not show variations: *B. raniceps* (ANOVA, $F_{1,6}$: 0.15; $p = 0.70$) and *R. diptycha* (Mann-Whitney, $U_{1,7}$: 0.97; $p = 0.32$) (Table 2).

The average volume of each oocyte did not differ for *B. raniceps* (Table 2). However, we observed differences for *R. diptycha*, which had significantly smaller oocytes in the Caatinga (mean = 0.0015 $\pm$ 0.0008 mm³) compared to the Atlantic Forest (mean = 0.0036 $\pm$ 0.0013 mm³); (ANOVA, $F_{1,7}$: 7.76; $p = 0.03$) (Table 2). The other species did not show variations: *B. raniceps* (ANOVA, $F_{1,6}$: 3.55; $p = 0.11$) and *L. macrosternum* (ANOVA, $F_{1,29}$: 0.20; $p = 0.66$) (Table 2).

DISCUSSION

Contrary to our expectations, neither males nor females differed in size between Caatinga and Atlantic Forest. Similarly, reproductive efforts in the Caatinga did not differ significantly from the Atlantic Forest, except for *L. macrosternum* and *R. diptycha*, which showed a lower number and a smaller size of oocytes, respectively. Adult frogs were not smaller in environments with irregular precipitation regimes and reduced resources availability during the extended dry season (Caatinga), suggesting that hydroperiod and prey availability may not be limiting factors for growth. Possibly to avoid compromising growth due to resource limitations, other strategies to minimize energy loss in the dry season seem to have been selected in amphibians from Caatinga, such as aestivation and use of subterranean shelters in periods of reduced activity (Varjão and Ribeiro, 2018; Jared et al., 2019; Moreira et al., 2021).

In the Caatinga, lower precipitation and shorter hydroperiods can hypothetically accelerate metamorpho-

sis and restrict resource availability for adults. Conversely, in the Atlantic Forest the hydrological stability can allow extended reproductive activity, but at the cost of expending more energy in vocalization, territory defense, partner encounter, courtship, and investment in oocytes (Arzabe et al., 1998; Afonso and Eterovick, 2007; Caldas et al., 2016). In both cases, energy deprivation would impact body size, as predicted by life history theory. Given limitations and finite resources, reproduction can incur costs that would ultimately reduce growth rate (Bradshaw and McMahon, 2008). In other words, body size patterns in the two ecoregions would be similar because growth would not be the main focus of energy investment, and thus, selective pressures would not promote an increase in size. In the Caatinga, the limited availability of trophic resources during the short rainy season would provide just enough energy for a rapid reproductive event. In the Atlantic Forest, the greater availability of trophic resources, ensured by annual water stability, would support a prolonged reproductive event. In both cases, the primary objective would be reproduction, and energy investment would be prioritized for this activity.

The expected patterns for hostile environments (Caatinga) and stable environments (Atlantic Forest) were not corroborated for most of the species' reproductive investment. The number of oocytes did not change in *B. raniceps*. In contrast, the volume of oocytes in *R. diptycha* was smaller in the Caatinga, contrary to some expectations for their sizes under harsh conditions (Morrison and Hero, 2003; Liao et al., 2016). Alternatively, harsh environments with short seasons for resource acquisition can result in low annual growth rates. Thus, smaller oocytes or clutches would be compensated by more reproductive events and greater longevity (Sinsch et al., 2015), a pattern common for large-size species (Stark and Meiri, 2018), like *Rana temporaria* (Sinsch et al., 2015). Indeed, *R. diptycha* is a large species (Sousa et al., 2022), and longevity has already been indicated as a key factor for the persistence of some bufonids in arid environments (Tevis Jr, 1966). Therefore, slow growth

rates and higher longevity resulting in more reproductive events in the Caatinga in *R. diptycha* may account for its smaller oocytes.

Leptodactylus macrosternum presented a lower number of oocytes in the Caatinga. However, contrary to what would be expected if the species in both regions allocated the same amount of energy for reproduction, these oocytes were not larger than those in the Atlantic Forest. Although it is not clear what drives this difference among areas, other factors can be driving egg number and size in this species (see Horato et al., 2024). The eggs of *L. macrosternum* are laid in the water (Heyer, 1969), and harsh insolation in arid environments can more severely affect eggs laid outside of water (Caldas et al., 2016). Similarly, there is less predation pressure in temporary aquatic environments subject to prolonged droughts (Woodward, 1983; Dayton and Fitzgerald, 2001; Schiwitz et al., 2020). The combination of such factors could prevent natural selection from favoring an increase in oocyte volume, resistance, and larval size. Thus, the qualitative nature of *L. macrosternum* reproduction would prevail. This hypothesis needs to be tested for the cause-and-effect relationships we discussed to be confirmed.

Studies focusing on the possible effects of environmental variables on life history traits in amphibian species from the Brazilian Forests remain scarce. Despite our moderate sample sizes, our data suggest that the differences between precipitation regimes are probably insufficient to promote significant reproductive and morphological adjustments in species that can thrive in both Caatinga and Atlantic Forest. However, the observed patterns require further investigation to be completely understood. In particular, future research should focus on other environmental factors and taxa, as well as increasing the number of samples analyzed.

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