

Factors determining the spatial and temporal variation in the abundance of *Pithecopus nordestinus* tadpoles (Anura: Phyllomedusidae) in a semi-arid Brazilian environment

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Abstract. Microhabitat choice by tadpoles is related to several physical or biological characteristics, and variations in these factors have a direct influence on their distribution and abundance at different scales (e.g. time, space). Our work sought to investigate how *Pithecopus nordestinus* tadpoles use water bodies at a Caatinga site and quantify how biotic and abiotic variables affects the occurrence of this tadpole species. We developed the study in the Protected Area Monumento Natural Grota do Angico/Sergipe, from December 2009 to November 2010 and collected samples (408 plots) using a “throw trap”. In addition to the tadpoles collected in the plots, we quantified five variables (competitors, percentage of emergent and aquatic vegetation, predators and depth) and acquired variation of some data throughout the year (size, maximum depth and hydroperiod) for each water bodies. Tadpoles were found in lentic water bodies that fit their habits and that were also suitable for mating by their adult relates. Most of the studied environments maintained water throughout the period of the study, with *P. nordestinus* tadpoles being present from April to October, with abundance peak both in July and May. The absence of *P. nordestinus* tadpoles from February to March may allow the establishment of other species during this period, minimizing the competition between them. The larvae of *P. nordestinus* showed an aggregate distribution ($I_d > 1$) in most of the water bodies throughout the year, which may reduce the predation. This could explain the positive relation that was found between the tadpole abundance and the predator’s presence. The aggregations were not intensified by the reduction of water bodies as the drought progressed. Among the ecological variables, the presence of competitors (other tadpoles) and the percentage of emergent and aquatic vegetation did not favor tadpole abundance. Interspecific competition can drastically reduce the amount of resources and damage metamorphosis in periods when there is still water regularity in the environments. Branching and abundant vegetation can damage the habit of *P. nordestinus* tadpoles, which are nektonic suspension-raspers, requiring that this portion of the space is unoccupied.

Key words. Amphibia, anurans, larvae, aggregations, spatial resources, temporal resources, Caatinga, predation, competition, throw trap.

Introduction

Species respond to a wide range of environmental factors (whether abiotic or biotic) that have a direct influence on their distribution and abundance at different scales (e.g. time, space); the understanding of the action of these factors is one of the major current issues in ecology (BLAUSTEIN et al. 1999, WARREN et al. 2014, ULRICH et al. 2017). In complex lifecycle organisms, such as amphibians, different environmental characteristics act on the adults and the larvae, as they use distinct spatial resources during their life stages. This antagonism directly influences how

they distribute and interact with their habitat (WILBUR 1980, TOFT 1985, LYNCH 2006). Ecological variations generate selective patterns that directly influences the growth rates of the larvae and, consequently, their development and metamorphosis time (ALFORD 1999, WELLS 2007).

Tadpoles distribution are also influenced by the occurrence of predators, and are considered to be the main cause of amphibian larvae mortality (HEYER et al. 1975, SMITH 1983, HERWIG et al. 2013, MAHER et al. 2018). However, the patterns of occurrence and the use of space by anuran larvae result from a complex interaction between biotic factors, such as competition, predation and the presence of

aquatic vegetation (MORIN 1983, HECNAR & M'CLOSKEY 1997, STRAUß et al. 2013, JOHNSON et al. 2015), and abiotic factors, such as rainfall distribution, humidity and temperature, in addition to physicochemical characteristics (e.g. pH, dissolved oxygen, salinity) (AICHINGER 1987, DEGANI & KAPLAN 1999, BERNABÒ et al. 2013, WASSENS et al. 2013). Potentially competing tadpoles can directly affect the growth, maximum metamorphosis size, and larval length of other amphibians, as they capture environmental resources more efficiently (PETRANKA 1989, CABRERA-GUZMÁN et al. 2013); however, the presence of aquatic vegetation favors survival, as it provides refuges against predators (BABBITT & JORDAN 1996, KOPP et al. 2006).

Rainfall, humidity and temperature are mainly related to the duration of the water bodies and, when depreciated, these characteristics contribute to the desiccation of puddles, which could lead to the mortality of tadpoles (GOMEZ-MESTRE et al. 2013, O'REGAN et al. 2014). In this sense, conspecifics could form larger aggregations that favor the acquisition of heat and the maintenance of body temperature, promoting the acceleration of metamorphosis (BRATTSTROM 1962, HARAMURA 2007). Another possibility is that decreasing the size of the water body would favor aggregations, and increasing intraspecific competition could hinder the acquisition of resources by causing the larvae to metamorphose rapidly, still at a reduced size (NEWMAN 1989, TEJEDO & REQUES 1994).

The Caatinga is located in the northeastern region of Brazil and has a semi-arid tropical climate with a predominance of two characteristic seasons: one is very dry and prolonged and the other has moderate, irregularly distributed rain (CHIANG & KOUTAVAS 2004, LEAL et al. 2005, BARBOSA et al. 2013). The low incidence of rainfall throughout the year, combined with high temperatures and high light intensity, results in a high rate of evaporation, the consequent desiccation of the soils and a short duration of temporary pools (AB'SABER 1977, REIS et al. 2006). Pools with reduced hydroperiods, such as those in arid or semi-arid climates, or areas with a pronounced dry season, are generally used by tadpoles that have a short larval stage with a rapid rate of development (BABBITT & TANNER 2000, LEIPS et al. 2000, SZÉKELY et al. 2017). They usually present a high activity rate, which is justified by the need for the rapid capture of resources from a transient environment that is susceptible to constant desiccations, and, according to some authors, has a low abundance or total absence of predators (MORIN 1983, WOODWARD 1983, SKELLY 1996).

Pitechopus tadpoles are usually nektonic (suspension-raspers), occupying the upper half of the water column and preferring to filter particles in suspension, but occasionally collecting and ingesting periphyton from solid surfaces and/or substrate (DUELLMAN & TRUEB 1994, MCDIARMID & ALTIG 1999, WELLS 2007). CRUZ (1982) described the tadpole that is the object of this study, previously identified as *Phyllomedusa hypochondrialis* (Hylidae) based on specimens obtained in Itagibá, State of Bahia, Brazil. Subsequently, CARAMASCHI (2006) redefined these specimens as a new species, *Phyllomedusa nordestina*. Recent-

ly, the genus *Pitechopus* was removed from the synonymy with *Phyllomedusa* and the species of interest in this study came to be identified as *Pithecopus nordestinus* (Caramaschi 2006), now belonging to the family Phyllomedusidae (DUELLMAN et al. 2016).

The present study aimed to investigate how *Pithecopus nordestinus* tadpoles use water bodies of an area of Caatinga and quantify the effects of biotic and abiotic variables in the occurrence of this tadpole species. Based on information obtained from the literature, we selected some biotic and abiotic parameters for evaluation, and we elaborated the following hypotheses: 1 – Higher rates of rainfall and humidity and milder temperatures favor the larvae remaining in the water bodies over time; 2 – As the water bodies dry, the distribution of the larvae would assume an even more aggregated pattern; 3 – A higher percentage of aquatic and emergent vegetation has a positive influence on the abundance of *P. nordestinus* tadpoles; 4 – The presence of potential competitors and predators has a negative influence on the abundance of *P. nordestinus* tadpoles; 5 – Larger depths positively influence *P. nordestinus* tadpoles.

Materials and Methods

Study area

The Monumento Natural Grota do Angico (MNGA; 37°40'W; 09°39'S – Fig. 1) occupies an area of 2,182 ha and is located in the morphoclimatic domain of the Caatinga, between the municipalities of Poço Redondo and Canidé do São Francisco, in the upper "Sertão" of Sergipe, Brazil (AB'SABER 1977), near the São Francisco river (RUIZ-ESPARZA et al. 2011). The climate is semi-arid, with sparse and irregular rain (NIMER 1972). The average precipitation is 500 mm per year, usually from April to August (RUIZ-ESPARZA et al. 2011). The MNGA presents a unique phytophysognomy, composed of vegetation in the process of secondary succession and more dense vegetation; this is distributed, respectively, in mountainous areas with species typical of Caatinga (*Poincianella pyramidalis* (Tul.) L. P. Queiroz and *Jatropha mollissima* (Pohl Baill.) and close to intermittent streams and in the riparian forest of the São Francisco river (SILVA et al. 2013).

Data collection

We sampled six water bodies (3 ponds, 1 puddle, 1 artificial reservoir and 1 partially dried stream branch), all of which were temporary (Table 1). The data were collected over a maximum period of four days, at variable intervals as a function of the reduction of water bodies during the dry season. Each environment was sampled once a month, performing 12 visits by water body and 72 in total. Data collection was performed in the afternoon, between 13:00 and 18:00 h, with one or two water bodies sampled per day, depending on the time needed due to their sizes. This study took place between the months of December 2009 and No-

Variation in abundance of *Pitechopus nordestinus* tadpoles

Table 1. Characterization of water bodies studied at Protected Area Monumento Natural Grota do Angico (MNGA), State of Sergipe, Brazil. Surrounding vegetation: Herb (herbaceous), Sh (shrub), Arbo (arboreal).

Water body	Surrounding vegetation	Months with water	Maximum depth (m)	Maximum size (m ²)	Geographical coordinates
Pond 1	Herb, Sh, Arbo	Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct	0.50	153.1	37°40'57"W, 9°39'50"S
Pond 2	Herb, Sh	Mar, Apr, May, Jun, Jul, Aug, Sep	0.37	130.2	37°41'08"W, 9°39'56"S
Pond 3	Herb, Sh	Mar, Apr, May, Jun, Jul, Aug, Sep	0.30	171.7	37°41'09"W, 9°39'46"S
Puddle	Herb, Sh, Arbo	Mar, Apr, Jun	0.17	84.78	37°40'55"W, 9°39'50"S
Artificial reservoir	Herb	Mar, Apr, May, Jun, Jul, Sep	0.15	8.84	37°40'08"W, 9°39'49"S
Stream section	Herb, Sh, Arbo	Feb, Mar, Apr, May, Jun, Jul, Sep, Oct, Nov	0.60	357.08	37°40'09"W, 9°39'59"S

vember 2010, aiming to cover the dry and rainy seasons, which are characteristic of the Caatinga domain.

We also assessed mean monthly temperature, relative humidity and accumulated monthly precipitation, which

were taken from the Climatological Data Collection Platform (Plataforma de Coleta de Dados Climatológicos – PCD Poço Redondo), located approximately 15 km from the Monumento Natural Grota do Angico (MNGA).

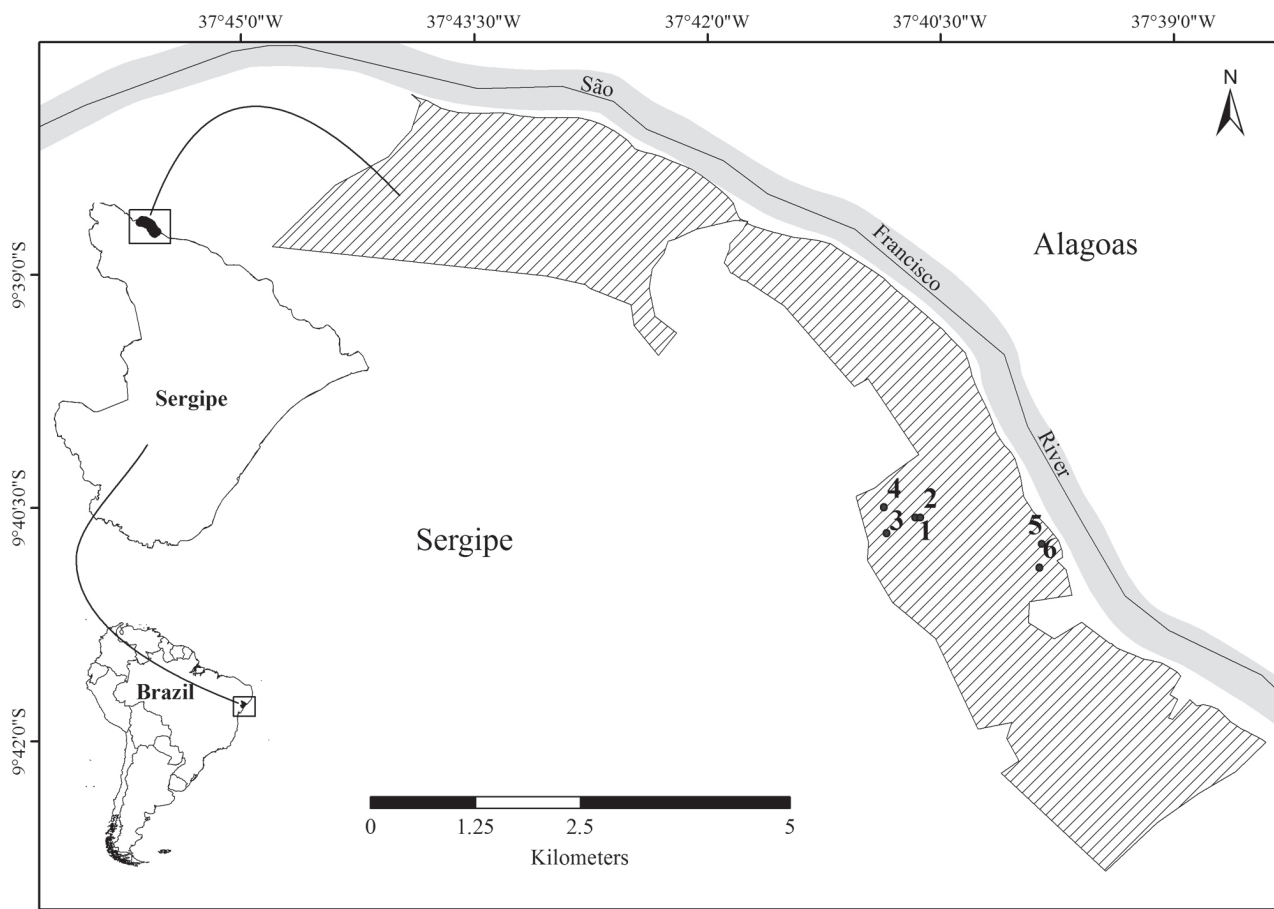


Figure 1. Location of the Protected Area Monumento Natural Grota do Angico (MNGA – hatched area), Poço Redondo – Sergipe. The numbers correspond to the water bodies sampled in this study: 1 = Pond 1, 2 = Puddle, 3 = Pond 2, 4 = Pond 3, 5 = Artificial reservoir and 6 = Stream section.

Characterization of water bodies

We measured the following data in each sampling month, in order to cover their variation (dry and rain), in each of the water bodies: 1 – size, in m^2 ; 2 – maximum depth, in cm; 3 – hydroperiod: number of months in which the environment retained water. These parameters are commonly used when sampling tadpoles residing in temporary aquatic environments that are subject to seasonal variations (HEYER 1973, NEWMAN 1989, GLOS et al. 2007). The size of each water body was estimated according to its format, using area calculations for ellipses ($A = \pi r^2$) in the case of ponds and the puddle, squares for the reservoir ($A = L^2$) and rectangles for the stream ($A = b \times h$). We also determined the vegetation around the aquatic environments to obtain information on the larvae habitat, based on different vegetation height (e.g. herbaceous, shrub, arboreal) (Table 1).

Collection of tadpoles and biotic variables

We collected samples of *P. nordestinus* tadpoles, predators and competitors using a “throw trap” (BABBITT et al. 2009, BROSTOFF et al. 2010), which consists of a $50 \times 50 \times 100$ cm PVC structure covered on the sides by a 1.5 mm mesh nylon screen to prevent the entry and exit of the animals (Fig. 2). The “throw trap” was submerged in the margin-center direction of the water body and was positioned vertically against the substrate for 10 minutes. Each immersion of the instrument was considered a plot, and three plots were made for each 1 m interval, starting from point o (margin) and advancing to the maximum depth. To randomize the plots, before each immersion, the direction of the pointer that marks the seconds on a wristwatch was determined,

which determined the direction in which the trap would be displaced. The total plots where asymmetrical, considering that each water body had a different size and varied in area throughout the year (Pond 1 = 127 plots, Pond 2 = 71 plots, Pond 3 = 87 plots, Puddle = 17 plots, Artificial reservoir = 17 plots, Stream section = 69 plots). Each sample (tadpoles, possible invertebrate predators and competitors) was collected from the enclosed area with the aid of a fine mesh sieve, identified (parcel number) and stored in plastic bags. At the end of sampling in the water body, the animals from each plot were identified, counted and then returned to the environment. We also visually estimated the amount of aquatic and emergent vegetation present in each plot (HARTEL et al. 2007). We established four categories, using the “throw trap” quadrant as a baseline: 1 – 25% plants when 1/4 of the quadrant was filled; 2 – 50% when 2/4 of the quadrant was filled; 3 – 75% when 3/4 of the quadrant was filled; 4 – 100% when 4/4 of the quadrant was filled.

The tadpoles of *P. nordestinus* have easily distinguishable characteristics and are the only representatives of the family Phyllomedusidae and of the genus *Pitechopus* in MNGA (GOUVEIA & FARIA 2015). We visually identified these tadpoles by observing the mouth in the anterior position of the head; the dorsal fin originating at the level of the beginning of the posterior third of the body with a curved contour to the end of the tail, which is slightly curved downwards; and the ventral fin with a height of approximately three times that of the dorsal fin, also originating at the level of the beginning of the posterior third of the body, presenting a curved contour (CRUZ 1982). The identification of tadpole predators was based on animals that are commonly reported in other studies (BABBITT & JORDAN 1996, KOPP et al. 2006, MUNIZ et al. 2008, MOGALI et al. 2012), being thus counted as insects belonging to the



Figure 2. Collection of tadpoles and insect predators using a “throw trap” in the Protected Area Monumento Natural Grota do Angico (MNGA), State of Sergipe, Brazil.

taxa Odonata (larvae) and Belostomatidae, since no fish were collected nor visualized in the environments during the year of sample collection. Finally, we considered competitors to be any tadpole other than *Pithecopus nordestinus* recorded in the plot, which could belong to the other 19 species of anurans recorded in the area (SANTANA et al. 2014, GOUVEIA & FARIA 2015).

During the use of the “throw trap”, attempts were made to avoid disturbance around the plot, and the collector was carefully moved in the water so as to not frighten the tadpoles.

Statistical analyses

First, we used a Shapiro–Wilk test (ZAR 1999) to evaluate the distribution of the data sets, in order to know which analyses would best fit the relationships we sought to investigate. To evaluate the influence of climate parameters on the total number of tadpoles, we used Spearman’s correlation coefficients (LEGENDRE & LEGENDRE 1998), based on the values for the average temperature, relative air humidity and monthly precipitation amounts.

To evaluate the distribution type of the tadpoles, we used the Morisita Dispersion Index (I_d) (MORISITA 1962), derived from the density data obtained for each plot of the sampled water bodies. We calculated this using the equation:

$$I_d = n \left[\frac{\sum x^2 - \sum x}{(\sum x)^2 - \sum x} \right],$$

where n represents the size of the sample, in this case the total number of plots sampled; $\sum x$ corresponds to the sum of the individuals of all the plots, given by $x_1 + x_2 + x_3 \dots + x_n$; and $\sum x^2$ is the sum of the total number of individuals in each plot squared, given by $x_1^2 + x_2^2 + x_3^2 \dots + x_n^2$. I_d values greater than 1 indicate an aggregate distribution, those equal to 1 indicate a random distribution and those less than 1 indicate an homogeneous distribution (KREBS 2009). To test whether the I_d value was significantly different from 1, we used the Morisita significance index using the equation:

$$\chi^2 = I_d (\sum x - 1) + n - \sum x,$$

where x represents the tabulated value of the Chi-square distribution for n degrees of freedom. If the value of I_d equals the tabulated value, the pattern is random; if it does not equal, the pattern is regular (homogeneous) when it is smaller than the tabulated value, or aggregated when it is larger.

After obtaining the distribution values, we tested the possibility that the size of the water bodies, during the year, could lead to greater or lower tadpole aggregation. For this, we used a simple linear regression (ZAR 1999), which correlated the values obtained by the Morisita index with the total area of each body of water, both obtained monthly.

In order to evaluate which factors most contributed to the abundance of *P. nordestinus* larvae, we used a generalized linear model (GLM) with a Poisson distribution and adjusted logarithmic functions to perform parametric

analysis (SOKAL & ROHLF 2012), including the ecological variables in plots (depth, total number of competitors, total number of predators, percentage of aquatic vegetation and percentage of emergent vegetation). The Akaike information criterion, or AIC, was used as the model selection criterion. According to BURNHAM & ANDERSON (2002), the AIC seeks to minimize the distance between the model and the truth, defined as the Kullback–Leibler distance (KULLBACK 1987), and searches for a model that best fits with the fewest parameters possible (the principle of parsimony). In algebraic terms, the AIC is defined by:

$$AIC = -2 (\ln (\text{risk})) + 2 K$$

where risk is the probability of the data in view of a model and K is the number of free parameters of the model. AIC scores are generally presented as ΔAIC (read as Delta Akaike), which consists of the difference between the AIC of each model and the AIC of the best model found (the lowest AIC), which therefore has a ΔAIC equal to zero. This procedure aims to define the scenario that best explains the variations between the number of individuals of the target species and the listed variables.

The significance level adopted for the hypothesis tests was 5%. All statistical analyses were conducted with R Project 3.5.1 software for Windows (R Development Core Team 2016).

Results

Habitat

We sampled 408 plots with the “throw trap”, and obtained data from 752 *P. nordestinus* tadpoles, 1325 predators (Belostomatidae and Odonata larvae) and 1404 tadpoles of other species across all the sampled water bodies. The larvae of *P. nordestinus* occupied lentic water bodies; the only exception was a single tadpole found in a temporary stream soon after a period of higher rainfall concentration. In addition, rainfall was not sufficient to generate a stream of water in the creek area, and one larva was found inside a large puddle that formed along its course. Temporary ponds had the highest abundance of *P. nordestinus* tadpoles, corresponding to 80.19% of the registered individuals.

Temporal distribution

We only recorded *P. nordestinus* tadpoles during the rainy season, between the months of April and October, in the water bodies of the MNGA. Larvae did not occur in the different habitats during the first rains, since tadpoles were not registered in the months of February and March, when water was already available in the environment. The highest abundances were observed in the months of July and May, respectively; these periods did not present the highest averages for accumulated precipitation, mean temperature and relative humidity (Fig. 3).

Table 2. Results of the monthly distributions of *Pithecopus nordestinus* tadpoles according to the Morisita index and monthly variations in the size (m²) of the water bodies.

Month	Pond 1		Pond 2		Pond 3		Artificial reservoir	
	Morisita Index	Size of water body (m ²)	Morisita Index	Size of water body (m ²)	Morisita Index	Size of water body (m ²)	Morisita Index	Size of water body (m ²)
April	2.4	123.1	–	–	5.04	131.9	2.94	8.84
May	1.65	112.6	5.64	102	0	50.7	1.65	8.84
June	1.95	153.1	0	130.2	0.75	171.7	1.08	8.84
July	2.25	142.9	10.08	120.2	2.85	171.7	3.15	8.84
August	2.7	116.8	2.1	31.4	4.8	83.7	2.28	8.84
September	3.15	107.7	–	–	–	–	5	8.84
October	2.31	17.5	–	–	–	–	–	–

Among the evaluated climatic parameters, significant correlations were found between the average temperatures and the monthly abundance of tadpoles ($r_{\text{temper}} = -0.8556$; $p = 0.0004$) and between the relative humidity and the monthly abundance of tadpoles ($r_{\text{umid}} = 0.8701$; $p = 0.0002$). However, accumulated precipitation had no influence on the number of individuals recorded in the different months ($r_{\text{precip}} = 0.4649$; $p = 0.1277$).

Spatial distribution

The monthly distribution values of *P. nordestinus*, obtained through the Morisita index, are shown in Table 2, as well as the size of the occupied water bodies. Most values were greater than 1, indicating an aggregate distribution pattern.

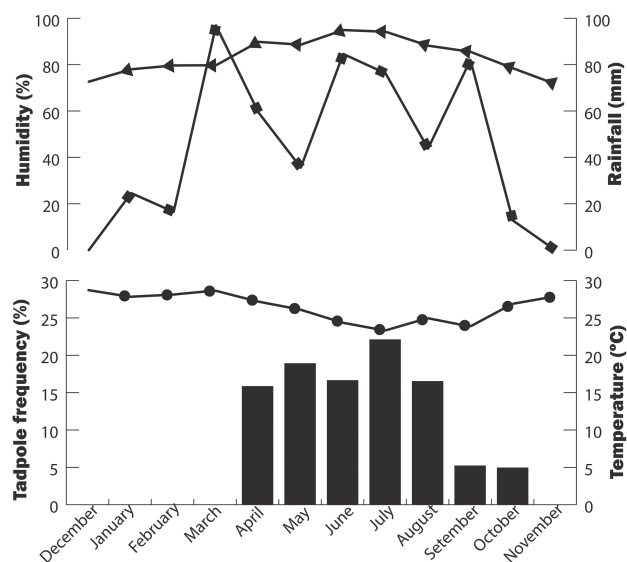


Figure 3. Monthly climatic variable values, measured at the nearest meteorological station (Poço Redondo/SE) for the Protected Area Monumento Natural Grota do Angico (MNGA - Caatinga) between December 2009 and November 2010. (–●–) average temperature (–■–); accumulated rainfall; (–▲–) relative humidity. The bars represent the monthly relative frequencies of *Pithecopus nordestinus* larvae in the sampled water bodies.

The significance test corroborated all the values obtained by the Morisita index. Of the six water bodies sampled, only one did not have *P. nordestinus* tadpoles (the puddle), which only retained water for 3 months of the year. In addition, the artificial reservoir could not vary in size, since its proportions were fixed. Thus, we excluded the puddle and stream section (which only presented one *P. nordestinus* tadpole) from the distribution analyses, and the relationship between the influence of the size of the water bodies on the distribution of larvae could not be tested for the reservoir.

The variation in the size of water bodies over time did not influence the aggregation values obtained by the Morisita index, suggesting that they should respond to other types of factors (Pond 1: $R^2 = -0.117$, $F = 0.368$, $p = 0.574$; Pond 2: $R^2 = -0.408$, $F = 0.130$, $p = 0.746$; Pond 3: $R^2 = 0.333$, $F = 0.0002$, $p = 0.986$).

Generalized linear model (GLM)

The generalized linear model, which investigated the relationships between the number of tadpoles found in the plots and the defined ecological variables, explained 16.12% of the variation ($AIC = 2447.7$, $p < 0.0001$). Most of the factors had a significant effect. Specifically, the competitors ($N = 408$, $Pseudo R^2 = 0.16$, $z = -11.05$, $p < 0.001$), percentage of emergent vegetation ($N = 408$, $Pseudo R^2 = 0.16$, $z = -7.73$, $p < 0.001$) and percentage of aquatic vegetation ($N = 408$, $Pseudo R^2 = 0.16$, $z = -5.81$, $p < 0.001$) negatively influenced the abundance of *P. nordestinus* larvae, whereas the predators ($N = 408$, $Pseudo R^2 = 0.16$, $z = 7.77$, $p < 0.001$) presented a positive relationship. However, no significant values were observed for depth ($N = 408$, $Pseudo R^2 = 0.16$, $z = 0.65$, $p = 0.52$).

Discussion

In MNGA, *P. nordestinus* tadpoles were found to occupy all lentic environments. Although no lotic water bodies were sampled, since they did not exist in the area, the selection of lentic habitats has already been reported for the species,

and is typical of some representatives of the genus *Pithechopus*, such as *P. azureus*, *P. hypochondrialis* and *P. rohdei* (PYBURN & GLIDEWELL 1971, COSTA et al. 2010, FAIVOVICH et al. 2010). Primarily, the tadpole registration in these environments can be explained by the reproductive mode of *Phyllomedusa nordestina* (= *Pithechopus nordestinus*), since adults use the vegetation marginal to puddles and ponds for laying their eggs (VIEIRA et al. 2007, CALDAS et al. 2016). Lentic environments appear to be most favorable to the development of *P. nordestinus* larvae, because they usually live in standing water environments, where they are usually found in the upper half of the water and in an oblique position relative to the surface. In addition, their anterior mouth seems to have derived from the ventral region, and is certainly related to the habit of catching food suspended in water (CRUZ 1982).

In seasonal environments with a well-defined and/or pronounced dry season, most tadpoles occur during a restricted period of the year, in other words, when water bodies are available (ROSSA-FERES & NOMURA 2006, LOWE et al. 2015, SZÉKELY et al. 2017). However, there was no influence of rainfall rates on the total abundance of *P. nordestinus* larvae. This reinforces the standpoint defended by some authors, who affirm that there is no single climatic variable that influences the reproduction of anurans and the permanence of tadpoles in the habitat (POMBAL JR. 1997, CONTE & MACHADO 2005). Rain seems to have considerable importance for filling the water bodies; however, once they are formed, other factors could have greater relevance to their maintenance. Within this, high humidity rates and milder temperatures would be of great importance for the durability of puddles and ponds in Caatinga environments, which are known to have high temperature, insolation and evaporation throughout the year (REIS et al. 2006, TROVÃO et al. 2007).

We did not observe *P. nordestinus* tadpoles in the environment in the first two months of rainfall. This absence may favor resource partitioning among larvae of different species, as those that colonize the environment faster could obtain resources from it before the establishment of other tadpoles. This temporal segregation may possibly be one of the mechanisms that reduces the negative effects of competition between the larvae of some anuran species, as has been discussed by other authors (DIXON & HEYER 1968, HEYER 1973, ETEROVICK & SAZIMA 2000).

The larvae presented an aggregate distribution in almost all the studied water bodies, and in most of the months in which they were effectively present. Schooling behavior has been observed in the tadpoles of *Phyllomedusa vailanti*, *Phasmahyla guttata* and *Phasmahyla cochranae*, other representatives of the family Phyllomedusidae (BRANCH 1983, COSTA & CARVALHO E SILVA 2008, LEÃO-PIRES et al. 2017). This may be related to factors that minimize the action of predators and morphological characteristics, and the behavioral and physiological needs of the species, which would promote a better use of resources and would be crucial factors for their spatial distribution in water bodies (BARRETO & MOREIRA 1996). Aggregations with conspe-

cifics represent a tadpole adaptation that minimizes predation, especially when the metamorphosis period is near, when they are more vulnerable (NICIEZA 1999, SPIELER & LINSENMAIR 1999, GLOS et al. 2007). In Phyllomedusidae, it has already been suggested that *Phyllomedusa vailanti* tadpoles would be able to identify kins and group evenly into size classes (BRANCH 1983), a behavior that can also occur on *P. nordestinus* tadpoles. We cannot disregard that aggregations aid in foraging, providing the acquisition of more diverse food items, as also noted for *Bufo crucifer* (= *Rhinella crucifer*) (ETEROVICK 2000). That would be an important advantage over solitary behavior tadpoles.

The gradual drying of the water bodies did not intensify the aggregations of *P. nordestinus*. This behavior would not be incoherent in a drastic and irregular environment, such as the Caatinga, since large aggregates could accelerate metamorphosis, either by the greater acquisition of temperature obtained by the larvae or by increased intraspecific competition and abandonment of the water body by means of a decrease in resources (BRATTSTROM 1962, TEJEDO & REQUES 1994, INDERMAUR et al. 2010). We suggest that *P. nordestinus* tadpoles do not heavily depend on this acceleration, even in critical situations, since the early stages of larval development occur outside the water, on the marginal vegetation (HADDAD & PRADO 2005, VIEIRA et al. 2009) and organisms reach the body of water in later stages than most other species (DUELLMAN & TRUEB 1994, WELLS 2007). We also emphasize that the sampling period was quite atypical, and there was rain and water available in the environment for about 8 months. Phenomena of this nature are expected in the Caatinga, and enduring periods of droughts and floods are recurrent, but it is normal for rain to be restricted to very short periods of the year (NIMER 1972, PRADO 2005). Although rainfall did not have a positive influence on tadpole abundance, it could have guaranteed a longer duration of the water bodies, avoiding the need for *P. nordestinus* tadpoles to adopt strategies to advance metamorphosis.

Tadpoles of other species negatively influenced the abundance of *P. nordestinus* in the different sampled plots. Competitors can capture resources more easily or inhibit growth by chemical mediation, directly affecting the larval period of other species (GRIFFITHS et al. 1991, SMITH et al. 2004, CABRERA-GUZMÁN et al. 2013, ARRIBAS et al. 2018). We know that an increase in intraspecific competition (aggregations) may favor the acceleration of metamorphosis in moments when the water bodies are drying. However, *P. nordestinus* tadpoles would have no advantage by anticipating this phase as a regular situation, as juveniles would reach a small size and would be more susceptible to pressures in the terrestrial environment (SMITH 1987, BECK & CONGDON 2000). Temporary aquatic environments are unpredictable in space and time, and the larvae of various species often adapt to this unpredictability, which may limit the degree of specialization for resource allocation. In these types of environments, most tadpoles are unspecialized filterers and may be potential competitors between themselves (FATORELLI & ROCHA 2008). In

this way, it would be important that *P. nordestinus* avoid sharing space with other species, because resource availability could seriously decline.

The abundance and action of invertebrate predators may exert an influence on the life of tadpoles, regulating population density and reducing metamorphic size (INDERMAUR et al. 2010), affecting locomotor capacity, swimming speed and the degree of larvae exposure, including biochemical changes to morphological characteristics (MOGALI et al. 2012, MAHER et al. 2018, RAMAMONJISOA et al. 2018), or selective action on different sized larvae (WILBUR 1997). Some studies have shown that predators cause changes in the distribution of tadpole species (HEYER et al. 1975, GASCON 1989, HECNAR & M'CLOSKEY 1997), or even lead to exclusion in some environments (TIBERTI & VON HARDENBERG 2012). We observed a positive relationship between predator abundance (Odonata larvae and Belostomatidae) and *P. nordestinus* larvae. Our results contradict the pattern of arid environments with ephemeral water bodies, in which there is usually a low occurrence of tadpole predators and a minor influence of predation on amphibian larval assemblages (MORIN 1983, DAYTON & FITZGERALD 2001, JARA & PEROTTI 2010). We do not believe that a greater number of predators offers favorable conditions for tadpoles, and justify the observed result in two ways: 1 – the sites that allow the establishment of more larvae may also have conditions that facilitate predator occupation, including some physical characteristics (e.g., oxygen, pH, temperature) that were not investigated in this study, but which usually influence odonates and belostomatids in ephemeral environments (FONSECA et al. 2008, JANSSEN et al. 2018, YAPO et al. 2018); 2 – the sites that have the highest predator numbers also present more *P. nordestinus* tadpoles, because the formation of shoals is an effective behavior against predation, as has been discussed previously, and these are the areas where larger aggregations occur. The larvae of amphibians that occur in ephemeral water bodies also usually have chemical defense mechanisms (ÁLVAREZ & NICIEZA 2009), a behavior that could act in conjunction with aggregations and should not be disregarded, and requires further investigations.

The emergent vegetation observed in the different water bodies was negatively related to the presence of *P. nordestinus* tadpoles. In most cases, this corresponded to typical Caatinga plants (mainly shrubs) that colonized the substrate of water bodies, dried and remained there after being flooded. We suggest that the accumulation of twigs and dry leaves makes it difficult for the tadpoles to swim and engage in feeding behavior, since *Pithecopus* larvae are usually found in the upper half of the water column, where they ingest suspended food particles (CRUZ 1982, MCDIARMID & ALTIG 1999, BRANDÃO 2002). On the other hand, aquatic vegetation would promote larvae survival, since densification creates effective refuges against predators, as already noted by other authors (KOPP et al. 2006, MUNIZ et al. 2008, VALDEZ et al. 2017). However, in this study, we detected a negative relationship between larvae abundance and the percentage of aquatic vegetation in the plots; we sug-

gest that this is because aggregates represent a more efficient alternative to minimizing predation. Thus, *P. nordestinus* larvae would avoid aquatic vegetation accumulation, as this would reduce space and impair the accommodation of a sufficient number of individuals for the shoal formation.

Finally, we did not observe an influence of depth on the occurrence of *P. nordestinus* tadpoles. This result is somewhat intriguing because we believed that sites with a greater depth should favor larval abundance due to the habits and adapted morphology of the species (theoretically more efficient in deep environments; CRUZ 1982, MCDIARMID 1994, DUELLMAN et al. 2016). However, we suggest that greater depths could also be occupied by competitors and emergent vegetation, forcing *P. nordestinus* tadpoles to diversify the occupation of space in the water bodies.

In this semi-arid Brazilian environment, the occurrence and distribution of *P. nordestinus* tadpoles seems to be influenced by the joint action of some factors (competitor presence, predators, emergent and aquatic vegetation, surface water retention time, milder temperatures and high humidity rates). Morphological and reproductive aspects also seem to contribute to the selection of the most appropriate sites for larval survival, especially for aquatic habitats (lentic water bodies, with the presence of marginal shrub-arboreal vegetation) and, to a certain extent, for the microhabitats that integrate them (emergent vegetation × tadpole habit). Individual aggregation can be a positive strategy against the action of predators, because establishment of predators in the water bodies does not seem to be a problem even in an environment with drastic conditions. The abundance of *P. nordestinus* larvae is not affected by variations in the size of water bodies throughout the year, suggesting that the acceleration of metamorphosis is not a critical factor, even in an environment that is subject to water irregularities most of the time.

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