










Reproductive biology of direct developing and threatened frog *Adelophryne maranguapensis* (Anura, Eleutherodactylidae) reveals a cryptic reproductive mode for anurans and the first record of parental care for the genus

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ABSTRACT

Anurans with direct development are among the most difficult species for conducting studies concerning ecology and natural history. This paper provides information on the reproduction of *Adelophryne maranguapensis*, a threatened species endemic to Serra de Maranguape, an Atlantic Forest relict surrounded by dry Caatinga phytophysionomies. Our objectives were to identify the reproductive periods, verify any preference for breeding sites, review the reproductive mode and describe parental care. The species reproduces during the rainy season and is not selective as to the species of bromeliad used for oviposition. This is the first report of parental care for the genus since females demonstrate egg attendance until the formation of the gel layer in all the eggs. We revisit the terms that define the reproductive mode of this species and propose the need to redefine it. The redefinition considers: (1) deposition of bromeligen and non-aquatics eggs around the phytotelm; (2) direct development; (3) parental care with egg attendance by the female.

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Introduction

The genus *Adelophryne* Hoogmoed, Lescure 1984 consists of small litter frogs, found from the Amazon to the Atlantic Forest and Guiana Region, and comprises 10 species (Frost 2020) with direct development (Cassiano-Lima et al. 2011). Little is known of its natural history, and only *Adelophryne maranguapensis* is formally recognised as endangered because of its estimated distribution area of 13 km² in the highlands of Serra de Maranguape, in the Caatinga domain (Silvano and Borges-Nojosa 2018; Haddad et al. 2018). Direct development is the most common reproductive strategy among frogs with

endotrophic larvae (Wells 2007), but the species that use this strategy are among the most difficult to study regarding their ecology and natural history (Townsend and Stewart 1985). For over 20 years, direct development was only a hypothesis for the genus *Adelophryne* (Hoogmoed and Lescure 1984; Hoogmoed et al. 1994), and although terrestrial eggs have been reported for *A. patamona* and *A. baturitensis* (MacCulloch et al. 2008; Cascon et al. 2014), direct development was fully confirmed in *A. maranguapensis*, with records of eggs laid in bromeliads (Cassiano-Lima et al. 2011).

Bromeliads, as well as any plant structure capable of accumulating water, are often used as breeding sites for frogs, and provide lower incidences of predation and competition for eggs and tadpoles (Lehtinen et al. 2004), maximising the reproductive fitness (Toledo et al. 2012). These structures form limnological environments with complex ecological relationships known as phytotelms (Richardson 1999; Kitching 2000; Mestre et al. 2001). Among the reproductive modes for anurans listed by Haddad and Prado (2005) only five (6, 8, 14, 26 and 36) are associated with phytotelmata. However, none of these directly refers to species with direct development, either in water or in environments influenced by the microclimate generated within phytotelms.

The concept of reproductive modes for anurans includes data relating to breeding sites, egg characteristics, spawning and development, and parental care, if any (Duellman and Trueb 1994; Pombal-Jr and Haddad 2007). Recently, Gomez-Mestre et al. (2012) provided evidence that the transition between baseline reproductive modes and derivatives may have occurred more suddenly than previously considered. This reproductive specialisation apparently occurs in rain forest environments, in response to predation (Magnusson and Hero 1991; Prado et al. 2002), parasitic relationships (Todd 2007) or local topography that constrains the formation of large natural water reservoirs (Haddad and Prado 2005).

Cassiano-Lima et al. (2011) regarded *A. maranguapensis* as sharing the characteristics of reproductive mode 27 (arboreal eggs hatching to froglets, *sensu* Haddad and Prado 2005). However, in this paper we consider that this category does not satisfactorily reflect the reproductive characteristics of this species, and based on natural history data, we suggest that the reproductive mode of *A. maranguapensis* should be redefined.

Crump (2015) emphasises that the best way to expand the understanding of anuran reproductive modes is by incorporating natural history data, which provides conservation strategies with major ecological relevance. This is particularly desirable for *A. maranguapensis*, not only because it is a threatened species (Silvano and Borges-Nojosa 2018), but also because its area of endemism has one of the highest priorities for the conservation of amphibians in the Caatinga domain (Camardelli and Napoli 2012).

Material and methods

Study area

The Serra de Maranguape (03°53'40.6"S, 38°43'21.2"W, 920 m asl.) is located 25 km inland from the coast of the state of Ceará, Brazil. It is a mountain, included in the domain of ancient shields and massifs, consisting of a precambrian crystalline base (Souza 2002). Elevation and proximity to the coast are two of the factors leading to the presence of woody vegetation taller than 5 m, interspersed with shrubs and epiphytes

(Fernandes 1998; Lima and Cascon 2008). Annual rainfall is 1,300 mm and mean temperature is between 23°C and 26°C, contrasting with high temperatures and low rainfall in the surrounding Caatinga. Because of these characteristics, as well as the several endemic species recorded, the Serra de Maranguape is considered one of the areas of highest priority for the conservation of amphibians in northeastern Brazil (Camardelli and Napoli 2012).

We concentrated our work in two areas (Figure 1):

- (1) Riacho Beija-Flor (03°53'44.3" S; 38°43'20.8" W; 890 m asl.): Area of approximately 2.500 m² with a permanent stream (one m in width and 45 cm in depth), and dense arboreal vegetation over 15 m with numerous mosses, ferns, bromeliads and orchids.
- (2) Pico da Rajada (03°53'44.2" S; 38° 43'20.8" W; 920 m asl.): Area of approximately 200 m². It is the highest point of the mountain, with a steep slope and exposed rock. The dominant tree (almost 3.5 m in height) is montane mangrove (*Clusia* sp), with understory of bromeliads, orchids, and other epiphytes, which also occur on exposed rock.

Record of egg clutches

Fieldwork consisted of monthly expeditions lasting two to four days between the months of April 2010 and April 2012. The surveys occurred between 0600–1200 and 1900–2100 h. In both areas we searched for the eggs in roots and aerial parts of plants, litter, cavities in tree trunks, moss, holes in the soil, under rocks and other places that could be used for oviposition. For each individual spawning, we counted the eggs, identified the bromeliad species used for oviposition and recorded the height above ground. We also used the records of four spawning observations registered in 1998 and 2003 (see Table 1). Parental care was observed in two instances. In both cases we directly observed the females' behaviour at a distance of 15 cm, and they did not attempt to escape. In both cases entire bromeliads containing female and eggs were removed and taken to our base camp. Clutches and adults remained under direct observation for approximately one hour, at which point the female abandoned the eggs. Immediately eggs were removed, immersed in 3% cysteine for 2 minutes (cf. Richardson et al. 1998), fixed in 2.5% glutaraldehyde and 4% paraformaldehyde in a 0.1 M sodium phosphate buffer for 2 h. After this the eggs were transported to the laboratory, where they were dehydrated, mounted on aluminium stubs, super-coated in gold and examined with a Quanta 250 electronic microscope (cf. Lima et al. 2016). Bromeliads were then returned to their original locations.

Availability of oviposition sites

To check the availability of bromeliads we performed three transects (see Brower and Zar 1984; Cullen-Jr and Rudran 2004) in the areas where eggs were found on 29 October 2012. Two transects were in the Riacho Beija-Flor (03°53' 48, 2 'S;



Figure 1. Fieldwork areas. Riacho Beija-flor (a) and Pico da Rajada (b).

38°43'19,3' W; 878 m asl.), and one in the Pico da Rajada (03°53'40,6 'S; 38°43'21,2' W; 920 m asl.). Each transect was 50 m long and 2 m wide, and we recorded all bromeliads up to 4 m above ground level. The short length of the transects was due to the difficult terrain, especially steep slopes.

Table 1. General data on the egg clutches of *Adelophryne maranguapensis*, with date of record, bromeliad species, number of eggs and bromeliad height. Clutches with parental care underlined; *Recorded at Pico da Rajada.

Clutch	Date	Bromeliad species	Eggs (n)	Height (m)
1	28.II.1998	<i>Guzmania lingulata</i>	5	1,5
2	12.I.2003	<i>G. lingulata</i>	3	0,5
3	26.IV.2003	<i>G. lingulata</i>	5	1,8
4	26.IV.2003	<i>G. lingulata</i>	6	1,8
5	21.IV.2010	<i>G. lingulata</i>	3	1,4
6*	21.IV.2010	<i>Vriesea cearensis</i>	6	1,6
7	21.IV.2010	<i>G. lingulata</i>	7	1,6
8	21.IV.2010	<i>Aechmea maranguapensis</i>	8	4,4
9	21.IV.2010	<i>G. lingulata</i>	5	2,5
10	21.IV.2010	<i>G. lingulata</i>	6	1,5
11	21.IV.2010	<i>Guzmania sanguinea</i>	6	1,3
12	21.IV.2010	<i>G. sanguinea</i>	3	1,3
<u>13*</u>	25.I.2011	<i>V. cearensis</i>	4	1,6
<u>14</u>	25.I.2011	<i>G. lingulata</i>	8	1,5
15	25.I.2011	<i>G. lingulata</i>	4	1,8
16	25.I.2011	<i>G. lingulata</i>	6	1,4
17	25.I.2011	<i>G. lingulata</i>	4	1,4
18	25.I.2011	<i>G. lingulata</i>	3	1,8
19*	26.I.2011	<i>V. cearensis</i>	4	1,5
20	25.II.2011	<i>G. lingulata</i>	3	1,6
21	25.II.2011	<i>G. lingulata</i>	4	1,9
22	26.III.2011	<i>G. lingulata</i>	4	1,9
23	26.III.2011	<i>G. lingulata</i>	4	1,5
24	26.III.2011	<i>G. lingulata</i>	5	1,6
25	26.III.2011	<i>G. lingulata</i>	5	2,2
<u>26</u>	26.III.2011	<i>G. lingulata</i>	6	1,5
<u>27</u>	26.III.2011	<i>G. lingulata</i>	8	2,0
28	26.III.2011	<i>G. lingulata</i>	5	1,5
29	26.III.2011	<i>G. lingulata</i>	5	1,4
30	26.III.2011	<i>G. lingulata</i>	5	1,8
31	30.IV.2011	<i>G. lingulata</i>	4	1,8
32	30.IV.2011	<i>G. lingulata</i>	7	1,0
33	30.I.2012	<i>G. lingulata</i>	4	1,8
34	30.I.2012	<i>G. lingulata</i>	6	1,1
35	30.I.2012	<i>G. lingulata</i>	4	1,6
36	17.IV.2012	<i>G. lingulata</i>	6	1,9
37	17.IV.2012	<i>G. lingulata</i>	3	1,4
38	17.IV.2012	<i>G. lingulata</i>	5	1,5
39	17.IV.2012	<i>G. lingulata</i>	4	1,5
40	17.IV.2012	<i>G. lingulata</i>	3	1,5
41*	17.IV.2012	<i>G. lingulata</i>	5	0,3

Climatic data

Humidity and temperature data were obtained with a wet bulb thermohygrometer located at the base camp (03°54'11,3 'S; 38°43'12,6' W; 719 m asl.), and monthly rainfall was obtained from Fundação Cearense de Meteorologia (FUNCEME), with measurements made at the Maranguape Station (03°54'06,64"S; 48°40'57,36" W, 4 km from base camp).

Results

Reproductive activity

Reproduction of *A. maranguapensis* is prolonged (cf. Wells 2007), but concentrated in the January–June rainy season (Figure 2). During this period, while walking to the

base camp to begin the monthly fieldwork, we could hear more than 100 individuals calling along the way.

Males vocalised continuously during daylight hours (0500–1730 h), decreasing gradually as the day darkened. Very few individuals called at night, and only during the rainy season. During the months with rainfall < 100 mm, fewer than 10 individuals, widely spaced, were heard calling.

Viable clutches of *A. maranguapensis* were recorded only in the rainy season, with monthly rainfall > 150 mm (Figure 2). At this time, differences between maximum and minimum relative humidity were very small (especially in April 2011 and March and April 2012). High humidity during the day is probably the main factor for the survival of egg masses. In January 2012, with monthly rain < 50 mm we found three clutches of *A. maranguapensis*, but the eggs were dead and infected by fungi. Although the first annual rainfall had already occurred, it is likely that the weather conditions, especially the large daily variation in relative humidity, were unfavourable to the development of the embryos. In February and March 2012 we did not carry out field work, and we could not confirm the presence of clutches. However, the high precipitation, and identification of clutches and animals vocalising in both January and April suggest the occurrence of eggs in bromeliads during this period.

All egg clutches ($n = 41$) were found in bromeliads. Each one had 3–8 eggs and all of them were at least 2 cm from the water accumulated in bromeliads. The most common bromeliad associated with spawning was *Guzmania lingulata* ($n = 35$; Table 1). In Pico da Rajada, three clutches (75%) occurred in *Vriesea cearensis*, and only one clutch (25%) was found in *G. lingulata* (Table 1). In Riacho Beija-Flor, most of the clutches ($n = 34$, or 91.9%)

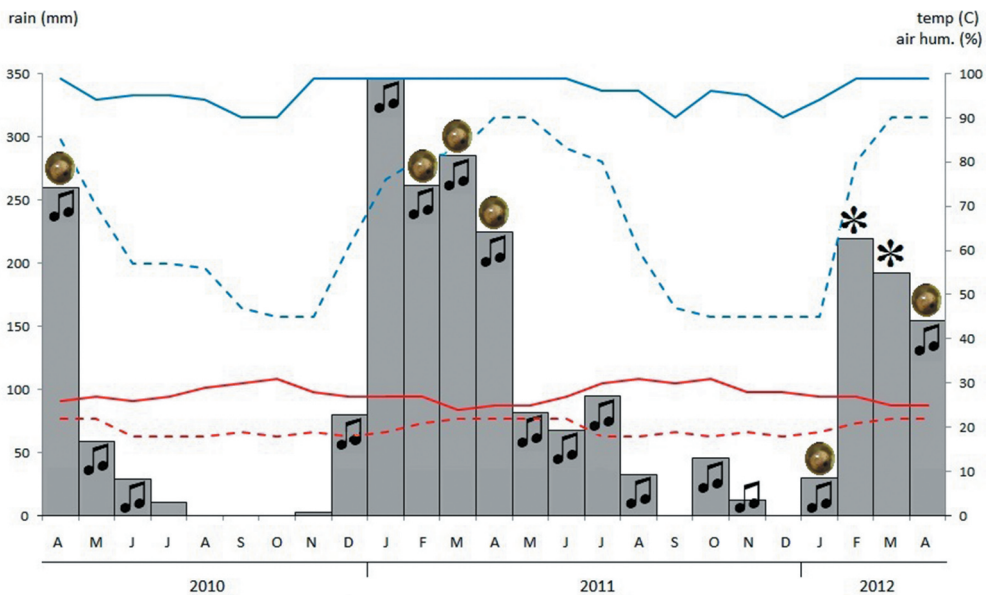


Figure 2. Climatic parameters in Serra de Maranguape between the months of April 2010 and April 2012. Precipitation (columns); maximum relative humidity of air (blue line), minimum relative humidity of air (blue dashes), maximum temperature (red line), minimum temperature (red dashes), musical note (occurrence of vocalisations), egg (presence of egg masses); * without field work.

were found in *G. lingulata*, and three clutches (8.1%) were found in *G. sanguinea* ($n = 2$) and *Aechmea maranguapensis* ($n = 1$) (Table 1).

Transects in both areas revealed that *V. cearensis* and *G. lingulata* are the most numerous bromeliads in Pico da Rajada (90.5%) and Riacho Beija-Flor (98.1%), respectively. This fact suggests that *Adelophryne maranguapensis* uses the most available bromeliad species, rather than being selective as to species.

We recorded parental care on two occasions: on 25 January 2011 at 0800 h in Pico da Rajada, and on 26 March 2011 at 1000 h in Riacho Beija-Flor (Table 1). In both cases a female was seated over the eggs and no males were seen. The females remained on the eggs, practically immobile, during handling of the bromeliad leaves for photography. If any egg seemed to move, the female restored it to its original location (Figure 3). In both cases one of the eggs appeared to be in an early stage of development. It was approximately 2 mm diameter and lacking a gel layer, consisting only of the yolk. The other eggs were almost 4 mm in diameter and morphologically similar to the eggs described for the species (Cassiano-Lima et al. 2011). Following transport to the base camp, the females exhibited the same behaviour for at least one hour before leaving the eggs. At this time there were no apparent differences between the eggs, and all displayed the developed gel.

Scanning electron microscopy indicated that all the eggs were fertilised, and at the second cleavage stage of development (Lima et al. 2016). These findings show behaviour of egg attendance by the female (cf. Crump 1995; Wells 2007), and the absence of males from the vicinity of females with newly spawned eggs raises the possibility of internal fertilisation.



Figure 3. Female *Adelophryne maranguapensis* showing parental care activity (clutch 13, Table 1).

Discussion

Site and reproductive period

Phytotelms are water bodies formed in leaves, flowers or cavities in plants (Maguirre-Jr 1971; Frank and Lounibos 1987). These environments can be used as temporary or permanent resources by many species and permit the formation of complex food webs (Walker et al. 1991; Kitching 2000; Waldemar and Irgang 2003; Oliveira 2004). Bromeliads are among the key-influencers concerning phytotelm environments, and amphibians are frequently observed in these plants (Sabagh et al. 2017). Studies focusing on the association between amphibians and bromeliads in Brazil are still incipient, and in many regions it is necessary to conduct inventories for both species of amphibians and bromeliads.

Egg clutches of *Adelophryne maranguapensis* were found predominantly in the bromeliads *Guzmania lingulata* and *Vriesea cearensis*. In Serra de Maranguape, these species have a restricted distribution and occur only in the humid parts of the mountain (Monteiro 2005). The prevalence of clutches in *G. lingulata* (98.1%) in the Riacho Beija-Flor, and *V. cearensis* (75%) in the Pico da Rajada, indicate that there is no specific selection, but suggest that *A. maranguapensis* uses the most abundant bromeliad species in each locality. In frogs, the selection of environments for oviposition increases the possibility of success in activities related to breeding, feeding, protection from predators and climatic fluctuations (Afonso and Eterovick 2007), and the bromeliculous environment provides all these advantages (Lehtinen et al. 2004; Lin et al. 2008). The placement of eggs with direct development in bromeliads by *A. maranguapensis* is perhaps the key factor for the full establishment of this species in the montane forest, because it avoids direct competition with other amphibians, as it is the only local bromeligen amphibian species (D. C. Lima, unpubl. data).

Although *Adelophryne maranguapensis* does not use the water accumulated in bromeliads for oviposition, we observed a relationship between species reproduction and the rainy season, as with other amphibians in dry areas in northeastern Brazil (Arzabe 1999; Xavier and Napoli 2011). The results showed that oviposition occurs in periods when temperature and air humidity fluctuate less (temp. max 27–28° C, min. air humidity above 70%). Except in January 2012, spawning occurred only in months when minimum humidity exceeded 70%, even in periods with less intense rainfall, such as April 2012 (Figure 2), suggesting that high minimum relative air humidity is a factor that favours the reproduction of the species.

Occurrence of specialised reproductive modes in anurans is directly related to humidity (Silva et al. 2012), and local climatic instability resulting from human action are risks especially for amphibians with arboreal eggs (Touchon and Warkentin 2008). In Serra de Maranguape, activities such as the conversion of forests into banana plantations and the collection of bromeliads and other epiphytes (Lima and Cascon 2008) have direct impacts on local populations of *A. maranguapensis*.

Redefinition of the reproductive mode

Previously, Cassiano-Lima et al. (2011) suggested that *Adelophryne maranguapensis* exhibited reproductive mode 27 (*sensu* Haddad and Prado 2005; arboreal eggs hatching into

froglets). The term 'arboreal' is generic for describing reproduction in amphibians and can be applied to eggs deposited in any aerial part of a plant, and even creeping plants such as mosses (Crump 2009). It is evident that this term, without any additional details, obscures features that may demonstrate the existence of other specific reproductive modes (Crump 2015). Holes in trees and bromeliads, for example, are 'arboreal' environments widely known due to their ability to hold water, forming phytotelms (Louton et al. 1996; Kitching 2000; Mestre et al. 2001).

Of the 39 reproductive modes listed for frogs, five (6, 8, 14, 26 and 36, *sensu* Haddad and Prado 2005) are formally related to the use of phytotelmata, but none of these is clearly linked to species with direct development. Based on this, we suggest that the reproductive mode of *Adelophryne maranguapensis* must be redefined. For this we adopted the term 'bromeligen' (previously used by Peixoto 1995 to classify species and not eggs or spawns) to specify and restrict the eggs as bromeliad dependent, and we propose the new term *Periphytotelmata* (gr. Peri = around) to indicate the specific location of oviposition in the bromeliad. Thus, the reproductive mode of *A. maranguapensis* would be a subdivision of the arboreal eggs category (cf. Haddad and Prado 2005), stated as follows: 'bromeligen periphytotelm eggs, with direct development'.

Periphytotelmata, as proposed here, indicates that the plant forms a phytotelm environment, but makes it clear that the eggs are not deposited into the water. These eggs portray an evolutionary adaptation that increases the chances of survival in face of three problems: low concentration of dissolved oxygen in phytotelm (Lehtinen et al. 2004); occurrence of predators and parasites associated with these water reservoirs (Lehtinen et al. 2004; Todd 2007; Lin et al. 2008); and desiccation of spawning by the sun (Pombal-Jr 1999).

Parental care

Parental care occurs in at least 10% of anuran species, and although its occurrence or absence is one of the reproductive mode components, this behaviour is not typically used to differentiate them (Crump 2015). In amphibians this behaviour is quite complex and is associated with events involving eggs or froglets, in which the male or female act singly or together to facilitate the survival of their offspring (McDiarmid 1978; Duellman and Trueb 1994).

Although there was no previous research on the natural history of the genus *Adelophryne* prior to 1998, Beck (1998), without providing the source of his information, reported that this genus has no parental care. Our findings demonstrate parental behaviour of egg attendance for *A. maranguapensis*. Egg attendance is the most common form of parental behaviour among amphibians, particularly for species with oviposition in terrestrial and arboreal environments (Lehtinen 2003). This behaviour involves protection from predators and pathogens, prevention of anomalies during embryonic development, aiding froglets at hatching, preventing dehydration (Crump 1995, 2015), and transmitting innate defences from parents to the eggs (Walke et al. 2011).

In *A. maranguapensis* this behaviour is probably related to the prevention of desiccation (cf. Stebins and Cohen 1995), and we assume that this behaviour occurs until the full formation of the gel layer in all the eggs. In 39 (95.12%) of clutches were observed embryos still undifferentiated and did not have females on them or nearby. It is possible

that female contact is necessary to transfer water to the egg capsule by osmosis, as reported for other Eleutherodactylid frogs (Taigen et al. 1984), until all the eggs are able to be maintained by the moisture provided by the phytotelm.

Species that exhibit egg attendance can also be classified according to the amount of time they perform parental care. Species with high attendance spend long periods close to the eggs during the day, while those with low attendance remain for a short time (Cheng and Kan 2010). Our results suggest that *A. maranguapensis* exhibits low attendance.

Parental care exercised by female frogs has sometimes been associated with internal fertilisation (Wells 1981), a rare condition for frogs (Wells 2007). Because we found females and newly oviposited fertilised eggs without males nearby, it is possible that internal fertilisation occurs in *A. maranguapensis*. This hypothesis requires further confirmatory studies describing the courtship behaviour, amplexus and oviposition activity. The information in this work contributes to our understanding of the natural history of the genus *Adelophryne* and provides support for the development of strategies for the conservation of *A. maranguapensis* and the Serra de Maranguape. Additionally, it reinforces the importance of research involving natural history of frogs with direct development.

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Disclosure statement

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