Breeding biology of *Phyllomedusa azurea* Cope, 1862 and *P. sauvagii* Boulenger, 1882 (Anura) from the Cerrado, Central Brazil

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Abstract

*Phyllomedusa azurea* and *P. sauvagii* are treefrogs from seasonal dry environments of Central Brazil. We report on reproductive and other natural history features of these species. The study was carried out in Serra da Bodoquena, Mato Grosso do Sul, Brazil. The reproductive period was determined by the presence of vocalizing males, amplexant pair or presence of tadpoles. The reproductive effort was measured as the ratio of gonad mass in relation to body mass (BM). The reproduction of both species was correlated with the rainy season. Female *P. sauvagii* produced more eggs and their eggs were larger than those of *P. azurea*. Both species showed sexual dimorphism in relation to the snout–vent length (SVL) and BM. The mating behaviour of both species was similar. Males in both species showed similar reproductive efforts, but females of *P. azurea* invested more in gonads compared to the males of *P. sauvagii*. *Phyllomedusa azurea* showed a significant relation between SVL versus number of the mature eggs (NME), and *P. sauvagii* between SVL versus NME and BM versus ovarian mass.

Keywords: Anura, Hylidae, Cerrado, clutch size, sexual dimorphism, Phyllomedusa

Introduction

Reproductive biology has been studied in many amphibian species (e.g. Crump 1974; Pröhl 1997). In temperate regions, the reproductive activity of anurans is generally cyclic or seasonal, usually occurring with rise of temperature and rainfall. In tropical seasonal environments, the breeding of anurans can be prolonged or explosive (e.g. Duellman and Trueb 1986; Prado et al. 2005), and rainfall seems to be the main factor determining the control of reproduction (Duellman and Trueb 1986). The environmental conditions in tropical regions during the wet season are favourable for the reproduction of amphibians...
during several months. However, some species reproduce only during a few days each year (Biever 1997).

The reproductive activity patterns of anurans were classified as: (1) explosive—species with breeding activity lasting a few days with synchronous arrival of males and females, a high, loud chorus formation, and males employing a mate-location behaviour defined as active searching (sensu Wells 1977); (2) prolonged or continuous—species reproducing for more than one month, exhibiting asynchronous arrival of females at the breeding sites, and with males often defending territories, or simply an acoustic space (sensu Wells 1977). However, intermediate or opportunistic patterns may occur and have characteristics similar to the explosive and prolonged breeders (Duellman and Trueb 1986; Bastos and Haddad 1999).

Different reproductive strategies may minimize the cost and/or risks associated with reproduction (e.g. Harvey and Pagel 1993; Prado et al. 2000; Rodrigues et al. 2005). The cost of reproduction is important to understanding life history patterns (e.g. Pough et al. 1998; Prado et al. 2000). The estimation of reproductive effort allows the measurement of energy expenditure in reproduction (Stearns 1992; Rodrigues et al. 2003, 2004). One method for measuring the reproductive effort in anurans is to correlate the size, mass, or volume of gonads, or clutches, to body size, mass, or volume (e.g. Crump 1974; Prado et al. 2000). In general, clutch volume is correlated with female size, simply because of the limited availability of space in the abdominal cavity of the female (Kaplan and Salthe 1979; Shine 1992; Prado et al. 2000).

In spite of the fact that Neotropical regions contain more than 50% of the anuran species of the world (Duellman 1999) and exhibit a great diversity of reproductive modes (Haddad and Prado 2005), information on their life histories is scarce or incomplete (Krügel and Richter 1995; Prado et al. 2000; Rodrigues et al. 2004). The majority of the detailed studies on reproduction were made from species with aquatic reproduction in temperate (e.g. Robertson 1986; Ritke et al. 1990) and tropical regions (e.g. Bastos and Haddad 1999; Pombal and Haddad 2005; Rodrigues et al. 2005). Studies of species with arboreal reproduction are increasing (Vaira 2001), but more specific studies, mainly focusing on reproductive effort, are rare (Prado et al. 2000; Rodrigues et al. 2005).

In Brazil, the majority of studies on reproduction in anurans have been made mostly in the south-eastern region (e.g. Silva et al. 2005) in the Atlantic Rainforest (e.g. Bastos and Haddad 1996; Pombal and Haddad 2005), and in the north region, in the Amazonian Rainforest (e.g. Juncá 1998; Neckel-Oliveira 2004). The Cerrado (Brazilian savanna) is one of the most threatened ecosystems in the world (Myers et al. 2000), due to high human impact on this environment (deforestation and soybean plantation) (Beebee 1996; Silva and Bates 2002). However, studies on the anuran fauna of the Cerrado are few and recent (Colli et al. 2002; Brasileiro et al. 2005), and their biology remains poorly known. Through great habitat loss, or land conversion for agriculture (Lavilla et al. 2000), the arboreal sites for breeding and the development of advanced larval stages are threatened. The Serra da Bodoquena is a preserved area of Cerrado classified by Myers et al. (2000) and Colli et al. (2002) as a priority area with regard to the biodiversity of the herpetofauna of Brazil.

The aims of this investigation were to examine several aspects of the natural history of *Phyllomedusa azurea* Cope, 1862 and *P. sauvegi* Boulenger, 1882 in order to: (1) identify the reproductive period; (2) determine the clutch, egg and test sizes in these species; (3) estimate the reproductive effort; (4) assess the existence of sexual dimorphism in size and body mass; (5) evaluate the relationship between body size and mass, and the number of mature ovarian eggs and ovarian mass in gravid females, and (6) evaluate the relationship between the SVL and body mass of males and females in relation to reproductive effort.
Study area and methods

This study was carried out in the Serra da Bodoquena at Canaa Farm (20°40'30.4"S, 56°45'20.2"W) and at Canaa Settlement (20°41'32.3"S, 56°44'34.3"W), municipality of Bodoquena, Mato Grosso do Sul State, Brazil. The mean annual temperature is 21°C, and the mean annual precipitation is 1500 mm (Alvarenga et al. 1982; Figure 1). The rainy period is from October to May, with a dry season from June to September (Rodrigues et al. 2004, 2005).

Serra da Bodoquena is located in the southern portion of the state, on the border of the Pantanal do Nabileque (Boggiani and Clemente 1999). The vegetation of the plateau varies according to relief and soil type, displaying semi-deciduous forest and fields of Gramineae (see Furtado et al. 1982; Rodrigues et al. 2005).

Populations of both species were surveyed in two temporary water bodies. One pond was approximately 100 m², with the depth ranging from 20 to 40 cm, and 30 m distant from a small forest. This pond was surrounded by Gramineae (Brachiaria decumbis) and Asteraceae shrubs (Vernonia sp.) only. The other body of water was a flooded Brachiaria decumbis field with an area of approximately 500 m², with depth ranging from 15 to 80 cm. The accumulation of water here occurs due to soil type and a surface depression. The two study sites were approximately 4 km apart.

Data were collected during 4 consecutive days in each month from October 2000 to September 2001 at each water body. However, a collaborator remained in these areas and recorded the precipitation and presence of species during our absence. The reproductive period was determined based on direct observation of males vocalizing, amplectant pairs or presence of tadpoles of the respective species. The plant family used by each breeder was recorded.

![Figure 1. Number of individuals present in monthly samples from October 2000 to September 2001 and total rainfall per month at the study site. Black bars, number of Phyllomedusa sauvagii; dotted white bars, number of P. azurea; black circles, total rainfall during the study; black triangles, rainfall recorded during 4 days by month of study.](image-url)
The collected individuals were transported, anaesthetized, and preserved in the laboratory. The snout–vent length (SVL) of adults was measured to the nearest 0.1 mm with a vernier caliper to verify size differences between the female and male of each species. The total body mass (BM) and gonad mass (GM) of males and females were determined to the nearest 0.001 g with a digital scale. The gonads were removed through a ventro-lateral incision and weighed individually. To assess the fecundity of gravid females, only the largest eggs were removed and counted. The egg diameters were measured with an ocular micrometer to the nearest 0.1 mm and considered to be mature (Crump 1974), at a size above 1.4 mm for *P. azurea* and 1.9 mm for *P. sauvagii*. Voucher specimens have been deposited in the Zoological Collection of the Federal University of Mato Grosso do Sul, Campo Grande, MS (*P. azurea*, ZUFMS-508–519 and *P. sauvagii*, ZUFMS-520–530).

To evaluate the correlations between female fecundity and body size, linear regression analyses were performed between the following variables: (1) SVL versus number of mature eggs (NME); (2) BM versus NME; (3) SVL versus ovary mass (OM); (4) BM versus OM.

The Student's *t* test was used to compare male and female SVL, BM, and reproductive effort (RE). RE was estimated as the percentage of GM relative to BM. To evaluate the influence of SVL and BM of females and males on RE, linear regressions were performed (RE versus SVL and RE versus BM).

The average number of eggs per clutch was determined based on the number of eggs deposited by amplexant pairs on vegetation. After egg deposition, the frogs were killed, and the abdominal cavity was opened to verify the presence and percentage of eggs in different stages of maturation. The eggs obtained were preserved in 5% formalin.

The number of leaves surrounding the clutches was recorded and predation intensity was estimated by dividing the number of clutches attacked by predators by the total number of clutches. Partially or totally damaged nests were assumed to have been attacked by predators. However, we do not identify the predators.

**Results**

The reproductive activity of both *Phyllomedusa azurea* and *P. sauvagii* coincided with the rainy season (October to May) (Figure 1). The species reproduced in both the pond and in the flooded field. *Phyllomedusa azurea* vocalized and mated through the whole rainy season, independent of rainfall volume. We observed asynchronous arrival of males and females of *P. azurea* at the water bodies. On the other hand, *P. sauvagii* vocalized and mated only on heavy rainfall days, or up to 2 days after. Males did not show active searching for females. We observed high numbers of individuals and more than 10 amplexant pairs at night after rainfall. In the dry period, individuals of *P. sauvagii* were found in small forest fragments near to ponds.

Males of *P. azurea* and *P. sauvagii* vocalized on shrubs and on the ground before going to the pond. When the males arrived at the temporary pond, they moved to elevated points of vegetation (shrubs). The oviposition behaviour of both species was similar. Males start vocalizing 2 h after sunset. In the flooded field, males vocalized on a grassy area above the water, and in temporary ponds mainly on shrubs. The oviposition behaviour was observed in two amplexant pairs of each species. Pairs in amplexus moved towards the stem of the leaf and, with their body weight and movement of the legs, folded the leaf. The clasping males helped the female with movement of legs and cloaca to shed the eggs. The couples in amplexus added gelatinous eggless capsules together with the eggs at the moment of
oviposition, which were deposited in the upper part of the clutch (great numbers) and among the eggs. The leaves are joined or folded with the aid of the male.

Sexual size dimorphism in SVL and BM were verified for *P. sauvagii* and *P. azurea*, females being, on average, larger and heavier than males (Table I). The RE of the males of both species was similar. But females of *P. azurea* had significantly higher RE than *P. sauvagii* (Table II).

Females of *P. azurea* showed significant and positive correlation of SVL versus NME (n=8; r²=0.49; P=0.05) (Figure 2A). SVL versus OM (P=0.9), BM versus OM (P=0.3), and BM versus NME (P=0.5) were not significantly correlated in *P. azurea*. Females of *P. sauvagii* showed significant and positive correlation of SVL versus OM (n=19; r²=0.21; P=0.048) (Figure 2B) and BM versus OM (n=26; r²=0.20; P=0.02) (Figure 2C). BM versus NME (P=0.13) and SVL versus NME (P=0.16) were not significantly correlated in *P. sauvagii*.

*Phyllomedusa azurea* did not show significant correlation of SVL versus RE for females (n=7; P=0.69) or males (n=18; P=0.80), or of BM versus RE for females (n=7; P=0.06) or males (n=18; P=0.98). *Phyllomedusa sauvagii* did not show significant correlation of SVL versus RE for males (n=36; P=0.12) or females (n=25; P=0.32), nor between BM versus RE for males (n=36; P=0.22). However, *P. sauvagii* females showed significant and negative correlation of BM versus RE (n=25; r²=0.16; P=0.04) (Figure 3).

Clutches of *P. azurea* were deposited only on single leaves of a plant of the Gramineae family (n=6), while *P. sauvagii* deposited clutches in one to three leaves (n=8) of plants of the Asteraceae family. Twenty-six clutches (14 for *P. sauvagii* and 12 for *P. azurea*) were attacked by predators. Eight clutches (57.1%) of *P. sauvagii* that were wrapped in two or more leaves showed signs of predation, while only two clutches (16.6%) were observed for *P. azurea*. Clutch sizes differed significantly between species (df=28; t=17.49; P<0.01). The average number of eggs per clutch was 594±192 (n=15 clutches; range=201–829 eggs) for *P. sauvagii* and 103±27 (n=14 clutches; range=50–142 eggs) for *P. azurea*. The average diameter of eggs was also larger (df=493; t=17.49; P<0.001) in *P. sauvagii* (2.54 mm±0.29; n=253) compared to *P. azurea* (2.14 mm±0.25; n=330). Females of *P. azurea* contained a great number of eggs in the ovary in different stages of maturation (35% in relation of clutch size), while those of *P. sauvagii* had fewer (15%).

**Discussion**

*Phyllomedusa azurea* displayed prolonged reproductive activity as defined by Wells (1977) and Prado et al. (2005). The reproductive activity of *P. azurea* recorded in this study was similar to that found by Gallardo (1987), Matos et al. (2000), and Prado et al. (2005). *Phyllomedusa sauvagii* exhibited characteristics of an explosive (e.g. concentration of male

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Table I. Mean ± SD, range and t test of snout–vent length (SVL, mm) and body mass (BM, g) of *Phyllomedusa azurea* and *P. sauvagii* males and females from the Cerrado, Central Brazil.

|        | Males   |        | Females  |        |        |        |        |
|--------|---------|--------|----------|--------|--------|--------|--------|
|        | N  | Mean ± SD | Range   | N  | Mean ± SD | Range   | t      | P      |
| *P. sauvagii* |        |        |          |        |        |        |        |
| SVL    | 36 | 77.32±4.95 | 69.0–89.2 | 27 | 88.45±3.63 | 83.4–96.6 | 9.86   | <0.01  |
| BM     | 36 | 32.50±7.22 | 21.6–47.4 | 26 | 59.41±6.89 | 49.6–71.7 | 14.8   | <0.01  |
| *P. azurea* |        |        |          |        |        |        |        |
| SVL    | 20 | 38.68±1.50 | 35.2–41.4 | 8  | 42.53±1.50 | 39.8–44.4 | 6.20   | <0.01  |
| BM     | 18 | 3.22±0.53  | 2.30–4.35 | 8  | 4.50±1.17  | 3.37–6.94 | 2.94   | <0.02  |
vocalizing after heavy rainfall) and prolonged breeder (e.g. more than 6 months reproductive period). Information regarding the period and sites of reproduction for *P. sauvaüii* are scarce. Duellman and Trueb (1986) suggested that the ability of anurans to use ephemeral environments was a response to the predation of eggs and tadpoles, which is higher in permanent environments. Cardoso (1981) showed that the larvae of *Dendropsophus sanborni* Schmidt, 1944 developed more quickly in temporary environments

|       | *P. sauvaüii* |       | *P. azurea* |       |     |     |
|-------|--------------|-------|-------------|-------|-----|-----|
|       | *N*          | **GM** | **RE**      | *N*   | **GM** | **RE** | **t** | **P** |
| Males | 36           | 0.21±0.08 | 0.63±0.19  | 18    | 0.022±0.008 | 0.67±0.23 | 0.65 | 0.51 |
| Females | 25   | 8.34±2.07 | 14.2±3.8  | 7     | 0.93±0.22   | 21.4±7.2 | 3.60 | 0.001 |

Table II. Mean ± SD and *t* test of gonads mass (GM) and reproductive effort (RE) of *Phyllomedusa azurea* and *P. sauvaüii* males and females measured as the percentage of mature gonad weight relative to body weight.

Figure 2. Females of *Phyllomedusa azurea* (A) and *P. sauvaüii* (B, C) collected at the study site from October 2000 to September 2001. Correlations between: (A) SVL versus NME (NME=6.411SVL−173.22); (B) SVL versus OM (OM=0.403SVL−21.79); (C) BM versus OM (OM=0.3043BM−5.41).
than in permanent ones. The predation on aquatic eggs and tadpoles (Magnusson and Hero 1991) and the competition for microhabitats were proposed as important factors influencing the evolution of complex oviposition behaviour (Crump 1974; Duellman and Trueb 1986; Magnusson and Hero 1991). Possibly, the reproductive pattern shown by *P. sauvgii* reduces the predation pressure on individuals through risk dilution (reducing an individual’s chance of being eaten) (Krebs and Davies 1993). Certainly, the study site has many species of predators, such as birds *Pitangus sulphuratus* (Linnaeus, 1766) and *Syrigma sibilatrix* (Temminck, 1824) and crocodilians, *Caiman crocodilus yacare* (Daudin, 1802) that actively search for prey in the surrounding habitats (Rodrigues and Arruda 2006).

In spite of the fact that a species reproduces in open and seasonal environments (Cei 1980; Arzabe 1998), the coincidence of the reproductive period with rainfall can be explained, in part, by the reproductive mode of the species (arboreal eggs, and eggs hatching into exotrophic tadpoles that drop in lentic water). These species depend on air humidity to prevent desiccation of eggs and embryos, which are wrapped in leaves above the water, or simply because heavy rainfall increases the hydroperiod of water bodies, forming a suitable environment for development of tadpoles.

Female *P. azurea* and *P. sauvgii* were larger and heavier than males. Similar results have been reported for other hylids (Shine 1979), such as *Hypsiboas faber* Wied-Neuwied, 1821 (Martins 1993) and *Dendropsophus elegans* Wied-Neuwied, 1824 (Bastos and Haddad 1996). Females are larger than males in 90% of the known species of anurans (Shine 1979), and the causes of this phenomenon are diverse (Stamps 1995) such as: capacity of larger females to produce larger clutches and eggs (Crump and Kaplan 1979; Prado et al. 2000; Rodrigues et al. 2003, 2004, 2005), differences in the age at first reproduction, or in the mortality rate caused by higher predation pressure on larger males (Howard 1981), or restricted growth of males due to energy demand linked to reproductive activity (Woolbright 1989).

Figure 3. The negative correlation of BM versus RE (RE = -0.217BM + 27.155) for *Phyllomedusa sauvgii* females.
Male *P. azurea* and *P. sauvagii* showed similar investment in gonads. On average, the males of *Scinax fuscovarius* (Lutz, 1925) (a relatively small species) had larger investment in gonads than *Trachicephalus venulosus* (Laurenti, 1768) (a relatively larger species) (Rodrigues et al. 2005). Variations in testes size can be found in numerous species of mammals, birds, and amphibians (Coker et al. 2002; Rodrigues et al. 2004). However, species involved in intense spermatic competition have larger testes than species that experience low competition intensity (Møller 1991; Møller and Briskie 1995). Polyandry (more than one male trying to fertilize the eggs of a female) has been reported for some anuran species (Roberts 1994; D’Orgeix and Turner 1995; Prado et al. 2000). In species exhibiting this behaviour, males had larger testes compared to species in which this behaviour is unknown (Prado et al. 2000; Rodrigues et al. 2005). Probably, the similar investment in gonads between the two species of *Phyllomedusa* studied here indicates that neither displays polyandry. Nevertheless, more research is necessary into ecological and reproductive aspects to explain why the RE is similar in males of both species, but different in females.

In contrast, females of *P. azurea* (ER 29.1%) invested more in gonads than *P. sauvagii* (ER 21.1%). Crump and Kaplan (1979) observed that small species allocate, proportionally, the same amount of energy to reproductive investment when compared with larger species. According to Pough et al. (1998), the amount of energy invested in reproduction is negatively correlated with the survival of adults. Also, the high allocation of reproduction energy may attract predators, causing individuals to become more vulnerable to predation (Pough et al. 1998). Small species generally have shorter life spans than large species, and thus a more limited chance of reproduction in the future. They should allocate relatively more energy to reproduction per season than larger species (Pough et al. 1998). Positive evidence for this hypothesis has been recorded in lizards by Tinkle (1969). Crump (1974) and Prado and Haddad (2005) observed that females of larger species tend to invest less in ovaries. These physiological adaptations could cause dissimilarity in the investment in gonads when comparing species of different size. Large species have a proportionately larger amount of supportive tissue and minor abdominal cavity space for the location of eggs (Crump 1974). As heavy rainfalls occur randomly and *P. sauvagii* mate only on such days, they may go to ponds after rain with many eggs immature.

Several studies have demonstrated that female size is positively correlated with the number of eggs or ovary mass (Prado et al. 2000). For females of *P. azurea*, 60% of the variation in NME was explained by SVL. For *P. sauvagii*, 21% and 20% of the variation in OM were explained by SVL and BM, respectively. For 41 species of anurans belonging to different families, studied by Crump (1974) in Ecuador, only 26.8% showed a positive relationship between SVL and NME. Larger body size confers reproductive advantages to females, such as an increase in egg production or egg size (Crump 1974; Howard 1978). Lang (1995) and Prado et al. (2000) verified that the body volume or mass are more appropriate measures to estimate the NME than SVL. However, our data showed a pattern different from that of Lang (1995), Prado et al. (2000), and Rodrigues et al. (2004, 2005). The most reasonable explanation for our result is the variation in weight, because weight of individuals depends on several factors (e.g. availability of resources, success in the capture and assimilation of prey). On the other hand, SVL is less variable in adults. According to Howard (1988), body growth among anurans never ceases totally and older individuals are more fertile and exhibit higher reproductive success (Howard 1988). However, the negative relationship observed between BM versus RE (Figure 3) for females of *P. sauvagii* means that larger females do not invest in gonads in the same proportion as smaller females do. One of the explanations could be that larger bodies have proportionately more supportive
tissue (Crump 1974; Prado and Haddad 2005), or body fat accumulated in the female’s abdominal cavity reduces the space available for eggs and, consequently, reduces the NME and RE.

The breeding behaviour and leaf nest construction of Phyllomedusa azurea and P. sauvagii were basically the same as that previously described in congeners such as P. bicolor (Boddaert, 1772) and P. vaillantii Boulenger, 1882 (Lescure et al. 1995). Phyllomedusa azurea oviposited in only one leaf. Matos et al. (2000) observed that P. azurea deposited its eggs on a single leaf when it was wide enough, but used two when they were too narrow. The same result was observed for P. sauvagii, a species that is heavier, with larger clutches, than P. azurea. However, Neckel-Oliveira and Wachlevski (2004) observed that the clutches of P. tarsius (Cope, 1868) had the lowest incidence (29%) of attack by predators (staphylinid beetles and phorid flies), while P. tomopterna (Cope, 1868) had 50% and P. bicolor 61%. They concluded that the lowest rate of attack was due to P. tarsius having a larger mean number of leaves wrapped around the eggs than P. bicolor and P. tomopterna. In this study, results differed from those of Neckel-Oliveira and Wachlevski (2004). The higher rate of attack occurred in P. sauvagii (the species with larger mean number of leaves for clutch), due to the type of vegetation used by this species. The leaves of Asteraceae found around the water bodies were small and narrow, exposing part of the clutch of this species to predation. Therefore, the reproductive success of two syntopic Phyllomedusa species depends on the availability of arboreal vegetation or shrubs around the aquatic bodies. Environments without this vegetation can be prejudicial for arboreal breeders such as hylids.

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