

Reproductive strategies of *Physalaemus nattereri* (Steindachner, 1863) and *P. albonotatus* (Steindachner, 1864) at Serra da Bodoquena, State of Mato Grosso do Sul, Brazil

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Abstract: There is a high diversity of activity patterns in the chorus and reproductive strategies of amphibians, mainly among species in tropical regions. In this study we analysed the reproductive period, reproductive effort, occurrence of sexual size dimorphism, and the relation between body size and fecundity in the gravid females of *Physalaemus nattereri* and *P. albonotatus*, at Serra da Bodoquena, Brazil. These two species commonly inhabit open areas at the Serra da Bodoquena. The reproductive period was determined through the observation of males vocalizing, couples in amplexus, and presence of tadpoles. The reproductive effort was measured as percentage of gonad mass relative to body mass. *Physalaemus nattereri* reproduced from October to January, while *P. albonotatus* reproduced from October to April. The males of *P. nattereri* invested more in reproduction than *P. albonotatus*, but the females of *P. albonotatus* had a higher reproductive effort than *P. nattereri*. *Physalaemus nattereri* presented sexual dimorphism in size and body mass, where females, on average, were larger than males. We found no sexual dimorphism in size and body mass for *P. albonotatus*. Females of both species presented a significant relation between snout-vent length (SVL) and the number of mature eggs and between the SVL and ovary mass. Both species presented the same egg laying behaviour, but differences in attraction behaviour were observed. Reproduction of *P. nattereri* is explosive, while *P. albonotatus* is continuous. Both species can adapt to several types of habitat due to behavioral and physiological plasticity.

Key words: anurans, *Physalaemus nattereri*, *P. albonotatus*, reproduction, Serra da Bodoquena.

Resumen: Estrategias reproductivas de *Physalaemus nattereri* (Steindachner, 1863) y *P. albonotatus* (Steindachner, 1864) en la Sierra de Bodoquena, Estado de Mato Grosso del Sur, Brasil. – Hay una elevada diversidad en los patrones de actividad de los coros y estrategias reproductivas de los anfibios, principalmente entre las especies de las regiones tropicales. En este estudio se analiza el periodo y esfuerzo reproductor, la existencia de dimorfismo en el tamaño de los ejemplares maduros y la relación entre el tamaño corporal y la fecundidad de las hembras grávidas de *Physalaemus nattereri* y *P. albonotatus*, dos especies habituales de áreas abiertas de la Sierra de Bodoquena, Brasil. El período reproductor se determinó mediante observación de machos vocalizando, parejas en *amplexus* y presencia de renacuajos. El esfuerzo reproductor fue medido como el porcentaje de masa gonadal respecto a la masa corporal. *Physalaemus nattereri* se reprodujo de octubre a enero, mientras *P. albonotatus* lo hizo de octubre a abril. Los machos de *P. nattereri* invirtieron más en la reproducción que los de *P. albonotatus*, pero las hembras de *P. albonotatus* mostraron mayor esfuerzo reproductor que las de *P. nattereri*. Los ejemplares de *P. nattereri* presentaron dimorfismo sexual en el tamaño y masa corporal, siendo las hembras, por término medio, más grandes que los machos, mientras que no se encontraron diferencias en el caso de *P. albonotatus*. Las hembras de ambas especies presentaron una relación significativa entre

la longitud hocico-cloaca (SVL) y el número de huevos maduros y también entre el SVL y masa ovárica. Ambas especies presentaron el mismo comportamiento de puesta, pero se observaron diferencias en el comportamiento de atracción. La reproducción de *P. nattereri* es explosiva, mientras la de *P. albonotatus* es continua. Ambas especies pueden adaptarse a varios tipos de hábitat debido a su plasticidad etológica y fisiológica.

Palabras clave: anuros, *Physalaemus nattereri*, *P. albonotatus*, reproducción, Sierra de Bodoquena.

INTRODUCTION

There is a great diversity of activity patterns and reproductive strategies in amphibians (BEVIER, 1997). In temperate regions, the reproductive activity depends on both temperature and rainfall, being usually cyclical (ROME *et al.*, 1992). But, in tropical regions, amphibians are capable of continuous reproduction, rainfall being the factor to determine seasonality (AICHINGER, 1987; DUELLMAN & TRUEB, 1994). The environmental conditions in tropical regions during the wet season are favorable for the reproduction of amphibians during several months. However, some species reproduce only during a few days every year (BEVIER, 1997). WELLS (1977) classified the diverse reproductive patterns of tropical anurans in two main types: explosive and continuous. Explosive reproduction is characterized mainly by occurring in short periods (hours or days), by the low selectivity of males (active search for females), chorus formations and arrival of females and males at the breeding pond is quite synchronous, while in the continuous reproduction the reproductive period is longer (several months), males are more selective and are territorial, there is an asynchrony in the arrival of males and females to the pond. Intermediate patterns can associate characteristics of continuous and explosive breeding (BASTOS, 1995).

A reproductive strategy may be viewed as the combination of physiological, morphological, and behavioral attributes that act in

concert to produce the optimum number of offspring under certain environmental conditions (DUELLMAN & TRUEB, 1994). In this way, different strategies can increase the efficiency of reproduction, minimizing the cost and/or risks associated with reproduction (HARVEY & PAGEL, 1993). The cost of reproduction is important to understand life history patterns (POUGH *et al.*, 1998) and sexual selection (TRIVERS, 1972). In oviparous species the energy content of the eggs is considered to be an estimation of the energy spent in reproduction (TINKLE *et al.*, 1970), but energy can be spent in other manners, such as nest construction, vocalization, mate and egg deposition (RYAN *et al.*, 1983). The estimation of reproductive effort allows to measure the energy spent with reproduction (STEARNS, 1992). A way to assess reproductive is to measure the size, mass or volume of gonads or clutches relative to body size, mass or volume (e.g. CRUMP, 1974; STEARNS, 1992; PRADO *et al.*, 2000). In general, clutch volume is correlated with female size, because of the limited availability of space in the abdominal cavity of the female (KAPLAN & SALTHER, 1979; SHINE, 1992; PRADO *et al.*, 2000).

More than 50% of the known anuran species live in the Neotropical region (DUELLMAN, 1999) and exhibit a great diversity of reproductive modes (CRUMP, 1974) that seemingly are correlated with the variety of habitats (POUGH *et al.*, 1998). Despite the high anuran diversity, the information about their life histories is

insufficient and there are few detailed studies about reproduction (e.g. CARDOSO *et al.*, 1989; KRÜGEL & RICHTER, 1995). More specific studies, such as reproductive effort, are rare (e.g. LAMPO & MEDIALDEA, 1996; PRADO *et al.*, 2000).

Studies on anuran reproduction in Brazil were made mostly in the southeastern region (e.g. BERTOLUCI, 1998; FREITAS *et al.*, 2001) and in the Central Amazonian rainforest (e.g. MARTINS, 1988; JUNCÁ, 1998). Studies on the anuran fauna of the Cerrado (Brazilian savanna) are recent (COLLI *et al.*, 2002) and, despite the high human impact on the environment on the cerrado (BEEBEE, 1996), the biology of anurans remains poorly known (POMBAL & BASTOS, 1996; RODRIGUES *et al.*, 2003).

The present study focused on some aspects of the reproduction of *Physalaemus nattereri* (Steindachner, 1863) and *P. albonotatus* (Steindachner, 1862) in temporary pond (artificial cattle drinking pond) and flooded area, at Serra da Bodoquena (Cerrado), State of Mato Grosso do Sul, Brazil. The aims of this investigation were: (a) to identify the reproductive period and pattern of both species, (b) to determine clutch and egg size, (c) to estimate reproductive effort, (d) to assess the existence of sexual dimorphism in size and body mass, and (e) to assess the relationship between body size and mass, and the number of mature ovarian eggs and ovarian mass in gravid females.

MATERIALS AND METHODS

The study was carried out at Serra da Bodoquena, Canaã Farm (20° 40' 30.4" S, 56° 45' 20.2" W) and Canaã Settlement (20° 41' 32.3" S, 56° 44' 34.3" W), municipality of Bodoquena, Mato Grosso do Sul State, southwestern Brazil. Mean annual temperature

is 21°C, and mean annual precipitation is approximately 1500 mm (ALVARENGA *et al.*, 1982) (Fig. 1). The rainy period occurs from October to April, with a dry season extending from May to September (RODRIGUES *et al.*, 2003).

The Serra da Bodoquena is located in the south-center portion of the State, on the border with the Pantanal of Nabileque floodplain (BOGGIANI & CLEMENTE, 1999). The vegetation of the plateau varies according to the relief and soil type (e.g. semi-deciduous forest and field of gramineae) (FURTADO *et al.*, 1982). Breeding population was surveyed in two temporary water bodies: (a) a pond of approximately 100 m², depth ranging from 20 to 40 cm, and vegetation composed of Gramineae and Asteraceae shrubs, and (b) a flooded field with an area of approximately 500 m², depth ranging from 15 to 80 cm, and vegetation composed of Gramineae. Accumulation of water in flooded

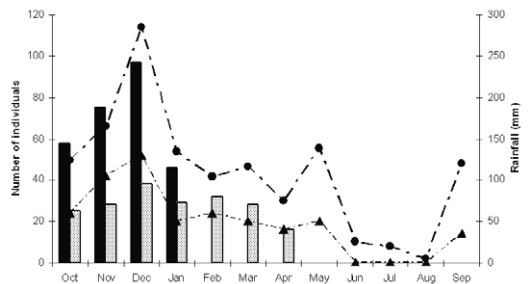


FIGURE 1. Number of individuals present in monthly samples (black bar is total of individuals of *P. nattereri* and dotted white bar is total of *P. albonotatus*) and total rainfall per month at the study site (black circle is total rainfall during the study and black triangle is rainfall anoted during four days by months of study).

FIGURA 1. Número de individuos presentes en los muestreos mensuales (la barra negra representa el total de individuos de *P. nattereri* y la punteada blanca el total de individuos de *P. albonotatus*) y precipitación mensual total en el lugar de estudio (el círculo negro representa la precipitación total durante el estudio y el triángulo negro la registrada durante cuatro días por mes de estudio).

field occurs due to soil type and small depression in land. The two study sites were approximately 4 km apart.

Data were collected during about 4 days each month from October 2000 to September 2001 in each water body. The reproductive period was determined based on direct observation of males vocalizing, amplexant pairs or presence of tadpoles. Oviposition sites were characterized by recording the presence or absence of vegetation.

The individuals collected were transported in plastic bags and sacrificed by freezing. The snout-vent length (SVL) of adults was measured to the nearest 0.1 mm with a vernier calliper. The total body mass (BM) and gonad mass (GM) of males and females were determined to the nearest 0.001 g with a digital balance. The gonads were removed through a ventro-lateral incision. The diameter of the eggs was measured with an ocular micrometer to the nearest of 0.1 mm. The largest and most pigmented eggs were considered to be mature (CRUMP, 1974), with a size of 0.5 mm for *Physalaemus albonotatus* and 0.7 mm for *P. nattereri*. Mean number of eggs per clutch was estimated based on the number of mature ovarian eggs (NME) found in the ovaries of the gravid females. Voucher specimens were deposited in the Zoological Collection of the Federal University of Mato Grosso do Sul (*Physalaemus nattereri* ZUFMS-526-529 and *P. albonotatus* ZUFMS-530-532).

To assess the relation of female fecundity with (SVL and BM) linear regression analyses were performed between the following variables: (1) snout-vent length (SVL) *versus* number of mature ovarian eggs (NME), (2) body mass (BM) *versus* NME, (3) SVL *versus* ovary mass (OM), and (4) BM *versus* OM.

Student's t-tests were used to compare male and female SVL, reproductive effort (RE)

and body mass. Reproductive effort was estimated as percentage of gonad mass (GM) relative to body mass.

RESULTS

The reproductive activity of *P. nattereri* occurred from October to January, and was related to the period of high rainfall (daily values > 50 mm) (Fig. 1). Most reproductive activity was observed at the pond and occurred up to three days after rainfall. Males formed choruses to attract females to the flooded area. Males also sought actively for females, swimming and vocalizing (choruses) on the water surface. When in amplexus, they used the margins of temporary pond and flooded area with presence and absence of vegetation (footprint of animals) to deposit the clutches. More than one pairs of *P. nattereri* were observed to deposit eggs in the same nest. The reproductive activity of *P. albonotatus* began in October and extended until April, corresponding to the wet season in the region (Fig. 1). Males of *P. albonotatus* were observed emitting calls from the margins of temporary pond and flooded area, hidden amidst the vegetation (Gramineae), and in small depressions caused mainly by footprints of animals.

Mean number of eggs per clutch was 3765 ± 1249 ($n = 39$) for *P. nattereri* and 1474 ± 418 ($n = 29$) for *P. albonotatus*. Clutches size differed significantly between species ($df = 49$, $t = 10.68$, $p < 0.001$). Mean diameter of eggs of *P. nattereri* ($1.20 \text{ mm} \pm 0.20$, $n = 85$) was larger compared to *P. albonotatus* ($0.98 \text{ mm} \pm 0.21$, $n = 239$, $df = 174$, $t = 8.29$, $p < 0.001$).

Sexual size dimorphism both in SVL and BM was observed for *P. nattereri*, females being, on average, larger and heavier than males (Table 1). For *P. albonotatus* no differences in size and body mass between

TABLE 1. Data of snout-vent length (SVL) (mm) and body mass (BM) (g) of males and females of *P. nattereri* and *P. albonotatus*.**TABLA 1.** Valores de la longitud hocico-cloaca (SVL) (mm) y masa corporal (BM) (g) de machos y hembras de *P. nattereri* y *P. albonotatus*.

		Males			Females				
		N	$\bar{x} \pm SD$	Range	N	$\bar{x} \pm SD$	Range	t	p
<i>P. nattereri</i>	SVL	42	47.3 \pm 2.4	42.8-55.0	42	51.3 \pm 2.7	43.0-56.4	7.22	< 0.001
	BM	41	11.4 \pm 1.7	7.59-16.0	41	19.2 \pm 4.0	9.78-26.9	11.7	< 0.001
<i>P. albonotatus</i>	SVL	35	29.6 \pm 1.20	27.4-32.4	30	30.2 \pm 1.80	26.4-34.1	1.73	> 0.05
	BM	36	2.36 \pm 0.38	1.57-3.48	24	2.20 \pm 0.50	1.18-3.33	1.4	> 0.05

males and females were detected. Males of *P. nattereri* had significantly higher RE than *P. albonotatus*, while the relation was inverted for females, *P. albonotatus* having significantly higher RE than *P. nattereri* (Table 2).

Females of *P. nattereri* showed a significant and positive relationship between SVL vs. NME ($n = 40$, $r^2 = 0.31$, $p < 0.001$) (Fig. 2A), BM vs. NME ($n = 42$, $r^2 = 0.34$, $p < 0.001$) (Fig. 2B), SVL vs. OM ($n = 39$, $r^2 = 0.53$, $p < 0.001$) (Fig. 2C), BM vs. OM ($n = 40$, $r^2 = 0.74$, $p < 0.001$) (Fig. 2D), and females of *P. albonotatus* showed a significant and positive relationship between SVL vs. NME ($n = 29$, $r^2 = 0.14$, $p = 0.04$) (Fig. 2E) and BM vs. OM ($n = 23$, $r^2 = 0.37$, $p = 0.002$) (Fig. 2F). The variables SVL vs. OM, and BM vs. NME were not significantly correlated in *P. albonotatus*.

DISCUSSION

The reproductive activity of *P. nattereri* and *P. albonotatus* occurred in the wet season in the study area as recorded for tropical anurans in other studies (AICHINGER, 1987; PRADO *et al.*, 2000). Despite the great difficulty in defining the reproductive pattern of a species, due to the great variation among populations (BASTOS, 1995), we considered *P. nattereri* to be an explosive breeder and *P. albonotatus* a continuous breeder, as defined by WELLS (1977) and ARAK (1985).

The reproductive pattern observed for *P. nattereri* is similar to that of *Bufo bufo* (males alternate between bouts of calling and searching; high densities of individuals in pond and eggs into huge communal masses or nest) (EIBL-EIBESFELDT, 1950) and other

TABLE 2. Data of gonad mass (GM) (g) and reproductive effort (RE) of males and females of *P. nattereri* and *P. albonotatus*.**TABLA 2.** Valores de la masa gonadal (GM) (g) y esfuerzo reproductivo (RE) de machos y hembras de *P. nattereri* y *P. albonotatus*.

		<i>P. nattereri</i>			<i>P. albonotatus</i>				
		N	GM ($\bar{x} \pm SD$)	RE ($\bar{x} \pm SD$)	N	GM ($\bar{x} \pm SD$)	RE ($\bar{x} \pm SD$)	t	p
Males		41	0.028 \pm 0.007	0.24 \pm 0.05	36	0.004 \pm 0.001	0.17 \pm 0.06	5.81	< 0.001
Females		41	4.343 \pm 1.558	22.2 \pm 5.0	23	0.812 \pm 0.19	27.3 \pm 5.10	3.9	< 0.001

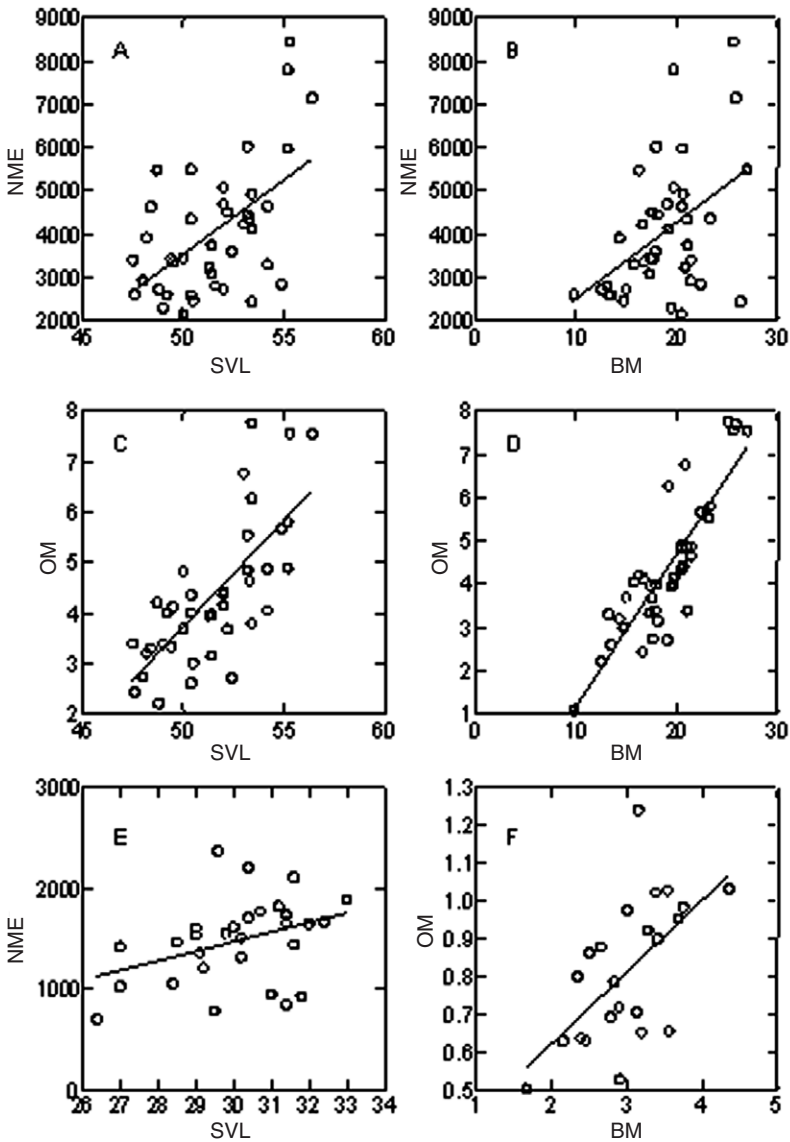


FIGURE 2. Relations between (A) snout-vent length (SLV) vs. number of mature ovarian eggs (NME) ($N = 40$, $r^2 = 0.31$, $p < 0.001$) of *P. nattereri* females, (B) body mass (BM) vs. NME ($N = 42$, $r^2 = 0.34$, $p < 0.001$) of *P. nattereri* females, (C) SLV vs. ovary mass (OM) ($N = 39$, $r^2 = 0.53$, $p < 0.001$) of *P. nattereri* females, (D) BM vs. OM ($N = 40$, $r^2 = 0.74$, $p < 0.001$) of *P. nattereri* females (E) SVL vs. NME ($N = 29$, $r^2 = 0.14$, $p = 0.04$) of *P. albonotatus* females, and (F) BM vs. OM ($N = 23$, $r^2 = 0.37$, $p = 0.002$) of *P. albonotatus* females. All specimens were collected at Serra da Bodoquena, MS, Brazil, from October 2000 to September 2001.

FIGURA 2. Relaciones entre (A) longitud hocico-cloaca (SLV) vs. número de huevos maduros (NME) ($N = 40$, $r^2 = 0.31$, $p < 0.001$) de hembras de *P. nattereri*, (B) peso corporal (BM) vs. NME ($N = 42$, $r^2 = 0.34$, $p < 0.001$) de hembras de *P. nattereri*, (C) SLV vs. peso del ovario (OM) ($N = 39$, $r^2 = 0.53$, $p < 0.001$) de hembras de *P. nattereri*, (D) BM vs. OM ($N = 40$, $r^2 = 0.74$, $p < 0.001$) de hembras de *P. nattereri*, (E) SVL vs. NME ($N = 29$, $r^2 = 0.14$, $p = 0.04$) de hembras de *P. albonotatus* y (F) BM vs. OM ($N = 23$, $r^2 = 0.37$, $p = 0.002$) de hembras de *P. albonotatus*. Todos los ejemplares fueron colectados en la Serra da Bodoquena, MS, Brazil, de octubre de 2000 a septiembre de 2001.

species (WELLS, 1977; ARAK, 1985). BEZERRA (1998) pointed out that *P. nattereri* is preyed upon by many terrestrial vertebrates. Possibly, this reproductive pattern reduces the predation pressure on individuals through risk dilution (an individual's lower chance of being eaten) (KREBS & DAVIES, 1993).

Physalaemus nattereri and *P. albonotatus* can vocalize and breed at several sites with the presence or absence of vegetation or in small depressions formed by footprints of animals, as observed in other species of *Physalaemus* (HADDAD *et al.*, 1988; DUELLMAN & TRUEB, 1994; KWET & DI-BERNARDO, 1999). CARDOSO *et al.* (1989) studied an anuran community in the southeastern Brazil and suggested that the different disposition of the clutches in the environment could be associated to different defensive tactics of the offspring. This way, clutches associated to the vegetation could be protected from predators.

Physalaemus nattereri and *P. albonotatus* exhibit the same reproductive mode (mode 8; Foam nest on pond; feeding tadpoles in pond), according to the classification proposed by DUELLMAN & TRUEB (1994). *Physalaemus nattereri*, the larger species, produced larger clutches and eggs, as compared to *P. albonotatus*, supporting the results of CRUMP (1974), DUELLMAN & TRUEB (1994), and PRADO *et al.* (2000), that among species exhibiting the same reproductive mode, larger species tend to produce larger clutches and larger eggs.

Many amplexant pairs of *P. nattereri* spawn in the same nest (communal nest) which was probably due to the great density of reproducing individuals. GIARETTA & MENIN (2004) observed communal nests in *P. cf. fuscomaculatus* and other *Physalaemus* species (probably *P. nattereri*) in Cerrado of South-eastern of Brazil. RYAN (1985) observed common nests for *P. pustulosus* and

suggested that the small surface area relative to egg mass volume produced by the construction of the common nests could reduce the exposure of eggs to the air, decreasing desiccation and predation risks. HÖDL (1990) and GIARETTA & MENIN (2004) observed that communal nesting is facultative for *P. cf. fuscomaculatus* and *P. ephippifer* respectively. More studies on reproductive biology are necessary to understand why some individuals of *P. nattereri* build communal nests while this behavior is absent in *P. albonotatus*.

Females of *P. nattereri* were, on average, larger than males, which is the case for other leptodactylids, such as *Leptodactylus podicipinus* (PRADO *et al.*, 2000), *Physalaemus cuvieri*, and *P. lisei* (KWET & DI-BERNARDO, 1999), and most anurans species (SHINE, 1979). The causes of that phenomenon are diverse: the capacity of larger females to produce larger clutches and eggs (CRUMP & KAPLAN, 1979; PRADO *et al.*, 2000), differences in the age of the first reproduction or in the mortality rate caused by higher predation pressure on larger males (HOWARD, 1981), or even restrictions to the growth of males due to energy demand linked to reproductive activity (WOOLBRIGHT, 1989). *Physalaemus albonotatus* did not exhibit sexual size dimorphism, which was also observed by MARTINS & HADDAD (1988) and MARTINS (1993) for *Hyla faber*. The nonexistence of sexual size dimorphism can be owed to similar growth rates of both sexes (POUGH *et al.*, 1998) or to male-male competition involving physical combat (SHINE, 1979). Nevertheless, more works are necessary on ecological and reproductive aspects to explain why there is sexual size dimorphism in *P. nattereri* but not in *P. albonotatus*.

Males of *P. nattereri* had relatively larger in gonads than *P. albonotatus*. PRADO *et al.*

(2000) observed that males of *Leptodactylus chaquensis* had larger gonads than *L. podicipinus*, and that behavioral differences between both species could partially explain this difference. Also, *L. chaquensis* and *L. podicipinus* exhibit polyandry (more than one male trying to fertilize the eggs of a female) (PRADO & HADDAD, 2003), which may be an important factor in determining testes size. Testes size is also related to the intensity of the sperm competition and occurrence of multimale spawning in anurans (PRADO & HADDAD, 2003). Species that occurs this behavior the males have larger testes than species where this behavior is absent (JENNIONS & PASSMORE, 1993; EMERSON, 1997). According to GROSS (1985), in cases of external fertilization, there are two possible strategies for males to increase their fertilization success: to release a great number of sperm or to be close to the female. The probability of fertilization through sperm retained in the foam nest is high (KUSANO *et al.*, 1991), and peripheral males in the same foam nest are capable of fertilizing the eggs (JENNIONS & PASSMORE, 1993). PRADO & HADDAD (2003) suggested that sperm competition can also be an important factor affecting testes size in *Leptodactylus chaquensis* and *L. podicipinus*. These observations can be plausible to explain the differences in testes size between the species of *Physalaemus* in the present study, as shown in *P. nattereri* the occurrence of multimale spawning.

Females of *P. albonotatus* (RE 27.3%) invested more in gonads than *P. nattereri* (RE 22.2%). Our results do not support CRUMP & KAPLAN (1979), who found that, independently of reproductive mode, females of any anuran species produce clutches with similar amounts of energy. If an individual allocates a larger amount of energy to reproduction in a particular reproductive

season, it can reduce the amount of available energy for growth or reproduction in the next season (POUGH *et al.*, 1998). Small species, as is the case of *P. albonotatus*, have shorter life spans than larger species, and, consequently, smaller chance of reproducing in the future. Therefore, females of smaller species probably allocate relatively more energy for a reproductive event than do larger species (POUGH *et al.*, 1998).

Several studies demonstrated that female size is positively correlated with the number of eggs or ovary weight (e.g. LANG, 1995; PRADO *et al.*, 2000). For females of *P. nattereri* 31 and 34% of the variation in NME, and 53 and 74% in OM were explained, respectively, by SVL and BM. For *P. albonotatus*, 14% of the variation in NME, and 37% of the variation in OM were explained, respectively, by SVL and BM. CRUMP (1974), studied 41 species of Ecuadorian anurans from different families, and found a positive relationship between SVL and NME in only 26.8% of the species. Larger body size confers reproductive advantages to females, such as an increase in the production or size of eggs (CRUMP, 1974; HOWARD, 1978). The variation of data was higher for BM than SVL in both species. Body volume or mass are more appropriate measures to estimate the NME than SVL (LANG, 1995; PRADO *et al.*, 2000). Among anurans body growth never ceases totally and older individuals are more fertile and exhibit higher reproductive success (HOWARD, 1988).

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