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REPRODUCTIVE BIOLOGY OF *Melanophryniscus devincenzii* (ANURA: BUFONIDAE) IN SOUTHERN BRAZIL

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ABSTRACT

The reproductive biology of *Melanophryniscus devincenzii* was described here, based on morphometrics and gonadal analysis of 86 individuals collected in the Sertão Municipal Natural Park, Rio Grande do Sul, Brazil. Individuals were captured both manually and using pitfall traps. We identified 63 males and 23 females, with the sex ratio biased towards males. Sexual dimorphism was observed, with females being larger than males. No significant correlation was found between female body size and oocyte number, nor between male body size and testicular mass, indicating that energetic investment may be more focused on reproduction than on growth. All analyzed females (except one) exhibited mature oocytes, immature and atretic oocytes in their ovaries, suggesting that females may be latent to reproductive event. This reproductive latency benefit to those species that have explosive reproductive events and depend on rainfall.

Keywords: Explosive reproduction, reproductive investment, fecundity, fat bodies.

RESUMEN

Biología reproductiva de *Melanophryniscus devincenzii* (Anura: Bufonidae) en el sur de Brasil. Se describe la biología reproductiva de *Melanophryniscus devincenzii* basada en el análisis morfométrico y gonadal de 86 individuos colectados en el Parque Natural Municipal de Sertão, Río Grande del Sur, Brasil. Los individuos fueron capturados (manualmente y usando trampas de caída). Identificamos 63 machos y 23 hembras. La proporción de sexos estuvo sesgada a favor de los machos, y se comprobó la existencia de dismorfismo sexual en la especie, con hembras más grandes que los machos. No se encontraron relaciones significativas entre el tamaño de las hembras y el número de oocitos; ni entre el tamaño de los machos y la masa testicular, indicando que la inversión energética estaría centrada más en la reproducción que en el crecimiento. Todas las hembras analizadas (con la excepción de una) presentaron oocitos maduros, acompañados de oocitos inmaduros y atrésicos en sus ovarios, evidenciando que las hembras estarían siempre preparadas para el evento reproductivo, lo cual resultaría beneficioso considerando que los eventos reproductivos del tipo explosivo dependen de las precipitaciones.

Palabras Clave: Reproducción explosiva, inversión reproductiva, fecundidad, cuerpos grasos.

INTRODUCTION

Amphibians exhibit a wide range of reproductive modes, which include variations in egg characteristics, oviposition sites, and the presence of parental care (Duellman & Trueb, 1986; Haddad & Prado, 2005). The reproduction of several anuran species is particularly influenced by abiotic variables. Temperature and precipitation are the primary climatic factors affecting anuran reproductive cycles (Cardoso & Martins, 1985), which can directly alter the timing and duration of the reproductive period (Lajmanovich, 2000). According to Wells (1977), there are two temporal reproductive strategies in anurans: prolonged and explosive breeding. However, these strategies represent the extremes of a continuum along which most species are distributed. Anurans with explosive reproduction concentrate their reproductive activity within hours or days, with males and females migrating synchronously to breeding sites. In prolonged breeders, the activity period extends over several weeks or months; the arrival of both sexes is asynchronous, and females may choose males (Wells, 1977; Wells, 2007).

Reproduction in amphibians may be influenced by other factors, such as the energy allocated to fat bodies (FB) (Jørgensen, 1992). Fat bodies serves as a crucial nutritional source during periods of drought or hibernation (Saidapur & Hoque, 1996; Hillman et al., 2009). These structures are located in the gonads of both males and females and are involved in the metabolism of gonadal processes (particularly lipid synthesis and storage), as well as in folliculogenesis and yolk production (Mendez-Tepepa et al., 2023). Previous studies have demonstrated an inverse relationship between FB abundance and gonadal development in anurans, confirming that these structures serve as energy reserves for reproduction (Díaz-Páez & Ortiz, 2001; Pereira & Maneyro, 2012; Pereira et al., 2015). In female anurans that do not exhibit parental care, reproductive success largely depends on the total energy stored in the oocytes (Grafe et al., 1992). Additionally, the quality of their offspring is directly affected by the amount of energy stored in the fat bodies (Díaz-Paéz & Ortiz, 2001), which supports oocyte development (Mendez-Tepepa et al., 2023).

Melanophryniscus Gallardo, 1961 is a monophyletic genus belonging to the family Bufonidae, distributed across Brazil (from Espírito Santo, Minas Gerais, and Mato Grosso do Sul to Rio Grande do Sul), Bolivia (with one species reaching the inter-Andean valleys in the south), central and northern Argentina (from Buenos Aires to Jujuy), Paraguay, and Uruguay (Frost, 2024). Currently, the genus comprises 31 species, commonly known as “South American red-bellied toads” (Frost, 2024). The first study on reproductive behavior in this genus was carried out on *Melanophryniscus stelzneri*, which determined an explosive reproduction (Fernández, 1927). Patterns of reproductive activity were studied on different species of the Genus *Melanoprhyniscus.* For instance, reproductive activity was reported to *M. rubriventris* (Vaira et al., 2005) and *M. diabolicus* (Cairo et al., 2008); while oviposition site selection was examined in *M. rubriventris* and *M. stelzneri* (Goldberg et al., 2006; Pereyra et al., 2011); and calling activity was studied in males of *M. stelzneri* (Pereyra et al., 2016); and *M. cupreuscapularis (*Duré et al., 2015). More recent investigations have focused on the, reproductive biology and use of microhabitats in *M. montevidensis* (Pereira & Maneyro, 2016; 2018), the reproductive traits of *M. atroluteus*, *M. devincenzii*, and *M. krauczuki* (Marangoni & Baldo, 2023); as well as the sexual dimorphism, and fertility aspects of *Melanophryniscus fulvoguttatus* (Carrillo et al., 2024) There are few studies on the natural history of *M. devincenzii* (i.e., Bortolini et al., 2013). Despite these advancements, more studies about natural history of *M. devincenzii* are nedded, to better understand the variation among poplations.

It is worth noting that several of these studies demonstrated a skewed sex ratio in favor of males during reproductive events in species of the genus *Melanophryniscus* (Bustos Singer & Gutiérrez, 1997; Vaira, 2005; Cairo, 2013; Pereira & Maneyro, 2018; Marangoni & Baldo, 2023), as well as the existence of sexual dimorphism, with females being larger than males (Pereira & Maneyro, 2018; Carrillo et al., 2024). Regarding the relationship between fecundity (F) and/or oocyte size with female size, the results are varied within the genus. For example, in species such as *M. diabolicus* and *M. montevidensis*, fecundity was not correlated with female size (Cairo et al., 2008; Pereira & Maneyro, 2018). Opposite results were reported for *M. fulvoguttatus*, where fecundity was positively correlated with female size (Carrillo et al., 2024). On the other hand, in *M. atroluteus*, a negative correlation was found between oocyte size and female size, while in *M. krauczuki*, this relationship was positive (Marangoni & Baldo, 2023). Finally, it is important to highlight that species with explosive reproductive dynamics tend to maintain a constant lipid reserve for the potential reproductive event (e.g., Valdez & Maneyro, 2016), which was demonstrated in *M. montevidensis* (Pereira & Maneyro, 2018).

The aim of this study was to describe the reproductive parameters of a *Melanophryniscus devincenzii* (Anura: Bufonidae) population from the Sertão Municipal Natural Park (PNMS), Rio Grande do Sul, Brazil, by analyzing the reproductive investment of females and the potential associations between fat body reserves and the reproductive activity of both males and females.

MATERIAL AND METHODS

Study Species

Melanophryniscus devincenzii (Klappenbach, 1968) (Fig. 1), commonly known as Devincenzi's toad or Rivera's toad, is a small-sized species characterized by a frontal swelling (Maneyro & Carreira, 2016). It is included in the phenetic group *M. tumifrons*, which comprises eight species with a restricted distribution across Paraguay, Uruguay, Argentina, and Brazil (Caramaschi & Cruz, 2002; Brusquetti & Lavilla, 2006; Airaldi et al., 2009). Some references regarding the natural history attributed to *M. aff. devincenzii* should currently be considered as *M. devincenzii* (Langone & Lavilla, 2024). In Brazil, it is found in the northern and central-western regions of the state of Rio Grande do Sul (Bastos et al., 2023). This species is primarily diurnal, although it may also be active at night, exhibiting explosive breeding dynamics associated with heavy rainfall and high humidity (Maneyro & Carreira, 2016). The species is not considered threatened at a local (Bastos et al., 2023) or global scale (IUCN, 2023).

Fig. 1. *Melanophryniscus devincenzii* individual in its natural habitat. Photo: Raúl Maneyro.

Study site and individual collection

Individuals of *M. devincenzii* were captured using manual capture and dry pitfall traps with drift fences (Cechin & Martins, 2000), between 2005 and 2011, from the Municipal Natural Park of Sertão (PNMS), Rio Grande do Sul, Brazil (28º02'31" S, 52º13'28" W) (Fig. 2). Four trap arrays were located, each consisting of 8 plastic containers placed 10 m apart and connected by a one-m-high drift fence. These traps were checked three times a week. Additionally, active searches for specimens were conducted during both day and night. All captured individuals are deposited in the Amphibian Collection of the University of Passo Fundo (CAUPF). We sexed all specimens, males were considered reproductively active if they had a developed vocal sac, or if they were found vocalizing or in amplexus at the study site.

Laboratory Work

Individuals of *M. devincenzii* were sexed via gonadal analysis. Before dissection, body mass (BM, in g) and snout-vent length (SVL, in mm) were recorded. In females, the gonads were removed to measure ovarian mass (OM) using a digital balance accurate to 0.001 g. Oocytes were subsequently classified by developmental stage as mature, immature (translucent), or atretic, following the criteria of Camargo et al. (2005) and Pereira & Maneyro (2012). Females were considered mature if they had mature oocytes in their ovaries, with the smallest female carrying mature oocytes serving as a reference to distinguish mature from immature females. Fecundity (F = number of mature oocytes) was recorded for both ovaries. Reproductive investment (RI) in reproductive females was then calculated as the ratio of F to SVL (RI = F/SVL) (Carrillo et al., 2024). The Kruskal-Wallis test was used to study the variation in the IR of females among reproductive events. To explore potential relationships between SVL and F, as well as between SVL and OM, linear regression analyses were performed on these variables.

The size (in mm) of the smallest male found in reproductive activity was used as a threshold to distinguish between mature and immature individuals. Testicular mass (TM, in g) of each individual was measured as an indicator of testicular activity in mature

Fig. 2. Collection site of *Melanophryniscus devincenzii* individuals. The black circle represents the location of the Municipal Natural Park of Sertão (PNMS) in Rio Grande do Sul.

males (de Oliveira et al., 2007; Bortolini et al., 2018). The relationship between SVL and TM was analyzed through linear regression of these variables, and monthly variation in TM of mature males was examined using the non-parametric Kruskal-Wallis test. Additionally, to determine the existence of sexual size dimorphism in the species, SVL and BM were compared between sexes using the non-parametric Mann-Whitney U test. To assess differences in the frequency of captured males and females, the sex ratio (SR = number of males / number of females) was calculated. Finally, to examine the association between the reproductive activity of *M. devincenzii* and fat accumulation, fat bodies (FB) in both males and females were categorized based on abundance (absent, small, intermediate, and large) (Pereira & Maneyro, 2012).

RESULTS

A total of 86 individuals of *M. devincenzii* were captured and analyzed, comprising 23 females and 63 males. Three instances of breeding activity were recorded for the species at the study site, where males were observed calling, amplectant pairs, and egg clutches in lotic water bodies and along stream margins. Peaks in capture numbers corresponded to these three breeding events that occurred in September 2009 (N=8 individuals), December 2010 (N=37), and July 2011 (N=22) (Fig. 3). During these events, males were more abundant than females (Fig. 3), and the sex ratio was skewed in favor of males (SR=3.6 in December 2010; and SR=2.7 in July 2011). The exception was in September 2009, where the sex ratio was balanced (SR=1). The mean SVL for males was 23.2 ± 1.7 (range: 17.7–27.4) mm, while the mean body mass (BM) was 1.4 ± 0.4 (range: 0.5–2.2) g. For females, these values were 27.5 ± 2.1 (range: 23.1–32.5) mm and 2.2 ± 0.6 (range: 1.3–3.7) g. The smallest female with mature oocytes measured 24.9 mm, and the smallest male found in reproductive activity measured 20.45 mm. All individuals found below these reference values for each sex were considered immature. A total of 22 mature females and 60 mature males were identified. Significant sexual size dimorphism was found in *M. devincenzii*, as females exhibited a greater SVL (U=72; $p<0.05$) (Fig. 4a) and greater BM (U=180.5; $p<0.05$) (Fig. 4b) than males.

The mean ovary mass (OM) in females was 0.25 ± 0.25 (range: 0.01–0.92) g. Of the 23 females analyzed, 22 exhibited all three types of oocytes in their ovaries: mature, immature, and atretic. The mean fecundity (F) was 126.5 ± 109.4 (range: 12–313) oocytes. No significant relationship was found between $\log_{10}$ SVL and $\log_{10}$ F ($R^2=0.08$; $p=0.19$; Fig. 5a); however, a significant positive relationship was found between $\log_{10}$ SVL and $\log_{10}$ OM ($R^2=0.19$; $p=0.04$) (Fig. 5b). The mean RI was 4.5 ± 3.8 (0.5–12.2) (Fig. 6), and no significant variation was observed in this parameter across different breeding events (H=5.55; $p=0.06$). For

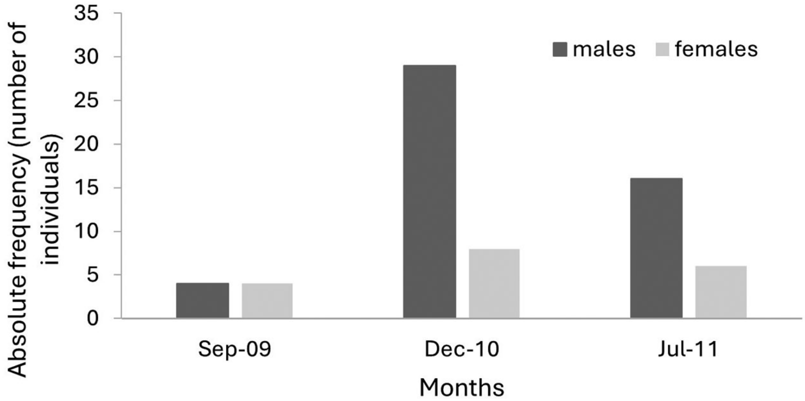

Fig. 3. Variation in the absolute frequency of *Melanophryniscus devincenzii* individuals observed during breeding activity at the study site.

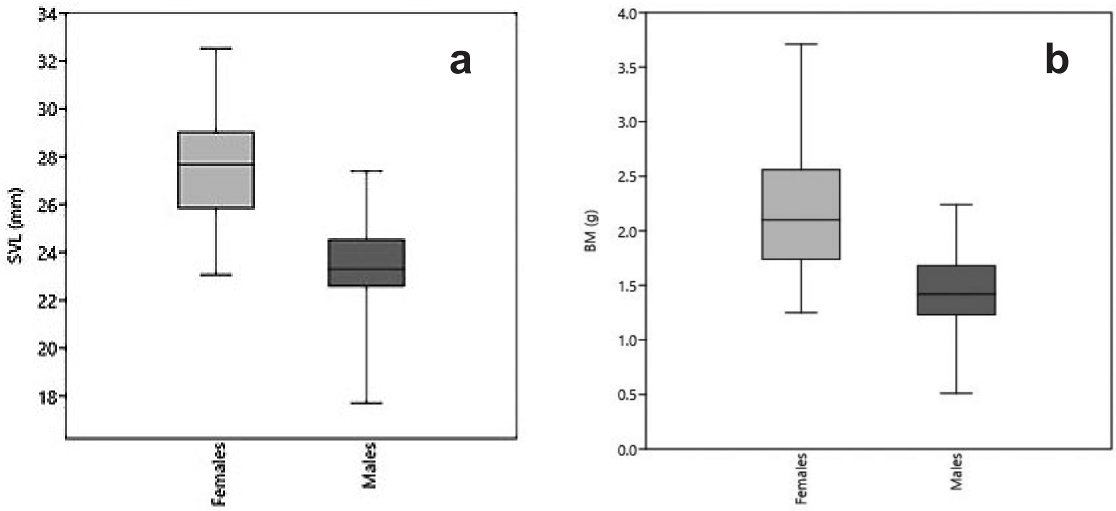

Fig. 4. a. Variation in snout-vent length (SVL, mm) and **b.** variation in body mass (BM, g), of males and females of *M. devincenzii*.

males, the mean testis mass (TM) was 0.004 ± 0.002 (range: 0.0007–0.001) g. No significant relationship was found between $\log_{10}$ SVL and $\log_{10}$ TM (R^2=0.0001; p=0.93) (Fig. 7), and there was no significant variation in TM across months (H=7.69; p=0.05).

Finally, 60.9% of the females analyzed did not display fat bodies (FB). In December 2010 and July 2011 (during reproductive activity events), females exhibited FB across different abundance categories (Fig. 8). In contrast, 83.3% of the males analyzed presented FB. Males found in reproductive activity exhibited FB, with the "abundant" category predominating in December 2010 and July 2011 (Fig. 9).

DISCUSSION

This study recorded three reproductive activity events for *Melanophryniscus devinzenzii*: in September 2009, December 2010, and July 2011. The species exhibits an explosive reproductive pattern, breeding in semi-permanent marshes in open environments following heavy rainfall. Reproductive events for this species have been reported at the study site following precipitation exceeding 60 mm (Bortolini et al., 2011). Reproductive activity associated with intense rainfall has been observed in most species of the genus, including *M. stelzneri* (Bustos Singer & Gutierrez, 1997), *M. montevidensis* (Prigioni & Garrido, 1989; Pereira & Maneyro, 2018), *M. rubiventris* (Vaira,

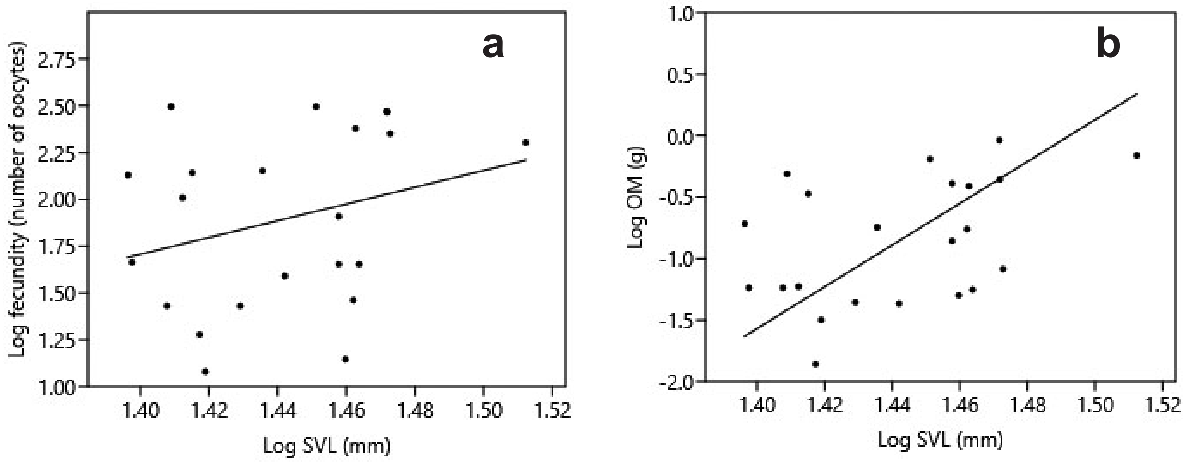

Fig. 5. a. Linear regression model between $\log_{10}$ SVL (mm) and $\log_{10}$ F (number of oocytes); and **b.** linear regression model between $\log_{10}$ SVL (mm) and $\log_{10}$ OM (g) in females of *M. devincenzii*.

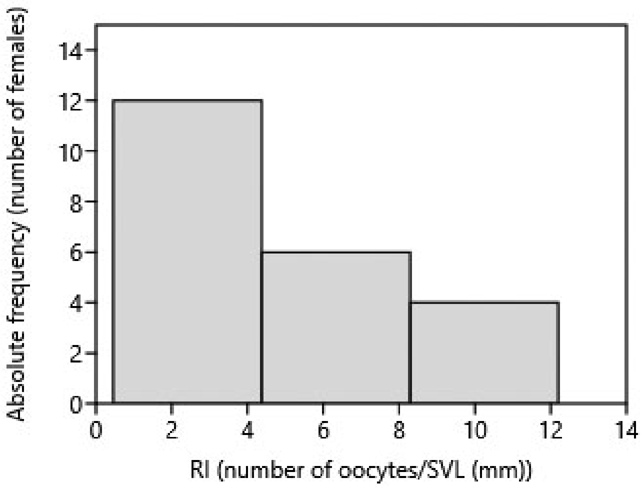

Fig. 6. Frequency distribution of Reproductive Investment (RI) in females of *M. devincenzii*.

2005), *M. diabolicus* (Cairo et al., 2008), and *M. cambaraensis* (Santos & Grant, 2011). During breeding events, clutches and exotrophic tadpoles were observed in flowing water bodies, indicating that the species exhibits reproductive mode 2 (Haddad & Prado, 2005). Egg deposition in lotic water bodies has also been observed in Uruguayan populations of *M. devincenzii* (Maneyro, 2008).

Throughout the study, 73.3% of all individuals analyzed were males. Additionally, in two of the three recorded reproductive events, male abundance was higher than that of females. Similar patterns have been reported in Uruguayan populations of *M. montevidensis*, another species with an explosive breeding strategy, where a sex ratios 3:1 or higher were recorded during reproductive events (Pereira & Maneyro, 2018).

Male-biased sex ratio during reproduction are common feature in explosive breeders, as documented by Wells (2007) and have been demonstrated in several species of the genus *Melanophryniscus,* such as *M. stelzneri*, *M. rubriventris* y *M. diabolicus;* (Bustos Singer & Gutiérrez, 1997; Vaira, 2005; Cairo, 2013). Furthermore, sexual size dimorphism was confirmed in *M. devincenzii*, with females being significantly larger and heavier than males. This pattern is consistent with observations in most anuran species (Shine, 1979), where larger females may produce larger clutches and oocytes of greater size (Prado et al., 2000; Camargo et al., 2008). However, Wells (2007) suggests that there are no differences in the sizes of amplectant males and females in explosive breeding dynamics. The results of this study contradict this assertion, since sexual dimorfism is evidente. However, this female biased

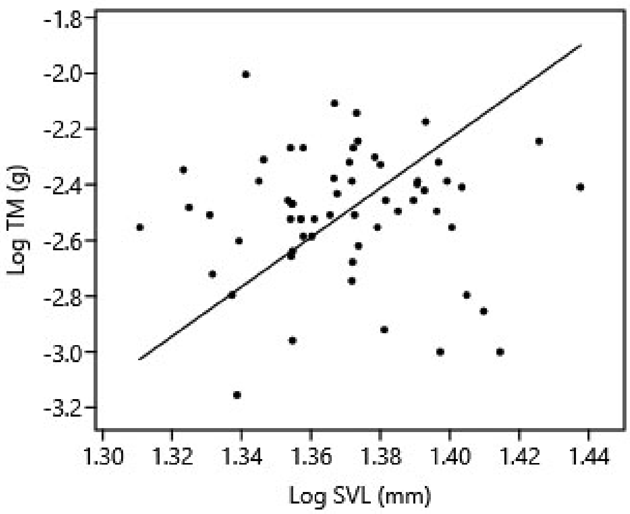

Fig. 7. Linear regression model between $\log_{10}$ SVL (mm) and $\log_{10}$ TM (g) in males of *M. devincenzii*.

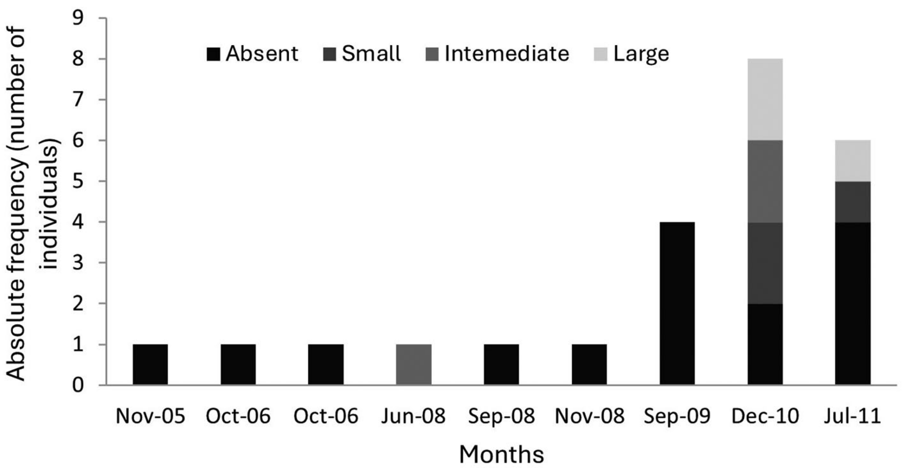

Fig. 8. Temporal variation in fat body abundance in females of *M. devincenzii*.

size dimorphism can not be associated to female fecundity. A possible explanation could be that *M. devincenzii* males initiate reproductive activity at smaller body sizes, allowing them to participate in multiple reproductive events, thus maximizing their reproductive success. This strategy would be advantageous considering that explosive breeding events are unpredictable due to their high dependence on rainfall.

All analyzed females (with the exception of one), including those collected outside reproductive events, exhibited mature oocytes in their ovaries, accompanied by immature oocytes in various stages and atretic oocytes. This finding suggests that the females are prepared for potential reproductive events by consistently maintaining a reserve of mature oocytes. The recorded fecundity for the females was comparable to that reported in other species of *Melanophryniscus*, such as *M. diabolicus* (Cairo et al., 2008), *M. cambaraensis* (Caorsi, 2011), and *M. montevidensis* (Pereira & Maneyro, 2018). No significant relationship was found between fecundity and body size, indicating that females allocate their energy resources to reproduction rather than growth in order to maximise future reproductive success, as observed in species with prolonged reproductive periods (Camargo et al., 2005; Pereira & Maneyro, 2012). Consistent with this, several females exhibited values close to the mean and high reproductive indices, previously reported in species exhibiting explosive reproduction (Pereira & Maneyro, 2018). Contrary to expectations, a significant relationship was

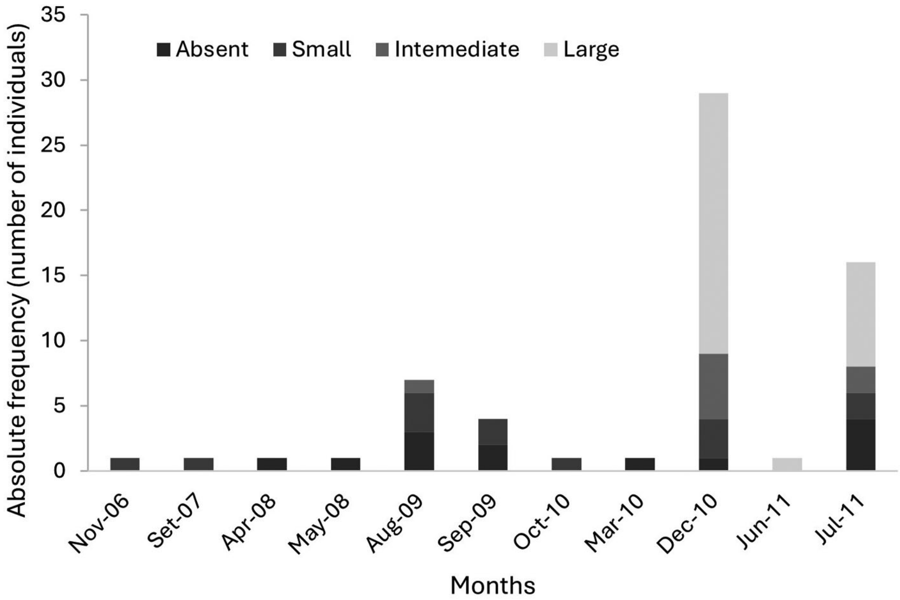

Fig. 9. Temporal variation in fat body abundance in males of *M. devincenzii*.

found between ovarian mass and female size. However, it is crucial to note that ovarian mass is influenced not only by mature oocytes but also by the immature and atretic oocytes observed in the analyzed females. In males, size did not correlate with testicular mass, and no monthly variation in this parameter was recorded, which is expected, as monthly variation in both gonadal volume and mass serves as indicators of prolonged reproductive activity (de Oliveira et al., 2007; Pereira & Maneyro, 2015).

Fat bodies can be used as energy reserves for gametogenesis; they are generally scarce during the spawning period and may decrease as oocytes develop (Frost, 1983; Jørgensen, 1992). In species with seasonal reproductive activity, an inverse relationship between fat body abundance and gonadal development has been reported, suggesting the utilization of fat bodies as energy reserves for reproduction (Díaz-Páez & Ortiz, 2001; Pereira & Maneyro, 2012; Pereira et al., 2015). In the present study, over 80% of the analyzed males exhibited fat bodies, indicating that they consistently maintain a lipid reserve that would enable increased testicular activity and calling in response to a potential reproductive event. In contrast, the analyzed females predominantly lacked fat bodies. However, females engaged in reproductive activity displayed fat bodies in various categories of abundance (with the exception of September 2009), which is consistent with an explosive reproductive pattern. Our results indicate that the species exhibits some of the expected characteristics for anuran explosive breeders; however, it should be important to analyze a greater number of females to determine whether the dynamics of fat bodies are consistent with this reproductive strategy.

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