TEMPORAL DISTRIBUTION, REPRODUCTIVE SYNCHRONY, AND MATING PATTERNS OF THE EXPLOSIVE BREEDER FROG *DERMATONOTUS MUELLERI* (ANURA: MICROHYLIDAE)

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Abstract: The knowledge about natural history of a species is fundamental for the proposition of theories in population, community, and behavioral ecology. *Dermatonotus muelleri* (Boettger, 1885) is one of the several Neotropical anuran species that still lacks basic information. These frogs are widely distributed in South America and present many peculiar morphological features, such as a reduced head size and a tongue morphology that suggests a specialized diet in ants and termites. In this study, we describe the reproductive ecology of *D. muelleri*, with special attention to the mechanisms that regulates (i) the reproductive synchrony between males and females, (ii) the operational sex ratio (OSR), and (iii) if size is a good predictor of pairs formation (assortative mating). We found that *D. muelleri* aggregates in short periods of reproductive activity (one to five consecutive nights) to reproduce. During the reproductive events, males and females arrive at the breeding sites in synchrony, using environmental (temperature and pluviosity) and biotic (termite reproductive swarms and male calling) cues. Also, there is a high population density (1,079 ± 816 individuals, n = 11 reproductive events), with a biased OSR toward the number of males. The intense male-male competition prevents any female choice, and the call function is related more to reduction of predation costs to females. We did not find size assortative mating in *D. muelleri*. The lack of size assortative mating may be a consequence of different pressure selection of males and females. While females where selected to have larger body size and offspring production, at the cost of reproductive lifespan, males are subject to an intense male-male competition which prevents the expression of female preferences.

Keywords: mating system, OSR, random mating, reproductive synchrony time lag.

DISTRIBUIÇÃO TEMPORAL, SINCRONIA REPRODUTIVA E PADRÕES DE ACASALAMENTO DO SAPO DE REPRODUÇÃO EXPLOSIVA *DERMATONOTUS MUELLERI* (ANURA: MICROHYLIDAE)

Resumo: O conhecimento sobre a história natural de uma espécie é fundamental para a proposição de teorias em ecologia de populações, comunidades e comportamental. *Dermatonotus muelleri* (Boettger, 1885) é uma das várias espécies de anuros Neotropicais que ainda carecem de informações

básicas. Essas rãs são amplamente distribuídas na América do Sul e têm muitas características morfológicas peculiares, como um tamanho reduzido da cabeça e morfologia da língua que sugere uma dieta especializada em formigas e cupins. Neste estudo, descrevemos a ecologia reprodutiva de *D. muelleri*, com especial atenção aos mecanismos que regulam (i) a sincronia reprodutiva entre machos e fêmeas e (ii) a razão sexual operacional (RSO). Nós encontramos que *D. muelleri* se reúne em curtos períodos para a atividade reprodutiva (de uma a cinco noites consecutivas). Durante os eventos reprodutivos, machos e fêmeas chegam em sincronia no ambiente estudado, usando pistas ambientais (temperatura e pluviosidade) e bióticas (enxames reprodutivos de cupins e canto de anúncio do macho). Durante os eventos, existe uma alta densidade populacional (1.079 ± 816 indivíduos, n = 11 eventos reprodutivos), com uma RSO desviada para o número de machos. A intensa competição macho-macho inibe a exibição de preferência pelas fêmeas, e a função da atividade de vocalização está mais relacionada a redução dos custos de predação para as fêmeas. Nós não encontramos acasalamento pareado por tamanho em *D. muelleri*. A falta de acasalamento pareado por tamanho pode ser uma consequência de diferentes pressões seletivas de machos e fêmeas. Enquanto fêmeas são selecionadas para um maior tamanho de corpo e produção de ovos, ao custo de oportunidades reprodutivas, machos estão expostos à uma intensa competição macho-macho o que evita a expressão de seleção pelas fêmeas.

Palavras-chave: sistema de acasalamento, OSR, acasalamento aleatório, atraso de sincronia reprodutiva.

INTRODUCTION

The importance of natural history knowledge of species to their conservation and to theories in population and communities' ecology is increasingly being recognized (Duellman, 1999a; Greene, 1986, 1994; Heyer et al., 1988; Machado et al., 1999; Martins et al., 2021; Scott Jr & Campbell, 1982). For example, the knowledge of reproduction is necessary for the success of most reintroduction and ex-situ conservation efforts (Michaels et al., 2014). One of the difficulties is that the natural history of many anuran species from different parts of the world is still poorly or unknown (Bastos et al., 2003; Haddad, 1998). In the Neotropics, particularly in Brazil, this scenario is not different. *Dermatonotus muelleri* (Boettger, 1885) is endemic to the Cerrado-Caatinga-Chaco biogeographic domain, an ecological region that covers areas in Brazil, Argentina, Bolivia, and Paraguay. This domain is characterized by a pronounced dry season and savannah like vegetation (Duellman, 1999b). Despite the wide geographical distribution, *D. muelleri* is rare in anuran surveys, because of the explosive breeding behavior characteristic of this species (Stanescu et al., 2014, 2016). Also, this frog has a semi-fossorial habit and remains hidden in underground chambers during most part of the year (Nomura and Rossa-Feres, 2011).

In this study, we describe some traits of the reproductive ecology of *D. muelleri*, with special attention to the mechanisms that regulates (i) the reproductive synchrony between males and females and (ii) the operational sex ratio (OSR). Particularly, we are interested to test if breeding synchrony between males and females depend on the temporal scales of environmental clues. Also, we (iii) tested if the size of males is a good predictor of mating pairs formation (assortative mating). Assortative mating by size is considered the most common pattern of pair formation in natural populations and has direct demographic implications for animal populations (see a review in Crespi, 1989).

Considering the fossorial habit of *D. muelleri* and the extensive and strong dry season of its ranging area, we hypothesized that the breeding synchrony between males and females of this species depended on environmental clues, such as the rain volume. Moreover, we also predicted that the OSR will be deviate to the male number, as is it common to other explosive breeder anurans (Sullivan, 1985; Wells, 2007; Wells, 1977). In such condition, we expected that mating pairs were assorted by size, once bigger females would have an advantage by coupling with bigger males. Moreover, *D. muelleri* has morphological adaptations to fossorial habit (Antoniazzi et al., 2022) and for forelimbs-head-first burrowing (Nomura et al., 2009), which includes a round body, a small head, and a short fore and hindlimbs. Because of these morphological adaptations, we expect that size differences would be a constraint to cloacal pairing, which is an ecological driver for assortative mating by size (Crespi, 1989).

MATERIAL AND METHODS

STUDY SITE

The field samplings and natural history observation was conducted at an artificial semi-permanent pond (60 m length x 31 m width x 2

m deep) located in a matrix of pasture and corn crops in the municipality of Vitória Brasil, São Paulo (SP) State, Brazil (20º 12' 12.6'' S, 50º 29' 52.9'' W, 474 a.s.l.) (Fig. 1). One margin of the pond (about eight meters long) had no vegetation and the other was predominantly covered by grass species and sparse bushes and few vegetation was found inside the pond. The pond's depth varied during the rainy season, from 15 cm centimeters in September, at the beginning of the rainy season, to almost two meters (in the pond's central area) in June, at the dry season. The bottom of the pond was mainly composed by sand/clay soil, which gave the water a reddish coloration.

Fig. 1. Semi-permanent pond (20º 12' 12.6'' S, 50º 29' 52.9 ' W, 474 a.s.l.) at Vitória Brasil, São Paulo, Brazil, where the study was conducted.

Fig. 2. Male (A) and female (B) of *Dermatonotus muelleri* (Boettger, 1885). Note the round body and short limbs of *D. muelleri* individuals. Photo not in scale.

BREEDING SYNCHRONY AND TEMPORAL SCALE

We performed 24 field trips between April/2001 and June/2003. We used the survey at breeding sites method (Scott Jr. & Woodward, 1994) to estimate the abundance of males and females during each sampling. On each field trip, we started the observations at 17:30 hs, before dusk. In the first observations hours, we search the surrounding area for males and females of *Dermatonotus muelleri* (Fig. 2) arriving to the pond, feeding or for dead individuals. Later, we started the abundance estimation after choruses' formation, which begins around 21:00 hs. Before that time, isolated males could be heard calling, but we wait until many males started to vocalize. To perform the abundance estimation, we slowly walked around the pond margins and registered all observed and/or heard males and observed females to the abundance estimates. To get the most accurate abundance estimate possible, we count the number of individuals along stretches of 50 m at pond ma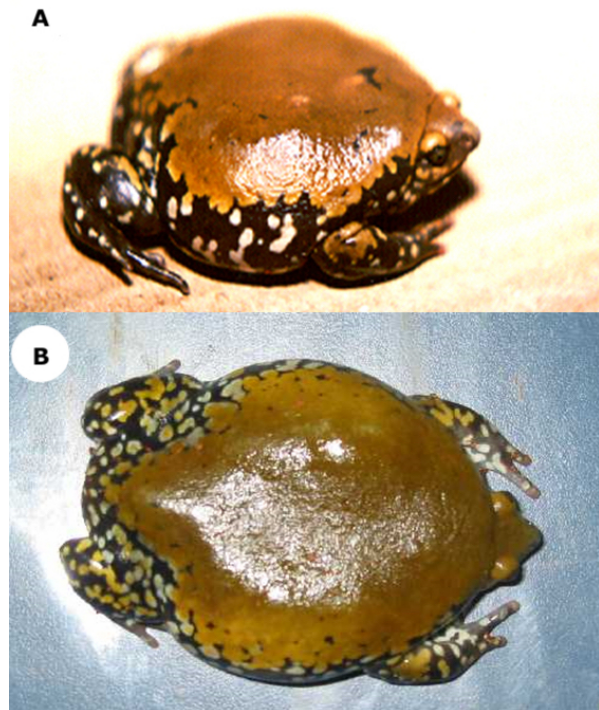rgin. Our sampling for abundance estimation last around 2 to 3 hours/per person, being finished when we complete a turn in the pond's perimeter. After the abundance estimation, we remained in the pond to perform ad *libitum* behavior observations. These surveys, abundance estimation and behavior observations, were carried out by two persons and for consecutive days, varying between 2 to 8 days by each field trip, depending on the reproductive period of males, to infer the total time of breeding activity of *D. muelleri*.

To test if breeding synchrony between males and females depend on the temporal scales of environmental clues, we accomplished daily surveys for three months of the sampling period: December/2001, January/2002 and February/2002. This daily dataset was used to test the effect of temperature, rainfall volume, and relative humidity on the (i) number of reproductive events in a month, (ii) duration of the reproductive events, and (iii) total abundance of *D. muelleri*. To these analyses we considered the rainfall data on different temporal scales (monthly, accumulated between reproductive events, and accumulated from the last three days before the reproductive event) to identify which one elicit the best demographic response. Temperature measures (mean, minimal, maxi-

mum, and daily variation) and relative humidity were obtained from the Brazilian Agricultural Research Corporation (Embrapa Uva e Vinho) at Jales, SP, and the daily rain data were obtained from the Secretary of Agriculture of Vitória Brasil, SP.

REPRODUCTIVE BEHAVIOR AND BODY SIZE

We characterized the calling sites (n = 37) used by *D. muelleri* males according to substrate type, depth and distance to the margin, margin type (visually classified as sloped or very sloped, respectively until and more than 30-40 degrees of inclination in relation to the water surface). This last trait described if the frog call floating, supporting at the edges of the pond, or partially submerged, but not floating. Depth was measured to the nearest cm with 2 m long graduate rod and the distance to the margin with a tape measure. We estimated the distribution of calling males in the pond by measuring the distance between on male to the nearest male in calling activity (n = 81 of calling males pairs).

We also calculated the linear density of males in calling activity to verify whether males of *D. muelleri* select the calling sites. For this, we conducted six transects on the margins with vegetation and four transects on the margins without vegetation in four different field trips (November 13th, December 20th, 21th and 22th, in 2002). We measured the snout-vent length (SVL) of amplectant males and females, solitary females, and the nearest solitary male of amplectant pairs, to test if the size of males is a good predictor of mating pairs formation, using a caliper with 0.05 mm of precision.

OPERATIONAL SEX RATIO (OSR)

We estimated the OSR of *D. muelleri* during reproductive events using the abundance of males and females at the margins of the pond and registering only individuals found by visual search, as females do not emit calls. We calculated the OSR as the ratio between the total number of females by the total number of males. We used this ratio to test whether larger choruses of males also have a larger number of females. Because the capture probability differed between males and females, the OSR is a better predictor of the competition among males and describes the number of males and females that are prone to mate in the population (Weir et al., 2011; Kvarnemo & Ahnesjö, 1996). Thus, as choruses of males increases, we expected that it attracts more females ready to reproduction, would increase the OSR closer to the 1:1 ratio (Sullivan, 1985).

STATISTICAL ANALYSIS

We tested for correlation between the environmental variables (temperature, relative humidity, and pluviosity) by the Spearman correlation test (Zar, 1999). For the months of December/2001, January/2002 and February/2002, we were able to perform daily surveys at the study site. Thus, we used these months to test whether the male abundance correlated with either the temperature measures or the daily rain using the Spearman test (Zar, 1999). By comparing daily and monthly correlations, we were able to verify if the same environmental clues were important to elicit breeding synchrony at different temporal scales.

We analyzed the distribution of males in calling activity at the study site by comparing the distance among the nearest neighbors to a null model of distribution. In this model, males maintain a constant distance to the nearest neighbors, in a uniform distribution (Lambshead & Hodda, 1994). The statistical significance was obtained by the χ^2 test (Zar, 1999). We compared the linear density of males between the two types of microhabitats (margins with or without vegetation) using the student's t-test (Zar, 1999).

We tested whether larger males had advantage to obtain a female by comparing the SVL of males in amplexus with their nearest neighbors using a paired t-test (Zar, 1999). To test for size-assortative mating in *D. muelleri*, we correlated the SVL of males and females in amplexus using linear regression (Zar, 1999). If size-assortative mating occurs, we should find a positive relationship between the SVL of males and females in amplexus (Crespi, 1989). We also used linear regression to test whether larger choruses had higher OSR, which indicate an increase in the number of females ready to mate, and whether males' distribution was determined by the SVL. For this last analysis, we compared the distance between neighbors and their SVL differences also using a linear regression (Zar, 1999).

RESULTS

In every studied year, we found individuals of *D. muelleri* in foraging activity since September, but the reproductive activity was restricted to the period between November and February (Fig. 3). We named this period in which we detected males in calling activity as reproductive event. Other sixteen anuran species, used the pond for reproduction during our surveys (Tab. 1). We registered 14 reproductive events, which lasted from two to five days (Fig. 4). As expected for a species with explosive reproductive pattern, males' distribution was aggregated (Tab. 2).

REPRODUCTIVE SYNCHRONY AND TEMPORAL SCALE

Males and females' abundances were positively correlated to the monthly pluviosity and

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Tab. 1. List of the registered species in the studied pond (20º 12' 12.6'' S, 50º 29' 52.9'' W) in Vitória Brasil municipality, São Paulo State, Brazil.

Taxon
Bufonidae
Rhinella diptycha (Cope, 1862)
Hylidae
Dendropsophus elianeae Napoli & Caramaschi, 2000
Dendropsophus nanus (Boulenger, 1889)
Dendropsophus minutus (Peters, 1872)
Boana raniceps (Cope, 1862)
Trachycephalus "vermiculatus"
Scinax fuscovarius (Lutz, 1925)
Scinax similis (Cochran, 1952)
Leptodactylidae
Leptodactylus fuscus (Schneider, 1799)
Leptodactylus mystacinus (Burmeister, 1861)
Leptodactylus luctator (1892)
Leptodactylus podicipinus (Cope, 1862)
Physalaemus cuvieri Fitzinger, 1826
Physalaemus marmoratus (Reinhardt and Lütken, 1862)
Physalaemus nattereri (Steindachner, 1863)
Microhylidae
Dermatonotus muelleri (Boettger, 1885)
Elachistocleis cesarii (Miranda-Ribeiro, 1920)

minimum temperature, and negatively correlated with the temperature variation (Tab. 3; Fig. 3). The length of the reproductive events was correlated with the accumulated pluviosity between reproductive events (Tab. 3; Fig. 4). At the daily scale, the male abundance was not correlated to any of the environmental variables (Tab. 4; Fig. 5). At this temporal scale though, it was possible to note a time lag of one or two days between rainfall and the formation of the reproductive aggregation (Fig. 5).

REPRODUCTIVE BEHAVIOR AND BODY SIZE

Males began their calling activity around 1900h. At first, males had a small abundance, around 20 to 30 individuals, but from 21:00 hs – 22:00 hs the number of males increased to more than 1,000 individuals (1,079 ± 816 individuals, n = 11 reproductive events). Males of *D. muelleri* selected either the marginal vegetation or the emergent vegetation in the interior of the pond as calling sites. In the second case, males used the emergent vegetation to keep their rostral side towards the margins and above surface. Regardless the calling site, males called with their arms straightened and with the snout upwards, showing the black coloration of their vocal sacs. The distance to the margin where males vocalized varied more than the depth of the calling site (Vocalization site distance to the margin = 2.04 ± 7.35 m; vocalization site depth = 0.09 ± 0.11 m).

Despite the high abundance of males during reproductive events, males of *D. muelleri* selected sites mainly near the highly sloped margins (*D. muelleri* density$_{sloped margins}$ = 2.69 ± 0.13 ind.m^{-1}; n = 6; *D. muelleri* density$_{shallow margins}$ = 1.07 ± 1.36 ind.m^{-1}; n = 4; t = -3.02; p < 0.05). Also, we found a negative correlation between the difference in body size and the distance among neighbors in calling activity, showing that small males stood near larger males (Body size difference = 3.91 ± 2.97 mm; distance between neighbor males = 32.60 ± 17.77 cm; n = 82; r = -0.30; p < 0.01). There was no significant difference between the body size of males in amplexus and their nearest neighbors (males in amplexus body size = 58.27 ± 3.25 mm, n = 33; nearest solitary male body size = 58.98 ± 3.88 mm, n = 33; t = 9.23, p = 1.99) nor did we find correlation between the size of males and females in amplexus (males in amplexus body size = 58.27 ± 3.25 mm; females body size = 68.99 ± 4.93 mm; r = 0.15, p > 0.05, n = 77 couples), which indicates that pair formation was not defined by a correlation between male and female size (larger females does not select larges males), denoting no assortative mating by size in *D. muelleri*.

OPERATIONAL SEX RATIO

Males of *D. muelleri* were more abundant than females, which resulted in a low OSR in all reproductive events (Fig. 6). Although the number of females was higher in reproductive events with a higher number of males, the OSR was correlated only with the female abundance (Tab. 3), which suggest that larger choruses did not attract more females.

Tab. 2. Spatial distribution of *Dermatonotus muelleri* (Boettger, 1885) in Vitória Brasil municipality, São Paulo State, Brazil.

Date	Distribution	Mean	Variance	Chi-square	DF	N
Nov-13-02	Aggregated	32.37	723.70	581.2	26	20
Dec-20-02	Aggregated	31.89	254.03	207.1	26	31
Dec-21-02	Aggregated	28.22	346.95	319.6	26	25
Dec-22-02	Aggregated	16.30	391.83	625.1	26	14
Total period	Aggregated	37.71	813.17	2156.2	100	90

DF: degrees of freedom; N: number of individuals.

Tab. 3. Spearman correlation (rs) between the number of reproductive events in a month and between the abundance of males and females with environmental and biotic variables. In bold, significant correlation. The symbol (*) indicates p< 0.05; the symbol (**) indicates p < 0.01.

Variables	Reproductive events	Abundance	
		Males	Females
Environmental	r_s	r_s	r_s
Pluviosity	**0.73****	**0.71****	**0.61****
Mean temp.	**0.39***	**0.41***	**0.43***
Min. temp.	**0.68****	**0.68****	**0.62****
Max. temp.	0.19	0.22	0.24
Temp. variation	**-0.67****	**-0.60****	**-0.66****
Relative humidity	0.34	0.29	0.29
Biotic	r_s	r	r
Number of males	**0.98****	-	**0.72***
Number of females	**0.91****	**0.72***	-
OSR	-	-0.08	**0.63***

temp.: temperature; min.: minimum; max.: maximum; OSR: Operational Sex Ratio; Temp. variation: difference between maximum and minimum temperatures.

Tab. 4. Spatial distribution of *Dermatonotus muelleri* (Boettger, 1885) in Vitória Brasil municipality, São Paulo State, Brazil.

Variables	December/01		January/02		February/02	
	r_s	p	r_s	p	r_s	p
Pluviosity	0.03	>0.05	0.12	>0.05	0.08	>0.05
Mean temp.	0.04	>0.05	0.01	>0.05	-0.16	>0.05
Min. temp.	0.17	>0.05	0.19	>0.05	0.17	>0.05
Max. temp.	-0.10	>0.05	-0.12	>0.05	-0.35	>0.05
Temp. variation	-0.28	>0.05	**-0.36**	**<0.05**	-0.36	>0.05

temp.: temperature; min.: minimum; max.: maximum; OSR: Operational Sex Ratio; Temp. variation: difference between maximum and minimum temperatures.
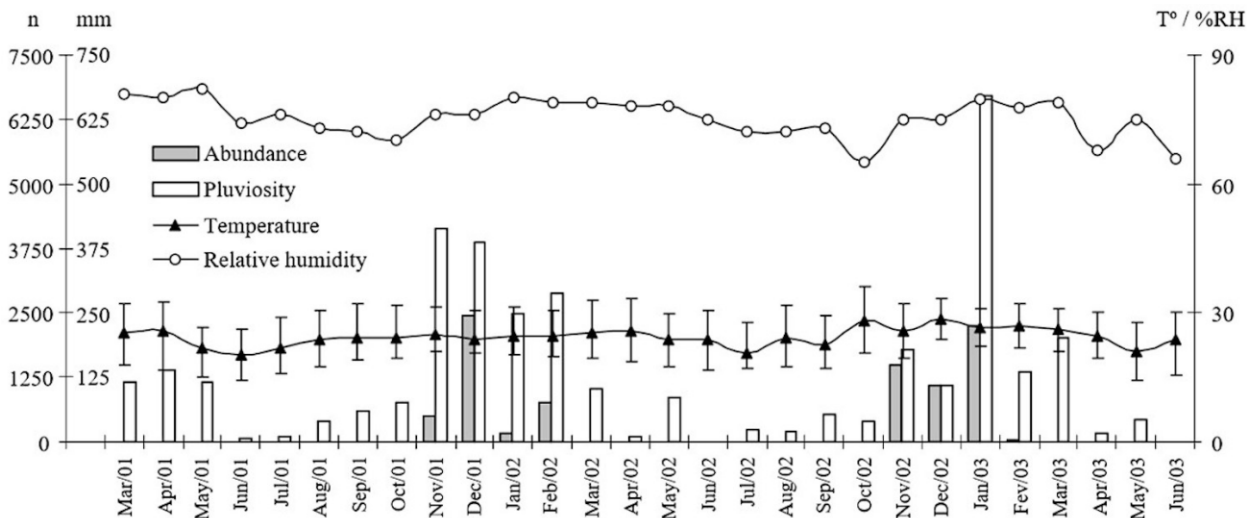
Fig. 3. Seasonal abundance (n) of a *Dermatonotus muelleri* (Boettger, 1885) population in Vitória Brasil municipality, São Paulo State, Brazil. Pluviometry data (mm) – Secretariat of Agriculture of Vitória Brasil, SP, Brazil. Vertical lines in the temperature line represent the minimum and maximum temperature for the month. Temperature (°C) and relative humidity (%RH) data – Embrapa Uva e Vinho, Jales, SP, Brazil.
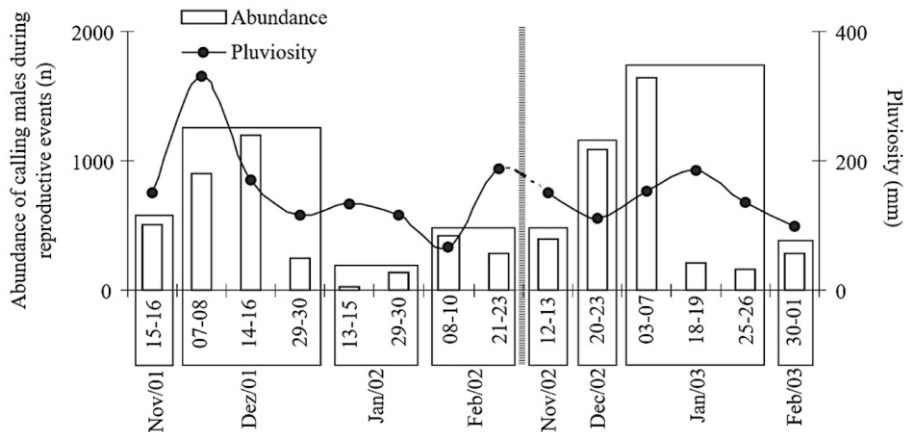
Fig. 4. Duration, in days, abundance (n), number of reproductive events per month of *Dermatonotus muelleri* (Boettger, 1885) and pluviosity in Vitória Brasil municipality, São Paulo State, Brazil. The rectangles represent reproductive events that occurs in the same month. The dashed bar represents the period when *D. muelleri* were not found in reproductive activity (March to October/2002).

DISCUSSION

D. muelleri is a typical explosive breeder species (*sensu* Wells, 1997), that aggregates in short periods of reproductive activity (one to five consecutive nights). During the reproductive events, males and females arrive at the breeding sites in synchrony, using environmental (temperature and pluviosity) and biotic (termite reproductive swarms and male calling) cues. Also, there is a high population density (1,079 ± 816 individuals, n = 11 reproductive events),

with a biased OSR toward the number of males, resulting in a lack of opportunity to sexual selection by females. Due to the high male-male competition, because of the high male density, females cannot reach any calling male before being intercepted by another male (males active search for female; Antoniazzi et al., 2022; F. Nomura and F. R. Carvalho, pers. obs.). While the calling activity of males does not allow female to show preferences, avoiding size assortative mating, it is important to elicit female displacement toward the reproductive sites only
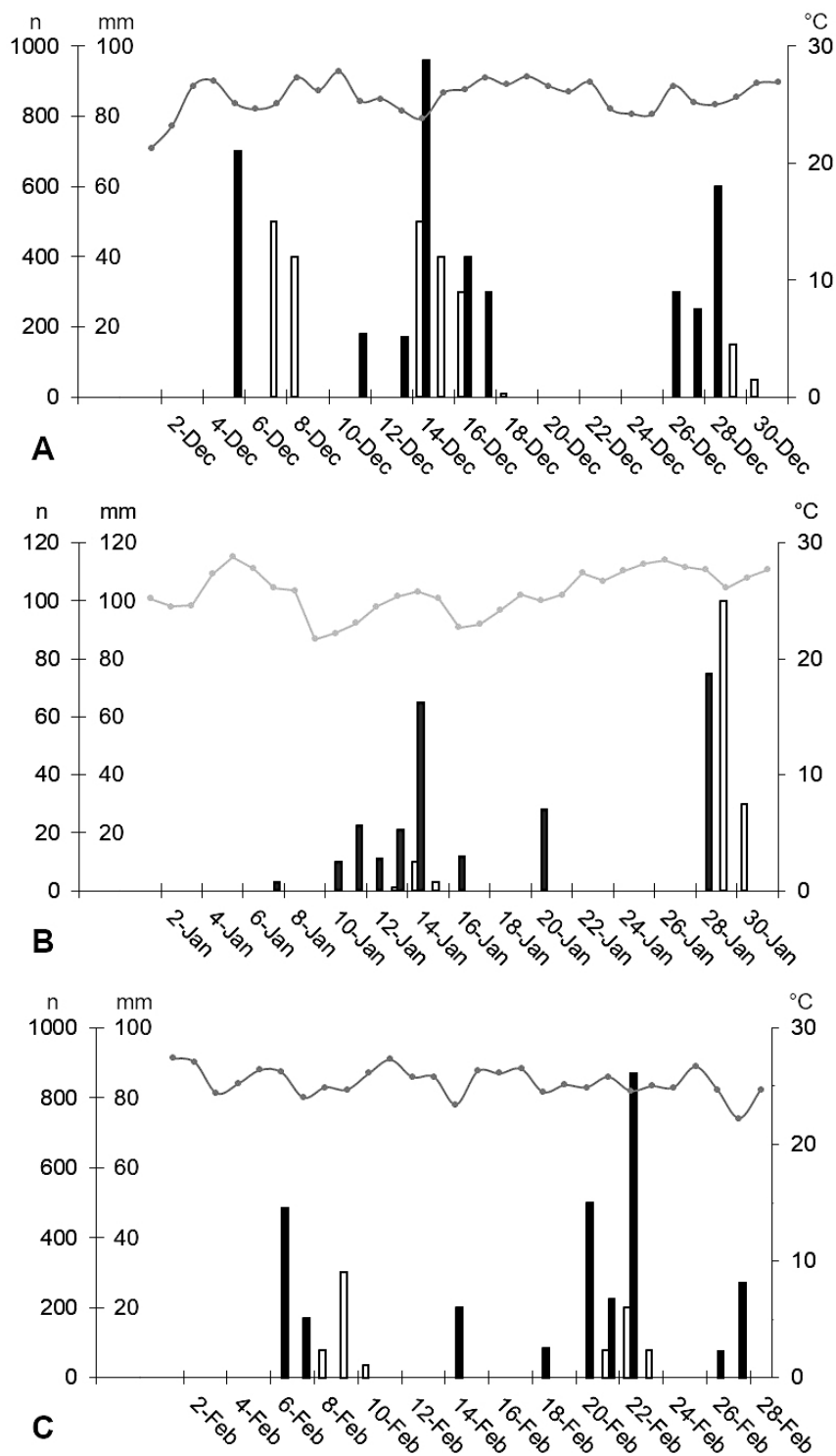
Fig. 5. Temporal distribution of *Dermatonotus muelleri* (Boettger, 1885) across December/2001 (A), January/2002 (B) and February/2002 (C), in an artificial pond in Vitória Brasil municipality, São Paulo State, Brazil. Black bars represent the pluviosity in 24h (mm), white bars represent the number of males in calling activity (n) and the gray lines represent the mean temperature (°C).

when males are reproductive available, reducing predation risk (Stanescu et al., 2014).

REPRODUCTIVE SYNCHRONY AND TEMPORAL SCALE

Daily temperature variation and total
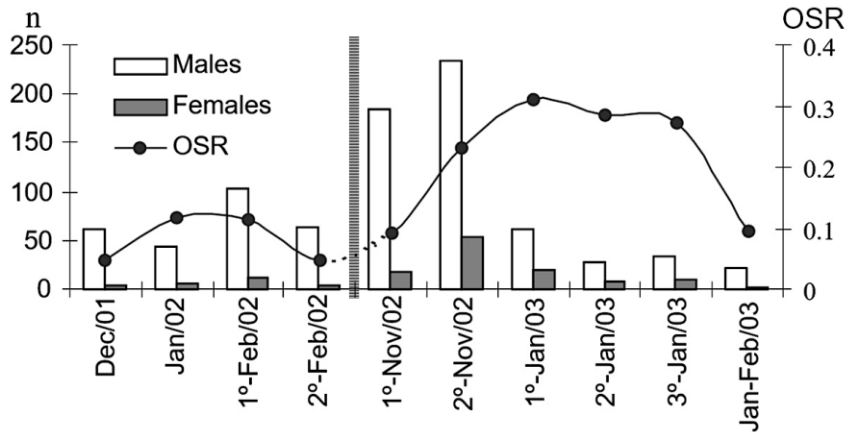
Fig. 6. Number of males (white bars) and females (gray bars) by event during the reproductive seasons of December/2001 to February/2002, and November/2002 to January-February/2003. The dashed bar represents the period when *Dermatonotus muelleri* (Boettger, 1885) were not found in reproductive activity (March to October/2002). Operational Sex Ratio (OSR) = F/M.

rainfall between reproductive events (> 50 mm) mediate the movement of individuals to the reproductive sites and seem to explain the breeding synchrony between males and females, as also detected for other explosive breeders (*e.g. Bufo calamita*, Tejedo, 1993). The use of environmental cues to synchronize reproductive activity was already described for other anuran species from xeric environments (Dimmit & Ruibal, 1980; Ruibal et al., 1969; Sullivan, 1985). However, we noted a time lag between the rainfall and the reproductive aggregations, which is only detected at the daily scale. This time lag suggests that *D. muelleri* does not rely only on environmental cues to achieve reproductive synchrony. During this time lag, males and females of *D. muelleri* were observed feeding on winged termites (Isoptera), a very caloric food (Basalingappa, 1970; Cmelik, 1969; Fast, 1964), before they aggregated at the pond for reproduction. Feeding events before reproductive events are common to anuran species from arid to semi-arid environments, as registered for *Scaphiopus couchii* and *Spea hammondii* (Dimmit & Ruibal, 1980; Ruibal et al., 1969). In such environments, during the wet season, there is an increase in the termite abundance, due to the reproductive dispersion elicited also by heavy rains (Dimmit & Ruibal, 1980; Pinheiro et al., 2002). Diet specialization is an important strategy to maximize the relation of feeding time and the total net energy yielded (Schoener, 1971).

The selection by vocalization site in *D. muelleri* is not related to lek formation. A lek formation is characterized by males' competition for females, who are often attracted to males bearing costly secondary sexual traits that are understood as a cue to signal male genetic quality (Botto & Castellano, 2016; Knopp et al.,

2008). *D. muelleri* males do not form lek, since (i) larger males did not have advantage in mating selection, (ii) there was no assortative size mating and (iii) we could see many males actively searching for females during reproductive events. Also, the amplexus in *D. muelleri* occurs in water and immediately after the female arriving, males' swims in the female direction and start to mount the female back (Antoniazzi et al., 2022; F. Nomura, pers. obs.). In such condition, the female is uncapable of reaching a calling male before being intercepted by another male. Why *D. muelleri* emit calls, if this behavior apparently does not increase individual reproductive fitness? The advertisement call of *D. muelleri* is characterized by notes with long duration, multipulsed structure and low frequency, that require a high energy investment (Ryan & Keddy-Hector, 1992). The same acoustic characteristics enable a long-distance propagation of the sound, which may attract more females to move to the pond. Therefore, males of *D. muelleri* may have behavioral strategies that reduce the energetic cost required by communication at long-distances. Among these strategies are (i) the emission of the advertisement call during a single contraction of the trunk muscles to reduce metabolic costs; (ii) the reproduction in open areas, which present lower interference to sound propagation; and (iii) the selection of specific microhabitats for vocalization (see Gerhardt, 1994). Although we did not find a factor to explain the selection of vocalization site, we found that males of *D. muelleri* congregate near the sloped margins to call.

Long-distance communication between males and females can also be advantageous for species that reproduce in unpredictable environments (Arak, 1983; Sinsch, 1990, 1991).

This is because an energetic balance is important to synchronize the reproductive activity. As females invest more in reproduction than males (Dimmit & Ruibal, 1980; Krebs & Davies, 1996; Stanescu et al., 2016), the long-distance communication avoids females to move to the reproductive site when males are not present. As such, long-distance communication saves energy for egg production, reduces females' predation risk (Arak, 1983; Sinsch, 1990, 1991, Stanescu et al., 2014), and is the main synchrony mechanism between males and females. Although the calling activity does not provide the opportunity of male selection by females in *D. muelleri* (Antoniazzi et al., 2022), it is still important to signal the beginning of the reproductive period and male availability.

REPRODUCTIVE BEHAVIOR, BODY SIZE

We found no assortative mating by size in *D. muelleri*. This result is surprising because the sexual sex dimorphism in *D. muelleri* is biased toward females that invest more in reproduction than males (Stanescu et al., 2016). Thus, large females that couple with larger males would gather greater reproductive output. Despite the environment where *D. muelleri* reproduces favors large females (Stanescu et al., 2016), females have no advantage by coupling with relatively large males. Many hypotheses have been proposed to explain the size assortative mating (see a review in Crespi, 1989), and physical constraints, such as size differences between males and females, are suggested as a driving factor. With longer size differences, the distance between male and female cloaca's increases, reducing fertilization efficiency (Antoniazzi et al., 2022; Crespi, 1989). Also, the round body shape and the small forelimbs of *D. muelleri* would increase the difficulty of males remaining in amplexus with females (Antoniazzi et al. 2022). However, as a common strategy with other microhylids, *D. muelleri* has a set of specialized glands in its ventral region that produces an adhesive secretion that binds the male with the female during reproduction (Antoniazzi et al., 2022), which prevents any difficulty in pairing due to size differences. Moreover, *D. muelleri* has shown behavioral adaptations that compensate for the mechanical constraints of cloacal pairing due to size differences between males and females (Antoniazzi et al., 2022). As suggested by Stanescu et al. (2016), females of *D. muelleri* would achieve a large reproductive output at the cost of a reduced reproductive lifespan as an adaptation to the Chaco climate. This scenario could increase the value of the reproductive opportunity more than the male quality, and the higher male-male competition, due to the large abundance of males during reproductive events, would select males despite female preference. The absence of female choice due to higher male density was already reported for other anuran species in arid and semi-arid environments (Sullivan, 1985) and is expected to occur for explosive breeder's anuran species (Wells, 1977; Wells, 2007).

FINAL CONSIDERATIONS

We found that *D. muelleri* use environmental (pluviosity and minimum temperature at monthly temporal scale) and biotic (termites reproductive swarms and long-distance communication at daily temporal scale) as clues to reproductive synchronization. Also, the long-distance call of *D. muelleri* males is an important stimulus to elicit female displacement toward the reproductive sites, avoiding random displacements and associated risks, as predation and loss of feeding opportunities (Ryan & Keddy-Hector, 1992; Sinsch, 1990, 1991). The lack of assortative mating by size may be a consequence of different pressure selection of males and females by the arid environment of the Caatinga-Cerrado-Chaco domain (Stanescu et al., 2016; Antoniazzi et al. 2022). While females where selected to have larger body size and offspring production, at the cost of reproductive lifespan (Stanescu et al., 2016), males are subject to an intense male-male competition which prevents the expression of female preferences (Antoniazzi et al. 2022).

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