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HEITOR TAVARES DE SOUSA MACHADO

VARIAÇÃO INTRAESPECÍFICA E EFEITO DAS INFECÇÕES ENDOPARASITÁRIAS NA VOCALIZAÇÃO E SELEÇÃO SEXUAL DE *Physalaemus cuvieri* FITZINGER, 1826

FORTALEZA
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Orientador: Prof. Dr. Robson Waldemar Ávila
Coorientadora: Profa. Dra. Cristiana Ferreira da Silva

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RESUMO

Os sinais acústicos emitidos pelos anfíbios fornecem informações sobre a localização, morfologia e contextos sociais e reprodutivos. Dentre estes, o canto de anúncio, que é usado para atrair fêmeas para o acasalamento e demarcar o território, é comumente mais estudado na literatura. A vocalização dos anfíbios pode ser influenciada por diferentes fatores bióticos e abióticos, que podem refletir uma variação intraespecífica. Desse modo, a presente tese de doutorado teve como objetivos principais (i) investigar a influência de variáveis ambientais e do tamanho dos anuros nos parâmetros acústicos de três populações de *Physalaemus cuvieri* do Brasil, (ii) testar como as infecções endoparasitárias afetam estes parâmetros acústicos e (iii) o sucesso reprodutivo em uma população de *P. cuvieri* localizada no município de Lavras da Mangabeira, pertencente ao Ceará, nordeste do Brasil. Observamos que o canto de anúncio das populações estudadas de *P. cuvieri* consistiu em uma nota simples com um envelope triangular que lembra uma forma de seta. As três populações apresentaram diferenças quanto à frequência dominante, duração do canto e os intervalos entre os cantos. Ademais, a massa dos indivíduos e a umidade influenciaram este último parâmetro. A frequência dominante foi afetada pelo tamanho dos anuros. Também observamos que as infecções por endoparasitas influenciaram apenas o intervalo entre os chamados. Além disso, observamos que apenas o tamanho dos indivíduos afetou o sucesso reprodutivo. Este estudo indica que diferentes populações de espécies podem exibir variações intraespecíficas em seus chamados de anúncio. Embora as infecções parasitárias afetem as vocalizações dos anuros, essas diferenças não são primariamente significativas na seleção sexual feminina.

Palavras-Chave: canto de anúncio; helmintos; parasito-hospedeiro; sucesso reprodutivo.

ABSTRACT

The acoustic signals emitted by amphibians provide information about location, morphology, and social and reproductive contexts. Among these, the advertisement call, used to attract females to mating and to demarcate the territory, is most commonly reported in the literature. Amphibian vocalization can be influenced by different biotic and abiotic factors, which may reflect intraspecific variation. Thus, the present doctoral thesis had as main objectives (i) to investigate the influence of environmental variables and anuran body size one the acoustic parameters of three populations of *Physalaemus cuvieri* from Brazil, (ii) to test how endoparasite infections affect these acoustic parameters and (iii) to evaluate the reproductive success in a population of *P. cuvieri* located in the municipality of Lavras da Mangabeira, state of Ceará, northeastern Brazil. We observed that the advertisement call of the studied populations of *P. cuvieri* consisted of a simple note with a triangular envelope resembling an arrow shape. The three populations exhibited variations in dominant frequency, call duration, and inter-call intervals. Additionally, the anuran body mass and humidity affected the last acoustic parameter. The dominant frequency was affected by the anuran body size. We also observed that the endoparasite infections only influenced the interval between calls. Additionally, we observed that only the size of the individuals affected reproductive success. This study indicates that different populations of species may exhibit intraspecific variations in their advertisement calls. While parasitic infections impact the vocalizations of anurans, these differences are not primarily significant in female sexual selection.

Keywords: advertisement call; helminths; host-parasite; reproductive success.

SUMÁRIO

1. INTRODUÇÃO GERAL

1.1. Comunicação acústica

A comunicação é uma transferência de informações por meio de um sinal e por um canal entre um emissor e um receptor (Hebets e Papaj, 2005; Toledo *et al*., 2015; Köhler *et al*., 2017). Existem diversos mecanismos de comunicação para que ocorram as interações sociais nos animais (Goodenough *et al*., 1993) e as populações possuem ajustes ecológicos para emitir e receber uma ampla variedade desses sinais (Bradbury e Vehrencamp, 2011).

Algumas espécies utilizam sinais para atrair parceiros sexuais, tais como espécies de lagartos que utilizam sinais visuais tanto para atração de fêmeas, como para afastar possíveis machos (Leal e Fleishman, 2004). Serpentes, por exemplo, podem liberar pistas químicas ao longo de trilhas, onde as fêmeas captam e seguem o macho escolhido (Richard *et al*., 2020). Dentre os vertebrados, os anfíbios possuem uma grande diversidade de modos de comunicação (Wells, 2007). Por exemplo, salamandras demonstram reciprocidade para acasalar liberando feromônios (Vaccaro *et al*., 2010), e algumas espécies também utilizam a biofluorescência na atração de parceiros sexuais (Lamb e Davis, 2020). Nos anfíbios anuros, a comunicação acontece por sinais visuais, químicos, táteis e acústicos (Wells, 2007; Preininger *et al*., 2013; Woodley, 2014; Toledo *et al*., 2015). Dentre estes modos, a vocalização parece ser o principal modo de comunicação nos anuros (Wells, 2007).

A variabilidade dos diferentes parâmetros acústicos relacionados à vocalização dos anfíbios pode ser classificada como estática ou dinâmica (Gerhardt, 1991; Bee *et al.*, 2010). Os parâmetros temporais, tais como a duração da chamada e o intervalo entre as chamadas, são classificados como dinâmicos, mostrando-se variáveis a nível intraespecífico (Bornschein *et al*., 2018; Turin *et al.,* 2018). Os parâmetros estáticos como as frequências máxima, mínima e dominante estão usualmente associados à morfologia do indivíduo (Bee *et al*., 2013; Guerra, 2020; Bezerra *et al*., 2021). Além disso, esses parâmetros acústicos são influenciados pelas interações sociais entre os indivíduos, como por exemplo, a presença de outros machos vocalizadores (Gerhardt, 1991; Tárano, 2001). Por fim, o próprio gasto energético dos machos emissores tem efeito em alguns parâmetros acústicos da vocalização (Pough *et al*. 1992; Bevier, 2016; Wells e Schwarts, 2007).

Dentre os anfíbios anuros, o canto de anúncio é o mais utilizado, pois contém informações importantes para o reconhecimento específico, bem como informações sobre sua

condição como competidor e parceiro (Gerhardt, 1994; Wells, 2007; Toledo *et al*., 2015; Liu *et al*., 2018). Além disso, cantos de cortejo e cantos durante o amplexo também são observados, onde na presença das fêmeas, os machos vocalizam em baixa intensidade e realizam movimentos musculares (Toledo *et al*., 2015). Essas características acústicas dos machos são determinantes para o seu sucesso reprodutivo (Pröhl, 2003; Ron, 2008), uma vez que as fêmeas selecionam os machos analisando tais características (Wells, 2007).

A vocalização de uma espécie é determinada por informações genéticas (Dawson e Ryan, 2009; Baugh *et al*., 2012); entretanto, outros fatores podem desarranjar o conjunto de características, aumentando ou diminuindo parâmetros fornecidos durante o canto, como ruídos de ações antrópicas (Penna e Zúniga, 2014; Caldart *et al*., 2016; Röhr *et al*., 2020), fatores ambientais como a temperatura (Lingnau e Bastos, 2007; Valetti e Martino, 2012), ruídos antrópicos (Leon *et al*., 2019), além de infecções endoparasitárias (Madelaire *et al*., 2013). Ademais, alguns estudos sustentam que o gradiente latitudinal (distância geográfica) tem um efeito significativo na vocalização dos anuros com ampla distribuição geográfica, refletindo uma variação intraespecífica em alguns parâmetros no canto de anúncio para algumas populações (Pröh *et al*., 2007; Baraquet *et al*., 2015; Tessarolo *et al*., 2016). Apesar de variações intraespecíficas na vocalização de diferentes populações terem sido reportadas para diferentes populações como *Scinax fuscomarginatus* (Lutz, 1925) na região central do Brasil (Souza *et al.*, 2023), *Eleutherodactylus glamyrus* (Estrada e Hedges, 1997) nas montanhas da Sierra Maestra no leste de Cuba (Rodríguez *et al*., 2010) e *Bokermannohyla ibitiguara* (Cardoso, 1983) no Parque Nacional Serra da Canastra, sudeste do Brasil (Turin *et al.,* 2018), ainda são pouco conhecidos quais fatores influenciam predominantemente essas diferenças.

1.2. Seleção sexual em anuros

Em diversos táxons, os espécimes podem ter vantagens escolhendo parceiros sexuais que possuem recursos e benefícios genéticos (Cunningham e Birkhead, 1998; Widemo e Saether, 1999; Jennions e Petrie, 2000). Portanto, como a vocalização é um mecanismo indispensável durante os comportamentos relacionados ao acasalamento de anuros (Wells, 2007), avaliar suas características é ideal para estudos de sinalização, reprodução e seleção sexual (Andersson e Iwasa, 1996; Gerhardt, 1994; Greenfield, 2005).

A escolha do parceiro sexual pode ser considerada um fator preditivo na evolução do comportamento social, presença de dimorfismo sexual e sistema de acasalamento (Miller, 2001; Greenfield, 2005; Schuett *et al*., 2010). Nesse sentido, a escolha da fêmea atua como uma

pressão seletiva sobre a evolução do comportamento dos machos (Schuett *et al*., 2010), direcionando as estratégias comportamentais dentro das populações (Dzieweczynski *et al*., 2014).

As fêmeas de anuros podem escolher os machos com base na qualidade dos padrões acústicos do seu canto (Gerhardt e Bee, 2007; Wells, 2007). Isto faz com que os machos compitam agressivamente contra rivais por acesso a fêmeas reprodutivas, a locais de vocalização de curto prazo ou a territórios de longo prazo (Bee *et al*., 2016). Dessa forma, a seletividade dos machos ocasionada pelas fêmeas, podem levar a competição entre os machos e a conservação das características escolhidas (Andersson e Iwasa, 1996). Portanto, a seleção sexual atua na competição dos machos pelas fêmeas, favorecendo espécimes que melhor atraem e competem por parceiros sexuais (Grafen, 1990; Gerhardt e Bee, 2007; Shuker *et al.,* 2021).

Estudos *ex situ* indicam que a seleção sexual de anuros não é aleatória (e.g., Gerhardt e Huber, 2002; Wogel e Pombal JR, 2007; Márquez *et al*., 2008). Por exemplo, fêmeas de *Cophixalus ornatus* (Fry, 1912) tenderam a selecionar machos que possuíam cantos de anúncio com baixa frequência dominante (Felton *et al*., 2006). Enquanto que, fêmeas de *Dendropsophus bipunctatus* (Spix, 1824) exibem uma preferência por sinais acústicos emitidos a uma elevada taxa de repetição (Wogel e Pombal jr, 2007). Por outro lado, alguns estudos realizados *in situ* demonstraram que essa seleção pode ser aleatória (Pfenning e Tinsley, 2002; Friedl, 2006; Glos *et al.,* 2019), permanecendo uma questão ainda não esclarecida em ecologia.

A partir da teoria da evolução pelo mecanismo de seleção natural surgiram muitos questionamentos, principalmente relacionados às características chamativas e características secundárias presentes em alguns indivíduos, não estando relacionadas com a sobrevivência da espécie (Danchin *et al*., 2010). Nesse sentido, a seleção natural é influenciada pelos atributos necessários para a existência, podendo levar à extinção da espécie. A seleção sexual relaciona-se às características secundárias presentes em indivíduos que levam à atração de parceiros, reprodução e sucesso reprodutivo (Andersson, 1982; Emerson e Ward, 1998).

A seleção sexual é uma forma de competição entre os indivíduos, visto que os espécimes competem para conseguir realizar a fertilização de gametas (Shuker *et al.,* 2021). Portanto, a seleção sexual atua quando existe a competição entre parceiros para o acasalamento, podendo gerar diferenças no sucesso reprodutivo de indivíduos de uma mesma população (Wells, 2007; Danchin *et al*., 2010).

1.3. Interação parasito-hospedeiro

Entende-se por parasitismo a interação de um organismo parasito que apresenta certo grau de coevolução com seu hospedeiro, alimentando-se dele e causando-lhe prejuízos (Poulin, 2007). Infecções endoparasitárias podem ser responsáveis por alterações no comportamento, crescimento e desenvolvimento dos seus hospedeiros (Poulin, 1994; Johnson *et al*., 2012; Marino Jr *et al*., 2013; Hernandez-Caballero *et al*., 2022). Apesar das infecções endoparasitárias alterarem o funcionamento do corpo do hospedeiro, inibindo ou reduzindo a capacidade reprodutiva do hospedeiro (Hurd, 2001; Heins *et al*., 2004), bem como na vocalização destes animais (Madelaire *et al*. 2013), ainda existem lacunas sobre os mecanismos pelos quais a vocalização dos anfíbios e consequentemente a seleção sexual são afetadas por infecções parasitárias.

Hurd (2001), explica que a redução da fecundidade devido à infecção parasitária é um resultado esperado e pode ser considerado um produto de alguma doença debilitante devido à infecção do parasita. Logo, a infecção parasitária é geralmente associada a um desequilíbrio do sistema imune, pois os custos aumentam com a resposta imunológica na reparação dos danos causados pela infecção (Tinsley *et al*., 2002; Belden e Kiesecker, 2005; Warne *et al*., 2010; Madelaire *et al*., 2017).

A discussão acerca da relação parasita hospedeiro na influência da vocalização dos machos traz informações importantes, pois infecções parasitárias consomem parte da energia do macho vocalizador (Ryan, 1988), podendo assim afetar a vocalização (Madelaire *et al*., 2013). É sabido que as infecções endoparasitárias dificultam a quantidade correta de distribuição de energia, deixando a alocação de energia dividida entre sobrevivência e reprodução (Martinez-Bakker e Helm, 2015). No entanto, entender o papel dessa relação parasito-hospedeiro em anfíbios ainda é controverso. Por exemplo, Madelaire *et al*. (2013) observaram que os machos de *Boana prasina* (Burmeister, 1856) que estavam parasitados produziram chamadas mais curtas. Um padrão oposto foi observado para *Dryophytes japonicus* (Günther, 1859), onde machos parasitados podem melhorar a qualidade da chamada, produzindo cantos mais longos (An e Waldman, 2016). Já para *Dryophytes versicolor* LeConte, 1825 não houve associação (Hausfater *et al*., 1990; Greenspan *et al*., 2016). Isto reforça a necessidade de mais estudos almejando compreender a influência de infecções endoparasitárias na comunicação e seleção sexual de anfíbios.

1.4 Organização e síntese da Tese

Nesta tese avaliamos como os parâmetros acústicos podem variar em função da distância geográfica, variáveis ambientais e características morfológicas dos anuros. Além disso, analisamos se infecções endoparasitárias podem trazer prejuízos na vocalização do hospedeiro e, consequentemente, se essa relação parasito-hospedeiro tem influência sobre a seleção sexual nos anuros. Para isso, utilizamos a espécie *Physalaemus cuvieri* Fitzinger (1826), uma rã de pequeno porte (Haddad e Sazima, 1992) amplamente distribuída, com ocorrência no Paraguai, Argentina e maior parte do território brasileiro (Mijares *et al*., 2010; Frost, 2023). A mesma habita ambientes antrópicos e conservados (Eterovick *et al*., 2020).

No capítulo 1, (manuscrito submetido no periódico científico Herpetological Conservation and Biology, Qualis B1, fator de impacto 0.8) apresentamos uma variação intraespecífica, nos parâmetros acústicos de três populações de *P. cuvieri* no Brasil. Nossa hipótese sugere que populações de localidades diferentes e, consequentemente, pressões abióticas e bióticas distintas apresentam diferenças nos seus parâmetros acústicos. Portanto, espera-se que tanto as características ambientais de cada localidade como as dos anuros influenciem os parâmetros acústicos de *P. cuvieri*.

No capítulo 2, (manuscrito aceito no periódico científico Annals of Parasitology, Qualis A4, fator de impacto 1.78) descrevemos seu canto de anúncio, a influência da carga parasitária na comunicação bioacústica e na seleção sexual, e como o tamanho dos anuros está relacionado com a abundância de endoparasitas. Nossas hipóteses propostas para o segundo capítulo são que: a abundância e riqueza de parasitos diminuem os parâmetros bioacústicos nas populações estudadas; indivíduos maiores apresentam maior quantidade de parasitos; a abundância de parasitos diminui o sucesso de acasalamento em machos de anfíbios anuros.

2. CAPÍTULO 1. Barker frog's accent: are there differences in the acoustic patterns of *Physalaemus cuvieri* populations?

Short title.—*Acoustic patterns of Physalaemus cuvieri populations*

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***Abstract.*—Vocalization is one of the most common communication modes for anurans, of which the advertisement call is used for sexual selection. Different factors may influence their vocalizations, resulting in an intraspecific variation. In this study, we described and investigated the influence of the temperature, humidity, and body size on the acoustic parameters of three populations of *Physalaemus cuvieri* from Brazil. In general, its typical advertisement call consists of a single note with a triangular envelope that resembles an arrow-like shape, a typical pattern for *Physalaemus* species. Our results indicated some intraspecific differences between the studied populations**

regarding dominant frequency, call duration and inter-call interval. The humidity and body mass influenced the inter-call intervals whereas the snout-vent length was inversely correlated to the dominant frequency. This study is an important contribution to understand the main factors driving vocalization variation in *P. cuvieri*. However, we suggest additional research into the influence of local environmental variables on anurans' acoustic properties.

Key Words.—advertisement call; anurans; Leptodactylidae; vocalization

INTRODUCTION

Animals produce various signals depending on their ecological context and function (Gerhardt and Huber 2002; Bee et al. 2010). Amphibians, for example, utilize multiple forms of communication, such as body movements and vocalizations (Wells 2010; Toledo et al. 2014). Typically, they generate calls in distinct social situations, including reproductive calls to attract females, aggressive calls to mark their territories, often involving confrontations, and defensive calls to escape or scare off potential predators (Toledo et al. 2014; Köhler et al. 2017; Brasileiro et al. 2021).

Research has examined anuran advertisement calls as valuable for identifying and characterizing new anuran species (Viuche-Lozano et al. 2018; Galindo et al. 2020). However, various factors can cause differences in singing characteristics among the same species, including their environment (Röhr et al. 2020a), the impact of traffic noise (Leon et al. 2019), and their morphological traits (Moser et al. 2022). Studies have highlighted intraspecific variations in the acoustic parameters of anurans. For instance, differences in call duration and peak frequency were noted among six anuran species commonly found in

Australia (Weaver et al. 2020). Additionally, monkey tree frogs (Phyllomedusidae) display variation in certain acoustic parameters from both intra and interspecific perspectives (Röhr et al. 2020a), as do *Eleutherodactylus* species in Puerto Rico Bank (Ríos-Franceschi and Joglar 2019). While most anuran species have advertisement calls described, the intraspecific call variability remains understudied for most of them.

The "Barker Frog", *Physalaemus cuvieri* (Fitzinger 1826), is widely distributed across Northeastern, Central, and Southern Brazil (Frost 2025). It is characterized by its small size and dorsal chromatic polymorphism, which varies from gray to brownish or greenish in juveniles. Additionally, the inguinal region and posterior thigh are reddish (Vaz-Silva et al. 2020). It is typically distinguished from other congeners mainly by its advertisement call, which resembles a barking dog (Mai and Loebmann 2010), giving rise to its common name (Frank and Ramus 1995).

The acoustic parameters of *P. cuvieri* were described in the 1960s (Barrio 1965) and revised nearly three decades later (Heyer et al. 1990). Subsequently, some bioacoustic studies have also reported its advertisement call (e.g., Silva et al. 2008; Lima et al. 2018; Hepp and Pombal-Jr 2020). Furthermore, its advertisement and courtship calls vary based on environmental, morphological, and social factors (Gambale and Bastos 2014; Borges 2022). Additionally, the latitudinal gradient may affect the advertisement call of some widespread anuran populations, resulting in intraspecific variations (Pröhl et al. 2007; Baraquet et al. 2015; Tessarolo et al. 2016). Therefore, (i) we described the advertisement call of three populations of *P. cuvieri*, (ii) tested if the acoustic parameters vary in response to the localities, (iii) investigated how temperature and humidity influence their acoustic parameters, and (iv) examined how their body size affects their calls.

MATERIAL AND METHODS

Study area.—This study was conducted in three areas within the Northeast Brazil (Fig. 1). The first sampling point is located in the Ubajara municipality, Ceará state (3°44'12.8" S, 40°55'40.7", 847.5 m a.s.l.). It is an Atlantic Rainforest enclave contained within the Ibiapaba plateau (Andrade-Lima 1982). This area is characterized to have a mean temperature ranging from 22° to 26° C and the mean rainfall is 1.346 mm with rains concentrated between January and May (Ipece 2018). The main vegetation types are Tropical Seasonal Deciduous Forest and Tropical Seasonal Evergreen Forest (Silveira et al. 2020). The second sampling point is located in a semiarid region (Caatinga *strictu sensu*) in the Lavras da Mangabeira municipality, Ceará state (06°49'53" S, 39°01'01" W, 260 m a.s.l.). This area is influenced by the climate tropical warm (even hot) with annual mean temperatures ranging from 26° to 28°C, characterized to have dry shrub vegetation (Ipece 2017; Moura et al. 2020). The mean rainfall is 866.4 mm, and the rains are concentrated between January and April (Ipece 2017). The last sampling point is located in "Serra dos Matões", Pedro II municipality, Piauí state (4°25'23" S, 41°27'34" W, 600 m. a.s.l.). This region is also part of the Ibiapaba bioregion, which makes the climate of this area milder than other municipalities in the Piauí state (Milanez and Pupim 2009). This area is characterized to have annual mean temperatures ranging from 18° to 28° C and the mean rainfall is 1.000 mm with rains concentrated between January and May (Aguiar e Gomes 2004). It is inserted in a transitional zone between Caatinga and Cerrado biomes, but the vegetation is composed predominantly of Cerrado typical species (Barros et al. 2014).

Sampling design.—Calls from 35 individuals of *P. cuvieri* were recorded across three localities during two periods: from January to February 2019 in the Ubajara municipality (10

individuals) and from February to April 2022 in Lavras da Mangabeira (20 individuals) and Pedro II (5 individuals). Temperature and humidity data were measured when *P. cuvieri* individuals were recorded using the portable weather station HTC2A Jiaxi. Once we located an adult male of *P. cuvieri* vocalizing, we approached the frog and remained motionless for five minutes before recording its advertisement calls. Each individual was recorded for 5 to 10 minutes using a professional Marantz PMD 660 digital recorder with a Yoga EM-9600 directional external microphone at a distance of approximately 70 cm from the calling male. Thereafter, we weighed each individual with a digital scale (accurate to 0.01 g), and measured the snout-vent length (SVL) with a digital caliper (accurate to 0.01 mm). We could not measure the anuran mass data from Pedro II due to problems with our digital precision scale. Voucher specimens were housed in the herpetological collections (NUROF) of Universidade Federal do Ceará, Fortaleza, Brazil, and of the Instituto Federal do Piauí-IFPI, Pedro II, Piauí, Brazil.

Data analyzes.—Digital recordings were sampled at 44.1 kHz with 16 bits resolution and saved in uncompressed wave files. Recordings were analyzed on a personal computer using Raven Pro 1.3 (Bioacoustic Research Program 2012), with the following settings: Hamming window function; DFT size 256-point samples; brightness = 74%; contrast = 76%; time grid overlap = 50%. To produce audiospectrograms and waveforms, we used the R packages "Seewave" (Sueur et al. 2008) and tuneR (Ligges et al. 2014), with the following settings: FFT size of 512 points, Hanning window, and 90% of overlap. We analyzed the following temporal and spectral parameters: call duration (CD), inter-calls intervals (CI), and dominant frequency (DF). Bioacoustics terminology follows Köhler et al. (2017).

We used the non-parametric Kruskal Wallis test (Shapiro-Wilk < 0.05) following by the Dunn's post-hoc test (Benjamini-Hochberg method) to investigate whether temporal and

spectral bioacoustics parameters vary in response to the environment where the individuals were found: Ubajara (Atlantic Rainforest enclave), Lavras (Caatinga), and Pedro II (Cerrado). We used transformed data (log x + 1) for better visualization in boxplot.

We first tested the normality of the response variables using the Shapiro-Wilk test (W), of which both CD (W = 0.884, p = 0.003), CI (W = 0.735, p = 5.381e-06), and DF (W = 0.806, p = 8.502e-05) did not have normal distribution data. Thereafter, we calculated the Variance Inflation Factors (VIF) to detect collinearity problems (James et al. 2013), of which no variable from the input variables had collinearity problems (VIF ≤ 2.96). Considering that our response variables are continuous with non-normal distribution, we used Generalized Linear Mixed-effects Models (GLMMs) to assess the effect of predictor variables—humidity, temperature, mass, and snout-vent-length (SVL)—on response variables (call duration, inter-calls intervals, and dominant frequency). We used the sampling point localities (Ubajara, Lavras da Mangabeira, and Pedro II) as a random effect (Local). Our general model was defined as: glmer (CD, CI, or DF ~ SVL + Mass + Temperature + Humidity + (1|Local), data = dados, family = Gamma (link = "log")). We measured the proportion of variation explained by random effects by dividing the random effects variation by the total variance. We checked the residuals' normal and homoscedastic distribution of all models with 5% significance values adopted using the Shapiro-Wilk and Breusch-Pagan tests, respectively. Statistical analyses were performed using the R packages *ggplot2* (Wickham 2016), *lme4* (Bates et al. 2015), *lmerTest* (Kuznetsova et al. 2017), *usdm* (Naimi et al. 2014), and *vegan* packages (Oksanen et al. 2023).

RESULTS

The advertisement call of *P. cuvieri* consists of a single note ranging from 0.24 s to 0.51 s (mean ± standard deviation: 0.31 ± 0.02 s). The inter-call intervals range from 0.51 s to 2.45 s (1.25 ± 0.8 s). The dominant frequency ranges from 562.5 Hz to 1280.5 Hz (806.1 ± 138.4 Hz) with five S-shaped pronounced harmonics and some subharmonics in the first half of the call (Fig. 2).

We observed a significant difference in acoustic parameters among the three *P. cuvieri* populations studied, including call duration ($H = 18.24$, $p < 0.001$), inter-call intervals ($H = 12.25$, $p = 0.002$), and dominant frequency ($H = 6.592$, $p = 0.037$). Individuals from Ubajara had longer call durations than those from Pedro II and Lavras da Mangabeira. In contrast, the dominant frequency in Pedro II was lower, but the inter-call intervals were longer than in the other locations (Table 1, Fig. 3).

Lastly, we observed that the inter-call intervals were influenced by the local humidity ($t = 2.140$, $p = 0.032$) and mass ($t = -2.175$, $p = 0.029$) of each individual. The dominant frequency was affected by the individuals' snout-vent length ($t = -2.134$, $p = 0.042$). Other input variables have no significant effect on their acoustic parameters ($p > 0.05$). The random influence is most noticeable in the call duration (31%) and inter-call intervals (45%). The absence of a general trend line in these relationships may linked to the random effects (Fig. 4).

DISCUSSION

We observed that the overall structure of the advertisement calls of *Physalaemus cuvieri* consisted of a single note, featuring a triangular envelope resembling an arrow-like shape – a typical pattern for *Physalaemus* species (Pimenta and Cruz 2004; Provete et al. 2012; Hepp

and Pombal-Jr 2020). However, we noted discrepancies in the call duration, inter-call interval and dominant frequency among the three populations examined. Differences in the acoustic parameters of certain anuran populations have been previously reported (Morton 1975; Kime et al. 2000; Gerhardt and Huber 2002) and might be interpreted as a frog advertisement call variation, or "anuran accents," (Weaver et al. 2020).

We found that individuals from Ubajara emitted longer calls than those in Pedro II and Lavras da Mangabeira. The local conditions of each environment may influence the acoustic efficiency of calls (Morton, 1975; Kime et al. 2000; Gerhardt and Huber, 2002). For example, in forested environments, anurans may produce longer advertisement calls (Ziegler et al., 2011; Röhr et al., 2020b). Thus, once the sampling point in Ubajara is regarded as an Atlantic Rainforest enclave (Moro et al. 2015), it could influence their call duration.

The Ubajara and Pedro II anuran populations also had the highest inter-call intervals. Anurans' vocalization behavior demands high energy expenditure (Pough et al. 1992; Bevier 2017) and influences different acoustic parameters (Wells and Schwarts 2007). Thus, we suggest these animals spend so much energy emitting longer call durations and require longer rest periods (inter-call intervals). This behavior has already been observed in other anurans (Cunnington and Fahrig 2010). In addition, we found an inverse relationship between the anurans' body mass and the inter-call intervals and a positive association with humidity. Comparisons are difficult to make because most studies do not include anurans' body mass (Erdtmann and Lima 2013) in the analyses, and the others have not supported this relationship (Wang et al. 2021; Almeida-Filho et al. 2024). The effect of humidity on inter-call intervals is supported for certain species, like *Leptodactylus bufonius* (Stănescu et al. 2022), but refuted for others, such as *Leptobrachella ventripunctata* (Feng et al. 2022). Thus, we recommend additional research to understand how humidity affects the anuran inter-call intervals.

Individuals from Lavras da Mangabeira had advertisement calls with a higher dominant frequency. Anurans can adjust the call frequency to disrupt barriers that can attenuate the signal quality of their advertisement calls (Roca et al. 2016; Leon et al. 2019). It is documented that the background noise is can favor higher frequencies (Preininger et al. 2007). However, the relationship between the dominant frequency and the local environmental characteristics is unclear (Erdtmann and Lima 2013). In contrast, the inverse relationship between the body size and the dominant frequency is common in anurans (e.g., Bee et al. 2013; Guerra 2020; Bezerra et al. 2021). Our results also support that smaller individuals have higher dominant frequency, but it is not possible to determine the environmental influence on their dominant frequency.

We concluded that individuals of *P. cuvieri* tend to have some acoustic parameters differences which reflects a kind of "accent" in each sampling site. Local populations geographically distant might have passed by different evolutive processes causing differences in their advertisement calls (Marova et al. 2010; Klymus et al. 2012; Weaver et al. 2020). Additionally, both anuran body conditions and environmental characteristics affect their calls (Castellano et al. 2002; Wong et al. 2004). However, more studies are needed to clarify the main factors driving vocalization variation in the populations studied. This research highlights the importance of emphasizing that intraspecific variations in the vocalizations of anurans do not always indicate speciation processes and that environmental factors may account for these differences.

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FIGURE CAPTIONS

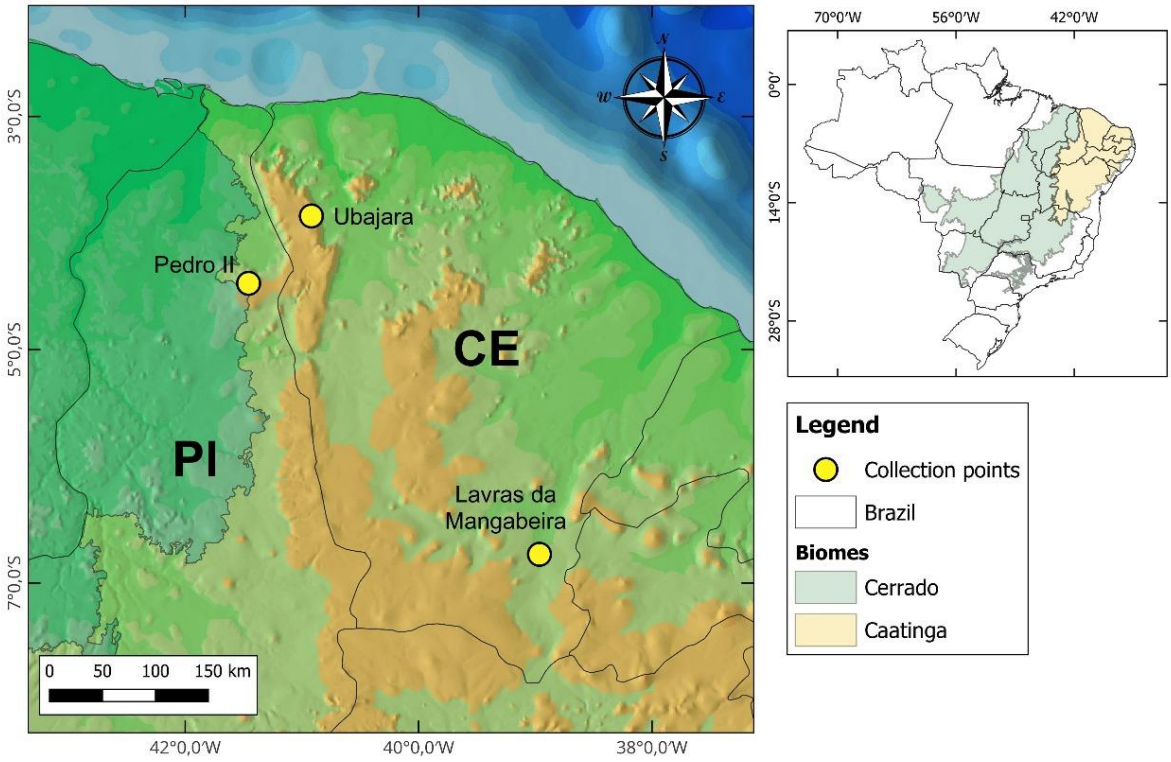

Fig. 1. Schematic map of the sampling points where individuals of *Physalaemus cuvieri* were recorded in Piauí (PI) and Ceará (CE) states, Northeast Brazil

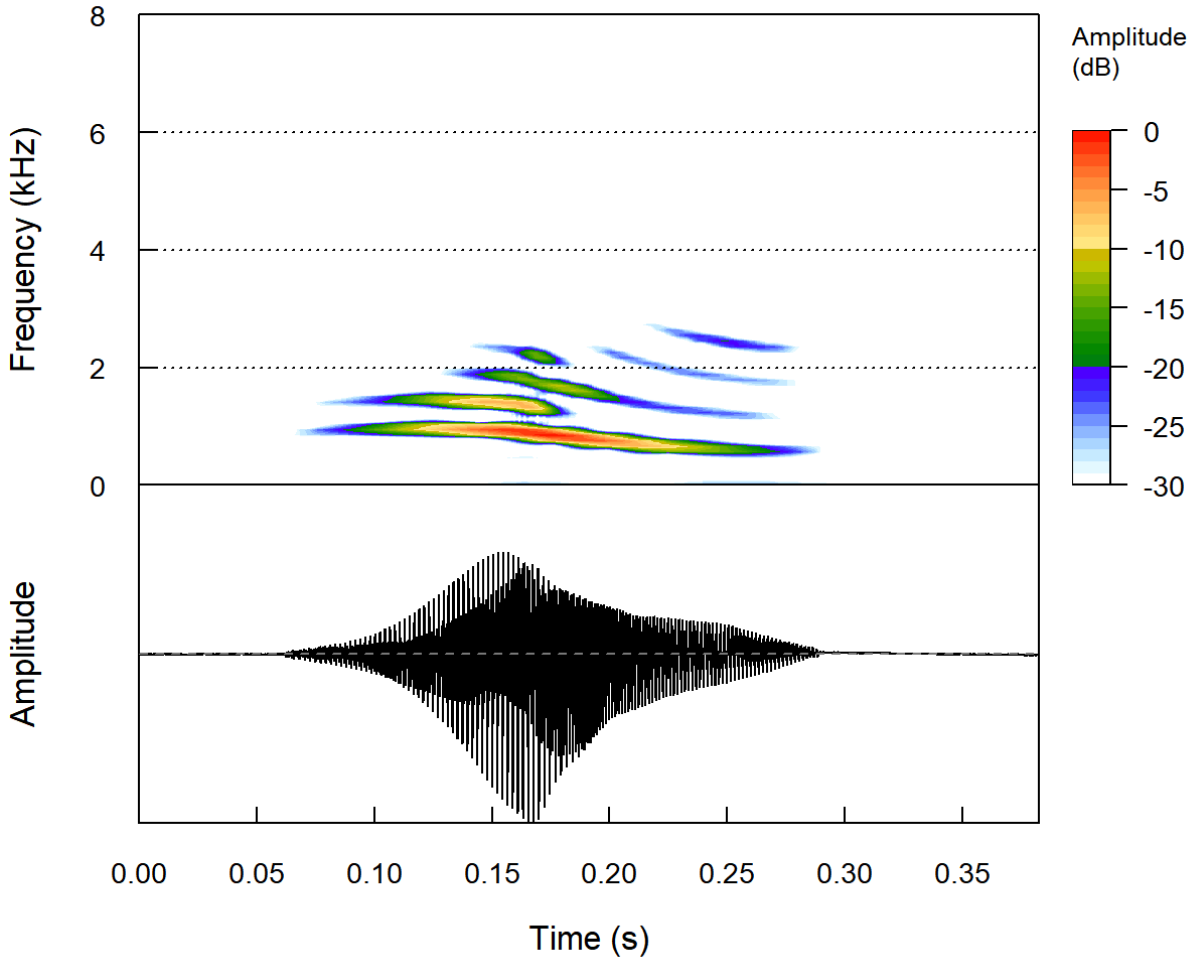

Fig. 2. Spectrogram and oscillogram of the advertisement call of *Physalaemus cuvieri*. Male recorded on April 18, 2019, in the Ubajara municipality, Ceará, Northeast Brazil.

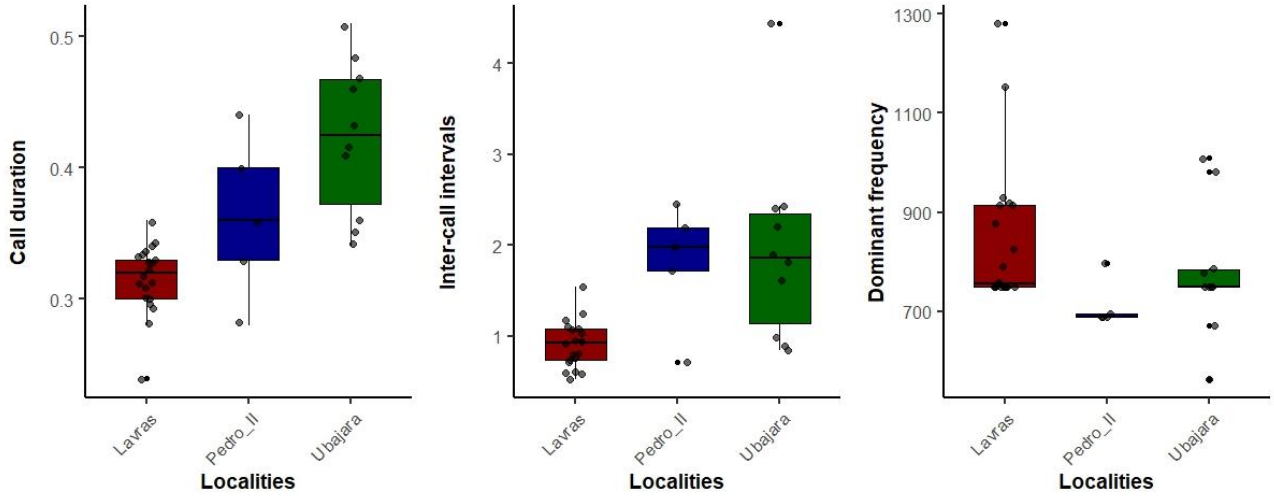

Fig. 3. Acoustic parameters between the populations of *Physalaemus cuvieri* from the tree localities in the Northeast Brazil

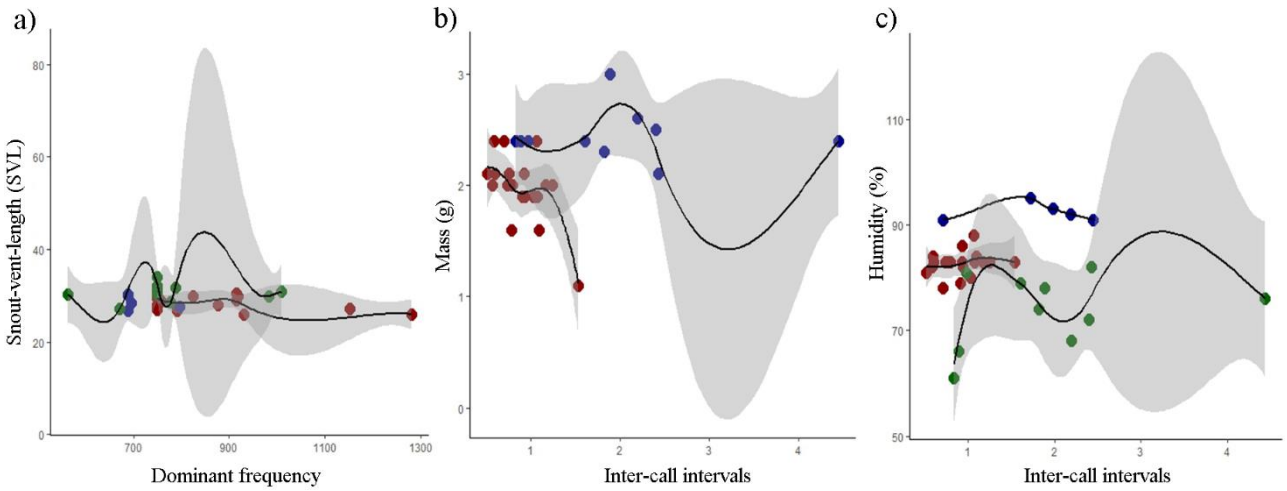

Fig. 4. Significant relationship between the acoustic parameters of *Physalaemus cuvieri* and the input variables studied. Lavras da Mangabeira (darkred circle), Pedro II (darkblue circle), and Ubajara (darkgreen circle)

TABLE CAPTION

Table 1. Acoustic parameters with respective maximum, minimum, mean, and standard deviation values of the individuals of *Physalaemus cuvieri* from Lavras da Manguabeira, Pedro II, and Ubajara municipalities, Northeast Brazil

Local	N	Recorded calls	Call duration	Inter-calls interval	Dominant frequency
Lavras da Mangabeira	20	1200	0.36 – 0.24 (0.31 ± 0.02)	1.54 – 0.52 (0.90 ± 0.25)	1280.4 – 750.0 (843.4 ± 146.4)
Pedro II	5	300	0.44 – 0.28 (0.36 ± 0.06)	2.45 – 0.71 (1.80 ± 0.67)	796.7 – 689.1 (711.9 ± 47.4)
Ubajara	10	600	0.51 – 0.34 (0.42 ± 0.05)	4.44 – 0.84 (1.94 ± 1.06)	1008.6 – 562.5 (778.8 ± 131.6)

N = number of individuals recorded.

Author photographs and biosketches.—

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3. CAPÍTULO 2. Endoparasites influence on vocalization and mating success of *Physalaemus cuvieri* Fitzinger, 1826

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ABSTRACT. Anurans vocalize in different social contexts, in which the advertisement call is the most disseminated. Different endoparasites usually parasitize these animals, but how these endoparasite infections affect anuran vocalizations remains unclear. Therefore, we investigate how endoparasite infections influence the advertisement call and mating success of *Physalaemus cuvieri*. For that, we searched and recorded the advertisement call of this anuran at a Caatinga area, during the rainy season from March to April 2021 and February to April 2022, totaling 63 sampling days. After recording the advertisement call, we monitored their success in starting amplexus with females. In the lab, we necropsied all collected individuals to see if some endoparasites infected them. We found a significant effect of the parasite load only on call intervals—more parasitized individuals exhibited higher call intervals. In addition, we observed that the less-weight individuals tended to be more parasitized. Lastly, only the male snout-vent lengths affected the matting success in the studied population of *Physalaemus cuvieri*. The present study is an essential contribution to understanding how anuran health influences communication and sexual selection.

Keywords: Advertisement call, Amphibians, Barker Frog, Leptodactylidae, Reproduction

Introduction

Different species usually emit visual and auditory signals to attract sexual partners [1–3], and amphibians are known to present a high diversity of communication modes [4–5]. Amongst them, vocal signals are predominant communication modes in amphibians, and they might be used in different social contexts, from territorial disputes to sexual behaviors. For instance, salamanders demonstrate reciprocity to mate by releasing pheromones [6], whereas anurans interact with each other through visual, chemical, and bioacoustic signals, besides tactile stimuli [4,7–8]. Vocalization is the most predominant means of communication in anuran

populations [4,9], which might be used in different social contexts, from territorial disputes to sexual behaviors [5].

Anurans might have different strategies to communicate with each other and attract females, including vocalization during the reproductive period [5,10]. The advertisement call is the most widespread within the anuran vocalization, acting as a reproductive isolation mechanism, because it contains characteristics for species recognition [4,10,11]. Additionally, it provides information about morphology, energy expenditure, and health status of the calling males [4,12].

Comprehending how endoparasite infections influence the bioacoustic parameters of anurans is still uncleared. For instance, the call duration of *Boana prasina* was negatively correlated with endoparasite abundance [13]. In contrast, the call effort increases with endoparasite infections in *Ranoidea rheocola* [14] and *Dryophytes japonicus* [15]. Lastly, no relation between endoparasite load and bioacoustic parameters was observed in *Dryophytes versicolor* and *Scaphiopus couchii* [16,17]. Thus, once females choose males, usually based on their advertisement calls [4,18], details in the acoustic characteristics of males might be valuable tools for their reproductive success [19,20].

Leptodactylids are one of the most conspicuous groups of Neotropical anurans [21], which implies a great variety of vocalizations since each species has a specific advertisement call [11]. Among them, *Physalaemus cuvieri* Fitzinger, 1826 is a small frog widely distributed inhabiting natural and anthropized lotic water ponds [22] and presents a characteristic vocalization like a barking dog [23]. Parasitological studies showed that this anuran tends to be infected by different endoparasite taxa [e.g., 24,25,26]; however, little is still known about how these infections influence their advertisement calls and sexual selection.

Herein, we investigate the relationship between endoparasite infections and bioacoustic communication and mating success of *P. cuvieri* in the Brazilian semiarid. We hypothesized

that (i) more parasitized anurans will emit lower and less prolonged calls with longer intervals, (ii) less successful matings, and (iii) larger frogs will have high parasite infection levels.

Material and Methods

Study area

The present study was carried out in the rural zone of the municipality of Lavras da Mangabeira (Fig. 1), Ceará State, Northeast Brazil (06°49'53" S, 039°01'01" W). It is located in the Brazilian semiarid region and has a tropical warm climate with mean temperatures ranging from 26º to 28ºC. Rainfall is concentrated between January and April, with an annual mean of 866.4 mm. It is inserted in the Caatinga biome, and the main vegetation comprises open shrubby caatinga [27].

Sampling

We searched for individuals of *P. cuvieri* during the rainy season from March to April 2021 and February to April 2022, totaling 63 sampling days. The field expeditions occurred at night (18 h to 00 h) using visual [28] and auditory [29] searches as sampling methodology.

When an active calling male was seen, his song was recorded using a professional digital recorder Marantz PMD660 with a unidirectional microphone positioned at a maximum distance of 50 cm in front of it for five minutes. To reduce the interference of observers on behavior, we started to record behavior 10 minutes after an individual had been detected. Then, we observed during the field expedition (18 h to 00 h) if the calling male mated (named as successful mating). All recorded calling males, regardless of their successful mating, were collected and carried out to the lab, where they were euthanized with an injection of lidocaine. We measured the snout-vent length (SVL) of each anuran with a digital calliper (0.01 mm) and weighed (mass) using a

weighing scale (Pesola®). These measures were used to investigate how the anuran body size is related to bioacoustic parameters and endoparasite infections.

Bioacoustic parameters

We sampled the digital recordings at 44.1 kHz with 16 bits resolution and saved in uncompressed wave files. We analyzed these recordings on a personal computer using Raven Pro 1.3 [30], with the following settings: Hamming window function; DFT size 256-point samples; brightness = 74%; contrast = 76%; time grid overlap = 50%. We used the R packages "Seewave" [31] and tuneR [32], with the following settings: FFT size of 512 points, Hanning window, and 90% of overlap to produce audiospectrograms and waveforms. For statistical analyses we described the following temporal and spectral parameters: call repetition rate (CR), call duration (CD), inter-calls intervals (CI), and dominant frequency (FD). See [11] for the bioacoustics terminology.

Parasitological procedures

In the lab, we necropsied and examined the presence of endoparasites in the gastrointestinal, respiratory, and urinary tract, and the abdominal cavity of each collected individual of *P. cuvieri*. Each endoparasite was treated following classic methodologies for each taxon [33,34]. Lastly, we measured the following parasitological descriptors: prevalence and abundance [35]. Endoparasites were deposited in the parasitological collection of the Universidade Federal do Ceará, Fortaleza, Brazil.

Statistical analyses

We used generalized linear models (GLM) to investigate the effect of endoparasite abundance on bioacoustic parameters. General model = (response variable (CI, CD, or FD) ~

endoparasite abundance, family = Gamma (link = "log"), data = dados). We checked the residuals' normal and homoscedastic distribution of all models with 5% significance values adopted using the Shapiro-Wilk and Breusch-Pagan tests, respectively. We also tested how the anuran body size influenced endoparasite infections using the GLM test [(SVL or mass) ~ endoparasite abundance, family = gaussian (link = "identity") and family = Gamma (link = "log"), data = dados)]. Residuals' normal and homoscedastic distribution were also checked.

Lastly, we tested if the bioacoustic parameters, endoparasite abundance and anuran body size influenced the mating success using the GLM test. General models were mating success ~ bioacoustic parameters, endoparasite abundance or anuran body size, family = binomial (link = "logit"), data = dados). Residuals' normal and homoscedastic distribution were also checked. Statistical analyses were performed using the r packages ggplot2 [36], performance [37], and vegan [38].

Results

We recorded 2050 calls from 41 males of *P. cuvieri*, whose typical advertisement call consists of a single note ranging from 0.24 s to 0.39 s (mean ± standard deviation: 0.32 ± 0.02 s). The dominant frequency ranges from 750.0 Hz to 1,280.0 Hz (826.1 ± 115.87 Hz) with five S-shaped pronounced harmonics and some subharmonics in the first half of the call, whereas the inter-call intervals range from 0.52 s to 1.72 s (0.94 ± 0.29 s) (Fig. 2).

Among the necropsied individuals of *P. cuvieri*, 23 were found to be infected by at least one species of endoparasite, resulting in a prevalence (Prev.) of 56.09%. We found 103 endoparasite specimens belonging to phyla Acanthocephala, Nematoda, and Platyhelminthes (class Trematoda) distributed in 11 taxa, in which *Oswaldocruzia belenensis* Santos, Giese, Maldonado, and Lanfredi, 2008 (N = 50, Prev. = 39.1%) and *Physaloptera* sp. (N = 21, Prev. =

39.1%) had the highest abundance and prevalence values, respectively (Table 1). It was the first record of *O. belenensis* parasitizing the *Physalaemus* genus.

We found a significant effect of endoparasite abundance only on inter-call intervals (T = 2.102, P = 0.04), whereas call repetition rate (T = -1.876, P = 0.07), call duration (T = -0.544, P = 0.592), and dominant frequency (T = 1.657, P = 0.111) were not influenced by the abundance of endoparasites. In this sense, more parasitized individuals had longer inter-call intervals (Fig. 3a). Additionally, we observed that less-weight individuals were significantly more parasitized (T = -3.92, P = 0.0006; Fig. 3b) whereas the SVL (T = -1.525, P = 0.14) had poor influence on parasitological infections.

In general, we observed that 21 males successfully mated, but neither the bioacoustic parameters ($p > 0.05$) nor the abundance of parasites affected the mating success ($z = -1.067$, $p = 0.286$). Only the SVL significantly influenced the mating success ($z = 2.061$, $p = 0.039$), whose larger individuals tended to mate more successfully (Fig. 3c).

Discussion

Almost half of the collected individuals were infected by at least one endoparasite taxa, with nematodes having the highest species richness and abundance. Nematodes are usually abundant in Neotropical frogs [39], moreover for terrestrial and semiaquatic species because it facilitates endoparasite infections with a direct lifecycle [40]. In addition to having the highest abundance in the population of *P. cuvieri* studied, *Oswaldocruzia belenensis* was rarely reported parasitizing anurans [e.g., 41,42], and our record represents the first record of this endoparasite infecting *P. cuvieri*. With the exception of *Cosmocerca parva* and *O. belenensis*, the remaining taxa could not be identified due to their developmental stage, or the lack of males present in the sample.

We noted that more parasitized individuals tended to have longer inter-call intervals, which may be associated with the energy expenditure to fight these infections because infected hosts may have different ways of allocating energy [43,44]. The energy expenditure to emit advertisement calls is related to some bioacoustic parameters [45,46,47]. Therefore, anurans with high levels of endoparasite infections have less energy to emit advertisement calls in a shorter period. Other bioacoustic parameters were not influenced by endoparasite abundance; however, more studies dealing with different species are still needed to understand how endoparasite infections affect the anuran health and, consequently, their advertisement call.

We also found an inverse relationship between endoparasite abundance and the mass of anurans, in which heavier individuals were less parasitized. Endoparasites infecting the gastrointestinal tract might consume the host's nutrients, thus reducing their weight [48]. This relationship was already reported for other anurans, such as bufonids [49,50]. Some endoparasite infections influence anuran growth [51], and our results suggest that high endoparasite infections might cause negative impacts on host health. Endoparasite infections have no relationship with anuran SVL as observed in other studies [e.g., 52,53].

We observed that anurans SVL had a pronounced influence on mating success, whose larger males tended to be more chosen by females. In general, larger anurans have the highest fitness and, consequently, might have greater survival capacity and reproduction, and they are better resource competitors [54,55,56]. Females use bioacoustic parameters from the anuran's advertisement calls to identify males of its species for mating [4]. Still, these parameters do not influence the sexual selection by females in the population of *P. cuvieri* studied. Therefore, females may use bioacoustic parameters to identify males of their species and locate him, later selecting the larger males visually.

The endoparasite infections did not affect mating success in the studied population. While reduced mating success is often a common consequence of endoparasite infections

[57,58,59], parasitized hosts can still reproduce normally if they become unrecognizable to females in terms of their parasitism [15,60]. In addition, the anuran SVL was the leading filter in explaining the mating success, which is not influenced by endoparasite infections. Therefore, as the endoparasite infections only influenced the inter-call intervals, which was also not a determining factor in the female choice, parasitized males went unnoticed by the females' choices.

Although endoparasite infections influence the bioacoustic parameters of *P. cuvieri*, our results support that they were not the primary driver of male mating success. In contrast, the anuran snout-vent length (SVL) had a pronounced effect on the female chosen, in which larger anurans had more mating success. The present study contributes to understanding how endoparasite infections affect a population of *P. cuvieri* regarding advertisement call and mating success; however, we suggest more studies testing these assumptions in controlled environments are still needed to understand the best drivers of anurans' sexual selection.

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Figure legends

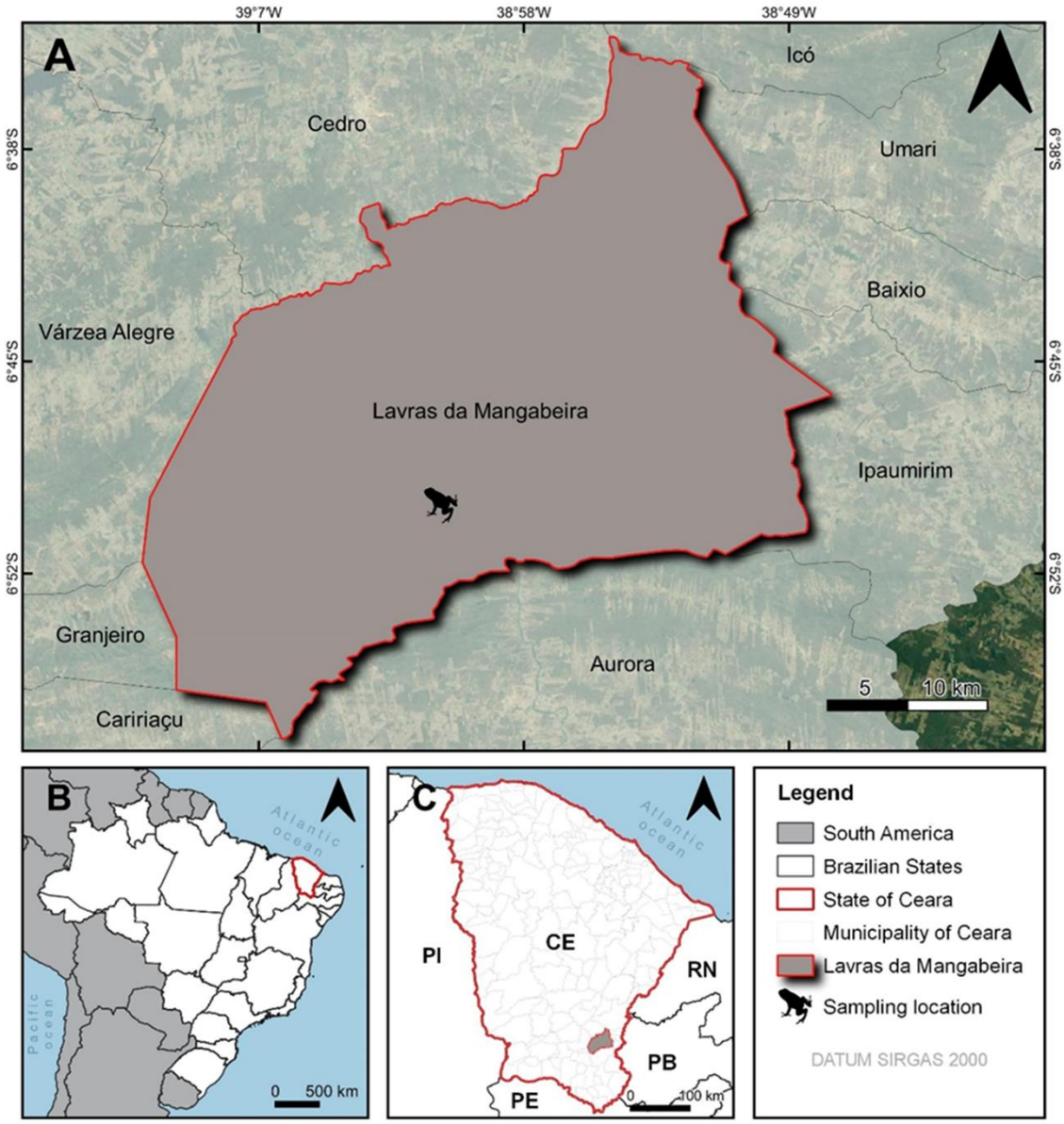

Fig. 1. Schematic map of the sampling point where individuals of *Physalaemus cuvieri* were recorded and collected in the state of Ceará, Northeastern Brazil.

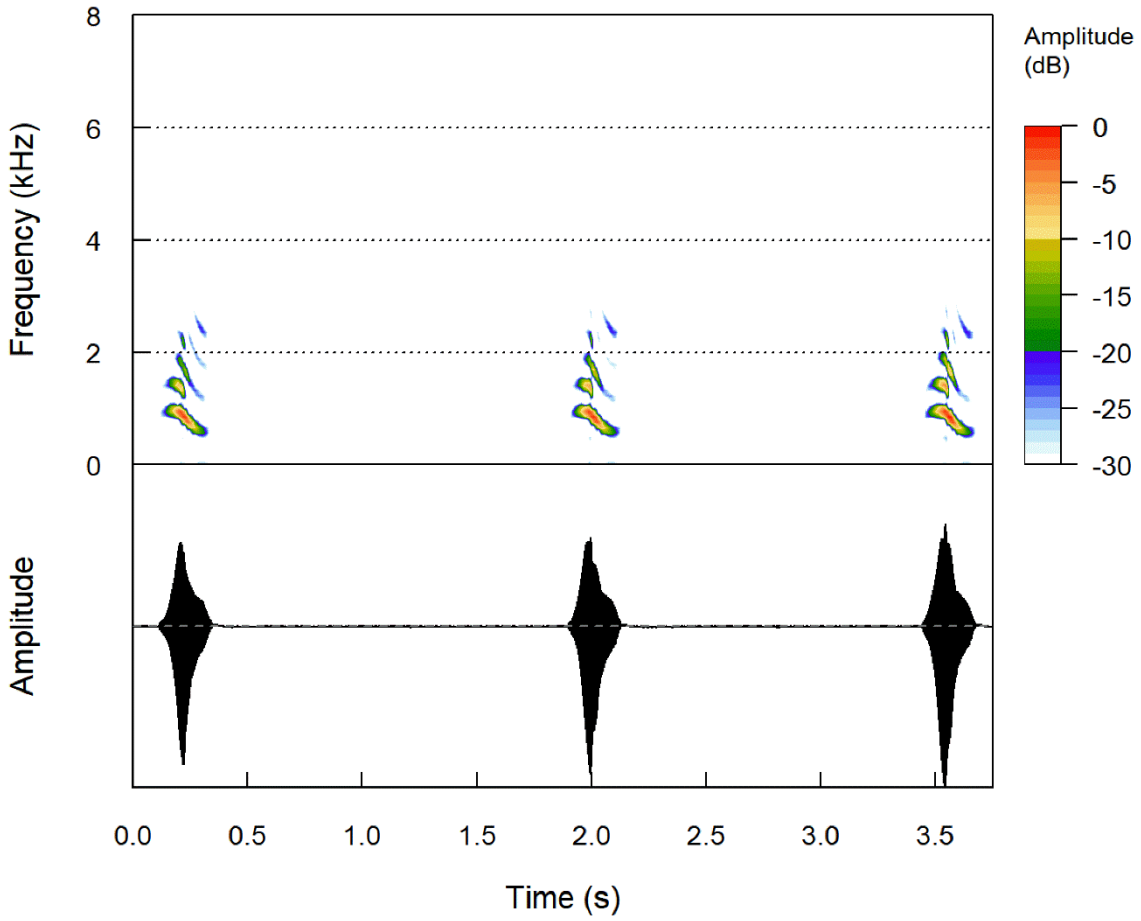

Fig. 2. Spectrogram and oscillogram of the advertisement call of *Physalaemus cuvieri* in the state of Ceará, Northeast Brazil.

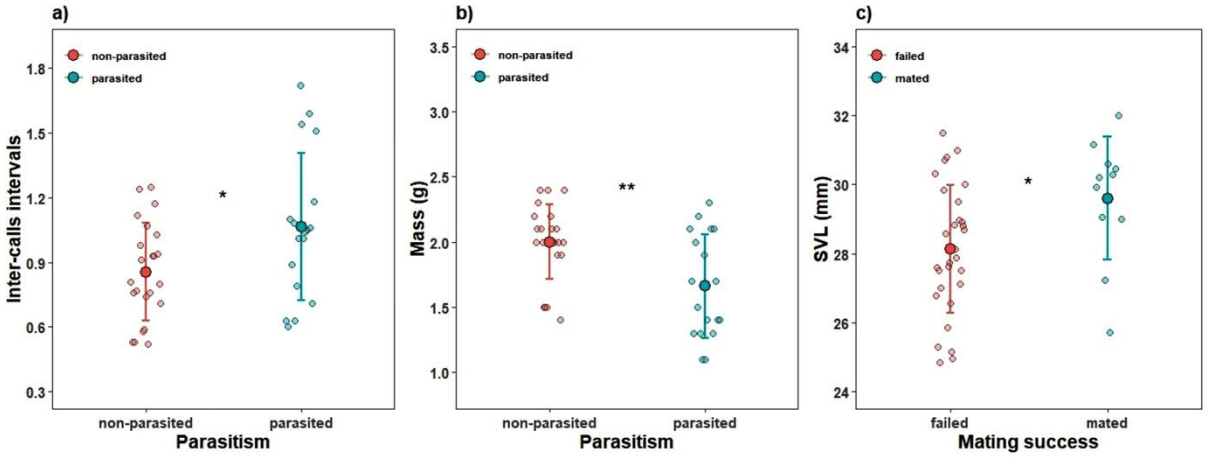

Fig. 3. Significative relationships between inter-call intervals (a) and mass (b) with the endoparasite abundance; and SVL with mating success (c) of *Physalaemus cuvieri*.

Table legend

Table 1. Endoparasite taxa infecting *Physalaemus cuvieri* in the municipality of Lavras da Mangabeira, Ceará State, Northeastern Brazil. Legends – endoparasite abundance (N), prevalence (P%), mean intensity of infection (MI), site of infection (SF): abdominal cavity (Ca), stomach (St), small intestine (Si), larger intestine (Li), lungs (Lg), and kidney (Kd).

Taxa	N	P%	MI	SF	Stage
Acanthocephala					
Cystacanths of Centrorhynchidae	1	4.35	1	Ca	Larvae
Cystacanths of Oligacanthorhynchidae	4	8.7	2	St, Ca	Larvae
Nematoda					
Aplectana sp.	1	8.7	1	Si, Li	Adult
Cosmocerca parva Travassos 1925	1	4.35	1	Si	Adult
Cosmocercidae	3	8.7	1.5	Li	Larvae
Oswaldocruzia belenensis Santos, Giese, Maldonado, and Lanfredi, 2008	50	39.13	5,5	Si	Adult
Oxyascaris sp.	18	4.35	18	Si	Adult
Filariidae	1	4.35	1	Ca	Larvae
Physaloptera sp.	21	39.13	2.3	St	Larvae
Rhabdias sp.	1	4.35	1	Lg	Adult
Trematoda					
Metacercaria	2	8.7	1	Kd	Larvae

4. CONSIDERAÇÕES FINAIS

A vocalização dos anfíbios anuros é determinada por informações genéticas, porém alguns fatores podem interferir no seu repertório acústico. Para entender alguns desses processos, utilizamos o canto de anúncio de *Physalaemus cuvieri*, um leptodactilídeo de médio porte que possui ampla distribuição geográfica no Brasil. Assim, nesta tese, investigamos a influência da temperatura, umidade e características morfológicas do anuros nos parâmetros acústicos de três populações de *Physalaemus cuvieri* do Brasil. Além disso, testamos como as infecções endoparasitárias afetam estes parâmetros acústico. Por fim, avaliamos o impacto dessas infecções no sucesso reprodutivo em uma população de *P. cuvieri* encontrada no município de Lavras da Mangabeira, estado do Ceará, nordeste do Brasil.

No primeiro capítulo investigamos se existem diferenças significativas no canto de anúncio em populações de *P. cuvieri* de três localidades do Brasil. Neste capítulo observamos que os parâmetros acústicos analisados do canto desta espécie variam em função da localidade e que a umidade, a massa e o tamanho do corpóreo do anuros influenciam estes parâmetros. Apesar dos resultados encontrados, sugerimos que mais estudos ainda são necessários para entender quais filtros ambientais permitem que ocorra essa variação intraespecífica no canto de anúncio entre as populações estudadas.

No segundo capítulo, usamos uma abordagem local para entender como as interações parasito-hospedeiro influenciam no canto de anúncio e, consequentemente, na seleção sexual de uma população de *P. cuvieri* localizada no município de Lavras da Mangabeira, estado do Ceará, nordeste do Brasil. Nossos resultados mostraram que a abundância parasitária dos hospedeiros influenciou apenas o intervalo entre os cantos — indivíduos mais parasitados exibiram intervalos maiores nos cantos. Além disso, não desempenhou um papel importante na seleção sexual. Por outro lado, o tamanho dos machos teve influência na escolha das fêmeas para o acasalamento. Esse estudo é uma importante contribuição para a compreensão do efeito das infecções endoparasitárias na vocalização e seleção sexual de anfíbios anuros.

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