

## Original paper

# Endoparasites influence on vocalization and mating success of *Physalaemus cuvieri* Fitzinger, 1826

Heitor T.S. MACHADO<sup>1</sup>, Kássio C. ARAÚJO<sup>2</sup>, Cristiana FERREIRA-SILVA<sup>3</sup>,  
Robson W. ÁVILA<sup>1,3</sup>

<sup>1</sup>Programa de Pós-Graduação em Ecologia e Recurso Naturais, Departamento de Biologia, Campus do Pici, Universidade Federal do Ceará, Bloco 906, Av. Mister Hull, s/n, Fortaleza, CE, 60440-900, Brasil

<sup>2</sup>Grupo de Pesquisa em Biodiversidade e Biotecnologia do Centro-Norte Piauiense, Instituto Federal de Educação, Ciência e Tecnologia do Piauí, Campus Pedro II, Rua Antonino Martins de Andrade, 750, Pedro II, PI, 64255-000, Brasil

<sup>3</sup>Núcleo Regional de Ofiologia, Universidade Federal do Ceará - UFC, Bloco 905, Centro de Ciências, Campus PICI, Fortaleza - CE, CEP: 60455-760, Brasil

Corresponding Author: Heitor T.S. Machado; e-mail: heitortdsm@gmail.com

**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 mating success in the studied population of *Physalaemus cuvieri*. The present study is an important 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 unclear. For instance, the call duration of *Boana prasina* was negatively correlated with endoparasite

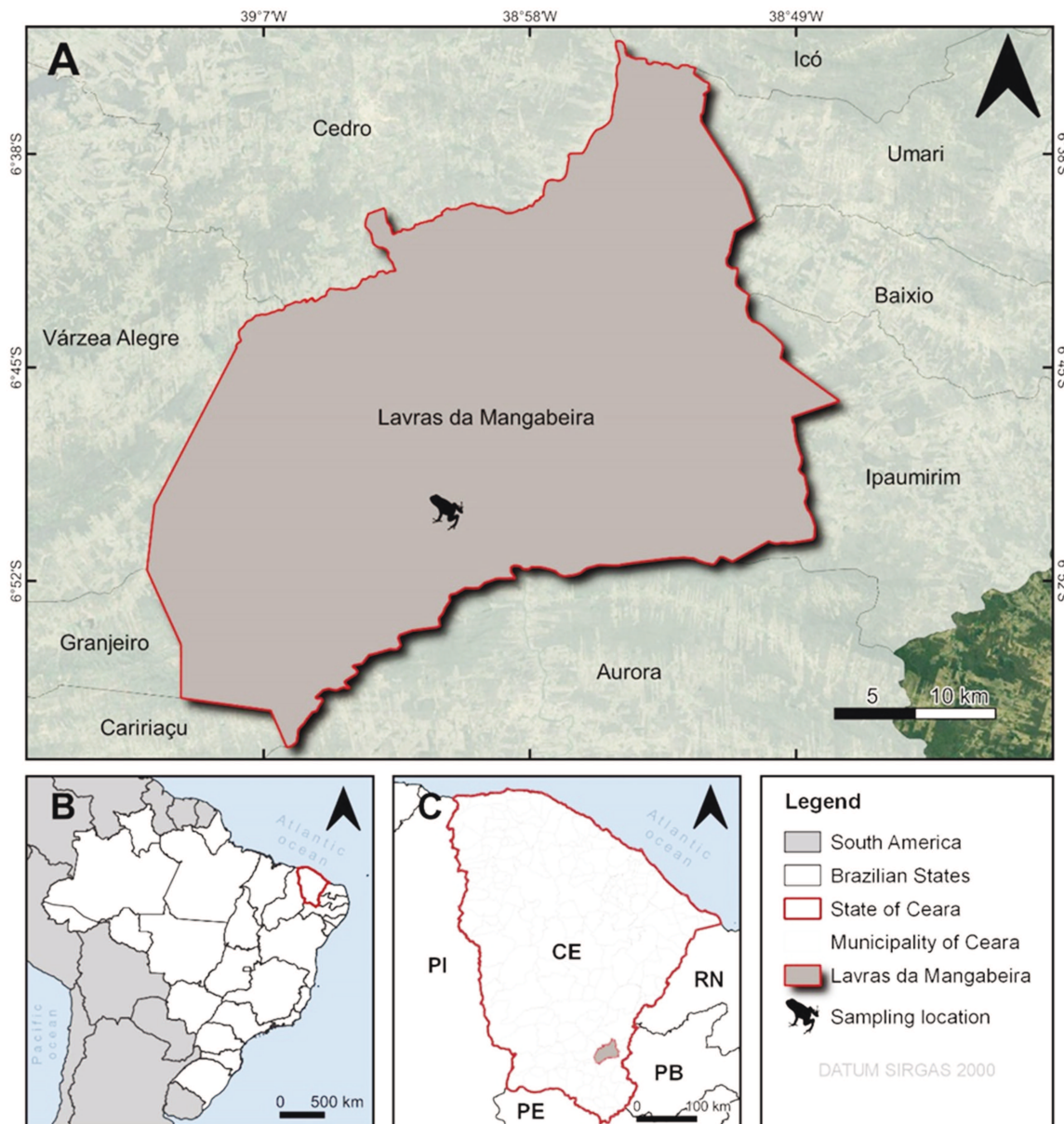


Figure 1. Schematic map of the sampling point where individuals of *Physalaemus cuvieri* were recorded and collected in the state of Ceará, Northeastern Brazil

abundance [13]. In contrast, the call effort increases with endoparasite infections in *Litoria rheocola* [14] and *Hyla japonica* [15]. Lastly, no relation between endoparasite load and bioacoustic parameters was observed in *Hyla 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., 24–26]; 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.

## Materials 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 26° to 28°C. 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.

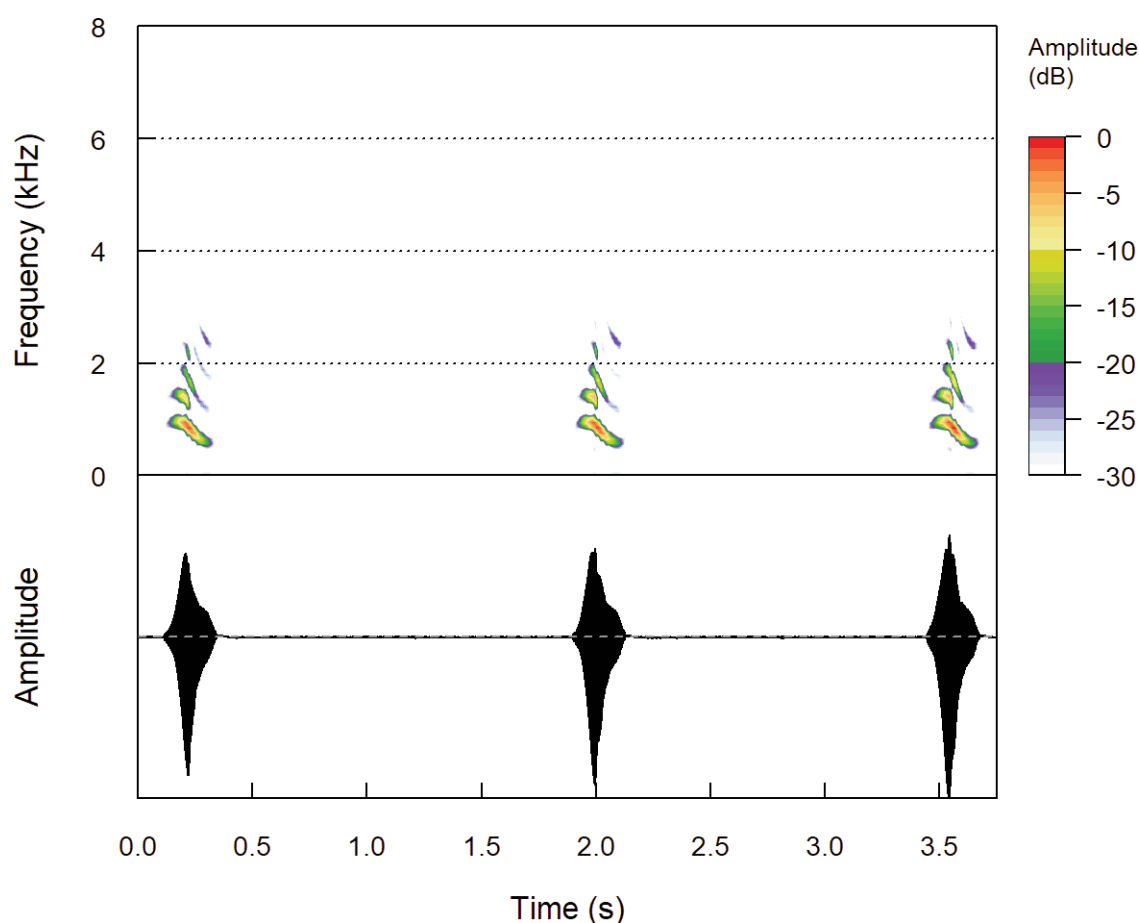


Figure 2. Spectrogram and oscillogram of the advertisement call of *Physalaemus cuvieri* in the state of Ceará, Northeast Brazil

### 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

Table 1. Endoparasite taxa infecting *Physalaemus cuvieri* in the municipality of Lavras da Mangabeira, Ceará State, Northeastern Brazil

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

Explanations: – 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)



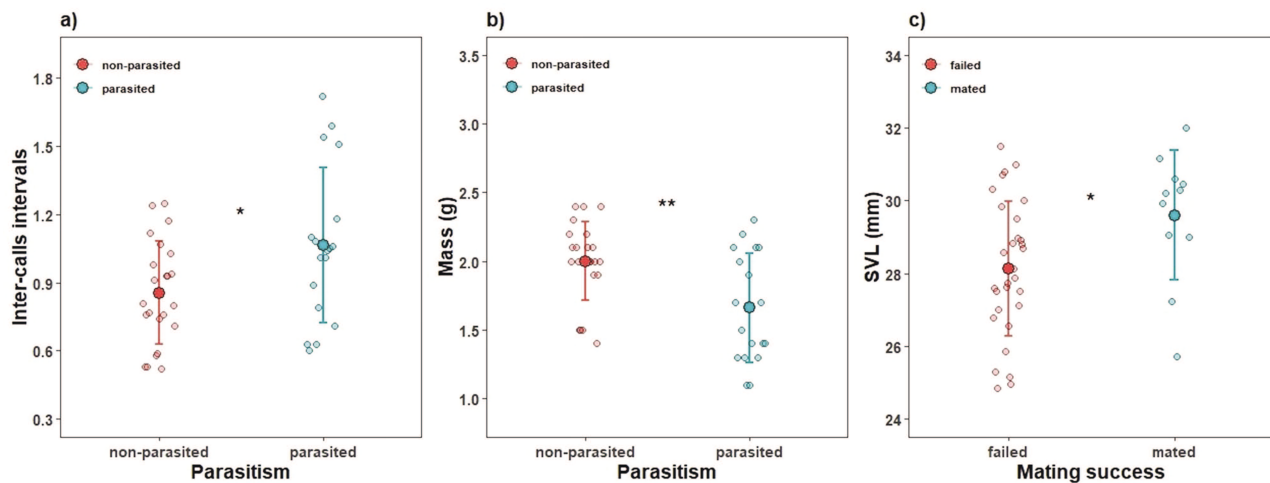


Figure 3. Significant relationships between inter-call intervals (a) and mass (b) with the endoparasite abundance; and SVL with mating success (c) of *Physalaemus cuvieri*

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  $\pm$  standard deviation:  $0.32 \pm 0.02$  s). The dominant frequency ranges from 750.0 Hz to 1,280.0 Hz ( $826.1 \pm 115.87$  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 ( $0.94 \pm 0.29$  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 taxon, 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 [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 [45–47]. 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 [52,53].

We observed that anurans SVL had a pronounced influence on mating success, with 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 [54–56]. 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 them, 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 [57–59], 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 choice, 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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## References

- [1] Leal M., Fleishman L.J. 2004. Differences in visual signal design and detectability between allopatric populations of *Anolis* lizards. *The American Naturalist* 163(1): 26–39. doi:10.1086/379794
- [2] Wilkins M.R., Seddon N., Safran R.J. 2013. Evolutionary divergence in acoustic signals: causes

- and consequences. *Trends in Ecology & Evolution* 28(3): 156–166. doi:10.1016/j.tree.2012.10.002
- [3] Arikawa K. 2017. The eyes and vision of butterflies. *Journal of Physiology* 595(16): 5457–5464. doi:10.1113/jp273917
- [4] Wells K.D. 2010. The ecology and behavior of amphibians. The University of Chicago Press, Chicago and London.
- [5] Toledo L.F., Martins I.A., Bruschi D.P., Passos M.A., Alexandre C., Haddad C.F.B. 2015. The anuran calling repertoire in the light of social context. *Acta Ethologica* 18: 87–99. doi:10.1007/s10211-014-0194-4
- [6] Vaccaro E.A., Feldhoff P.W., Feldhoff R.C., Houck L.D. 2010. A pheromone mechanism for swaying female mate choice: enhanced affinity for a sexual stimulus in a woodland salamander. *Animal Behaviour* 80(6): 983–989. doi:10.1016/j.anbehav.2010.08.020
- [7] Ryan M.J. 2009. Communication in frogs and toads. In: *Encyclopedia of neuroscience*. (Eds. L.R. Squire). Academic Press: 1159–1166.
- [8] Preininger D., Boeckle M., Freudmann A., Starnberger I., Sztatecsny M., Hodl W. 2013. Multimodal signaling in the small torrente frog (*Micrixalus saxicola*) in a complex acoustic environment. *Behavioral Ecology and Sociology* 67: 1449–1456. doi:10.1007/s00265-013-1489-6
- [9] Dorcas M.E., Price S.J., Walls S.C., Barichivich W.J. 2010. Auditory monitoring of anuran populations. In: *Amphibian ecology and conservation: a handbook of techniques*. (Eds. K.C. Dodd). Oxford University Press: 281–298.
- [10] Guerra V., Llusia D., Gambale P.G., Morais A.R.D., Marquez R., Bastos R.P. 2018. The advertisement calls of Brazilian anurans: historical review, current knowledge and future directions. *PLoS One* 13(1): e0191691. doi:10.1371/journal.pone.0191691
- [11] Köhler J., Jansen M., Rodríguez A., Kok P.J.R., Toledo O.L.F., Emmrich M., Glaw F., Haddad C.F.B., Rödel M.O., Vences M. 2017. The use of bioacoustics in anuran taxonomy: theory, terminology, methods and recommendations for best practice. *Zootaxa* 4251(1): 1–124. doi:10.11646/zootaxa.4251.1.1
- [12] Liu Q., Wang T., Zhai X., Wang J. 2018. Call characteristics of two sympatric and morphologically similar tree frogs species, *Polypedates megacephalus* and *Polypedates mutus* (Anura: Rhacophoridae), from Hainan, China. *Asian Herpetological Research* 9(4): 240–249. doi:10.16373/j.cnki.ahr.180025
- [13] Madelaire C.B., Silva R.J., Gomes F.R. 2013. Calling behavior and parasite intensity in treefrogs, *Hypsiboas prasinus*. *Journal of Herpetology* 47: 450–455.
- [14] Roznik E.A., Sapsford S.J., Pike D.A., Schwarzkopf L., Alford R.A. 2015. Condition dependent reproductive effort in frogs infected by a widespread pathogen. *Proceedings of the Royal Society B: Biological Sciences* 282: 20150694. doi:10.1098/rspb.2015.0694
- [15] An D., Waldman B. 2016. Enhanced call effort in Japanese tree frogs infected by amphibian chytrid fungus. *Biology Letters* 12: 20160018. doi:10.1098/rsbl.2016.0018
- [16] Hausfater G., Gerhardt H.C., Klump G.M. 1990. Parasites and mate choice in Gray Treefrog, *Hyla versicolor*. *American Zoologist* 30(2): 299–311.
- [17] Tinsley R.C. 1990. The influence of parasite infection on mating success in spadefoot toads, *Scaphiopus couchii*. *American Zoologist* 30(2): 313–324.
- [18] Gerhardt H.C., Bee M.A. 2007. Recognition and localization of acoustic signals. In: *Hearing and sound communication in amphibians*. (Eds. P.M. Narins, A.S. Feng, R.R. Fay, A.N. Popper). Springer: 113–146.
- [19] Pröhl H. 2003. Variation in male calling behaviour and relation to male mating success in the strawberry poison frog (*Dendrobates pumilio*). *Ethology* 109(4): 273–290. doi:10.1046/j.1439-0310.2003.00863.x
- [20] Ron S.R. 2008. The evolution of female mate choice for complex calls in túngara frogs. *Animal Behaviour* 76(6): 1783–1794. doi:10.1016/j.anbehav.2008.07.024
- [21] Frost D.R. 2025. Amphibian species of the world: an online reference. Version 6.2. Accessed on 11 January 2025. <https://amphibiansoftheworld.amnh.org/index.php>. American Museum of Natural History, New York, USA. doi:10.5531/db.vz.0001
- [22] Eterovick P.C., Souza A.M., Sazima I. 2020. Anuran amphibians from the Serra do Cipó, Brazil: Gráfiön Estúdio Editorial, Belo Horizonte.
- [23] Barrio A. 1965. El genero *Physalaemus* (Anura, Leptodactylidae) en la Argentina. *Physis* 25: 421–488.
- [24] Toledo G.M., Aguiar A., Silva R.J., Anjos L.A. 2013. Helminth fauna of two species of *Physalaemus* (Anura: Leiuperidae) from an undisturbed fragment of the Atlantic rainforest, Southeastern Brazil. *The Journal of Parasitology* 99(5): 919–922.
- [25] Leivas P.T., Leivas F.W.T., Campião K.M. 2018. Diet and parasites of the anuran *Physalaemus cuvieri* Fitzinger, 1826 (Anura: Leiuperidae) from an Atlantic Forest fragment. *Herpetology Notes* 11: 109–113.
- [26] Oliveira C.R., Ávila R.W., Morais D.H. 2019. Helminths associated with three *Physalaemus* species (Anura: Leptodactylidae) from Caatinga biome, Brazil. *Acta Parasitologica* 64: 205–212. doi:10.2478/s11686-018-00022-8
- [27] IPECE. Instituto de Pesquisa e Estratégia Econômicas do Ceará. 2024. Perfil municipal Lavra da Mangabeira.

- [https://www.ipece.ce.gov.br/wp-content/uploads/sites/45/2018/09/Lavras\\_da\\_Mangabeira\\_2017.pdf](https://www.ipece.ce.gov.br/wp-content/uploads/sites/45/2018/09/Lavras_da_Mangabeira_2017.pdf) (accessed 27 Jan 2025).
- [28] Crump M.L., Scott-Junior N.J. 1994. Visual encounter surveys. In: *Measuring and monitoring biological diversity: standard methods for amphibians*. (Eds. W.R. Heyer, M.A. Donnelley, R.W. McDiarmid, L.C. Hayek, M.S. Foster). Smithsonian Institution Press: 84–92.
- [29] Zimmerman B.L. 1994. Audio strip transects. In: *Measuring and monitoring biological diversity: standard methods for amphibians*. (Eds. W.R. Heyer, M.A. Donnelley, R.W. McDiarmid, L.C. Hayek, M.S. Foster). Smithsonian Institution Press: 92–97.
- [30] Bioacoustic Research Program. 2012. RAVEN PRO: interactive sound analysis software, Version 1.5. Accessible at: [www.birds.cornell.edu/raven](http://www.birds.cornell.edu/raven)
- [31] Sueur J., Aubin T., Simonis, C. 2008. Seewave, a free modular tool for sound analysis and synthesis. *Bioacoustics* 18: 213–226.
- [32] Ligges U., Krey S., Mersmann O., Schnackenberg O. 2023. Analysis of music and speech. R package version 1.4.7. <https://CRAN.R-project.org/package=tuneR> (accessed on 11 January 2025)
- [33] Amato F.R., Boeger W.A., Amato S.B. 1991. Protocolos para Laboratório Coleta e Processamento de Parasitos de Pescado. Imprensa Universitária – UFRJ, Rio de Janeiro.
- [34] Andrade C.M. 2000. Meios e soluções comumente empregados em laboratórios. Editora Universidade Rural, Rio de Janeiro.
- [35] Bush A.O., Lafferty K.D., Lotz J.M., Shostak A.W. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *The Journal of Parasitology* 83(4): 575–583.
- [36] Wickham H. 2016. ggplot2: elegant graphics for data analysis. 2nd edition. Springer.
- [37] Nikolai S.R. 2024. Performance: assessment of regression models performance. R package version 0.9.3. <https://cran.r-project.org/web/packages/performance/index.html> (accessed on 11 January 2025)
- [38] Oksanen J., Blanchet F.G., Friendly M., Kindt R., Legendre P., McGlinn D., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H., Szoecs E. 2023. vegan: Community Ecology Package. R package version 2.6-4. <https://cran.r-project.org/web/packages/vegan/index.html> (accessed on 11 January 2025)
- [39] Campião K.M., Morais D.H., Dias O.T., Aguiar A., Toledo G., Tavares L.E.R., Silva R.J. 2014. Checklist of helminth parasites of amphibians from South America. *Zootaxa* 3843(1): 1–93. doi:10.11646/zootaxa.3843.1.1
- [40] Anderson R.C. 2000. Nematode parasites of vertebrates. Their development and transmission. CABI Publishing, New York.
- [41] Santos J.N., Giese E.G., Maldonado-Junior A., Lanfredi R.M. 2008. A new species of *Oswaldocruzia* (Molineidae: Nematoda) in *Chaunus marinus* (Amphibian: Bufonidae) (Linnaeus, 1758) from Brazil. *Journal of Parasitology* 94(1): 264–268. doi:10.1645/GE-1336.1
- [42] Willkens Y., Furtado A.P., Santos J.N., Melo F.T.V. 2021. Do host habitat use and cospeciation matter in the evolution of *Oswaldocruzia* (Nematoda, Molineidae) from neotropical amphibians?. *Journal of Helminthology* 95: e33. doi:10.1017/S0022149X21000250
- [43] Nadler L.E., Adamo S.A., Hawley D.M., Binning S.A. 2023. Mechanisms and consequences of infection induced phenotypes. *Functional Ecology* 37(4): 796–800. doi:10.1111/1365-2435.14309
- [44] Wright M., Oleson L., Witty R., Fritz K.A., Kirschman L.J. 2023. Infection causes trade-offs between development and growth in larval amphibians. *Physiological and Biochemical Zoology* 96(6): 430–437. doi:10.1086/727729
- [45] Pough F.H., Magnusson W.E., Ryan M.J., Taigen T.L., Wells K.D. 1992. Behavioral energetics. In: *Environmental physiology of the amphibians*. (Eds. M.E. Feder, W.W. Burggren). University of Chicago Press: 395–436.
- [46] Wells, K.D., Schwartz J.J. 2007. The behavioral ecology of anuran communication. In: *Hearing and sound communication in amphibians*. (Eds. P.M. Narins, A.S. Feng, R.R. Fay, A.N. Popper). Springer: 44–86.
- [47] Bevier C.R. 2017. Physiological and biochemical correlates of calling behavior in anurans with different calling strategies. In: *Amphibian and reptile adaptations to the environment*. (Eds. D.V. Andrade, C.R. Bevier, J.E. Carvalho). Boca Raton: CRC Press: 1–18.
- [48] Poulin R. 2007. Evolutionary ecology of parasites. Princeton University Press, Princeton.
- [49] Kelehear C., Brown G.P., Shine R. 2011. Influence of lung parasites on the growth rates of free-ranging and captive adult cane toads. *Oecologia* 165: 585–592. doi:10.1007/s00442-010-1836-5
- [50] Finnerty P.B., Shilton C.M., Shine R., Brown G.P. 2017. Using experimental de-worming to measure the immunological and pathological impacts of lungworm infection in cane toads. *International Journal for Parasitology: Parasites and Wildlife* 6(3): 310–319. doi:10.1016/j.ijppaw.2017.09.006
- [51] Marino Jr J.A., Holland M.P., Werner, E.E. 2016. Competition and host size mediate larval anuran interactions with trematode parasites. *Freshwater Biology* 61(5): 621–632. doi:10.1111/fwb.12730
- [52] Cardoso E.L., Jesus R.F., Silva-Filho H.F., Willkens Y., Santana G.L., Santos A.N., Santos J.N., Melo F.T. 2021. Do environmental and host variables influence the parasite community of *Leptodactylus fuscus*



- (Anura: Leptodactylidae) in the Amazon Region?. *The Journal of Parasitology* 107(6): 904–911. doi:10.1645/21-53
- [53] Machado H.T.S., Oliveira S.S., Benício R.A., Araújo K.C., Ávila R.W. 2022. Helminths infecting sympatric congeneric treefrogs in Northeastern Brazil. *Acta Parasitologica* 67: 1–10. doi:10.1007/s11686-021-00497-y
- [54] Brooks R., Kemp D.J. 2001. Can older males deliver the good genes?. *Trends in Ecology & Evolution* 16(6): 308–313. doi:10.1016/s0169-5347(01)02147-4
- [55] Rausch A.M., Sztatecsny M., Jehle R., Ringler E., Hödl W. 2014. Male body size and parental relatedness but not nuptial colouration influence paternity success during scramble competition in *Rana arvalis*. *Behaviour* 151: 1869–1884. doi:10.1163/1568539X-00003220
- [56] Kelleher S.R., Scheele B.C., Silla A.J., Keogh J.S., Hunter D.A., Byrne P.G. 2021. Disease influences male advertisement and mating outcomes in a critically endangered amphibian. *Animal Behaviour* 173: 145–157. doi:10.1016/j.anbehav.2021.01.007
- [57] Hurd H. 2001. Host fecundity reduction: a strategy for damage limitation?. *Trends in Parasitology* 17(8): 363–368. doi:10.1016/s1471-4922(01)01927-4
- [58] Klein S.L. 2005. Parasite manipulation of host behavior: mechanisms, ecology, and future directions. *Behavioural Processes* 68(3): 219–221. doi:10.1016/j.beproc.2004.07.009
- [59] Beltran-Bech S., Richard F.J. 2014. Impact of infection on mate choice. *Animal Behaviour* 90: 159–170. doi:10.1016/j.anbehav.2014.01.026
- [60] Pfennig K.S., Tinsley R.C. 2002. Different mate preferences by parasitized and unparasitized females potentially reduces sexual selection. *Journal of Evolutionary Biology* 15(3): 399–406. doi:10.1046/j.1420-9101.2002.00406.x

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