

Advertisement call of Johnstone's whistling frog *Eleutherodactylus johnstonei* in Brazil

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ABSTRACT – Anuran advertisement calls play a role in attracting potential mates and can vary among individuals and populations. Here we describe the advertisement call of a non-native population of *Eleutherodactylus johnstonei* in São Paulo, Brazil and compare our data with other non-native populations in other countries. The advertisement calls of *E. johnstonei* show two-tonal frequency-modulated notes differing in spectral and temporal patterns. The first note is shorter and has lower frequencies than the second note. Our comparisons indicate that, except for the Montserrat population, the calls of the Brazilian population of *E. johnstonei* are similar to the other populations in terms of the call and note duration. Concerning spectral parameters, except for Bucaramanga (Colombia) and Caracas (Venezuela) populations, the dominant frequency of the first note is lower in the Brazilian population than in other localities. The advertisement call variations of *E. johnstonei* seem unrelated to morphological differentiation or the length of time since the population was introduced, but may reflect local female preferences or adaptation to environmental factors.

INTRODUCTION

Anurans exhibit acoustic, visual, chemical, and tactile modes of communication (Hödl & Amézquita, 2001; Wells, 2007; Belanger & Corkum, 2009). However, acoustic communication is the primary, most widespread, and most studied. Males of many species show a vast acoustic repertoire emitted in different social contexts, such as mate choice, sexual selection, kin recognition, and territoriality (Ryan, 2001). The advertisement call is the most conspicuous, highly studied, and has two main functions: i) to attract females to mate, and ii) to prevent agonistic interaction with other males (Littlejohn, 1977; Wells, 2007). Advertisement calls are species-specific and easy to record, making them helpful for species identification (Gerhardt & Davis, 1988).

Advertisement calls vary among individuals and conspecific populations (e.g., Castellano et al., 2002; Pettitt et al., 2013; Guerra et al., 2017). Individual call variations depend on intrinsic factors such as body size and conditions (Rodríguez et al., 2015; Ziegler et al., 2015). Also, extrinsic factors such as the presence of conspecific or heterospecific signals, background noise, and environmental temperature may influence call parameters at any given time (Lopez et al., 1988; Howard & Young, 1998; Wells, 2007; Schwartz & Bee, 2013). On the other hand, call variation among populations may follow a geographic cline resulting from genetic, morphological, and/or environmental factors (Castellano et al., 2000; Pröhl et al., 2007; Klymus et al., 2010). These variations directly impact sexual selection due to female mate choice (Gerhardt, 1991), leading to changes in communication systems and, ultimately, the evolution of

mating signals (Boul & Ryan, 2004; Wilkins et al., 2013).

Since non-native species are outside of their native habitat, they offer excellent opportunities to examine variation in call parameters among recently established populations. They may live without natural ecological pressure, such as competition in the acoustic niche between species in the community to minimise overlapping signals (Narins, 1995), and can show rapid differentiation in call parameters, as has been noted in the invasive cane-toad (*Rhinella marina*) and coqui frog (*Eleutherodactylus coqui*) (O'Neill & Beard, 2011; Yasumiba et al., 2016). The Australian populations of the invasive cane-toad have presented differences in dominant frequency and call duration (Yasumiba et al., 2016). On the other hand, the coqui frog exhibits differences in call frequencies, call rate, and call duration among populations at different elevations in its introduced range in Hawaii (O'Neill & Beard, 2011).

Eleutherodactylus johnstonei Barbour, 1914 (Anura: Eleutherodactylidae) is a nocturnal frog native to the Lesser Antilles (Lever, 2003) with successful populations in some other Caribbean islands, Venezuela, Colombia, the Guianas, Panama, and Costa Rica (Kaiser et al., 2002; Kraus, 2008). These countries were invaded by the frog over a period of 46 to 142 years (Hardy & Harris, 1979; Kaiser & Hardy, 1994). In Brazil, populations occur only in the urban megalopolis of São Paulo (Melo et al., 2014), where introduction occurred sometime before 1995 and appears to have been intentional (Toledo & Measey, 2018). *E. johnstonei* shows direct development (i.e., the fully metamorphosed froglet emerges from the egg), has a generalist diet and habitat (e.g., Kaiser et al., 2002; Ortega et al., 2005), and ecological modeling

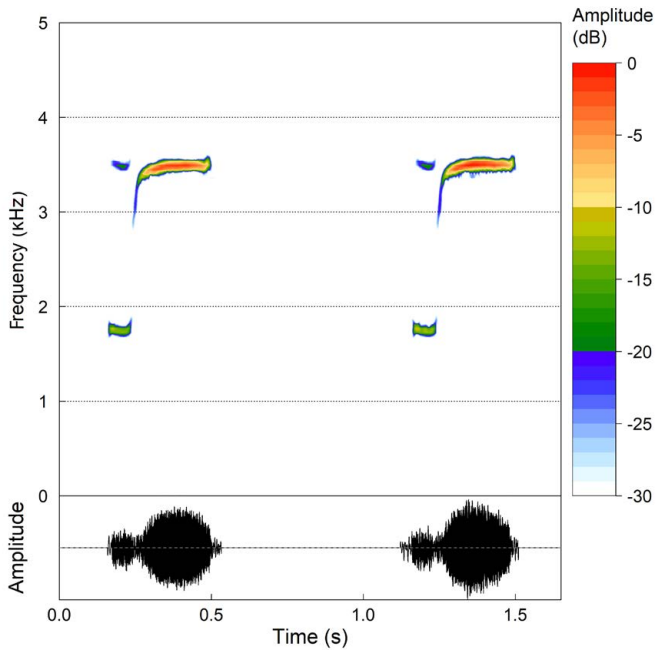


Figure 1. Spectrogram (top) and oscillogram (bottom) of the advertisement call of *Eleutherodactylus johnstonei* (Air temperature = 25.3 °C, relative humidity = 64 %, voucher FNVJ 50606). Spectrogram parameters: window size = 1.024, overlap = 90 %, window type = “Hann”. Figure created with the R package ‘Seewave’ (Sueur et al., 2008)

predicts a high potential to occur in different biomes in Brazil (Forti et al., 2017; Brasileiro et al., 2021). Herein we describe the advertisement call of the Brazilian population of *E. johnstonei* and compare our data with other non-native populations.

MATERIALS & METHODS

Data collection

We recorded advertisement calls of six male *E. johnstonei* on 16 March 2020 between 20:00h and 22:00h, in the urban area of the municipality of São Paulo, São Paulo State, southeastern Brazil (23° 38'02" S, 46° 40'55" W). We recorded each individual for 1–3 minutes using a Tascam DR-22WL digital record and measured the call intensity using a sound level meter, keeping a distance of 1 m from the recorded individual. We also measured the air temperature and relative humidity during each recording using a portable thermo-hygrometer (Icel, HT-200). All voucher specimens were anaesthetised and euthanised with 5 % lidocaine, fixed in 10 % formalin, preserved in 70 % ethanol, and deposited in the Amphibian Collection (ZUEC), at the Museu de Diversidade Biológica, Universidade Estadual de Campinas, state of São Paulo, Brazil (ZUEC25183 - 25188).

Bioacoustics analysis

We digitalised the recordings at 44.1 kHz with a resolution of 16 bits and undertook acoustic analyses using the Raven Pro 1.6.1 software (Bioacoustics Research Program, 2019). For call selection, we used the waveform window. We adjusted a fast Fourier transformation of 1.024 points for spectral

measurements, with a window of 90 % overlap, temporal hop size of 102 samples, and grid spacing of 43.1 Hz. We followed the note-centered approach and the concepts of notes, pulses, and calls defined by Köhler et al. (2017). Five calls from each male’s recordings were sampled at random to measure call parameters, totaling 30 calls. Estimates were made of call duration (ms), note duration (ms), intercall interval (ms), call rate (calls/min), dominant frequency of each note (kHz), low frequency of each note (kHz), and high frequency of each note (kHz). We obtained data for intercall interval (ms) and call rate (notes/min) by analysing the entire oscillogram (waveform) of the recording of each male (Charif et al., 2010) and constructed audio spectrograms in R using the Seewave package (Sueur et al., 2008). We have deposited our audio files of frog calls in the audio archive of Fonoteca Neotropical Jacques Vielliard (FNJV), Universidade Estadual de Campinas, State of São Paulo, Brazil (FNJV 50605–50610).

We compared the advertisement call of the Brazilian population of *E. johnstonei* with descriptions of nine populations available in the literature (Watkins et al., 1970; Lemon, 1971; Hardy & Harris, 1979; Kaiser, 1992; Kaiser & Hardy, 1994; Kaiser et al., 1994; Tárano & Fuenmayor, 2008; Flechas et al., 2018). However, some of the descriptions did not include all the call parameters that we analysed, this prevented us making certain comparisons.

RESULTS

The advertisement call of the recorded individuals of *E. johnstonei* in Brazil shows two types of notes differing in spectral and temporal patterns (Table 1; Fig. 1). The advertisement call of *E. johnstonei* has harmonic structures, in which the lowest band (fundamental frequency) concentrates most of the energy. The first note has two harmonics, and the second note has three to five harmonics (Fig. 1). On average, the first note lasted 76 ms with a dominant frequency of 1.77 kHz, a low frequency of 1.61 kHz, and a high frequency of 1.96 kHz. The second note is longer than the first note and lasted 212 ms on average with a dominant frequency of 3.42 kHz, a low frequency of 2.87 kHz, and a high frequency of 3.54 kHz. The advertisement call (first and second notes combined) presents a duration of 288 ms. The average call rate was 36 calls/min with an average intercall interval of 989 ms. The air temperature during the recordings was 25.3 ± 0.6 °C, and the relative humidity was 64 ± 3 %. The call intensity was registered between 75 and 78.5 Db recorded a metre away from each male. All six recorded frogs were in ornamental vegetation in gardens less than 1 m from the ground.

The advertisement call of all populations of *E. johnstonei* is composed of two notes. Except for the Montserrat population, the Brazilian population’s calls are similar to the other populations in terms of the call duration and the duration of the first and second note. In the Montserrat population, the call duration and second note duration are longer (Table 2). Concerning spectral parameters, the dominant frequency of the first note is lower in the present study than in other localities when considering average and variation range, except for in Bucaramanga (Colombia) and Caracas (Venezuela). The dominant frequency of the second

Table 1. Temporal and spectral characteristics of the advertisement call of *Eleutherodactylus johnstonei*. Calls were recorded from 6 males (totalising 30 calls) at Jardim Cordeiro, São Paulo, state of São Paulo, south-western Brazil. Each parameter includes mean \pm standard deviation, minimum and maximum values.

Call parameters	Mean \pm std (min – max)
Call duration (ms)	288 \pm 30 (236 – 340)
Intercall interval (ms)	989 \pm 220 (581 – 1500)
Call rate (call/min)	36 \pm 10 (25 – 49)
First note duration (ms)	76 \pm 10 (49 – 100)
Second note duration (ms)	212 \pm 20 (167.4 – 247.4)
Dominant frequency of the first note (kHz)	1.77 \pm 0.03 (1.72 – 1.81)
Dominant frequency of the second note (kHz)	3.42 \pm 0.13 (3.14 – 3.53)
Low frequency of the first note (kHz)	1.61 \pm 0.04 (1.5 – 1.7)
Low frequency of the second note (kHz)	2.87 \pm 0.12 (2.62 – 3.05)
High frequency of the first note (kHz)	1.96 \pm 0.07 (1.88 – 2.08)
High frequency of the second note (kHz)	3.54 \pm 0.13 (3.25 – 3.66)

note in the Brazilian population is similar to the populations of Caracas and Bermuda, but higher than the Bucaramanga population and lower than the Montserrat, Grenada, Georgetown (Guyana), Cumaná (Venezuela), and Barbados populations (Table 2).

DISCUSSION

The advertisement calls of the Brazilian population of *E. johnstonei* consist of two adjacent notes with distinct temporal and spectral parameters. Both notes are tonally frequency-modulated, with frequency modulation at the end of the first note and the beginning of the second note. Both notes present harmonics, however it can sometimes be challenging to visualise them in the spectrogram and therefore only the first harmonic of the first note is visible (Fig. 1). The harmonic structure of the call establishes a broad prevalent bandwidth (1.6–13.8 kHz).

While both notes play a role in male interactions, the function of the second note in the advertisement call of *E. johnstonei* is related to female attraction (Tárano & Fuenmayor, 2013). The harmonic structures recently identified in the advertisement call of *E. johnstonei* (Tárano & Fuenmayor, 2008, and this study) do not yet have a defined biological function. It is possible that harmonics were not detected in the older analysed recordings due to equipment limitations, as the first descriptions of these calls were documented in the 1970s (Watkins et al., 1970; Lemon, 1971; Hardy & Harris, 1979). The

function of harmonics has continued to be poorly investigated for anurans (Foratto et al., 2021).

The advertisement call structure of *E. johnstonei* in Brazil and the other nine non-native populations has revealed differences among them mainly in their dominant frequencies. Comparing the population of Brazil and Montserrat, differences occur both in temporal and spectral parameters. Usually, the dominant frequency among populations varies with the individual body size, while variations in temporal parameters occur due to temperature (Gerhardt & Huber, 2002; Ziegler et al., 2015; Tonini et al., 2020). Body size is positively associated with the mass of vocal cords that vibrate at lower fundamental frequencies as male size increases (Gerhardt, 1994). For *E. johnstonei*, the dominant frequency of the call can indicate the size of a male's body, but only in a limited way (Tárano & Fuenmayor, 2008). On average, males sampled in Montserrat are smaller than males in Brazil (Table 3), explaining the higher dominant frequencies in the Montserrat population.

Although the time since introduction varies among *E. johnstonei* populations, this factor does not seem to explain the variation in the advertisement call parameters (see Table 3). It was not possible to identify a pattern among newly established or long-established non-native populations. The cane-toad (*Rhinella marina*) in Australia also shows divergence in its advertisement call among invasive populations, and the variation has not been attributed to the time of invasion of each population, but to differences in adaptation to environmental, behavioral and/or ecological conditions (Yasumiba et al., 2016).

The variation in advertisement calls can be related to geographic distance gradients among populations (e.g. Smith et al., 2003; Smith & Hunter, 2005). For example, latitude and longitude largely explain the geographic variation in the advertisement call of *Litoria verreauxii* in the Australian Snowy Mountains (Smith et al., 2003). São Paulo, Brazil has the southernmost latitude (-23°) of the evaluated populations. Changes in environmental conditions associated with different latitudes may be responsible for call variations among *E. johnstonei* populations. Besides latitude, we should also consider the possible influence of social interactions (Gerhardt, 1994), sexual selection (Ryan et al., 1996), and the local acoustic environment (Ryan et al., 1990).

Unfortunately, variations both in sample size and the technology used in the analyses of previous studies has limited the comparisons that we could make with other introduced populations of *E. johnstonei*. For the future, we suggest detailed studies i) across the native distribution, including introduced populations of *E. johnstonei*, to focus on the ecological and behavioural characteristics of individuals to clarify the causes of call variation, and ii) far from the native distribution, to observe the effect of *E. johnstonei* introductions and consequences on established populations.

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Table 2. Comparison of the advertisement call of *Eleutherodactylus johnstonei* from several locations. Values are means ± standard deviation and/or variation ranges (in parenthesis).

Call Parameters					
Location	Call duration (ms)	First note duration (ms)	Second note duration (ms)	Dominant frequency of the first note (kHz)	Dominant frequency of the second note (kHz)
São Paulo (Brazil, this study)	288 ± 30 (236 - 340)	76 ± 10 (49 - 100)	212 ± 20 (167.4 - 247.4)	1.77 ± 0.03 (1.72 - 1.8)	3.42 ± 0.13 (3.14 - 3.5)
Bucaramanga (Colombia)	277 ± 23.1 (215.5 - 316.6)	77 ± 18.4 (1.5 - 107.5)	200.6 ± 17.5 (176 - 234)	1.723 ± 0.042 (1.6 - 1.9)	2.78 ± 0.146 (2.5 - 3.0)
Caracas	314 (226 - 400)	86 (53 - 111)	223 (142 - 307)	1.8 (1.6 - 1.9)	3.3 (3 - 3.6)
Montserrat	363	57	306	2.1	3.7
Grenada	271	71	200	1.9	3.6
Curaçao	271	71	200	1.85	3.5
Georgetown (Guyana)	264	57	187	2	3.6
Cumaná (Venezuela)	257	86	171	2	3.7
Barbados	(240 - 300)	(70 - 90)	(180 - 220)	(2 - 2.2)	(3.6 - 4.1)
Bermuda	–	85	180	2	3.5

Bucaramanga- Flechas et al. (2018); Caracas-Tárano & Fuenmayor (2008); Montserrat & Grenada-Kaiser (1992); Kaiser et al. (1994)*. Curaçao, Cumaná and Georgetown - Hardy & Harris (1979)*; Barbados-Lemon (1971); Bermuda-Watkins et al. (1970). (*) values estimated from sonograms as they were not given in the text

Table 3. Comparison of the snout–vent length (SVL) of *Eleutherodactylus johnstonei*, local air temperature and invasion time from non-native populations. Values are means ± standard deviation.

Location	SVL (mm)	Temperature (°C)	Invasion time (years)	References
São Paulo (Brazil, this study)	21.8 ± 0.9	25.3 ± 0.6	26	Toledo & Measey (2018)
Bucaramanga (Colombia)	–	–	–	–
Caracas (Venezuela)	23.08 ± 0.75	–	63	Tárano & Fuenmayor (2008); Hardy & Harris (1979)
Montserrat	20.5 ± 3.1	24 ± 2	-	Kaiser (1992), Kaiser et al. (1994)
Grenada	–	24 ± 2	136	Kaiser (1992), Kaiser et al. (1994)
Curaçao	–	-	46	Hardy & Harris (1979)
Georgetown (Guyana)	–	-	98	Hardy & Harris (1979)
Cumaná (Venezuela)	–	-	54	Hardy & Harris (1979)
Barbados	(20-23)	26	142	Lemon (1971), Kaiser & Hardy (1994)
Bermuda	–	–	141	Kaiser & Hardy (1994)

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REFERENCES

Belanger, R.M. & Corkum, L.D. (2009). Review of aquatic sex pheromones and chemical communication in anurans. *Journal of Herpetology* 43(2): 184–191.
 Boul, K.E. & Ryan, M.J. (2004). Population variation of

- complex advertisement calls in *Physalaemus petersi* and comparative laryngeal morphology. *Copeia* 2004(3): 624–631.
- Brasileiro, C.A., Fonseca, E., Giovanelli, J.G.R., Melo, N.B.V. & Both, C. (2021). Herpetofauna invasora no Brasil: presente e futuro. *Herpetologia Brasileira Contemporânea*, São Paulo, *Anolis Book* 2021(1): 263–273.
- Castellano, S., Giacoma, C. & Dujsebayaeva, T. (2000). Morphometric and advertisement call geographic variation in polyploid green toads. *Biological Journal of the Linnean Society* 70(2): 341–360.
- Castellano, S., Tonttini, L., Giacoma, C., Lates, A. & Balletto, E. (2002) The evolution of the release and advertisement calls in the Green Toads (*Bufo viridis* complex). *Biological Journal of the Linnean Society* 77: 379–391.
- Charif, R.A., Waack, A.M. & Strickman, L.M. (2010). RAVEN PRO v. 1.4 user's manual. Ithaca, NY. *The Cornell Lab of Ornithology*.
- Flechas, S.V., Ortega-Chinchilla, J.E., Arenas, L.M. & Amézquita, A. (2018). The Function of Supplementary Notes in the Communication System of Johnstone's Whistling Frog, *Eleutherodactylus johnstonei*. *Herpetological Review* 49(4): 626–632.
- Foratto, R.M., Llusia, D., Toledo, L.F. & Forti, L.R. (2021). Treefrogs adjust their acoustic signals in response to harmonics structure of intruder calls. *Behavioral Ecology* 32(3): 416–427.
- Forti, L.R., Becker, C.G., Tacioli, L., Pereira, V.R., Santos, A.C.F.A., Oliveira, I., Haddad, C.F.B. & Toledo, L.F. (2017). Perspectives on invasive amphibians in Brazil. *PLoS ONE* 12(9): e0184703.
- Gerhardt, H.C. & Davis, M.S. (1988). Variation in the coding of species identity in the advertisement calls of *Litoria verreauxi* (Anura: Hylidae). *Evolution* 42(3): 556–565.
- Gerhardt, H.C. & Huber, F. (2002). Acoustic Communication in Insects and Anurans: Common Problems and Diverse Solutions. *University of Chicago Press*. 542 pp.
- Gerhardt, H.C. (1991). Female mate choice in treefrogs: static and dynamic acoustic criteria. *Animal Behaviour* 42(4): 615–635.
- Gerhardt, H.C. (1994). The evolution of vocalization in frogs and toads. *Annual review of ecology and systematics*: 293–324.
- Guerra, V., de Moraes, A.R., Gambale, P.G., Oda, F.H. & Pereira Bastos, R. (2017). Variation of the advertisement call of *Physalaemus centralis* Bokermann, 1962 (Anura: Leptodactylidae) in the Cerrado of central Brazil. *Studies on Neotropical Fauna and Environment* 52(2): 103–111.
- Hardy Jr, J.D. & Harris Jr, H.S. (1979). Occurrence of the West Indian frog, *Eleutherodactylus johnstonei*. South America and on the island of Curaçao. *Bulletin of the Maryland Herpetological Society* 15: 124–133.
- Howard, R.D. & Young, J.R. (1998). Individual variation in male vocal traits and female mating preferences in *Bufo americanus*. *Animal Behaviour* 55(5): 1165–1179.
- Hödl, W. & Amézquita, A. (2001). Visual signaling in anuran amphibians. In: *Anuran Communication*, 121–141 pp. Ryan M.J. (Ed.). Smithsonian Institution Press, Washington.
- Kaiser, H. (1992). The trade-mediated introduction of *Eleutherodactylus martinicensis* (Anura: Leptodactylidae) on St. Barthélemy, French Antilles, and its implications for lesser Antillean biogeography. *Journal of Herpetology* 26(3): 264–273.
- Kaiser, H., Green, D.M. & Schmid, M. (1994). Systematics and biogeography of Eastern Caribbean frogs (Leptodactylidae: *Eleutherodactylus*), with the description of a new species from Dominica. *Canadian Journal of Zoology* 72(12): 2217–2237.
- Kaiser, H., Barrio-Amoros, C.L., Trujillo, J.D. & Lynch, J.D. (2002). Expansion of *Eleutherodactylus johnstonei* in northern South America: rapid dispersal through human interactions. *Herpetological Review* 33(4): 290–293.
- Kaiser, H. & Hardy Jr, J.D. (1994). *Eleutherodactylus johnstonei*. *Catalogue of American Amphibians and Reptiles* (CAAR). 581.3
- Kraus, F. (2008). Alien Reptiles and Amphibians: A *Scientific Compendium and Analysis*. Springer Science & Business Media. 563 pp.
- Klymus, K.E., Humfeld, S.C., Marshall, V.T., Cannatella, D. & Gerhardt, H.C. (2010). Molecular patterns of differentiation in canyon treefrogs (*Hyla arenicolor*): evidence for introgressive hybridization with the Arizona treefrog (*H. wrightorum*) and correlations with advertisement call differences. *Journal of Evolutionary Biology* 23(7): 1425–1435.
- Köhler J., Jansen M., Rodríguez A., Kok P.J.R., Toledo 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.
- K. Lisa Yang Center for Conservation Bioacoustics (2019). Raven Pro: Interactive Sound Analysis Software (Version 1.6.1) [Computer software]. Ithaca, NY: The Cornell Lab of Ornithology. Available from <http://ravensoundsoftware.com>.
- Lemon, R.E. (1971). Vocal communication by the frog *Eleutherodactylus martinicensis*. *Canadian Journal of Zoology* 49(2): 211–217.
- Lever, C. (2003). *Naturalized Reptiles and Amphibians of the World*. Oxford University Press, Oxford, U.K., 318 pp.
- Littlejohn, M.J. (1977). Long-range acoustic communication in anurans: an integrated and evolutionary approach. In *The Reproductive Biology of Amphibians*. pp. 263–294, Taylor, D.H. & Guttman, G.I. (Eds.). Plenum, New York.
- Lopez, P.T., Narins, P.M., Lewis, E.R. & Moore, S.W. (1988). Acoustically induced call modification in the white-lipped frog, *Leptodactylus albilabris*. *Animal Behaviour* 36(5): 1295–1308.
- Melo, M.A., Lyra, M.L., Brischi, A.M., Geraldini, V.C. & Haddad, C.F.B. (2014). First record of the invasive frog *Eleutherodactylus johnstonei* (Anura: Eleutherodactylidae) in São Paulo, Brazil. *Salamandra* 50(3): 177–80.
- Narins, P.M. (1995). Frog communication. *Scientific American* 273 (2): 78–83.
- O'Neill, E.M. & Beard, K.H. (2011). Clinal variation in calls of native and introduced populations of *Eleutherodactylus coqui*. *Copeia* 2011(1): 18–28.
- Ortega, J.E., Serrano-Cardozo, V.H. & Pinilla, M.P.R. (2005).

- Diet composition and microhabitat of *Eleutherodactylus johnstonei* in an introduced population at Bucaramanga, Colombia. *Herpetological Review* 36(3): 238–241.
- Pettitt, B.A., Bourne, G.R. & Bee, M.A. (2013). Advertisement call variation in the golden rocket frog (*Anomaloglossus beebei*): evidence for individual distinctiveness. *Ethology* 119(3): 244–256.
- Pröhl, H., Hagemann, S., Karsch, J. & Höbel, G. (2007). Geographic variation in male sexual signals in strawberry poison frogs (*Dendrobates pumilio*). *Ethology* 113(9): 825–837.
- Rodríguez, A., Börner, M., Pabijan, M., Gehara, M., Haddad, C.F.B. & Vences, M. (2015). Genetic divergence in tropical anurans: deeper phylogeographic structure in forest specialists and in topographically complex regions. *Evolutionary Ecology* 29(5): 765–785.
- Ryan, M.J., Cocroft, R.B. & Wilczynski, W. (1990). The role of environmental selection in intraspecific divergence of mate recognition signals in the cricket frog, *Acris crepitans*. *Evolution* 44(7): 1869–1872.
- Ryan, M.J., Rand, A.S. & Weigt, L.A. (1996). Allozyme and advertisement call variation in the túngara frog, *Physalaemus pustulosus*. *Evolution* 50(6): 2435–2453.
- Ryan M.J. (2001). *Anuran Communication*. Smithsonian Institution Press. Washington and London. 252 pp
- Schwartz, J.J. & Bee, M.A. (2013). Anuran acoustic signal production in noisy environments. In *Animal Communication and Noise*, 91–132 pp. Brumm, H. (Ed.). Springer, Berlin, Heidelberg.
- Smith, M.J. & Hunter, D. (2005). Temporal and geographic variation in the advertisement call of the booroolong frog (*Litoria booroolongensis*: Anura: Hylidae). *Ethology* 111(12): 1103–1115.
- Smith, M.J., Osborne, W. & Hunter, D. (2003). Geographic variation in the advertisement call structure of *Litoria verreauxii* (Anura: Hylidae). *Copeia* 2003(4): 750–758.
- Sueur, J., Aubin, T. & Simonis, C. (2008). Seewave, a free modular tool for sound analysis and synthesis. *Bioacoustics* 18(2): 213–226.
- Tárano, Z. & Fuenmayor, E. (2008). Analysis of the vocalizations of Johnstone's whistling frog (*Eleutherodactylus johnstonei*: Eleutherodactylidae) in northern–central Venezuela. *South American Journal of Herpetology* 3(3): 229–238.
- Tárano, Z. & Fuenmayor, E. (2013). Experimental analysis of the dimorphic function of the biphasic call of *Eleutherodactylus johnstonei* (Anura: Eleutherodactylidae). *South American Journal of Herpetology* 8(2): 73–80.
- Toledo, L.F. & Measey, J. (2018). Invasive frogs in São Paulo display a substantial invasion lag. *BioInvasions Records* 7: 1–4.
- Tonini, J.F.R., Provete, D.B., Maciel, N.M., Morais, A.R., Goutte, S., Toledo, L.F. & Pyron, R.A. (2020). Allometric escape from acoustic constraints is rare for frog calls. *Ecology and evolution* 10(8): 3686–3695.
- Watkins, W.A., Baylor, E.R. & Bowen, A.T. (1970). The call of *Eleutherodactylus johnstonei*, the whistling frog of Bermuda. *Copeia* 1970: 558–561.
- Wells, K.D. (2007) *The Ecology and Behavior of Amphibians*. University of Chicago Press, 1400 pp.
- 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.
- Yasumiba, K., Duffy, R.L., Parsons, S.A., Alford, R.A. & Schwarzkopf, L. (2016). Rapid differentiation of sexual signals in invasive toads: call variation among populations. *Scientific reports* 6(1): 1–7.
- Ziegler, L., Arim, M. & Bozinovic, F. (2015). Intraspecific scaling in frog calls: the interplay of temperature, body size and metabolic condition. *Oecologia* 181(3): 673–681.

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