JEE ISSN: 2288-1220
https://doi.org/10.5141/jee.24.040
Journal of Ecology and Environment (2024) 48:49

SHORT COMMUNICATION

Comparison of the responses of male Japanese treefrog (*Dryophytes japonicus*) to the rain and advertisement calls

Hahyun Nam, Jin-Kyoung Kim, Jiho Park, Jongsun Kim, Min-Woo Park, Jiyeon Cheon and Daesik Park*

Division of Science Education, Kangwon National University, Chuncheon 24341, Republic of Korea

ARTICLE INFO
Received April 17, 2024
Revised November 15, 2024
Accepted December 3, 2024
Published on December 18, 2024

***Corresponding author**
Daesik Park
E-mail parkda@kangwon.ac.kr

Anurans communicate with others using several types of calls such as advertisement, encounter, release, and rain calls. Some treefrog species produce rain calls from their daytime shelters, such as trees and bushes, during both the breeding and non-breeding seasons. However, the function of rain calls is poorly understood. We investigated the potential functions of rain calls by comparing the responses of male *Dryophytes japonicus* to the playback of advertisement and rain calls. During one minute of playback and three minutes post-playback, the frequencies of orientation and approach of male *D. japonicus* towards the call-producing speaker did not differ in the rain and advertisement calls. However, the number of individuals, who finally arrived at the speaker among the males, approached towards the speaker, was significantly lower for the rain call compared to the advertisement call during one-minute playback. Our results suggest that both types of calls evoke the attention of conspecific males, but rain calls do not attract conspecific males, unlike advertisement calls. This difference may reflect the distinct functions of rain and advertisement calls.

Keywords: animal communication, anuran, playback test, vocalization

Introduction

Acoustic signals of animals include the substantial proportion of the behavioral repertoire of animals (Laiolo 2010). Many animal taxa, including anurans, birds, and insects, use their acoustic signals for species recognition, mate selection, and territorial defense (Halfwerk et al. 2016; Luther and Gentry 2013). These signals are diverse and can function in sexual selection. Therefore, they have been extensively studied in terms of bioacoustics, evolution, behavior, ecology, and physiology (Podos and Webster 2022; Prestwich 1994; Toledo et al. 2015).

The vocalization of anurans is representative of acoustic signaling in animals. Anurans use their vocalizations in various social contexts to communicate with conspecifics (Taigen and Wells 1985; Toledo et al. 2015; Wells 1977). They commonly use several types of calls depending on the social context. The most studied and common type of anuran call is the advertisement call. Nearly all anuran species, including the Hylidae family, produce advertisement calls. These calls function to attract potential mates and play a key role in sexual selection (Toledo et al. 2015; Wells 1977; Zhu et al. 2017). Advertisement calls are also used to maintain individual distance between calling males during breeding aggregation (Bee and Perrill 1996; Brozoska et al. 1982; Wells 1977). When a male intrudes into the calling space or territory of a resident male, the resident male emits encounter calls as a form of aggressive behavior (Park and Choe 1998; Whitney 1980). Encounter calls often progress to direct physical combat. Release calls are emitted by females or males when forced or heterospecific amplexus occurs. Distress calls are emitted when seized by potential predators or when they escape from predators. Most of the functions of these call types are well understood. Unlike these calls, an additional call type, called the rain call, is one of the less-studied anuran call types (Toledo et al. 2015).

Several anurans of the Hylidae family, such as *Dryophytes squirella* and *Dryophytes gratiosus*, emit rain calls. It has been known that frogs primarily emit rain calls before or during rainfall as coined its term (Blair 1958; Neill 1952, 1958; Toledo et al. 2015). Although the vocal characteristics of rain calls have not been studied in detail, they typically have a shorter call and note durations, a smaller number of notes, and a higher note repetition rate compared to advertisement calls. Especially, rain calls have irregularly shaped pulse structure compared to advertisement calls (Fig. 1) (Park et al. unpublished data). Usually, rain calls are emitted diurnally by nocturnal species during both the breeding and non-breeding seasons (Toledo et al. 2015). Frogs that emit rain calls usually stay in their daytime retreat sites adjacent to the breeding site, such as trees or bushes, although they are sometimes found relatively far from the breeding sites (Blair 1958; Toledo et al. 2015). As rain calls are often produced on trees, they are also referred to as tree calls (Neill 1952, 1958; Toledo et al. 2015). Anuran species that emit rain calls are limited, and their functions are poorly understood (Köhler et al. 2017; Toledo et al. 2015).

Japanese treefrog (*Dryophytes japonicus*), the study subject species, are known to emit rain calls (Honda and Matui 1996; Inukai and Ochiai 1931). *D. japonicus* is widely distributed in Northeast Asia, from Japan, Korea, China, and Mongolia. They aggregate in their breeding pools, such as rice paddies, between June and August, when males produce advertisement calls to attract females (Borzée et al. 2018, 2019). Although several studies have been conducted on the advertisement calls of *D. japonicus*, no studies have been conducted on the characteristics and functions of their rain calls.

In this study, we conducted playback tests using rain and advertisement calls from *D. japonicus*. The playback of advertisement calls generally causes phonotaxis and vocalizing responses in male anurans (Hödl et al. 2004; Moreno-Gómez et al. 2015; Narins et al. 2003; Zhu et al. 2017). Therefore, we investigated the potential functions of rain calls by comparing the responses of male *D. japonicus* to rain calls and advertisement calls. This is the first study to use an experimental approach to study the function of rain calls in male *D. japonicus*.

Materials and Methods

Capture and handling of subjects

From June 23 to 27, 2023, we captured 45 calling males of *D. japonicus* over four days. Captures were performed in rice paddies in Dongnae-myeon (37.85404 N, 127.77432E), Chuncheon-si, Gangwon-do. The captured subjects were transferred to an indoor laboratory and housed individually in plastic containers (10 cm × 18 cm × 10 cm, *W* × *L* × *H*). The lids of each container had ten small holes with a diameter of 5 mm, allowing ventilation and air circulation from the outside to the containers. Paper towels soaked in water collected from the capture site were placed inside each container to allow the subjects to freely access the moisture and acclimatize to the experimental environment. All researchers wore latex gloves and changed them for each individual when handling the subjects to minimize the stress caused by the odors of other frogs or humans (Mumualem 2016). The containers were placed in an indoor room (receiving 16L:8D cycle of natural sunlight through the window) maintained at room temperature, separate from the experimental area used for the playback tests. There was no control over the temperature or humidity in the room where the containers were placed. All subjects were tested on the day of capture and released back to the capture site within two days.

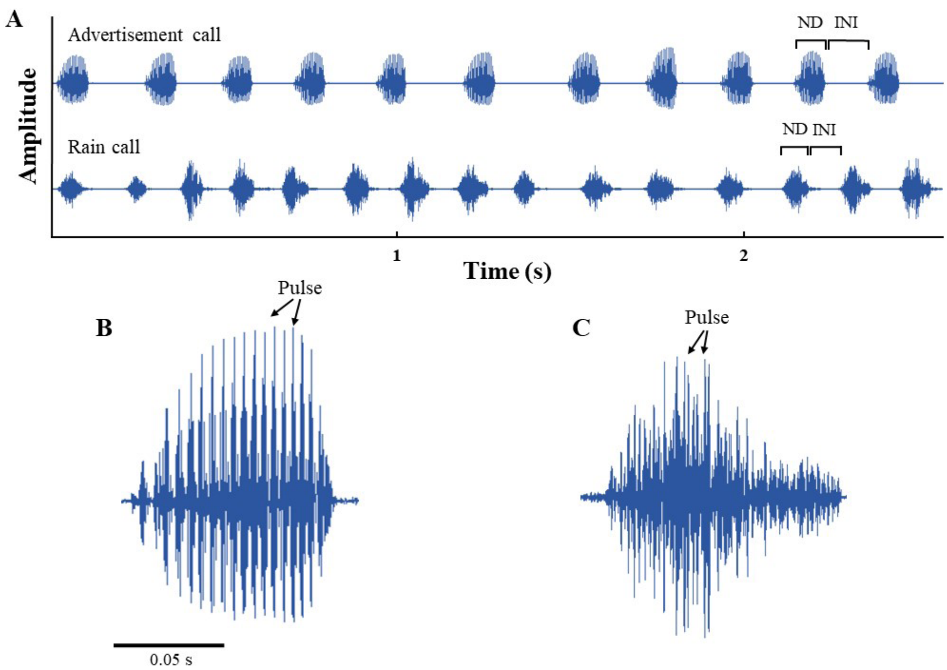

Fig. 1 Oscillograms of the advertisement and rain calls used in the playback tests as stimuli (A) and pulse structures within the note of advertisement (B) and rain (C) call stimulus. ND: note duration; INI: inter-note interval.

Acoustic stimuli

Three acoustic stimuli–advertisement call, rain call, and control (white noise, traffic sounds) stimuli–were used in our playback tests. Preceding the playback tests, we recorded the rain call and advertisement call of male *D. japonicus*, using a digital audio recorder (Marantz PMD660; 44.1 kHz sampling rate, 16-bit PCM files) connected to a directional microphone (Sennheiser ME-67), in May 2023 at the capture site. We selected the highest-quality and representative sound file for each call type based on its definition and used as a stimulus in the playback test. The advertisement and rain call stimuli were composed of 11 and 24 notes with durations of 3.6 and 9.3 seconds, respectively. The audio files of both stimuli were modified by applying noise reduction using the Audacity software v. 3.3.3 (http://audacity.sourceforge.net). The call characteristics of both stimuli, including note duration (the duration of a single note), inter-note interval (the interval between two consecutive note), and note repetition rate (number of notes repeated within the periods between first and last notes), are presented in Table 1 and Figure 1. Vocal characteristics were analyzed using Raven Pro 1.6.3 (Cornell Lab of Ornithology, New York, NY, USA), following the methods outlined by Park et al. (2013) and Köhler et al. (2017). We used traffic noise on YouTube (https://youtu.be/oc6rCY0d6mA) as a control stimulus, rather than white noise or silence (Baugh and Ryan 2017; Buxton et al. 2015; Halfwerk et al. 2016), because the road was located near the frog capture site.

Table 1 Characteristics of the advertisement and rain calls, which used in the playback tests as stimuli

Call type	Advertisement call	Rain call
ND	0.095 ± 0.004	0.089 ± 0.012
INI	0.142 ± 0.028	0.118 ± 0.021
NRR	4.454	4.943

Values are presented as mean ± standard deviation.
The number of notes in the advertisement call was 11 and those in the rain call was 24.
ND: note duration (s); INI: inter-note interval (s); NRR: note repetition rate (/s).

Experimental settings

Playback tests were conducted inside a rectangular hemi-anechoic styrofoam chamber (20 × 40 × 20 cm, W × L × H; Fig. 2). An 8 cm diameter speaker (PLEOMAX S1; PLEOMAX, Seoul, South Korea), employed for playing back acoustic stimuli, was installed on one wall of the chamber. The acoustic stimuli were played on a desktop and broadcast through a speaker. The opposite side of the speaker wall was covered with a polyurethane soundproof sponge (2081362766; Hysponge, Seoul, South Korea), and the adjacent sides of the speaker were covered with polyester soundproof boards (3519862573; Best Bang-eum, Seoul, South Korea) (Baugh and Ryan 2017). The bottom of the chamber was covered with paper towels soaked in water collected from the capture site to replicate the environment of the capture site. To prevent the effects of odors from other subjects, the floor of the chamber was washed with clean tap water, and paper towels were replaced for each test. To allow the subjects to acclimate to the experimental conditions, a small underground box (10 × 5 × 1 cm) was placed 35 cm away from the speaker. The male subjects were placed in a box before the playback tests. An acrylic sheet was used to cover the box to prevent the subjects from escaping before the experiment. The acrylic sheet had five holes (5 mm in diameter) that allowed circulation from the outside to the box. A string was attached to the acrylic sheet enabling it to be opened from outside the chamber without disturbing the subjects (see below). The cover of the playback test chamber was made of polyester mesh (20 × 40 cm, 1.4 × 0.9 mm mesh size, W × L). The temperature and relative humidity in the experimental area were maintained at 25.8°C ± 1.0°C and 55.7% ± 3.7%, respectively, using air conditioner (AR06R1130HZN; Samsung, Seoul, South Korea).

Experimental protocols

All experiments were conducted over four days from 22:00 to 01:00 and were completed within 5 hours of individual capture. A total of 45 male *D. japonicus* individuals were tested, with 15 males per stimulus. The test order and stimuli used for each individual were randomly selected,

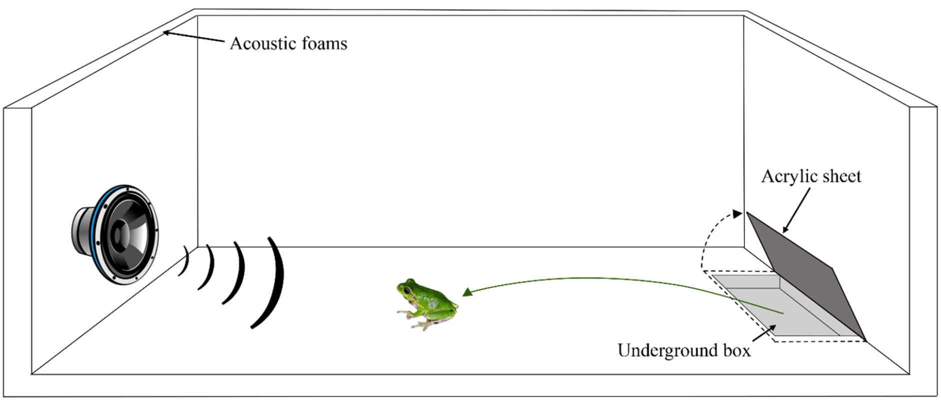

Fig. 2 The schematic diagram of the playback test chamber.

and each individual was tested only once.

Each test began by placing the subject in a box in the chamber and covering the box with an acrylic sheet. The subjects were allowed to acclimate to the box for 15 minutes. The acrylic sheet cover was then removed and the subjects were allowed to move freely into the chamber. The acoustic stimulus was broadcasted repeatedly for one minute through the speaker immediately after the acrylic sheet cover was opened. The maximum sound amplitude of the stimuli was adjusted to 65 dB at a distance of 35 cm from the speaker. After one minute of playback, we observed additional post-playback responses from the subjects for three minutes. Therefore, the entire process was recorded using a camcorder (DCR-SR65; Sony, Tokyo, Japan) installed above the chamber. After the tests, the snout-vent length (SVL) and body weight of each subject were measured using a digital Vernier caliper (CD15CPX; Mitutoyo Korea Corporation, Gunpo, South Korea) and a balance (RE-700; CAS, Yangju, South Korea) to evaluate the potential effects of the subject's body size on their responses to playback (Kelleher et al. 2017).

Statistical analysis

The playback test results were analyzed using the recorded video files. In our analysis, we selected four response parameters: orientation, where subjects oriented their head or body towards the speaker; approach, where subjects initiated their movements toward the speaker; arrival, where approaching subjects finally reached the speaker; and call, where subjects emitted their calls. When the subjects were facing the speaker before the stimulus was broadcasted, we considered their orientation as positive only when they approached the speaker directly. Subsequently, we measured the number of responses for each parameter in each test group during one minute of playback and three minutes of post-playback.

To analyze the significant differences in responses between the test groups, we first performed chi-square tests for each parameter. We then performed post-hoc analyses between each pair of test groups using Fisher's exact test, where significant differences ($p < 0.05$) were observed using chi-square tests. We also performed one-way ANOVA to examine the differences in body weight and SVL among the test groups. All statistical analyses were performed using R software v. 4.3.1 (R Core Team 2017). All mean values were presented as mean ± standard deviation.

Results and Discussion

The mean SVL of the subjects in the advertisement call, rain call, and control stimulus playbacks was 30.4 ± 2.3 mm, 31.1 ± 2.1 mm, and 30.9 ± 1.6 mm, respectively. The body weights of each test group were 2.3 ± 0.3 g, 2.21 ± 0.4 g, and 2.2 ± 0.3 g, respectively. There were no significant differences in SVL ($F = 0.383$, df = 2, $p = 0.684$) or body weight ($F = 0.062$, df = 2, $p = 0.940$) between the test groups. This indicates that there was no bias in the body sizes of the test groups so that the results of the playback tests were not influenced by this factor.

During one minute of playback, the number of orientations was significantly different between the test groups ($X^2 = 9.249$, $p = 0.010$, Table 2). Advertisement calls induced significantly more orientation than the control ($p < 0.05$, Fig. 3). However, the remaining comparisons were not significant ($p > 0.05$). The number of arrivals during one minute of playback was also significantly different between the test groups ($X^2 = 10.489$, $p < 0.01$, Table 2). The rain calls and controls induced significantly lower arrival responses among approaching male *D. japonicus* than advertisement calls ($p < 0.05$, Fig. 3). The comparison between the rain calls and the control was not significant ($p > 0.05$). During three minutes of post-playback, none of the measured parameters showed any significant differences among the three stimulus groups ($p > 0.05$, Table 2).

In this study, we confirmed that the number of orientations and approaches to the stimuli did not differ between the two call types. However, fewer male *D. japonicus* arrived at the acoustic stimuli of rain calls during playback than during the playback of advertisement calls. Our results indicate that both rain and advertisement calls attract the attention of conspecific males, but rain calls may not elicit conspecific males to approach the calling site. The rain calls of *D. japonicus*, as well as the advertisement

Table 2 Summarized results of the playback tests using advertisement and rain calls

Stimulus	During playback (1 min)				During post-playback (3 min)			
	Orientation	Approach	Arrival	Call	Orientation	Approach	Arrival	Call
Advertisement call	11	6	6	2	3	3	2	0
Rain call	9	4	1	0	3	2	3	0
Control	3	2	0	0	5	5	4	1
X^2	9.249	2.727	10.489	4.186	0.963	2.015	0.833	2.046
p-value	0.010	0.256	0.005	0.123	0.618	0.365	0.659	0.360

We used 15 male *Dryophytes japonicus* for each stimulus test and measured the number of subject males, who oriented, approached, arrived, and called towards or at the playback speaker during playback and post-playback. Control stimulus was traffic noise. The degree of freedom in all tests was 2.

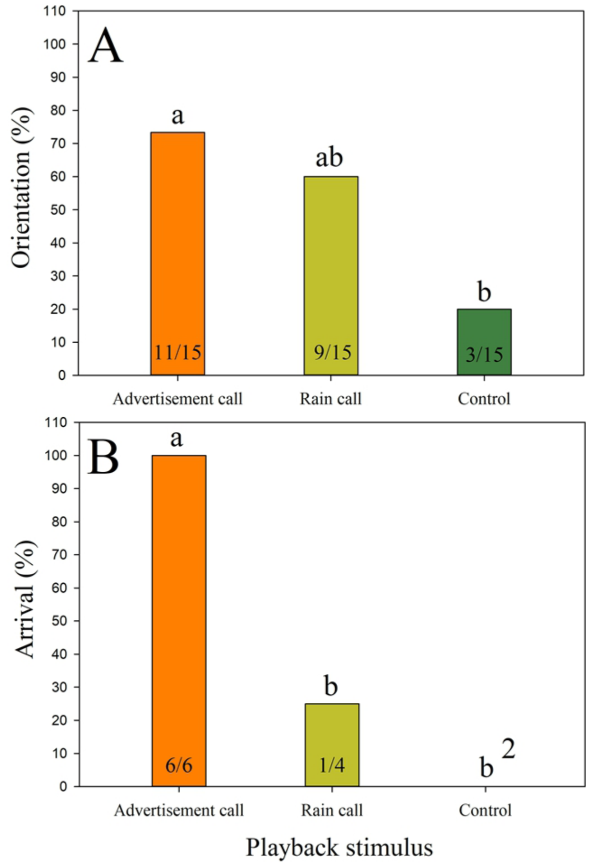

Fig. 3 The number of subject *Dryophytes japonicus* who orientated (A) and arrived at the speaker (B) during one-minute playback of advertisement call, rain call, and control (traffic noise). Numbers in the bars are the number of the subject males, who participated in a specific response stage. Different characters on the bars indicate *$p < 0.05$ in Fisher's exact post-hoc test.

calls, seem to convey specific information to conspecific males and elicit their responses. The vocalizations of anurans can convey several types of information to conspecifics. The advertisement calls of male anurans, for instance, convey information on their location to conspecific females, as well as information on the location of the breeding site and physical characteristics, such as the body size of calling males, to conspecific males (Buxton et al. 2015; Hoskin et al. 2009; Wells 1977). The orientation towards advertisement calls of frogs is the response in which frogs locate the calling site, allowing their approach to the site (Hödl et al. 2004; Lindquist and Hetherington 1996; Narins et al. 2003; Rheinlaender et al. 1979). In our playback tests, male *D. japonicus* exhibited an orientation towards both rain and advertisement calls, and the number of orientations was not significantly different between the two types of calls. This result suggests that rain calls convey information about their location, similar to advertisement calls. However, further studies are needed to evaluate whether male *D. japonicus* actively advertise their location or whether conspecific males actively use calls to locate the calling males.

Unlike advertisement calls, rain calls did not significantly elicit arrival responses in male *D. japonicus*. There are several possible explanations for these results. First, the call characteristics of rain calls, such as the pulse structure and relatively short call duration (see introduction and Fig. 1), may make it difficult for the receiver to accurately localize the location of males emitting rain calls (Jones and Ratnam 2023). Considering that the arrivals of male *D. japonicus* were very few during the three minutes of post-playback for both the advertisement and rain call stimuli, this explanation is plausible. Second, male frogs may not be eager to arrive at sites where rain calls occur. Generally, male *D. japonicus* emits rain calls at sites where breeding does not occur (Neill 1958; Toledo et al. 2015). Therefore, male subjects do not need to visit the site for potential breeding opportunities or male-male competition (Buxton et al. 2015; Fellers 1979; Narins et al. 2003, 2005; Perrill et al. 1978). Finally, considering the size of the playback chamber and the amplitude of the acoustic stimuli, subject males may have perceived that the males emitting rain calls did not intrude into their territories. However, this may not be a factor because, unlike rain calls, advertisement calls induced a significant arrival response in male subjects.

Based on the results of this study, several suggestions can be made for future research. First, rain calls occur not only during the breeding season but also during the non-breeding season (Toledo et al. 2015). Therefore, the function of the rain calls should be evaluated throughout the year. Second, because frog responses are influenced by the amplitude of the acoustic stimuli, their responses to different amplitudes of stimuli need to be studied. The amplitudes of acoustic stimuli often provide physical information to animals (Gerhardt and Huber 2002). Finally, rain calls occur diurnally (Neill 1958; Toledo et al. 2015) so playback tests during the daytime are required.

Abbreviations
Not applicable.

Acknowledgements
We thank Il-Kook Park, Jaejin Park, Hyerim Kwon and Yucheol Shin for their help during our research.

Authors' contributions
HN did sample collection, data curation, formal analysis, investigation, and writing original draft. JKK did sample collection and conducted playback test. JP, JK, MWP, and JC did sample collection and formal anlaysis. DP did conceptualization, supervision, writing-original draft, and writing-review and editing. All authors read and approved the final manuscript.

Funding
Not applicable.

Availability of data and materials
The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate
This study was reviewed and approved by the Institutional Animal Care and Use Committee of Kangwon National University (KW-230411-1).

Consent for publication
Not applicable

Competing interests
The authors declare that they have no competing interests.

References

Baugh AT, Ryan MJ. Vasotocin induces sexually dimorphic effects on acoustically-guided behavior in a tropical frog. J Comp Physiol A Neuroethol Sens Neural Behav Physiol. 2017;203(4):265-73. https://doi.org/10.1007/s00359-017-1155-y.

Bee MA, Perrill SA. Responses to conspecific advertisement calls in the Green frog (Rana clamitans) and their role in male-male communication. Behaviour. 1996;133(3-4):283-301. https://doi.org/10.1163/156853996X00152.

Blair WF. Mating call in the speciation of anuran amphibians. Am Nat. 1958;92(862):27-51. https://doi.org/10.1086/282007.

Borzée A, Kim M, Kim JY, Kim T, Jang Y. Microhabitat use during brumation in the Japanese treefrog, *Dryophytes japonicus*. Amphibia-Reptilia. 2018;39(2):163-75. https://doi.org/10.1163/15685381-17000036.

Borzée A, Purevdorj Z, Kim YI, Kong S, Choe M, Yi Y, et al. Breeding preferences in the treefrogs *Dryophytes japonicus* (Hylidae) in Mongolia. J Nat Hist. 2019;53(43-44):2685-98. https://doi.org/10.1080/00222933.2019.1704458.

Brozoska J, Schneider H, Nevo E. Territorial behavior and vocal response in male *Hyla arborea savignyi* (Amphibia: Anura). Isr J Zool. 1982;31(1-2):27-37. https://doi.org/10.1080/00212210.1982.10688518.

Buxton VL, Ward MP, Sperry JH. Use of chorus sounds for location of breeding habitats in 2 species of anuran amphibians. Behav Ecol. 2015;26(4):1111-8. https://doi.org/10.1093/beheco/arv059.

Fellers GM. Aggression, territoriality, and mating behavior in North American treefrogs. Anim Behav. 1979;27(1):107-19. https://doi.org/10.1016/0003-3472(79)90131-3.

Gerhardt HC, Huber F. Acoustic communication in insects and anurans. Chicago: University of Chicago Press; 2002.

Halfwerk W, Lea AM, Guerra MA, Page RA, Ryan MJ. Vocal responses to noise reveal the presence of the Lombard effect in a frog. Behav Ecol. 2016;27(2):669-76. https://doi.org/10.1093/beheco/arv204.

Hödl W, Amézquita A, Narins PM. The rôle of call frequency and the auditory papillae in phonotactic behavior in male Dart-poison frogs *Epipedobates femoralis* (Dendrobatidae). J Comp Physiol A. 2004;190:823-9. https://doi.org/10.1007/s00359-004-0536-1.

Honda M, Matsui M. Call repertoires of the Japanese treefrog, *Hyla japonica*. J Acoust Soc Am. 1996;100(4):2709. https://doi.org/10.1121/1.416103.

Hoskin CJ, James S, Grigg GC. Ecology and taxonomy-driven deviations in the frog call–body size relationship across the diverse Australian frog fauna. J Zool. 2009;278(1):36-41. https://doi.org/10.1111/j.1469-7998.2009.00550.x.

Inukai T, Ochiai S. A study on the breeding habits of Hyla arborea japonica Guenther. J Fac Sci Hokkaido Imp Univ Ser 6. 1931;1(3):111-6.

Jones DL, Ratnam R. Are frog calls relatively difficult to locate by mammalian predators? J Comp Physiol A. 2023;209:11-30. https://doi.org/10.1007/s00359-022-01594-7.

Kelleher SR, Silla AJ, Dingemanse NJ, Byrne PG. Body size predicts between-individual differences in exploration behavior in the southern corroboree frog. Anim Behav. 2017;129:161-70. https://doi.org/10.1016/j.anbehav.2017.05.013.

Köhler J, Jansen M, Rodríguez A, Kok PJR, Toledo LF, Emmrich M, et al. The use of bioacoustics in anuran taxonomy: theory, terminology, methods and recommendations for best practice. Zootaxa. 2017;4251(1):1-124. https://doi.org/10.11646/zootaxa.4251.1.1.

Laiolo P. The emerging significance of bioacoustics in animal species conservation. Biol Conserv. 2010;143(7):1635-45. https://doi.org/10.1016/j.biocon.2010.03.025.

Lindquist ED, Hetherington TE. Field studies on visual and acoustic signals in the “earless” Panamanian golden frog, *Atelopus zeteki*. J Herpetol. 1996;30(3):347-54. https://doi.org/10.2307/1565171.

Luther D, Gentry K. Sources of background noise and their influence on vertebrate acoustic communication. Behaviour. 2013;150(9-10):1045-68. https://doi.org/10.1163/1568539X-00003054.

Moreno-Gómez FN, Bacigalupe LD, Silva-Escobar AA, Soto-Gamboa M. Female and male phonotactic responses and the potential effect of sexual selection on the advertisement calls of a frog. Anim Behav. 2015;104:79-86. https://doi.org/10.1016/j.anbehav.2015.03.010.

Mumualem G. Review of field protocols on herpetological investigation: a working guide for junior herpetologists in Ethiopia. J Zool St. 2016;3(1):27-33.

Narins PM, Grabul DS, Soma KK, Gaucher P, Hödl W. Cross-modal integration in a dart-poison frog. Proc Natl Acad Sci U S A. 2005;102(7):2425-9. https://doi.org/10.1073/pnas.0406407102.

Narins PM, Hödl W, Grabul DS. Bimodal signal requisite for agonistic behavior in a dart-poison frog, Epipedobates femoralis. Proc Natl Acad Sci U S A. 2003;100(2):577-80. https://doi.org/10.1073/pnas.0237165100.

Neill WT. Burrowing habits of Hyla gratiosa. Copeia. 1952;1952(3):196. https://doi.org/10.2307/1439722.

Neill WT. The varied calls of the Barking Treefrog, Hyla gratiosa Leconte. Copeia. 1958;1958(1):44-6. https://doi.org/10.2307/1439539.

Park KB, Choe JC. Plasticity of mating calls of *Hyla japonica* (Amphibia: Hylidae). Korean J Biol Sci. 1998;2(4):463-9. https://doi.org/10.1080/12265071.1998.9647446.

Park S, Jeong G, Jang Y. No reproductive character displacement in male advertisement signals of *Hyla japonica* in relation to the sympatric *H. suweonensis*. Behav Ecol Sociobiol. 2013;67:1345-55. https://doi.org/10.1007/s00265-013-1563-0.

Perrill SA, Gerhardt HC, Daniel R. Sexual parasitism in the green tree frog (*Hyla cinerea*). Science. 1978;200(4346):1179-80. https://doi.org/10.1126/science.200.4346.1179.

Podos J, Webster MS. Ecology and evolution of bird sounds. Curr Biol. 2022;32(20):R1100-4. https://doi.org/10.1016/j.cub.2022.07.073.

Prestwich KN. The energetics of acoustic signals in anurans and insects. Am Zool. 1994;34(6):625-43. https://doi.org/10.1093/icb/34.6.625.

R Core Team. R: a language and environment for statistical computing. 2017. http://www.R-project.org/. Accessed 10 Sep 2023.

Rheinlaender J, Gerhardt HC, Yager DD, Capranica RR. Accuracy of phonotaxis by the green treefrog (*Hyla cinerea*). J Comp Physiol. 1979;133:247-55. https://doi.org/10.1007/BF00661127.

Taigen TL, Wells KD. Energetics of vocalization by an anuran amphibian (*Hyla versicolor*). J Comp Physiol B. 1985;155:163-70. https://doi.org/10.1007/BF00685209.

Toledo LF, Martins IA, Bruschi DP, Passos MA, Alexandre C, Haddad CFB. The anuran calling repertoire in the light of social context. Acta Ethol. 2015;18:87-99. https://doi.org/10.1007/s10211-014-0194-4.

Wells KD. The courtship of frogs. In: Taylor DH, Guttman SI, editors. The reproductive biology of amphibians. Boston: Springer;1977. p. 233-62.

Whitney CL. The role of the "encounter" call in spacing of Pacific tree frogs, *Hyla regilla*. Can J Zool. 1980;58(1):75-8. https://doi.org/10.1139/z80-010.

Zhu B, Wang J, Zhao L, Chen Q, Sun Z, Yang Y, et al. Male-male competition and female choice are differentially affected by male call acoustics in the serrate-legged small treefrog, *Kurixalus odontotarsus*. PeerJ. 2017;5:e3980. https://doi.org/10.7717/peerj.3980.