



The Vocalizations and Hearing Sensitivity of an Explosive-Breeding Tropical Toad from Southern China: A Test of the Matched Filter Hypothesis

Tongliang Wang¹, Lele Jia¹, Xiaofei Zhai¹, Jianguo Cui² and Jichao Wang^{1,*}

¹Ministry of Education Key Laboratory for Ecology of Tropical Islands, College of Life Sciences, Hainan Normal University, Haikou 571158, China

²Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu 610041, China

ABSTRACT

The matched filter hypothesis proposes that the tuning of auditory sensitivity should match the spectral character of calls, suggesting that sender calls and receiver auditory systems have co-evolved. However, studies provide mixed evidence, and in some species, this match is imprecise. Here, we analyzed the acoustic characteristics of male calls and both male and female hearing sensitivity in an explosive-breeding toad *Duttaphrynus melanostictus* to test the matched filter hypothesis. Male toads emitted a series of multisyllabic calls that were composed of single notes with a dominant frequency of 1494 ± 80 Hz. The dominant frequency reflected body size and was static between males, suggesting it may be under stabilizing selection and used in species recognition. Sexual dimorphism in peripheral auditory sensitivity was also observed as females exhibited lower auditory thresholds than males across 600–2400 Hz frequency range. The relationship between vocalizations and hearing corresponded to the matched filter hypothesis, suggesting that male call spectral structure and hearing sensitivity in males and females may have co-evolved under sexual selection in *D. melanostictus*.

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Authors' Contribution

JW conceived and designed the experiments, reviewed drafts of the paper. TW, LJ and XZ performed the experiments and analyzed the data. TW wrote the paper and prepared figures and/or tables with the help of LJ. JC reviewed drafts of the paper.

Key words

Acoustic properties, *Duttaphrynus melanostictus*, Hearing sensitivity, Matched filter hypothesis, Sexual selection.

INTRODUCTION

Acoustic communication plays an important role in survival and reproduction (Davies and Halliday, 1978; Bee *et al.*, 1999; Gerhardt and Huber, 2002; Cui *et al.*, 2012). Acoustic properties and hearing sensitivity jointly affect acoustic communication (Ron, 2008; Brittan-Powell *et al.*, 2010; Cui *et al.*, 2012). In anurans, acoustic properties (*i.e.*, dominant frequency, note duration) are usually influenced by body size (Cocroft and Ryan, 1995; Tárrano, 2001; Wang *et al.*, 2012), suggesting they could facilitate decision-making related to male–male competition and/or female choice. However, some studies have found no relationship between acoustic properties and morphological characteristics, such as snout-vent length and head length (Penna, 2004; Márquez *et al.*, 2005; Cui *et al.*, 2012).

Females receive and analyze the courtship calls produced by males to select suitable mates during the breeding season. Therefore, females may have the sensitive auditory perception to receive and analyze male attractive

signals that are under sexual selection (Gall *et al.*, 2011; Forstmeier *et al.*, 2014). Interestingly, studies of the American bullfrog (*Rana catesbeiana*; Hetherington, 1994), the Hylidae (*Eleutherodactylus coqui*; Narins and Capranica, 1976), and the Ranidae (*Odorrana tormota* and *O. graminea*, Shen *et al.*, 2011; Liu *et al.*, 2014; Wang *et al.*, 2016) suggest that hearing sensitivity differs between the two sexes, as evidenced by morphological characteristics, such as body size and the tympanic membrane, which could result in sexual dimorphism in hearing sensitivity in fishes and frogs (Yan *et al.*, 2000; van Dijk *et al.*, 2002; Wang *et al.*, 2016). However, other studies contradict the hypothesis of sexual dimorphism in hearing sensitivity (Caras *et al.*, 2010; Schrode *et al.*, 2014).

The match between the sensitivity of the auditory system and the energy spectrum of sender vocalizations influences the signal-to-noise ratio for receivers (Capranica and Moffat, 1983; Endler, 1992; Gerhardt and Schwartz, 2001). The so-called “match filter hypothesis” has been widely verified in fishes (Blaxter, 1981; Ladich and Yan, 1998), birds (Endler, 1992; Henry and Lucas, 2008), insects (Kostarakos *et al.*, 2008), and frogs (Márquez and Bosch, 1997; Yu *et al.*, 2006; Moreno-Gómez *et al.*, 2013). However, recently studies found the match filter hypothesis was not always applicable in anurans (Gerhardt and

* Corresponding author: wjc@hainnu.edu.cn
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Schwartz, 2001; Zhao *et al.*, 2017). At present, no studies concerning hearing sensitivity and sexual differences in auditory sensitivity have been conducted in tropical island toads.

The black-spectacled toad *Duttaphrynus melanostictus* is a typical explosive breeder, with females larger than males (Ngo and Ngo, 2013), and males that produce mating calls (Wei *et al.*, 2012). The species is widely distributed throughout Southeast Asia, with a range that spans Taiwan, southwestern and southern China (including Hainan Island), southward towards Indonesia, and westwards to India and Sri Lanka (Shieh, 1993; Fei *et al.*, 2012). The acoustic properties of this species were found to vary in individuals from Thailand (Heyer, 1971), India (Hampson and Bennett, 2002), Myanmar (Wogan *et al.*, 2003), and Indonesia (Márquez and Eekhout, 2006). In China, Wei *et al.* (2012) reported that the acoustic properties were highly variable across recording times, and analyzed the relationship between acoustic property and body size based on data from non-one by one individual under semi natural conditions. In this study, we addressed the following questions: (1) whether acoustic properties reflect the body size of the individual under natural conditions; and (2) whether there is sexual dimorphism in peripheral auditory sensitivity in this species. Finally, we tested the match filter hypothesis in *D. melanostictus*.

MATERIALS AND METHODS

Animals

The experiment was conducted in an ecological park of Hainan Normal University (19° 59' 54" N, 110° 20' 18.7" E, elevation 35 m a.s.l.) in Hainan Province, China. Calls were recorded from 17 male *D. melanostictus* in November 2017. Nine females and 14 males were used in the auditory brainstem response (ABR) experiment. After the ABR experiments and individuals had recovered from anesthesia, they were returned to their original site within 24 h of being hand captured. The treatment procedures were approved by the Animal Care and Use Committee of the Chengdu Institute of Biology, Chinese Academy of Sciences.

Vocalization recordings

The vocalizations of male *D. melanostictus* were recorded using a directional microphone (Sennheiser ME66 with K6 power module) connected to a digital audio recorder (Marantz PMD 661, 16-bit, 44.1 kHz) placed approximately 1 m from subjects, from 20:30 to 23:30, at ambient temperature 19–26°C, and relative humidity 75–90%.

Morphological data

Individuals were captured after calls were recorded

to investigate possible relationships between vocalization characteristics and body size. Snout-vent length, head length, and head width were measured using a digital caliper (10810206, Berryllion, China).

Auditory brainstem response measurements

The experiment was conducted at the same study site range from Nov 2017 to Jan 2018. In total, 23 toads (14 males, 9 females) were used. We used noninvasive ABR to measure hearing in toads that were lightly anesthetized via water immersion for 8–11 min (males) or 18–24 min (females), using a 0.2% solution of MS-222 (Tricaine Methane Sulfonate). Individuals were then placed in a soundproof acoustic chamber (0.5 × 0.5 × 0.5 m) (Carey and Zelick, 1993; Zhang *et al.*, 2012). When an individual showed no pain response to stimulation of the hind leg muscles using forceps, it was proceeded to the next stage of the experiment. The stimulus, ABR acquisition, equipment control, and data management procedures were similar to those in our previous studies (Zhang *et al.*, 2012; Cui *et al.*, 2017). In brief, for each specimen, three 27-gauge stainless steel electrodes (Rochester Electro-Medical, Inc. FL, USA) were inserted subdermally at (1) the midline above the medulla (approximately 3 cm caudally to the snout), and (2) above the tympanum, and (3) in the ipsilateral front leg as inverting, noninverting, and ground electrodes, respectively. The recording electrodes were connected to a head stage and amplifier (PA4 and RA4, 20 gain, TDT) via wires wrapped in tin foil.

The stimulus was generated and the ABR was recorded using a digital signal processor RM2 (Tucker-Davis Technologies, Gainesville, USA), via fiber optic cables linked to RA4 and a USB linked to a laptop computer running custom software (Open ABR). Two types of stimuli, tone pips and clicks, were generated using Open ABR and delivered using a portable amplified field speaker (SME-AFS, Saul Miner of Electronic Inc., USA), which was driven by an RM2 and positioned on the table (at a height of 105 cm), approximately 110 cm in front of the individual's head. ABR recording stimulus levels were calibrated using a G.R.A.S. 46 BE ¼-inch microphone (G.R.A.S. Sound and Vibration, Denmark, tianjia) with a CCP Supply (Type 12 AL, G.R.A.S. Sound and Vibration, Denmark) to a 60-dB sound pressure level (dB SPL re: 20 uPa) positioned at the individual's head. Stimuli were synthesized digitally at octave intervals from 0.6 kHz to 7 kHz, with a 1 ms rise/fall time, a 3 ms plateau time, and a sample rate of 24,414 Hz. The authors recognize that the brief stimuli and short rise/fall times of the tone bursts used in this study were not ideal for accurately determining thresholds for low frequency sounds. However, increased rise/fall times and longer stimulus durations affect the brainstem response morphology. Given these constraints, we chose a 5 ms tone train with a 1 ms rise/fall time. All

biological signals were notch-filtered at 50 Hz during data collection (Zhang *et al.*, 2012; Wang *et al.*, 2016; Cui *et al.*, 2017).

The ABR thresholds were determined using methods similar to those in our previous studies (Zhang *et al.*, 2012; Cui *et al.*, 2017). Threshold measurements were defined as the lowest stimulus level for which no repeatable responses were recognized and were initiated at 90 dB SPL and reduced in 5 dB steps. We assumed that the 90-dB level was higher than all ABR thresholds of *D. melanostictus* for the stimuli used. ABRs were obtained from each individual at frequencies between 0.6 kHz and 7 kHz for ABR threshold estimation (Brittan-Powell *et al.*, 2010; Zhang *et al.*, 2012).

Analysis and statistics

SPSS 19.0 (IBM SPSS Inc., Chicago, IL, USA) was used for analysis. All data were examined for assumptions of normality and homogeneity of variance using the Shapiro–Wilk and Levene’s tests, respectively. Spontaneous vocalizations from 17 males were obtained from the recordings, and the acoustic properties (dominant

frequency, fundamental frequency, note number, inter-note interval, note duration, and call duration) of the calls were analyzed. The sonograms of calls were prepared using Praat software (Boersma and Weenink, Version 5.1.11, University of Amsterdam, The Netherlands). The files were analyzed and displayed using Adobe Audition 3.0 and Praat. The coefficient of variation ($CV = SD/X \times 100\%$, where X is mean) for each acoustic property was computed separately to identify patterns of variation. Call properties were classified as static or dynamic based on inter-individual variation (CV) during bouts of calling (Gerhardt, 1991; Zhu *et al.*, 2017). If the CV of a given call property was less than 5%, it was identified as “static” as there was little variation between calls. Conversely, call properties were identified as “dynamic” when the CV was greater than 10%. Pearson correlation analysis was used to detect relationships between the call properties. ABR thresholds obtained from females and males in response to tone and click stimuli were sorted and analyzed using Independent samples t-tests. Results were expressed as mean \pm SD, and $P < 0.05$ was considered statistically significant.

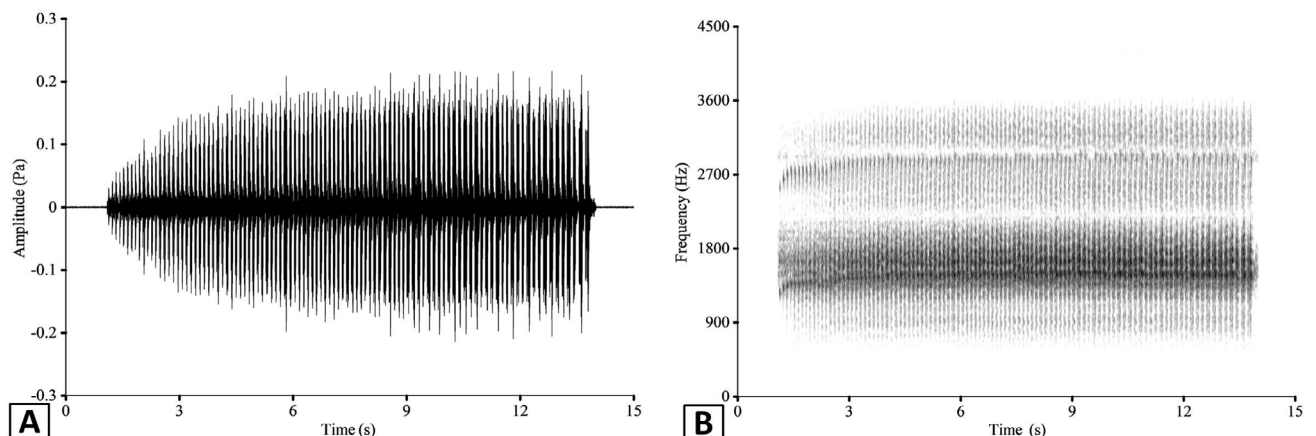


Fig. 1. The waveform (A) and sonograms (B) obtained for advertisement calls of *Duttaphrynus melanostictus*.

Table I.- Acoustic properties and morphological data of male *Duttaphrynus melanostictus*.

	Sample size	Mean \pm SD	Max	Min	CV (%)	Type
Dominant frequency (Hz)	17	1494.27 \pm 80.29	1636.00	1291.33	5.37	Static
Fundamental frequency (Hz)	17	569.73 \pm 77.96	660.30	322.92	13.68	Dynamic
Note number	17	145.71 \pm 62.39	315	52	42.82	Dynamic
Inter-note interval (s)	17	0.05 \pm 0.02	0.09	0.03	29.69	Dynamic
Note duration (s)	17	0.11 \pm 0.02	0.16	0.08	20.58	Dynamic
Call duration (s)	17	21.52 \pm 8.70	45.30	6.97	40.41	Dynamic
Snout-vent length (mm)	17	72.39 \pm 3.54	77.21	64.54	-	-
Head length (mm)	17	18.08 \pm 1.49	18.09	19.98	-	-
Head width (mm)	17	25.86 \pm 1.69	27.80	2.87	-	-

CV, coefficient of variation.

RESULTS

Acoustic structure

Male toads emitted a series of multisyllabic calls that were composed of single notes with a dominant frequency of 1494 ± 80 Hz. Figure 1 depicts the waveform (A) and sonograms (B) of the types of calls of males. The call properties and morphological data are summarized in Table I. The dominant frequency was static, while the fundamental frequency, note number, inter-note interval, note duration, and call duration were dynamic. Mean CV for static property was 5.37% for dominant frequencies, whereas that for dynamic properties was 13.68% or greater (Table I).

Relationship between acoustic structure and body size

Correlation analysis (Fig. 2) showed that the dominant frequency was negatively correlated with snout-vent length (Fig. 2A) and head width (Fig. 2B). The note duration

was significantly, positively correlated with head length (Fig. 2C). However, there were no significant correlations between fundamental frequency, note number, inter-note interval, or body size (all $P > 0.05$). The correlations between acoustic properties and body size are shown in Table II.

Table II.- Correlation analysis between acoustic properties and body size.

	Snout-vent length	Head length	Head width
Dominant frequency	0.01	0.07	0.02
Fundamental frequency	0.41	0.58	0.39
Note number	0.88	0.81	0.50
Inter-note interval	0.32	0.42	0.36
Note duration	0.94	0.01	0.09
Call duration	0.96	0.51	0.36

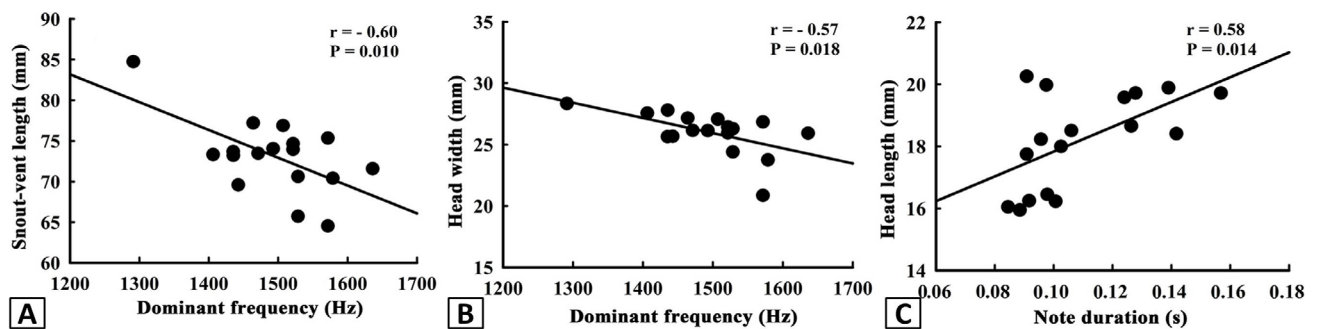


Fig. 2. Relationships between male dominant frequency and snout-vent length (A) and head width (B) and note duration and head length (C).

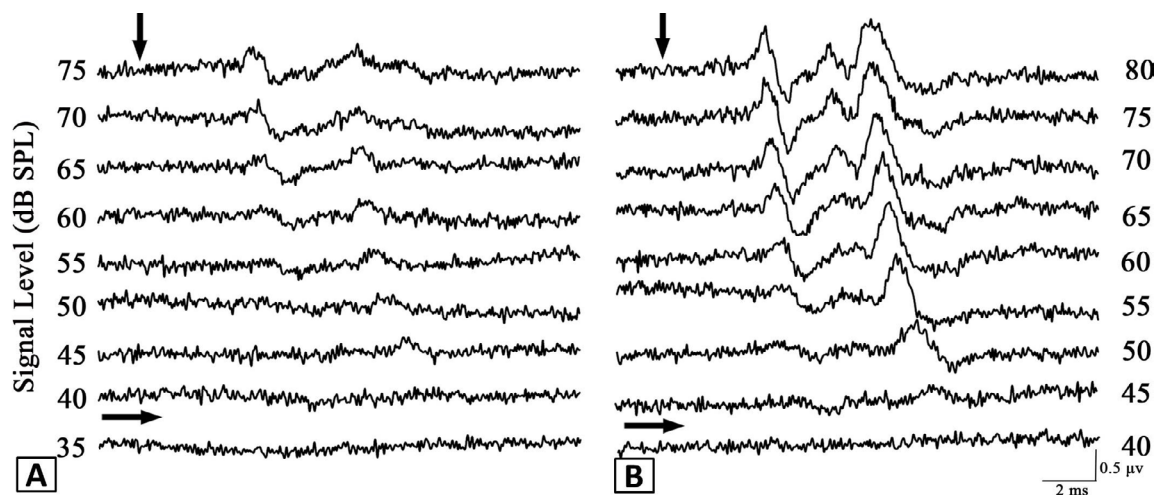


Fig. 3. Auditory brainstem responses (ABR) as a function of stimulus intensity evoked by 1.8 kHz tone pips from a female (A) and a male (B).

Sex differences in peripheral auditory sensitivity

Figure 3 shows a typical ABR response level series measured in one female and one male, for which thresholds of 40 dB SPL and 50 dB SPL were obtained, respectively. ABR thresholds are shown in Figure 4 (female, $n = 9$; male, $n = 14$). Figure 4 shows that the hearing frequency range was 0.6–2.0 kHz for females and 1.0–2.0 kHz for males. Remarkably, the best excitatory frequencies were 1.2–1.8 kHz in both females and males. Compared with males, the ABR thresholds in females were significantly smaller at 0.6–2.4 kHz ($P < 0.05$).

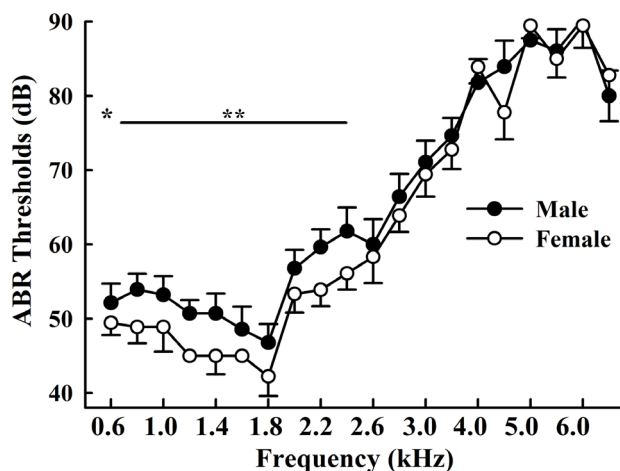


Fig. 4. Auditory brainstem response (ABR) thresholds for *Duttaphrynus melanostictus* recorded in males and females. The data are represented as mean \pm SD. * $P < 0.05$, ** $P < 0.01$.

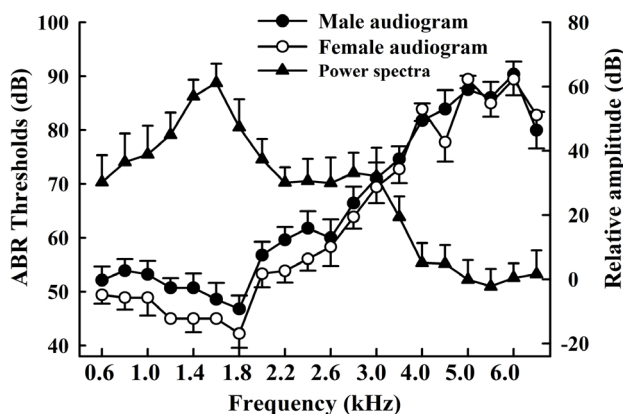


Fig. 5. Audiogram and power spectra of *Duttaphrynus melanostictus*. Data are presented as mean \pm SD.

Relationship between hearing sensitivity and vocalization characteristics

The ABR thresholds were lowest at a frequency of 1.8 kHz (42.2 ± 2.6 dB) (Fig. 5). The main energy spectrum

of male vocalizations was 1.0–2.0 kHz, during which both male and female *D. melanostictus* showed sensitive auditory perception. In general, the spectral structures of male vocalizations matched both male and female hearing sensitivity.

DISCUSSION

In anurans, classifying the diversification of calls is important for understanding their behavior and the evolution of acoustic communication (Krishna and Bosch, 2007). Sexual selection produces individuals that emit calls with longer call duration and more notes (Ryan and Keddy-Hector, 1992; Gerhardt and Huber, 2002; Gridi-Papp *et al.*, 2006). The male *D. melanostictus* emit a series of multisyllabic calls which are composed of single notes with dominant frequency 1494 ± 80 Hz. These results were similar to those from another study of this species in Zhejiang Province, China (Wei *et al.*, 2012), which showed a dominant frequency of about 1.5 kHz in males from the Bali population, Republic of Indonesia (Márquez and Eekhout, 2006). However, they were different from results of males in Bangkok that have a dominant frequency of 1.0–1.7 kHz (Heyer, 1971), and those in the Coorg population of Karnataka that have an average dominant frequency of 1.6 kHz (Hampson and Bennett, 2002), and those with a frequency over 3.0 kHz in Burma (Wogan *et al.*, 2003). Our results suggest that males compete by increasing the number of notes to make their acoustic signal more complex, and that the dominant frequency represents geographic variation in complexity. Geographic variation in anuran calls was also reported in *Leptodactylus fuscus* (Heyer and Reid, 2003), *Colostethus palmatus* (Bernal *et al.*, 2005), and *Dendropsophus cruzi* (Tessarolo *et al.*, 2016).

As previously reported in *Hyla labialis* (Gutiérrez and Lüddecke, 2002), *Rhacophorus dennysi* (Wang *et al.*, 2012), and *Philautus odontotarsus* (Zhu *et al.*, 2017), the acoustic properties could also have reflected the body size of *D. melanostictus*. Furthermore, the dominant frequency was classified as static, suggesting it may be under stabilizing selection and is probably used in species recognition. However, the note and call durations were dynamic, suggesting they may be under directional selection and more likely used in mate choice (Gerhardt, 1991; Zhu *et al.*, 2017).

Studies have verified that hearing sensitivity at all frequencies within the hearing range can be influenced by sex, and also influence thresholds in a stimulus-specific manner (Miranda and Wilczynski, 2009; Shen *et al.*, 2011). There was a significant sex difference in peripheral auditory sensitivity in *D. melanostictus*-females had more

sensitive hearing than males. However, this conclusion contradicts those from concave-eared torrent frogs, *Odorrana tormota* (Shen *et al.*, 2011) and large odorous frogs, *O. graminea* (Liu *et al.*, 2014), in which males are more sensitive than females to ultrasound. Furthermore, in American bullfrogs, the males are more sensitive than females to low frequencies (Werner *et al.*, 2009). Although these studies suggest sex-related differences in hearing sensitivity is species specific, the dimorphism in peripheral auditory sensitivity may result from differences in the breeding roles of the sexes. Interesting, our previous work suggested female choice plays a major role in shaping the mating behavior of this tropical toads (Wang *et al.*, 2018).

The match between male acoustic signals and female hearing abilities is a common feature in call-producing and hearing species (Ladich and Yan, 1998; Henry and Lucas, 2008; Kostarakos *et al.*, 2008; Moreno-Gómez *et al.*, 2013); however, there are studies that contradict this (Gerhardt and Schwartz, 2001; Wright *et al.*, 2003; Zhao *et al.*, 2017). The match is thought to have arisen over evolutionary time, as it promotes conspecific information transfer and reduces interference from natural environments (Moreno-Gómez *et al.*, 2013). In this study, we found that the tuning of female and male hearing sensitivity was well matched with the frequencies of male calls. This result clarified two aspects: for efficient communication in mixed-species choruses, the frequencies used in vocalizations and hearing was matched in each anuran species, and successful reproduction requires that females detect, recognize, and localize the vocalizations of a conspecific male (Gerhardt and Huber, 2002; Nityananda and Bee, 2011). Moreover, in anurans, the auditory receiving systems are thought to have coevolved with acoustic sender signals specifically (Ryan and Wilczynski, 1988; Gerhardt and Huber, 2002; Witte *et al.*, 2005). The match between frequencies used in hearing and vocalizations in *D. melanostictus* suggested that they have co-evolved. Sexual selection produces males that produce more complex calls, and female evolved selective pressure lead to improved acoustic communication (Hetherington, 1994; Feng *et al.*, 2006).

In conclusion, our results show that male *D. melanostictus* emit complex multisyllabic calls by increasing the number of notes. Dominant frequency and note duration could reflect body size in this species. The sexual dimorphism in peripheral auditory sensitivity, and the spectral structures of male vocalizations matched both male and female hearing sensitivity. Although receiving systems and acoustic communication signals are thought to have co-evolved, sexual dimorphism in the peripheral auditory sensitivity was observed. This suggested that female choice may play a more important role than male-male competition during breeding of this species.

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Statement of conflict of interest

The authors declare there are no competing interests.

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