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SPECTRAL FLUCTUATION ANALYSIS REVEALS VARIATION IN CICADA ADVERTISEMENT-SONG STRUCTURES

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Abstract. Understanding song structure is a fundamental step in any bioacoustic study because it provides a basis for interpreting signal production and behavioral function. Previously, an analytical framework based on spectral fluctuation analysis of peak frequency and amplitude was proposed, considering peak frequency as a species-specific signal perceived by females. In this study, advertisement songs of three cicada species with varying structural complexity, *Cryptotympana atrata*, *Graptopsaltria nigrofuscata*, and *Meimuna opalifera*, were analyzed to evaluate the applicability of this framework. Spectral fluctuations were examined using the strucchange package in R, and generalized linear regression models were fitted between peak frequency and root-mean-square amplitude to identify structural breakpoints. The results showed that songs of *C. atrata* were primarily divided into two non-repetitive parts, whereas *G. nigrofuscata* produced songs comprising five distinct segments. In *M. opalifera*, advertisement songs consisted of five sequential parts, each containing multiple frequency- and amplitude-modulated echemes. These findings demonstrate the robustness of the proposed approach in identifying song structures across species with different levels of complexity and provide an informative foundation for subsequent bioacoustic and behavioral studies.
Keywords: spectral fluctuation analysis, advertisement song, cicada.

1. Introduction

Cicadas belong to a group of insects that mainly rely on advertisement songs for species recognition and pair formation [1]. Accordingly, males convey species-specific information in both spectral and amplitude modulations of the song and send those acoustic signals toward conspecific females. In return, females recognize species-specific signals by vibrating their tympanal ridge at the peak frequency in conspecific male songs to identify and orient towards their potential mates [2]-[4]. Even in multi-species dynamics, the apodeme in female ears can act as a bandpass filter of background noise and tune in closely to the fluctuation of peak frequency, which assures an efficient phonotactic orientation to conspecific males afterwards [5]. After approaching their potential mates, females focus on the temporal characteristics of male songs for courtship responses [6]. For all those reasons, both spectral and temporal attributes of advertisement songs are critical for intraspecific intersexual communication in cicadas [6].

Songs are diverse among cicada taxa in both temporal and spectral attributes, which reflect differences in neural control and sound-producing morphology [7]. In the temporal domain, songs can be discriminated based on syllable structure, tymbal-apparatus level, or echeme structure as proxies for underlying motor patterning. Some species have simple songs composed of one or two types of echemes [8]-[10], whereas others include several types alternatively repeated during the song [10]-[13]. With regard to spectral domains, frequency spectra also vary from pure-tone spectra [14] to wideband [15]-[17], as well as peak frequency varying from 800 Hz [16] to ultrasonic frequency [18]-[19]. This diversity in both time and frequency poses a challenge for developing general, quantitative tools that can reliably detect and characterize structural organization across species with markedly different song architectures.

In a recent study, Nguyen et al. [20] proposed a spectral fluctuation analysis scheme that exploits time series of acoustic features, such as peak frequency and amplitude, to detect systematic changes in song structure using statistical break-point detection. Although the approach has successfully detected different patterns within the songs of *Hyalessa maculaticollis*, it remains unclear whether the same analytical framework is applicable across the full range of temporal and spectral complexity observed in cicadas. Demonstrating such robustness is essential if this approach is to be used as a general tool for bioacoustic analysis across taxa.

In this study, advertisement songs of three cicada species, *Cryptotympana atrata*, *Graptopsaltria nigrofuscata*, and *Meimuna opalifera*, were selected explicitly to span a gradient from relatively simple to more complex temporal and spectral song structures. Building on the previously developed spectral fluctuation analysis scheme, time series of peak frequency and amplitude were modeled using generalized linear regression, and the consistency of regression coefficients was evaluated across each recording. The strucchange package in R was then applied to these models to identify statistically significant breakpoints, that is, locations within a song where the underlying spectral–temporal relationship changes abruptly. By successfully detecting structural changes in songs that differ markedly in their temporal organization and spectral composition, this work demonstrates the applicability and versatility of the proposed spectral fluctuation analysis scheme to cicada songs of various structural types, thereby extending its potential use to broader comparative and taxonomic contexts.

2. Materials and methods

2.1. Song recording

From July to August 2013, songs of *C. atrata*, *G. nigrofuscata*, and *M. opalifera* were recorded in and around metropolitan Seoul, Republic of Korea. Each location was visited randomly twice from 9 am to 5 pm during the sampling period. The average temperature and humidity of each sampling location are provided in Table 1. On rainy days, no recordings were made.

Table 1. Information on each sampling locality. Temp: temperature; Hum: humidity

Date	Temp (°C)	Hum (%)	Location name	Latitude (°N)	Longitude (°E)	Area (m^2)
2013.08.01	30.2	73	Jamsil Complex	37.643611	127.076389	66000
2013.08.02	27	88.3	Byung Mok An Park	37.384400	126.908889	60,200
2013.08.07	29.6	80.4	Jungang Complex	37.4314389	126.992778	75355
2013.08.08	29.1	82.3	Jamsil Complex	37.6436111	127.076389	66000
2013.08.14	30.8	63.7	Jamsil Complex	37.6436111	127.076389	66000
2013.08.03	30.6	83.4	Jungang Complex	37.431439	126.992778	75,355
2013.08.05	29.3	89.3	Jungang Complex	37.431439	126.992778	75,355
2013.08.15	30.1	73	Hanok Village	37.559314	126.994444	58,000
2013.08.16	29.5	77.9	Hanok Village	37.559314	126.994444	58,000

Song recording and preprocessing followed the procedures described in Nguyen et al. [20]. Specifically, we recorded one complete advertisement song from each cicada, capturing the entire duration from beginning to end without interruptions. The recorder was positioned horizontally relative to the male cicada's body, and a distance of approximately 20 - 30 cm was maintained throughout each 1-minute recording to obtain high-quality acoustic signals while minimizing disturbance to the calling individual. Songs were recorded using a digital recorder (PCM-D50; Sony Electronics Inc., China) with a built-in microphone and a head-cover windshield to minimize background noise. Recordings were obtained at a 44.1 kHz sampling rate and 16-bit resolution.

2.2. Spectral fluctuation analysis

We followed Nguyen et al. [20] in analyzing the spectral fluctuation of cicada advertisement songs. Briefly, time series of peak frequency (PF) and root-mean-square amplitude (RMS) of each song recording were used to construct a regression model (PF ~ RMS). The null hypothesis of constant regression coefficients over time was tested using empirical fluctuation processes implemented in the strucchange package (version 1.5-0) in R (version 4.4.1) [21]. A significant test result indicated at least one structural change in the sequence.

To estimate the number and positions of structural changes, we evaluated both (i) peaks in the empirical fluctuation process and (ii) changes in fluctuation patterns. Breakpoints were subsequently determined using the breakpoints () function, which identifies segmentation points that minimize residual variation across the time series. The minimal segment size parameter (h) was selected based on two criteria: the number of peaks detected in the empirical fluctuation processes and the number of different patterns observed in the empirical fluctuation processes. In other words, we relied on both the number of peaks and the number of different patterns in estimating the number and locations of potential structural changes. As the duration of each segment could be varied among songs, the parameter h was refined through comparison of different fluctuation patterns among candidate models.

2.3. Hierarchical terminology of cicada song description

Hierarchical terminology employed to describe cicada songs commonly consists of pulse, syllable, echeme, phrase, and song [1], in which pulses are the smallest unit produced when the tymbal apparatus contracts and relaxes, and phrases are one complete complex song structure repeated in time. A syllable is one cycle of tymbal muscle movement, and an echeme is constituted by groups of syllables. A song is the totality of an advertisement signal with at least one phrase. In this study, we introduced a new structure, part, as an aggregation of echemes, so that one phrase is constituted by several parts.

After defining the structures of each song, we continued with temporal and spectral measurements. Definitions of Phrase Duration (PD), Part Duration (PaD), Echeme Duration (ED), Peak Frequency (PF), and Bandwidth 90% (BW) followed Nguyen et al. [20]. In addition, Inter-phrase interval (IPI) indicated the silent time between two consecutive phrases, and Phrase period (PP) summed up consecutive PD and IPI.

3. Results

In general, *C. atrata* was the species whose positions were maintained during calling, whereas the other species frequently changed calling perches between consecutive songs. Moreover, *C. atrata*'s songs were the least complex in structure, followed by *G. nigrofuscata*; the songs of *M. opalifera* consisted of multiple repetitions at both part- and echeme-levels.

3.1. *Cryptotympana atrata*

The advertisement song of *C. atrata* was a long, continuous call with a gradual increase of both PF and RMS at the beginning, followed by relatively constant spectral patterns in the main body. Examination of 79 empirical fluctuation processes in 21 songs showed that most phrases contained one prominent peak in the empirical fluctuation process (71 phrases), seven phrases included two peaks, and only in one phrase did we find three distinct peaks. All processes crossed the significance level, indicating at least one significant structural change in *C. atrata*'s songs. For that reason, one phrase of *C. atrata* was divided into two or more parts (Figure 1). The duration of one phrase was approximately 22.39 ± 2.68 s, with 26.77 ± 10.22 s in between consecutive phrases, which resulted in a phrase period of 48.97 ± 11.13 s. Descriptive analysis of other parameters related to the part structure of *C. atrata*'s songs is shown in Table 2.

Table 2. Spectral and temporal properties of C. atrata's advertisement songs (n = 21).

	PaD (s)	PF (kHz)	BW (kHz)
Part A	5.54 ± 1.81	5.81 ± 0.53	6.35 ± 0.49
In two-part songs			
Part B	16.85 ± 2.39	6.47 ± 0.60	6.42 ± 0.41
In three-part songs			
Part B	11.98 ± 2.92	6.20 ± 0.53	6.63 ± 0.47
Part C	8.34 ± 2.67	6.34 ± 0.94	6.64 ± 0.28
In four-part songs			
Part B	4.83	6.38	6.64
Part C	4.43	6.20	6.30
Part D	5.71	5.89	6.13

PD: phrase duration, PaD: part duration, ED: echeme duration, PF: peak frequency, BW: bandwidth 90%

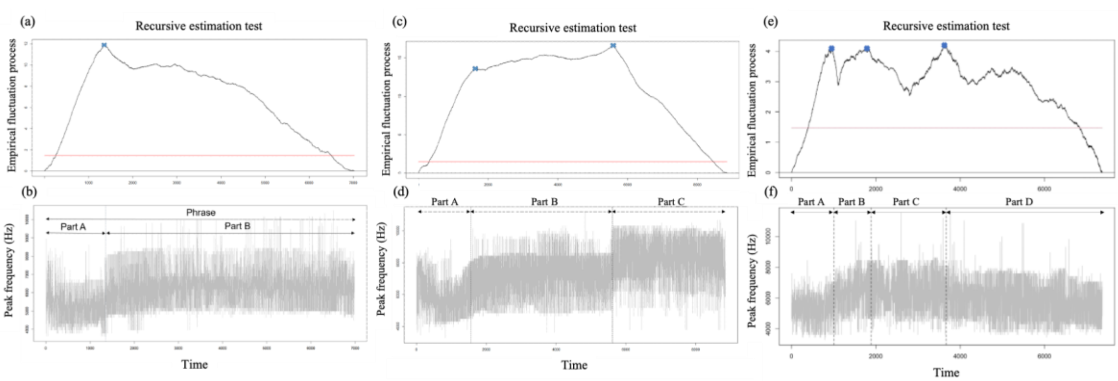

Figure 1. Advertisement songs of C. atrata, in which one phrase consisted of two to four parts. Empirical fluctuation processes and time-series of peak frequency of: (a) & (b) a song containing two parts A and B, (c) and (d) a song containing three parts A to C, (e) and (f) a song containing four parts A to D, respectively.

3.2. *Graptopsaltria nigrofuscata*

Song of *G. nigrofuscata* could be primarily described by two parts, in which the first part, represented by low frequency fluctuation, was assumed to build up energy for multiple fluctuations between profoundly distinct high and low frequencies in the second part. This coincided with one significant peak found in almost all empirical fluctuation processes of this species. Additionally, in some callings, we also identified sub-structures either within part A, part C, or part E, and we further analyzed them for a better understanding of their detailed structures. Consequently, songs of *G. nigrofuscata* could be divided into five main parts from A to E (Figure 2), in which echeme structure could be identified in certain parts. Detailed descriptive statistics of temporal and spectral properties are provided in Table 3.

3.3. *Meimuna opalifera*

The advertisement song of *M. opalifera* was the most complicated among cicada species in this study. This species produced songs that not only contained a variety of fluctuations but also, within each structure, repeated several distinct sub-structures. In general, we distinguished songs by *M. opalifera* based on five separate parts, with each part produced once. Calculation of the location of breakpoints also provided delimitation of five different parts A to E in one phrase (Figure 3). In some phrases, part B could be divided into sub-parts owing to intra-song variation, and detailed echeme structures could be clearly determined within these sub-parts (Figure 3). Descriptive statistics from phrase- to echeme structures are shown in Table 4.

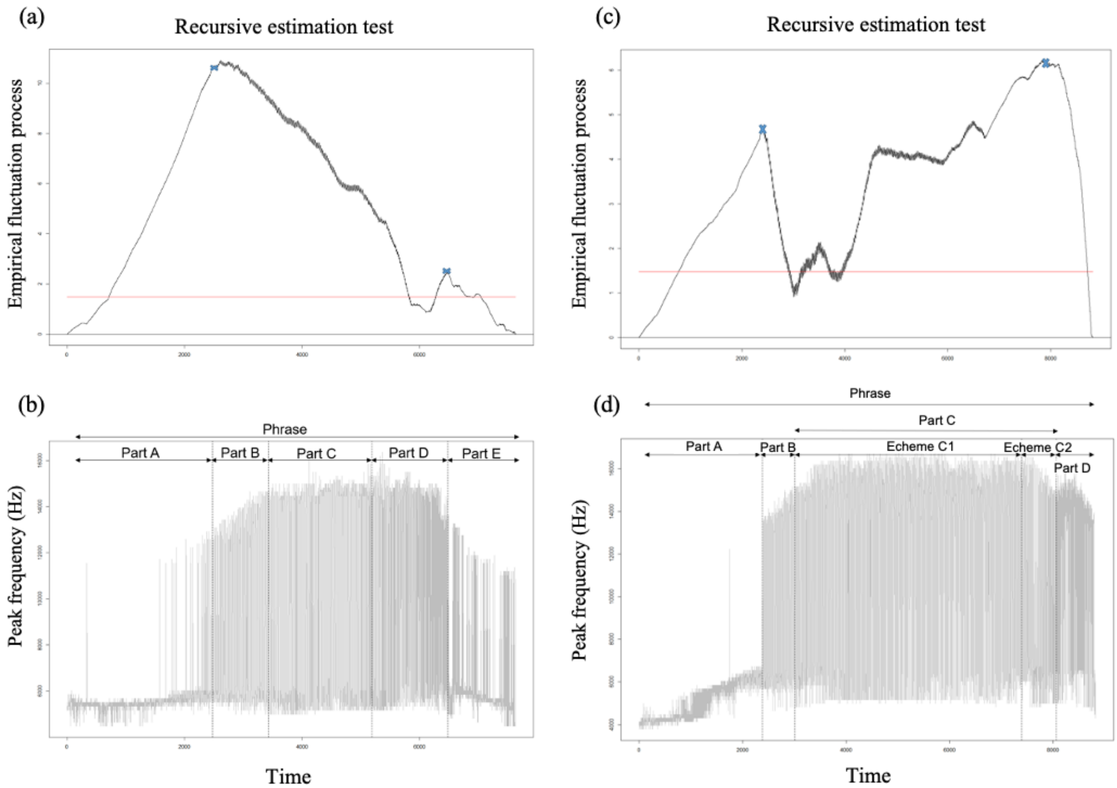

Figure 2. Advertisement songs of G. nigrofuscata, in which one phrase consisted of four to five main parts. Empirical fluctuation processes and time-series of peak frequency of: (a) & (b) a song containing five main parts A to E, (c) and (d) a song containing four parts A to D, in which part C was divided into two echemes, C1 and C2, respectively

Table 3. Acoustic properties of G. nigrofuscata's advertisement song (n=12)

	PaD (s)	ED (s)	PF (kHz)	BW (kHz)
Part A	12.67 ± 7.34			
Part B	5.12 ± 3.32		8.90 ± 0.95	8.18 ± 0.35
Part C	10.28 ± 4.75			
Part D	4.6 ± 2.3		10.15 ± 1.39	8.84 ± 0.47
Part E	19.05 ± 9.33			
Echeme A1		16.98 ± 10.3	5.90 ± 0.51	6.58 ± 1.07
Echeme A2		8.3 ± 7.54	5.90 ± 0.35	6.44 ± 1.30
Echeme C1		5.06 ± 3.1	10.44 ± 1.31	8.67 ± 0.55
Echeme C2		5.82 ± 3.94	10.57 ± 1.41	8.50 ± 0.39
Echeme E1		17.52 ± 8.08	6.42 ± 0.69	7.16 ± 0.88
Echeme E2		16.28 ± 8.31	6.29 ± 0.46	8.26 ± 1.30

For those parts that contained echeme-structure, spectral measurements were conducted at the *echeme-level. For the other parts that contained no echeme-structure, all measurements were performed at the part-level. PaD: part duration, ED: echeme duration, PF: peak frequency, BW: bandwidth 90%.*

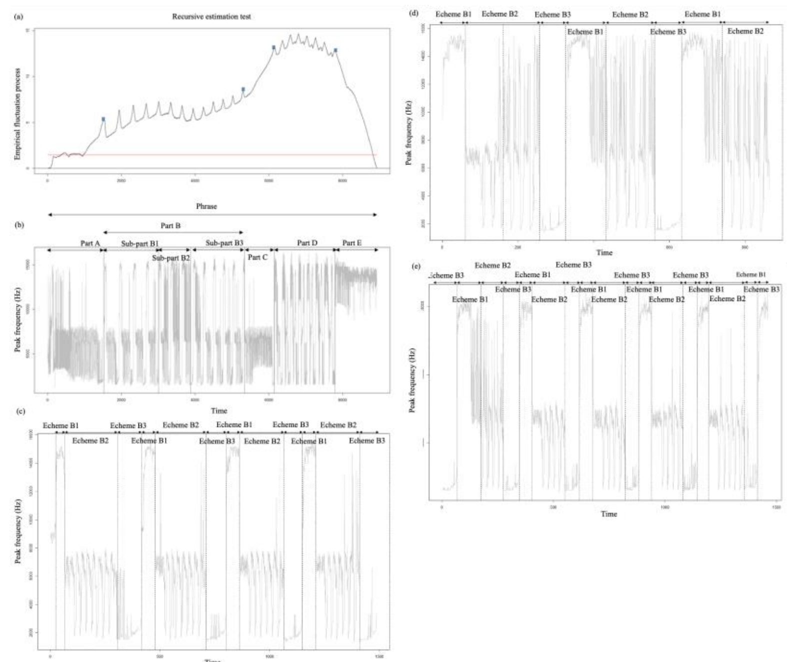

Figure 3. Advertisement song of M. opalifera in which one phrase consisted of five parts A-E, and part B containing three subparts and three types of echemes B1 to B3. (a) Empirical fluctuation process with four estimated peaks in one advertisement song; (b) Plot of peak frequency with identified structures; (c) Detailed echeme structures in sub-part B1; (d) Detailed echeme structures in sub-part B2; (e) Detailed echeme structures in sub-part B3.

Table 4. Acoustic properties of 25 M. opalifera's advertisement songs

	n	PaD (s)	ED (s)	PF (kHz)	BW (kHz)
Part A	1	5.36 ± 1.99			
Part B	1	11.48 ± 2.51			
Part C	1	2.79 ± 0.68			
Part D	1	4.07 ± 0.99			
Part E	1	3.9 ± 0.86			
Echeme A1	1		0.72 ± 0.64	6.76 ± 0.95	10.80 ± 1.92
Echeme A2	1		1.41 ± 0.52	5.40 ± 1.25	9.61 ± 1.10
Echeme A3	1		2.99 ± 1.94	5.90 ± 0.65	9.97 ± 1.24
Echeme A4	1		0.6 ± 0.35	7.27 ± 1.01	9.84 ± 1.30
Echeme A5	1		0.45 ± 0.22	3.30 ± 1.48	9.94 ± 1.69
Echeme B1	11.92 ± 2.6		0.24 ± 0.04	12.70 ± 0.85	8.26 ± 0.84
Echeme B2	10.96 ± 2.67		0.59 ± 0.07	5.67 ± 0.83	10.11 ± 1.05
Echeme B3	10.56 ± 2.69		0.2 ± 0.04	2.58 ± 0.45	9.48 ± 1.59
Echeme C1	1.42 ± 0.5		0.75 ± 0.41	5.67 ± 0.71	9.82 ± 1.21
Echeme C2	1.4 ± 0.5		1.33 ± 0.67	5.96 ± 0.51	8.28 ± 1.34
Echeme C3	1.08 ± 0.29		0.24 ± 0.24	9.30 ± 2.469	8.68 ± 0.78
Echeme D1	6.24 ± 1.3		0.22 ± 0.02	2.66 ± 0.66	9.60 ± 1.53
Echeme D2	5.32 ± 1.31		0.22 ± 0.02	13.17 ± 1.04	7.045 ± 0.65
Echeme D3	3.67 ± 1.49		0.12 ± 0.06	5.71 ± 0.77	10.26 ± 1.08
Echeme D4	4.68 ± 1.43		0.16 ± 0.04	7.03 ± 0.62	9.36 ± 1.00
Echeme D5	3.17 ± 1.2		0.09 ± 0.02	11.94 ± 1.36	8.97 ± 1.28
Echeme E1	1		1.7 ± 1.04	13.14 ± 1.00	6.77 ± 0.76
Echeme E2	1		2.2 ± 1.07	10.98 ± 1.23	7.75 ± 1.62

n = number of units produced in a phrase. PaD: part duration, ED: echeme duration, PF: peak frequency, BW: bandwidth 90%

4. Discussion

In this study, we demonstrated the applicability of spectral fluctuation analysis for delimiting distinct structures within cicada advertisement songs, ranging from the simple two-part structure of *C. atrata* to the highly complex, multi-fluctuating and repetitive patterns observed in *G. nigrofuscata* and *M. opalifera*. Traditionally, song analysis has relied largely on subjective interpretation to distinguish different structural units within songs. For species with relatively simple song patterns and minimal spectral variation, such subjective approaches may suffice. However, for species exhibiting complex acoustic structures, such as cicadas, birds, and primates, objective analytical methods are essential to accurately segregate different song components. The present results demonstrate that spectral fluctuation analysis provides a powerful, objective tool for such investigations.

In addition, intraspecific variation in calling song structures was observed among the three cicada species studied. This phenotypic plasticity in acoustic features may play a crucial role in courtship behavior across taxa. First, variation within species is often interpreted as a reflection of male quality since the production of more complex songs can serve as a proxy for male fitness and overall condition [22]. In birds, for example, female mate choice is frequently influenced by the complexity of male songs [23]. Furthermore, song complexity has been linked to nutritional competence and exposure to early-life stress, making it a reliable indicator of male quality [24]. Second, variation in male song structure may facilitate individual recognition. In species such as cicadas, chorusing behavior can increase mating opportunities but also mask individual acoustic signatures. In this context, intraspecific variation helps maintain conspecific recognition while allowing females to focus on distinctive individual traits.

Interspecific variation in song structure, on the other hand, likely arises from differences in the song-producing apparatus, which is primarily controlled by the tymbal mechanism and the nervous system. Divergence in either component can lead to structural differences in song and thereby contribute to the diversity of cicada song evolution. For instance, variation in tymbal morphology is often reflected in the distinct pulse patterns observed among closely related species [25], whereas neural variation influences fluctuations in peak frequency. In this study, we focused particularly on large-scale fluctuations in peak frequency, as this trait is crucial for species recognition and mate attraction. Overall, our findings highlight that spectral fluctuation analysis is an effective and versatile approach for acoustic studies of cicadas and other animals exhibiting complex song structures.

5. Conclusions

Spectral fluctuation analysis provides a robust and objective framework for characterizing cicada advertisement songs. By detecting breakpoints in the relationship between peak frequency and amplitude, we identified clear structural differences among three species, ranging from the simple two-part organization of *C. atrata* to the highly complex, multi-part structure of *M. opalifera*. The approach also captured intraspecific variability, demonstrating its sensitivity to subtle acoustic variation while reducing reliance on subjective interpretation. As such, it enables reproducible delimitation of song components, particularly in species with intricate acoustic patterns. Future studies should examine the functional significance of these patterns, including links to mate choice, individual recognition, and evolutionary divergence in song production mechanisms. Overall, this study provides a quantitative foundation for advancing research on acoustic communication and signal evolution in cicadas as well as other acoustic animals.

Note for contributor

- Short bio: Nguyen Quynh Hoa is a lecturer at the University of Science and Technology of Hanoi, Vietnam Academy of Science and Technology, Vietnam; Yikweon Jang is a Full Professor at Ewha Womans University, Republic of Korea.

- Author's contributions**:** Nguyen Quynh Hoa: conceptualization, data analysis, writing; Yikweon Jang: supervision, review, and editing.

***Conflict of interest*:** The authors declare no conflict of interest.

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