

RESEARCH ARTICLE

The mechanics of acoustic signal evolution in field crickets

Vamsy Godthi^{1,*}, Rohini Balakrishnan^{2,§} and Rudra Pratap^{1,‡}

ABSTRACT

Field crickets (Family Gryllidae, Subfamily Gryllinae) typically produce tonal calls with carrier frequencies in the range 3–8 kHz. In this study, we explored the use of a finite element model (FEM) of the stridulatory apparatus of a field cricket, *Gryllus bimaculatus*, based on experimental measurements of resonator geometry and mechanical properties, to predict the measured call carrier frequencies of eight other field cricket species, ranging between 3 and 7 kHz. The model allowed accurate predictions of carrier frequencies for all eight species to within a few hundred hertz from morphological measurements of their resonators. We then used the model to explore the plausible evolutionary design space for field cricket call carrier frequency along the axes of resonator size and thickness, and mapped the locations of the nine experimentally measured species in this design space. Although the nine species spanned the evolutionarily conserved spectrum of carrier frequency and body size in field crickets, they were clustered in a small region of the available design space. We then explored the reasons for this apparent evolutionary constraint on field cricket carrier frequencies at both the lower and higher limit. We found that body size and sound radiation efficiency were the main constraints at the lower limits, whereas the energetics of stridulation using the clockwork mechanism may pose a constraint at higher frequencies.

KEY WORDS: Evolutionary constraints, Wing mechanics, Cricket sound production, Finite element models, Signal evolution

INTRODUCTION

Crickets and bushcrickets are among the most ancient acoustically communicating terrestrial species on Earth, producing a vast diversity of species-specific calls. These calls range from frequencies as low as 600 Hz in some bushcricket species to as high as 150 kHz, and from pure tones to extremely high bandwidth calls (Chivers et al., 2017). Interestingly, this spectral diversity is generated via a highly conserved stridulatory mechanism, where a plectrum on the margin of one forewing scrapes against a row of pegs or file teeth on the other forewing (Fig. 1). An interesting contrast between true crickets (Gryllidae) and bushcrickets (Tettigoniidae) is that the former typically produce tonal calls with carrier frequencies in the range 2–9 kHz, whereas the latter group exhibits much higher spectral diversity (Chivers et al., 2017).

There have been two kinds of approaches to understanding the links between morphology and stridulatory structures on the one hand, and the emanated sound signal on the other. The first is pattern oriented and correlative, wherein statistical techniques such as regression and correlation are employed to examine the relationship between structure and sound output, across a large number of taxa, and used as predictive models to infer signal structure in species where only morphological data are available (Chivers et al., 2017; Montealegre-Z et al., 2017). The second is mechanistic and process oriented, using physics-based and simulation models of the mechanics of the stridulatory process to understand the production and attributes of the output sound signal (Godthi and Pratap, 2015). The mechanism of sound production is best understood in field crickets (true crickets of the subfamily Gryllinae: Elliott and Koch, 1985; Montealegre-Z et al., 2009). Nonetheless, this understanding has not, to the best of our knowledge, been used to develop predictive models wherein signal features of cricket species may be inferred from morphology. Our study aims to fill this gap and develop predictive models that are based on an understanding of the mechanics of sound production, using a comparative approach.

Sound production mechanism in crickets

The sound production mechanism in crickets can be thought of as consisting of three stages of transduction as shown in Fig. 1: actuation, frequency multiplication and amplification (Bennet-Clark, 1999). First, the contractions of wing muscles drive the two forewings to open and close at a low frequency (around 30 Hz for the field cricket *Gryllus bimaculatus*). Second, this low frequency actuation drives a plectrum present on one wing across a file of teeth present on the other wing (during the closing of the forewings). As the plectrum engages the teeth intermittently, it produces a series of high-frequency (around 5 kHz for the field cricket *G. bimaculatus*) displacement impulses on the wing. The plectrum-and-file act as a frequency multiplier by taking the low-frequency wing beat and producing a high-frequency impulse train as excitation for the next stage of transduction. Third, the impulse train excites the harp, which vibrates in response to produce the characteristic song (Fig. 1).

The input to the sound production mechanism is the muscle power given to the forewings to drive them together (Fig. 1). This energy is transformed by the actuation mechanism into angular motion. Depending on the overlap between the plectrum and the file tooth, the frequency multiplier mechanism uses the angular momentum to displace the file vertically by a proportionate amount (Fig. 1). For field crickets, the time period between two consecutive displacement impulses on the file is such that it coincides with the fundamental time period (resonance frequency) of the harp: this is called the ‘clockwork mechanism’ (Elliott and Koch, 1985). Thus, the harp vibrates with a large amplitude, acting as an amplifier, resulting in acoustic power radiation (Bennet-Clark, 1999). For bushcrickets, the mechanism is slightly different: the wings are asymmetric, and the main resonant structure is the mirror (see Montealegre-Z, 2009).

¹Centre for Nano Science and Engineering, Indian Institute of Science, Bangalore, Karnataka 560012, India. ²Centre for Ecological Sciences, Indian Institute of Science, Bangalore, Karnataka 560012, India.

*Present address: SABIC Research and Technology Pvt Ltd, Hosahalli, Karnataka 562125, India. ‡Present address: Plaksha University, Mohali, Punjab 140306, India.

§Author for correspondence (brohini@isc.ac.in)

© V.G., 0000-0001-5726-3387; R.B., 0000-0003-0935-3884; R.P., 0000-0001-6821-277X

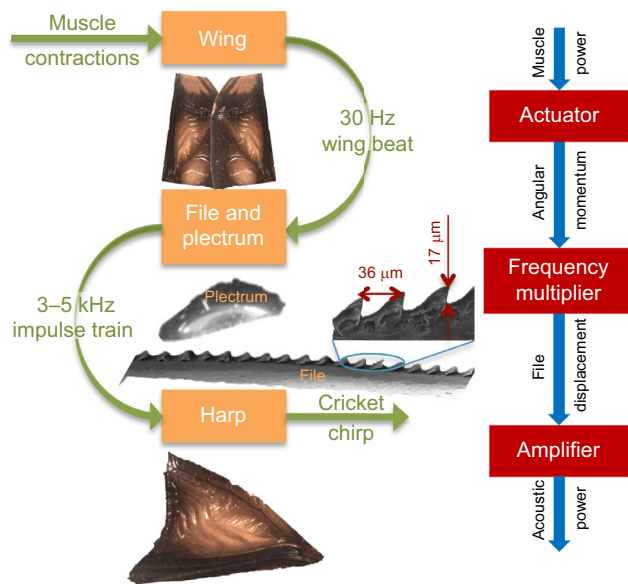


Fig. 1. The different stages of transduction involved in sound production by field crickets. The contractions of wing muscles drive the two forewings at a low frequency. This low-frequency motion drives a plectrum across a file of teeth resulting in a high-frequency impulse train which excites the harp to produce sound. Mean values for tooth spacing and height for *Gryllus bimaculatus* are shown.

Statistical models to predict call frequencies in crickets

Call carrier frequencies are expected to be higher for smaller cricket and bushcricket species, from reasons of allometric scaling (Bennet-Clark, 1998). Smaller species are expected to have smaller wings and thus smaller resonant structures (harps or mirrors in true crickets and bushcrickets, respectively), which should result in higher call frequencies. Similarly, smaller species are also expected to have shorter stridulatory files, possibly with smaller teeth packed at higher density (Montealegre-Z et al., 2009). This should result in the file teeth being struck at a higher rate and, with a match between the tooth strike rate and the resonant frequency of the harp (with the tooth strike period corresponding to the period of the carrier frequency), this should result in higher-frequency calls.

For 94 bushcricket (katydid) species (with resonant calls) that were previously examined (Montealegre-Z et al., 2017), body size was found to be a poor (though significant) predictor of call carrier frequency. The area of the mirror (main resonant structure in bushcricket wings) and the stridulatory file length were better and significant predictors of carrier frequency (with correlation coefficients of 0.52 and 0.62, respectively). A statistical model incorporating left mirror area and stridulatory file length was a strong predictor of call carrier frequency. The difference between predicted and actual carrier frequency for the species validated with this model was in the range 1–2 kHz (Montealegre-Z et al., 2017).

Even within a closely related group of crickets or bushcrickets, there are several reasons why these predicted call carrier frequencies are unlikely to be accurate. The expectation that call frequency can be predicted from resonator area alone is simplistic, given the mechanics of the resonator (harp or mirror). One expects that the resonant frequency is dependent on material properties (mass and Young's modulus), shape and thickness of the resonator. If the harps or mirrors of closely related species are similar in shape and made of the same material, then the call frequency should be predictable from a combination of size and thickness, and not from only one of these features. Regarding the second argument, that of

file size and morphology, this is again too simplistic: the tooth strike rate is determined by a combination of tooth spacing, plectrum radius and wing rotational speed; and the song frequency is unlikely to be accurately predictable from one of these features alone.

Finite element models

Over the past decade, finite element modelling (FEM), a computational tool employed in engineering (especially in the field of structural mechanics), has allowed a deeper understanding of the mechanics of cricket sound production. FEM allows one to model realistic geometries of resonators in 2D and 3D, and to examine resonance modes of these simulated structures, given specified boundary conditions and material properties (Godthi and Pratap, 2015). It is thus a very useful tool for biologists interested in the mechanics of sound production, given that biological structures typically have complex geometries that also vary between taxa. Mhatre et al. (2012) used FEM to examine the effects of resonator geometry on resonance modes of tree cricket wings (Subfamily Oecanthinae, Family Gryllidae), and concluded that the elongated forewings of tree crickets resulted in multiple resonant modes that were close together in frequency and amplitude, enabling the shift in song carrier frequency with temperature observed in these crickets. More recently, Jonsson et al. (2017) used a FEM to validate that the unusual pronotal cover over the stridulatory structures of a tropical katydid species functioned as a Helmholtz resonator.

Godthi and Pratap (2015) were the first to use a FEM to model the entire stridulation process in a cricket, from actuation to the output sound signal. Combining experimental determination of resonator material properties (Young's modulus = 6.88 ± 1.09 GPa for *G. bimaculatus*) and geometry with FEM, they were able to successfully recreate the temporal and spectral features of *G. bimaculatus* song. They also used the finite element model to examine the effects of damage to the stridulatory system, such as loss of some of the file teeth, as well as changes to tooth spacing, on the output signal, and found the system to be remarkably robust. FEM has not, however, been deployed so far to develop predictive models of sound signals from morphology across cricket taxa.

In this study, we use finite element models to (1) develop and validate predictive models of call carrier frequency across field cricket species based on morphological measurements; (2) compute and explore the plausible hypothetical design space for the evolution of cricket carrier frequencies given the mechanics of the stridulatory process; and (3) examine possible mechanistic reasons why field cricket call carrier frequencies have apparently been constrained between 3 and 8 kHz over evolutionary time.

MATERIALS AND METHODS

Song measurements

Values of mean carrier frequency of the songs of eight field cricket species examined in this study were taken from Jaiswara et al. (2013), which contains the details of song recording and analysis. Song recordings were made of the ninth species, *Tarbinskiellus portentosus*, from Kadari village, Dakshin Kannada district, Karnataka, India, using the methods detailed in Jaiswara et al. (2013). A subset (2–4 crickets of each species) of the individual crickets whose song recordings are described in Jaiswara et al. (2013), and *T. portentosus*, all of which were captured and preserved in 70% ethanol (at the Centre for Ecological Sciences, Indian Institute of Science), were used for the morphological measurements in the current study, which are detailed below.

Morphological measurements

To characterise the dimensions of the various structures involved in the sound production mechanism, we took optical images of the forewing. To determine the thickness of the harp to be used in the finite element model, we captured images of the cross-section of the harps of various species using scanning electron microscopy (SEM).

Measurement of forewing dorsal features

We used crickets stored in 70% ethanol for the morphological measurements. We carefully separated the forewings from the body of the insects and kept the samples flat by covering them with a glass slide. We captured images of the forewings of the crickets using a stereo-microscope (Leica S6D, Leica Microsystems, Wetzlar, Germany) connected to a 3.1 megapixel camera (EC3). We took calibrated images at the lowest magnification so that all the parts of the forewing associated with sound production were captured in the image (Fig. 2). We performed image processing in Photoshop (CS6, Adobe, San Jose, CA, USA) to measure the following features of the forewing: (1) area of the harp, (2) area of the mirror cell, (3) area of the forewing below the file, (4) file length and (5) distance of the plectrum from the wing pivot point (plectrum radius).

We also captured images of the insect bodies and measured the maximum pronotum width (as a measure of insect body size). We used a microscope with a 10 \times magnification lens (BX41M, Olympus, Tokyo, Japan) connected to a 5.0 megapixel camera (MicroPublisher 5.0 RTV, Qimaging) to capture images of the file (at the centre) on all the forewings. To estimate the mean file tooth spacing, we measured the average distance spanning five teeth in the middle of the file and then divided by 5 (see ‘Computation of rotational speed’, below, for why the middle five teeth were chosen). To get an estimate of variation in the triangular harp shape across the field cricket species, we measured the length of two sides of the harp

(l_f and l_d in Fig. 2) and calculated their ratio. Fig. 2 shows how the various measurements were defined using the images of the forewing of *Teleogryllus* spp.

Estimation of harp cuticle thickness

Sample preparation

We separated the forewings from the body of the crickets stored in 70% ethanol and first took all the images as described above. Then, we cut the harp of all the specimens at a specified location as shown in Fig. S1. We used a conductive carbon tape to glue the sectioned harp (containing the file) to the vertical face of a square aluminium stub for cross-sectional imaging in the scanning electron microscope (shown in Fig. S1). During SEM imaging, the sample was put in a chamber where an ultra-high vacuum is created. As the samples are organic in nature, they have a tendency to de-gas and either contaminate the chamber or block the aperture (from which the electron beam is focused). To prevent de-gassing, we desiccated the sample for at least 24 h and then sputtered a thin layer of gold (~10 nm) on the sample. The sputtered gold also helps to prevent charging of the sample when imaging (as the harp sample is not a good conductor of electricity).

SEM

We used a scanning electron microscope (ULTRA 55, Zeiss, Germany) to capture cross-sectional images of the harp. As the samples were not very rigid, the part of the sample projecting from the stub did not lie straight. To obtain the correct value of thickness from the SEM images, we needed to make sure that the plane of the cross-section was perpendicular to the electron beam when capturing the images. We achieved this by tilting the sample until the surface to be imaged lay in the horizontal plane. We captured multiple images along the width of the sectioned harp (tilting the sample as necessary). We used Photoshop (CS6, Adobe, San Jose,

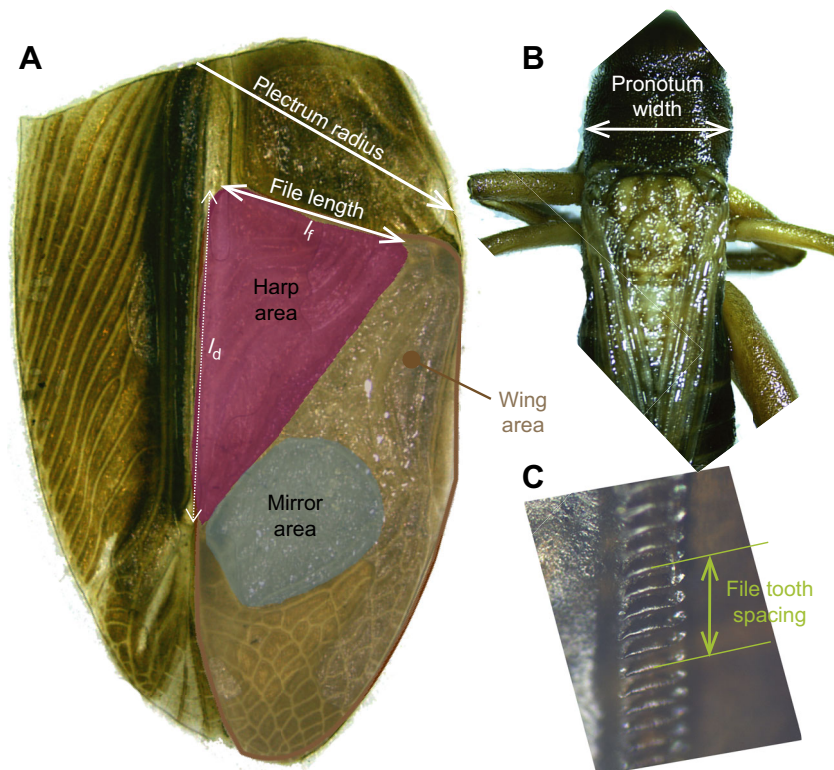


Fig. 2. Morphological measurements. (A) Forewing of a field cricket showing the features measured. l_d , harp length; l_f , file length. (B) Dorsal view of the thorax. (C) Close-up view of a stridulatory file.

CA, USA) to measure the average thickness of the harp from all the images (Fig. S2). We repeated this procedure on the harps of all the specimens.

Statistical analysis

The relationship between pairs of morphological variables or between carrier frequency and morphological variables was examined using linear regression analysis. We could not correct for non-independence of the data points (features of different species) which occurs as a result of their phylogenetic relatedness, as there is no phylogeny available for this set of species. This is unlikely to affect our conclusions, however, because our aim was not to reconstruct ancestral traits or test for correlated evolution, but only to predict song frequency from structure.

Finite element simulations

The harp model and its design space

As the harp is the key structural element for sound production and amplification, its accurate modelling is key to a good and reliable model for cricket song simulations and numerical experiments on what-if scenarios. FEM is a numerical technique in which any arbitrarily shaped geometry is divided into small discrete domains (called elements) of standard shapes such as lines, triangles, rectangles, tetrahedra, triangular prisms or rectangular bricks. Interpolation functions are used to approximate the solution within these domains and the boundary value problem (partial differential equation with prescribed boundary conditions) is converted into a set of algebraic expressions that are easy to solve. This allows us to numerically model any arbitrarily shaped geometry with a set of algebraic equations and solve for the response of the structure subjected to a set of boundary conditions and applied forces. The inputs of the finite element model of the harp include harp size and shape captured by geometric dimensions, material properties and boundary conditions. These details can be found in Godthi and Pratap (2015); the number of finite elements used and the meshing details can be found in the same reference.

This finite element model of the harp allows us to change the dimensions of the harp at will and run simulations to find the corresponding natural frequency (the possible cricket song frequency) of thousands of imaginary harps. The natural frequencies are the inherent dynamic characteristics of any system, and are the frequencies at which the system tends to oscillate freely in the absence of external forces. When driven by external force at these natural frequencies, the response is very high. Modal analysis is a finite element simulation method for identifying the natural frequencies, by determining the eigen values of the system of algebraic equations of the finite element model. A systematic exploration of these frequencies corresponding to the harp dimensions normalised with respect to that of *G. bimaculatus* defines the design space we studied. The first goal was to discover the correct scaling model of the song frequency with respect to the harp dimensions.

Acoustic radiation efficiency calculations

When a source of vibration radiates into a medium, in this case air, maximum energy transfer occurs when the acoustic resistance of the source (R_{rad}) matches the acoustic resistance of the fluid (Kinsler et al., 2000). The acoustic resistance of a radiating source depends on the nature and size of the source (a , which is the equivalent radius of the source), and the wave number ($k=2\pi/\lambda$, where $\lambda=c/\text{sound frequency}$ is the wavelength of sound) of the radiated sound. The acoustic radiation efficiency is defined as $R_{\text{rad}}/\rho_0 c S$, where ρ_0 is the

density of air, c is the speed of sound in air and S is the area of the radiating source (Leppington et al., 1982). The radiation of sound from the harp is similar to the radiation from a baffled circular piston. The efficiency of radiation from the harp depends on the ratio of its equivalent radius (a) to the sound wavelength (Kinsler et al., 2000). By determining the area of the harp and the wavelength of sound being radiated, one can estimate the efficiency of the sound radiation.

To estimate the radiation efficiency of the harp (which is of a non-trivial shape, i.e. it is not a standard geometric shape such as a circle/rectangle for which closed form analytical expressions for acoustic radiation exist), we developed an acoustic model using finite elements (3D acoustic elements in ANSYS: Fluid 30 and Fluid 130) as shown in Fig. S3A. We first optimised the parameters of the acoustic model by simulating the radiation from a piston in an infinite baffle and comparing it with the analytical solution as shown in Fig. S3C. Then, we used the same parameters and simulated the radiation from the harp. Fig. S3B shows the simulated sound pressure distribution near the harp at a particular frequency of radiation. We repeated the simulation at different frequencies to populate the graph of radiation efficiency $R_{\text{rad}}/\rho_0 c S$ versus ka as shown in Fig. S3D. Subsequently, we used a 2D grid of the normalised harp area and the calling frequency to compute the corresponding acoustic radiation efficiency (%) and generate a contour plot of iso-efficiency lines. We also computed the acoustic radiation efficiency for the 9 field cricket species studied and overlaid these on the same graph for a comparative study.

Computation of rotational speed

The required rotational speed during closing of the wing is governed by the frequency multiplier. During wing closing, each forewing rotates about a fixed point at a rotational speed of ω . The plectrum-and-file mechanism is located at a radial distance, called the plectrum radius (r), from the point of attachment of the wing to the insect body. The linear speed of the plectrum and file is each $v_p=\omega \times r$. As the two forewings close simultaneously, the relative speed (v) between the plectrum and the file is related to the rotational speed of each wing (ω) as $v=2(\omega \times r)$. Because they are moving with the same speed towards each other, the relative speed is twice the speed of the individual element. This relative speed (v) between the plectrum and the file is related to the frequency of impulses (f_{load}) through the inter-tooth spacing (p) as:

$$v = p \times f_{\text{load}} \quad (1)$$

The loading frequency is required to be close to the fundamental resonant frequency of the amplifier ($f_{\text{load}}=f_n$), in order to achieve the maximum output. Thus, the frequency multiplier mechanism relates resonant frequency of the harp to the closing rotational speed of the wing based on the morphology of the plectrum and the file.

From experimental observations, Koch et al. (1988) have also shown that there is a one-to-one correspondence between the file tooth spacing and the speed of the plectrum in order to maintain constant loading frequency (which is also close to the call frequency). Others (Bennet-Clark, 2003; Prestwich and O'Sullivan, 2005; Montealegre-Z, 2009) have reported that for different species of crickets, the tooth spacing increases steadily along the length of the file, reaching a maximum around the middle, after which it either becomes constant or decreases towards the end of the file. Hence, by measuring the maximum inter-tooth spacing (average spacing in the middle of the file), one can estimate the maximum relative speed needed and hence the maximum rotational speed that the forewings

Table 1. Average values of morphological measurements of forewings of different species of field crickets

No.	Species	Harp area (mm ²)	Mirror area (mm ²)	Wing area (mm ²)	File length (mm)	Plectrum radius (mm)	Pronotum width (mm)	Mean file tooth spacing (μm)	Mean thickness (μm)
1	<i>Gryllus bimaculatus</i> (3)	18.7	7.5	69.6	4.60	6.47	7.23	36.0	6.31
2	<i>Tarbinskiellus portentosus</i> (4)	24.7	13.7	90.6	4.02	7.57	10.3	106	7.31
3	<i>Teleogryllus</i> sp. (3)	19.0	8.76	56.2	4.19	6.44	6.97	34.0	4.53
4	<i>Itaropsis parviceps</i> (2)	10.2	7.05	38.3	3.47	4.50	4.45	19.1	4.41
5	<i>Velarifictorus</i> sp. (3)	7.15	2.15	15.9	2.22	3.67	3.26	24.9	2.23
6	<i>Coiblemmus compactus</i> (3)	11.5	5.05	29.4	2.87	5.60	4.95	39.8	4.01
7	<i>Platygryllus</i> sp. (2)	7.78	3.49	21.0	2.24	3.80	3.97	25.3	2.40
8	<i>Gryllodes</i> sp. (3)	6.14	1.52	12.0	1.90	2.80	3.81	22.0	2.41
9	<i>Plebeiogryllus guttiventris</i> (3)	7.18	2.81	21.6	2.34	3.50	4.22	19.1	3.10

Numbers in parentheses in the Species column are number of individuals.

have to achieve to maintain the loading frequency close to the resonant frequency of the amplifier (see Table S1 for details of calculations). For instance, in order to call at 5 kHz with an average tooth spacing of 36 μm, the relative speed between the file and the plectrum of *G. bimaculatus* has to be 90 mm s^{−1} and the corresponding rotational speed during stridulation has to be 13.8 rad s^{−1} (with a plectrum radius of 6.5 mm).

RESULTS
Prediction of carrier frequency from FEM and morphology
The measured morphological features of the stridulatory apparatus and the pronotum width (a measure of body size) of nine field cricket species are shown in Table 1. Both resonator (harp) area and forewing area scaled positively with and were highly predictable from body size in these species (Fig. 3A,B). In spite of this tight

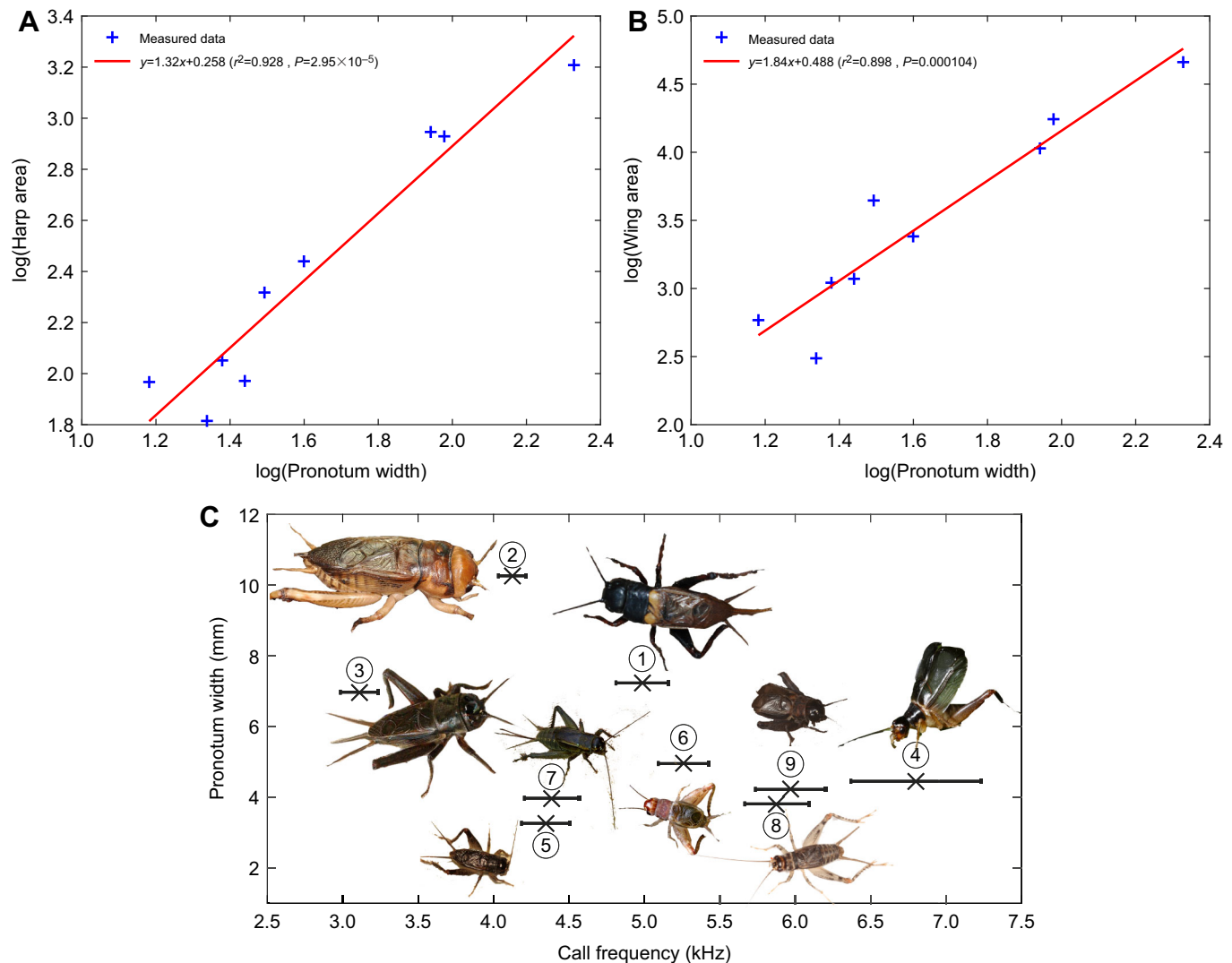


Fig. 3. Allometric scaling. (A) Harp area and (B) forewing area scale positively with body size (pronotum width). (C) Relationship between body size (pronotum width) and song carrier frequency in nine field cricket species (names corresponding to species number can be found in Table 1).

correlation, however, body size, resonator (harp) area, stridulatory file length and tooth spacing were poor predictors of field cricket song frequency when examined using the classical correlative approach between the individual morphological features (Table 1) and song frequency (Fig. 3C, Fig. 4A–D).

We then used a finite element model, detailed in Godthi and Pratap (2015), to estimate the changes in the resonant frequency of the harp with variations in area and thickness. It was seen from the analysis of images of harps of the nine species that there was very little variation in the shape of the harp: the standard deviation of the ratio of side dimensions was within 8%. Hence, we considered the shape to be constant and performed the analysis considering the variation in the area of the harp. We normalised the harp area of the eight species with respect to the area of *G. bimaculatus* harp and called this number η_A . Similarly, we normalised the thickness and called this number η_t . We performed modal analysis for different combinations of η_A and η_t and recorded the fundamental frequency. Fig. 5 shows the contour plot of the song carrier frequency with variation in area and thickness of the harp.

The iso-frequency lines represent the combinations of harp area and thickness that should result in a given song frequency (Fig. 5A), assuming the known clockwork mechanism of resonant sound

production in field crickets (Elliott and Koch, 1985). The song frequencies predicted by the fundamental vibrational modes for measured values of the mean harp thickness and area of 9 field cricket species are close to their measured mean song frequencies (less than 8% deviation from mean song frequencies in 8 of 9 species), as shown in Fig. 5C and Table 2. We also deduced from Fig. 5 (the iso-frequency lines seem to indicate a single parameter family of curves) that the song frequency scaling could be captured by a simple parameter η_t/η_A . Fig. 5C shows that the ratio of the measured harp thickness to the harp area is an excellent predictor of song frequency.

This scaling parameter is a very significant finding. What it indicates is that the harp is a ‘plate-like’ structural element, and not a ‘membrane-like’ element, although it is extremely thin compared with its lateral dimensions. This inference is based on known classical mechanics results in vibration theory. For example, the resonant frequency (ω_n) of a simply supported square plate is given by the expression (Timoshenko and Woinowsky-Krieger, 1959):

$$\omega_n = \alpha_n^2 \sqrt{\frac{E}{12(1-\nu^2)\rho}} \frac{t}{l^2}, \quad (2)$$

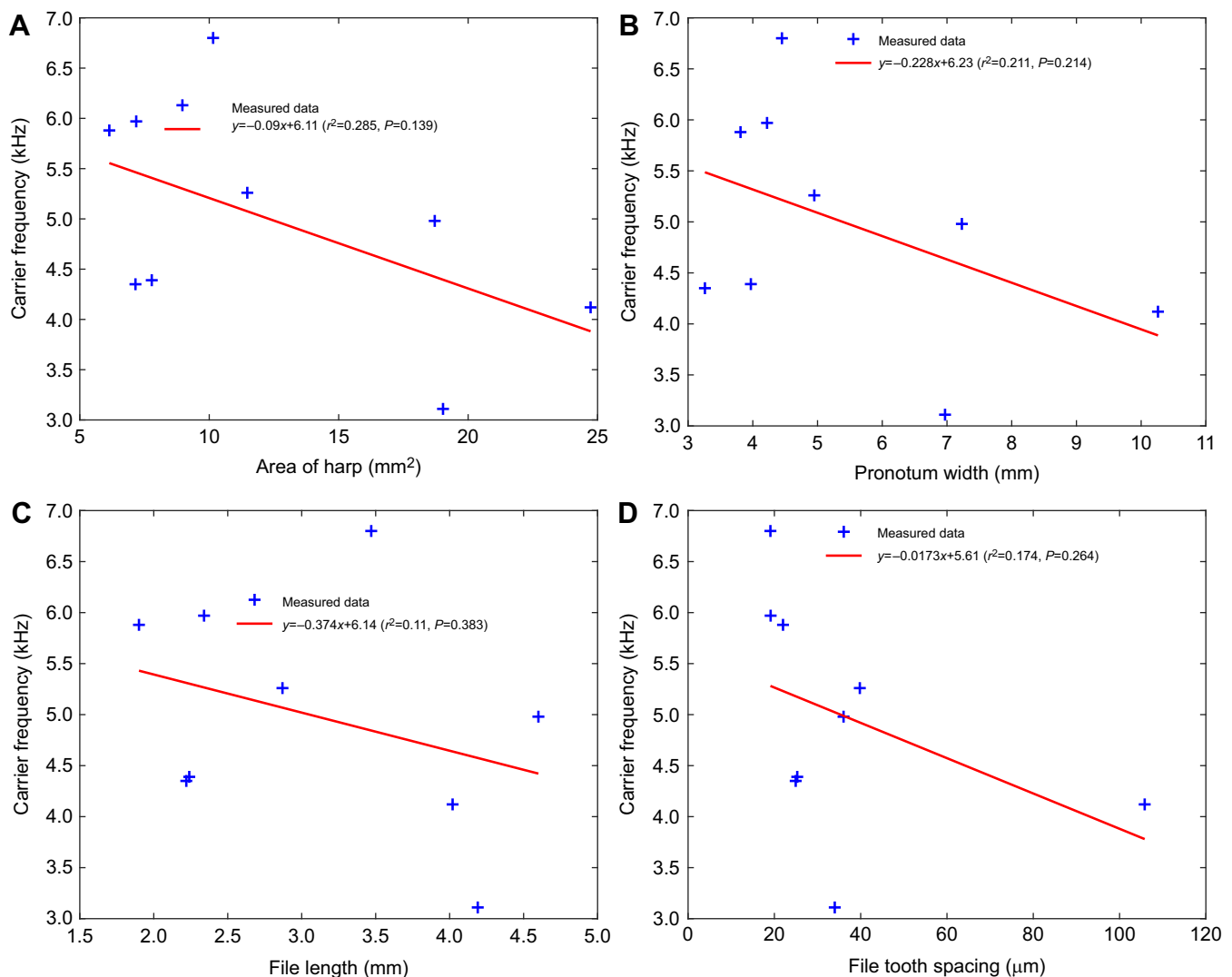


Fig. 4. Relationship between carrier frequency and individual morphological features. (A) Harp area, (B) body size, (C) file length and (D) file tooth spacing.

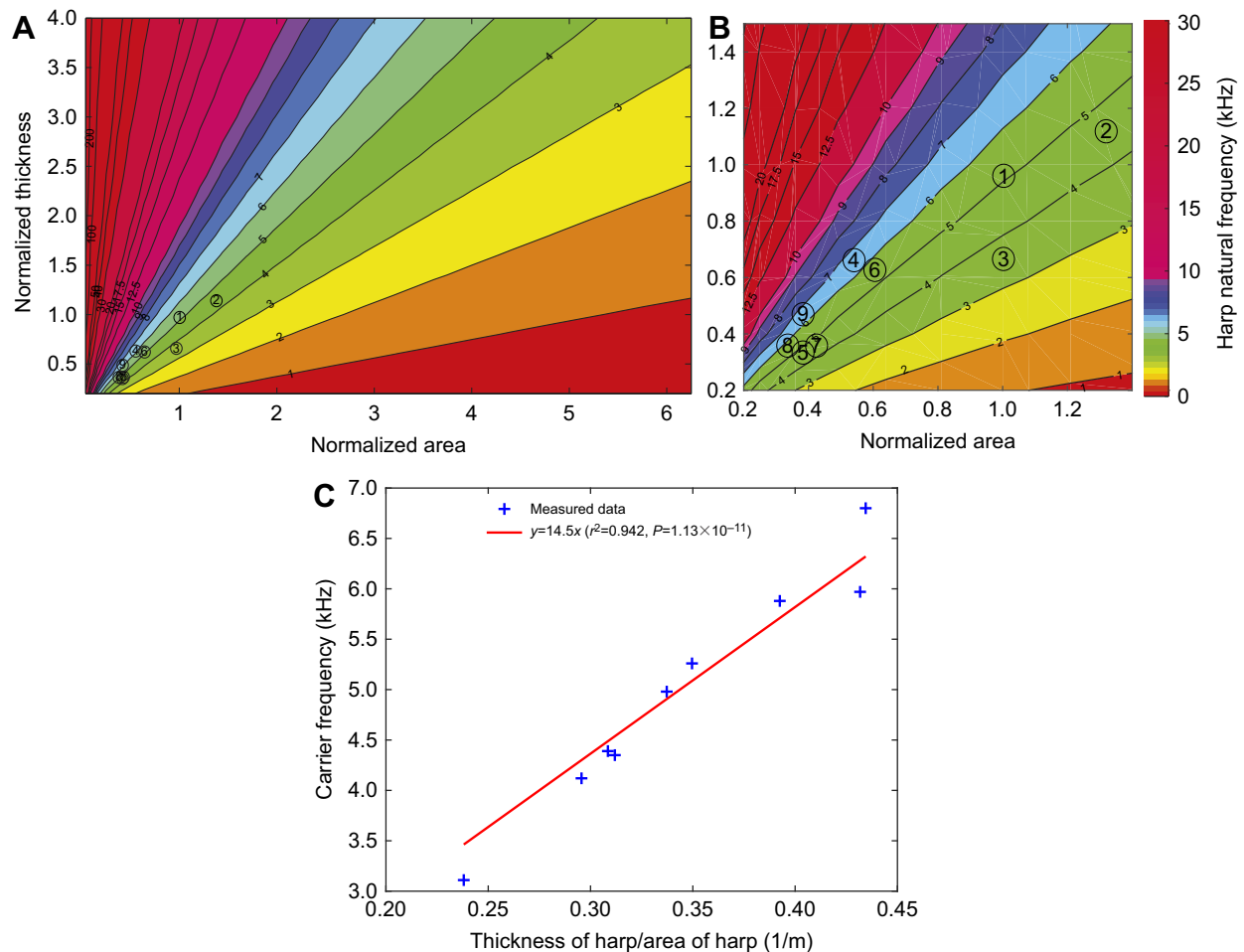


Fig. 5. Prediction of song frequency using the finite element model. (A) The contour plot of song carrier frequency estimated using the finite element model with variation in area and thickness of the harp. (B) A close-up of the contour plot populated with the measured values of the mean harp thickness and area of 9 field cricket species (numbers in circles are species identities corresponding to those in Table 1). (C) The ratio of harp thickness/area is an accurate predictor of cricket species song carrier frequency. Solid line, predicted relationship between the two variables; crosses, observed values of different field cricket species.

where α_n is a non-dimensional number corresponding to the mode, E is Young's modulus, ν is Poisson's ratio, ρ is the density, t is the thickness and l is the side length of the square plate. In contrast, the resonant frequency (ω_n) of a clamped circular membrane is given by the expression:

$$\omega_n = \alpha_n \sqrt{\frac{T}{\rho}} \frac{1}{tR}, \quad (3)$$

where α_n is a non-dimensional number corresponding to the mode, T is the surface tension per unit length, ρ is the density, t is the thickness and R is the radius of the membrane. If we focus on just the geometric dimensions, the scaling of frequency is clearly based on the ratio of the thickness and the area of the plate. This discovery of the scaling parameter for the song frequency tells us that the harp has a certain flexural stiffness that makes it a plate-like structure and that is why the harp resonant frequency scales the way it does.

Clustering in design space

Field crickets occupy a very limited part of the theoretically available design space (combinations of harp area and thickness that can produce particular frequencies). The song frequencies of field crickets lie between 3 and 8 kHz and, even within this frequency range, they exploit only a limited range of harp area/thickness:

Fig. 5A shows that, even when considering a small part of the theoretically available design space for these frequencies, values for field crickets are clustered within it. We examined what may constrain them to occupy this limited area of design space.

Low-frequency limit

If we first examine the case of evolving towards lower song frequencies, there are two ways to achieve this (Fig. 5A): keeping the harp thickness constant and increasing the area, or keeping the harp area constant and decreasing its thickness (co-varying them is also possible but we consider here the extreme cases for simplicity). A cricket with harp area and body size of *G. bimaculatus* (calling at 5 kHz) or *Teleogryllus* sp. (calling at 3.1 kHz) should in principle be able to produce a song frequency of 1 kHz by decreasing harp thickness by a factor of around 5 for *G. bimaculatus* and 3 for *Teleogryllus* sp. But field crickets, even the largest ones such as *Teleogryllus* sp. and *T. portentosus*, have not evolved to produce such low frequency songs, suggesting that there is a cost. Changing the harp thickness changes not only the song frequency but also the acoustic radiation efficiency. We found that the acoustic radiation efficiency varied between 0.7% and 2.5% (Table 3) for the different species.

Fig. 6 is a contour plot showing acoustic iso-efficiency lines with variation in the area and frequency of the harp. Upon examining the

Table 2. Measured values of song frequency, normalised harp area, thickness and the finite element model-predicted values of song frequency, and deviation from measured values

No.	Species	Measured				Predicted		
		Mean song frequency (kHz)	Normalised harp area (η_A)	Normalised harp thickness (η_t)	η_t/η_A	Song frequency (kHz)	Deviation	
							%	Hz
1	<i>Gryllus bimaculatus</i>	4.98 (6)	1	1	1	5.0 (ref.)	Ref.	Ref.
2	<i>Tarbinskiellus portentosus</i>	4.12 (6)	1.32	1.16	0.88	4.37	6	246
3	<i>Teleogryllus</i> sp.	3.11 (6)	1.02	0.72	0.71	3.52	13	406
4	<i>Itaropsis parviceps</i>	6.60 (6)	0.54	0.70	1.29	6.43	5	374
5	<i>Velarifictorus</i> sp.	4.35 (5)	0.38	0.35	0.92	4.62	6	266
6	<i>Coiblemmus compactus</i>	5.26 (5)	0.61	0.64	1.05	5.15	2	108
7	<i>Platygyryllus</i> sp.	4.39 (8)	0.42	0.38	0.91	4.56	4	175
8	<i>Gryllodes</i> sp.	5.88 (6)	0.33	0.38	1.15	5.81	1	70
9	<i>Plebeioigryllus guttiventris</i>	5.97 (7)	0.38	0.49	1.29	6.37	7	396

Numbers in parentheses in the mean song frequency column are number of individuals. Ref., values for *G. bimaculatus* were used as the reference.

nature of the iso-efficiency lines, we observe that the slope reduces as the normalised area increases. This indicates that the crickets should have increasingly larger harp sizes to be able to call with the same efficiency at lower frequencies. For example, if *Teleogryllus* sp. (calling at 3.1 kHz) decreases its harp thickness such that it can call at 1.5 kHz, its acoustic radiation efficiency would fall to 0.1%. This amounts to a 20 dB SPL reduction in radiated sound pressure (Table 3). To maintain the same efficiency of 1%, if we try to follow the iso-efficiency line (0.01 in Fig. 6), the area of the harp of *Teleogryllus* sp. should increase by a factor of 9. If allometric relationships between harp size and body size are preserved, this implies that the cricket has to become 5.3 times bigger to call at the same efficiency.

High-frequency limit

In contrast, changing song frequency towards higher values is unlikely to be constrained by the problem of low acoustic radiation efficiency (Fig. S3D). In fact, as the iso-efficiency lines in Fig. 6 show, it is possible to decrease harp area, increase song frequency and maintain or even increase radiation efficiency. To understand why field crickets do not call at high frequencies, we examined the structure of the frequency multiplier mechanism that provides the input to the resonator.

By the clockwork mechanism, a periodic displacement impulse is provided by the repeated tooth strikes of the plectrum over the file during a single wing closure, ensuring a cycle-by-cycle input matched to the resonant frequency of the harp. For a given plectrum speed, the highest achievable song frequency will thus be determined by the minimum achievable inter-tooth distance. From measurements of tooth size (basal width and height), we computed

the minimum theoretically possible distance between two consecutive teeth for the smallest tooth sizes among the 9 species, which was found to be 12 μm . To achieve a song frequency of 20 kHz with this minimum possible inter-tooth distance, the required plectrum speed was computed to be 120 mm s^{-1} , which is within the range of plectrum speeds computed for the 9 species of field crickets (53 to 218 mm s^{-1} as shown in Table 3) and should not pose a constraint.

The energy of the rotating wing is proportional to the product of rotational inertia (which in turn is directly proportional to mass) of the wing and square of the rotational speed. The required rotational speed is itself dependent on the radial distance of the plectrum from the wing hinge. The computed rotational speeds for the 9 species ranged from 8.210 to 28.8 rad s^{-1} (Table 3).

Previous studies (Prestwich and O'Sullivan, 2005) suggest that most of the energy (about 70%) generated by the muscle is expended to accelerate and decelerate the wing and the rest of the energy (30%) is spent in the file–plectrum catch and release (referred to as stridulation energy). First, we examined the consequences of increasing the harp thickness on energy requirements, while keeping the harp size constant, to achieve a resonant frequency of 20 kHz (with minimum inter-tooth distance). For the smallest species in our study (*Gryllodes* sp.), this would require 3.4 times the mass to be accelerated to 1.86 times its rotational speed, increasing the rotational energy required by a factor of about 12 and the stridulation energy by a factor of 1.8 (see Table 4 for results, and Table S1 for details of calculations). Similarly, for the largest species (*T. portentosus*), this would require about 5 times the mass to be accelerated but to half (0.55) the rotational speed, increasing the rotational energy required by a factor of 1.47 and the

Table 3. The computed wing rotational speed, acoustic efficiency and decrease in song sound pressure level (SPL) due to the reduction in efficiency if calling at 1 kHz for the nine field cricket species

No.	Species	Mean song frequency, f_n (kHz)	Tooth spacing, p (μm)	Plectrum speed, $v_p = \omega \times r$ (mm s^{-1})	Plectrum radius, r (mm)	Rotational speed, ω (rad s^{-1})	Acoustic efficiency (%)	Acoustic loss at 1 kHz (dB SPL)
1	<i>Gryllus bimaculatus</i>	4.98	36.0	89.7	6.47	13.85	2.5	−28
2	<i>Tarbinskiellus portentosus</i>	4.12	106	218	7.57	28.80	2.2	−24
3	<i>Teleogryllus</i> sp.	3.11	34.0	52.9	6.44	8.210	1.0	−20
4	<i>Itaropsis parviceps</i>	6.80	19.1	64.9	4.50	14.42	2.5	−33
5	<i>Velarifictorus</i> sp.	4.35	24.9	54.2	3.67	14.78	0.7	−25
6	<i>Coiblemmus compactus</i>	5.26	39.8	105	5.60	18.69	1.7	−28
7	<i>Platygyryllus</i> sp.	4.39	25.3	55.5	3.80	14.61	0.8	−25
8	<i>Gryllodes</i> sp.	5.88	22.0	64.7	2.80	23.10	1.1	−30
9	<i>Plebeioigryllus guttiventris</i>	5.97	19.1	57.1	3.50	16.32	1.4	−31

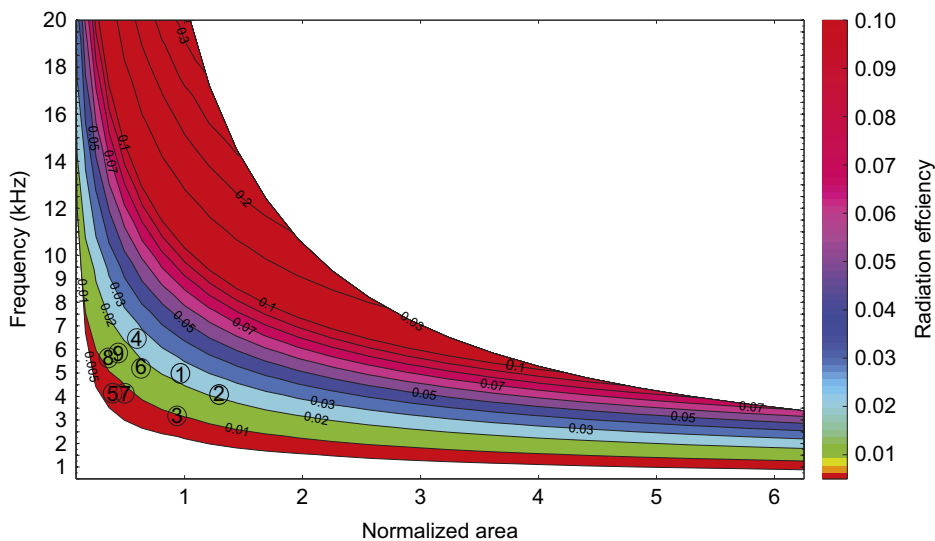


Fig. 6. Contour plot of acoustic radiation efficiency with variation in area and frequency of the harp. Values of harp area and carrier frequency were normalised with respect to those of *Gryllus bimaculatus*.

stridulation energy by a factor of 8.8 (Table 4). To call at 20 kHz, the increase in total energy expended for stridulation ranges from 3.7 times for the largest species to 8.7 times for the smallest. We repeated these calculations for a hypothetical carrier frequency of 10 kHz and found that total energy for stridulation again increased but only 1.5–2.8 times (Table 4).

We then examined an alternative approach to increasing song frequency to 20 kHz, i.e. keeping the thickness constant and decreasing the harp area. For the smallest species (*Gryllodes* sp.), this would require 0.3 times the mass to be accelerated to 3.4 times its rotational speed, increasing the rotational energy required by a factor of 3.5 and the overall energy required for stridulation by a factor of 2.7 in stridulation energy (Table 4). For the largest species (*T. portentosus*), this would require 0.2 times the mass to be accelerated to 1.2 times its rotational speed, reducing the rotational energy required by a factor of 0.4 but increasing the overall energy for stridulation by a factor of 1.4. Overall, the fold-increase in total energy for stridulation ranged from 1.4 for the largest species to 2.7 for the smallest. To call at 10 kHz using this strategy, however, only the largest species showed an increase in energy required for stridulation.

Changes in both harp thickness and area (intermediate to the above extreme cases) also resulted in increased energy expenditure,

indicating that, to call at 20 or 10 kHz, there are no combinations of harp area and thickness that would result in a decrease in energy expenditure (Table S2).

DISCUSSION

In this study, we used morphological measurements of the stridulatory apparatus of nine field cricket species, together with finite element models, to develop a predictive model for field cricket song carrier frequency, and validated the accuracy of the prediction to be within a few hundred hertz. We also used the finite element model to examine the available design space for the evolution of field cricket call carrier frequency in terms of the combinations of resonator area, thickness and sound radiation efficiency. We mapped the experimentally determined values from nine field cricket species on to this contour plot and found them to be clustered in a relatively small part of the design space. Finally, we explored the possible reasons, given the structural constraints of the stridulatory apparatus, and the process of stridulation, why field cricket song carrier frequencies appear to be limited to a narrow band of sound frequencies. We conclude that the lower frequency limit is imposed by allometric scaling between body size and resonator size, and speculate that the higher frequency limit could be imposed by energetic constraints on stridulation.

Table 4. Implications of high song carrier frequencies for stridulation energetics

Species	Song frequency (kHz)	Fold-change in mass of harp, <i>a</i>	Fold-change in rotational speed, <i>b</i>	Fold-change in rotational energy (70%), $a \times b^2$	Fold-increase in stridulation energy (30%)	0.7×rotational energy+0.3×stridulation energy
<i>Gryllodes</i> sp. ¹	20	3.40	1.86	11.696	1.8	8.73
<i>T. portentosus</i> ¹	20	4.85	0.55	1.469	8.8	3.67
<i>G. bimaculatus</i> ¹	20	4.02	1.338	7.194	3	5.94
<i>Gryllodes</i> sp. ²	20	0.294	3.42	3.44	1	2.71
<i>T. portentosus</i> ²	20	0.206	1.213	0.303	4	1.41
<i>G. bimaculatus</i> ²	20	0.25	2.68	1.79	1.5	1.70
<i>Gryllodes</i> sp. ¹	10	1.7	0.9275	1.46	1.8	1.56
<i>T. portentosus</i> ¹	10	2.425	0.275	0.183	8.8	2.77
<i>G. bimaculatus</i> ¹	10	2.01	0.669	0.9	3	1.53
<i>Gryllodes</i> sp. ²	10	0.59	1.2	0.86	1.41	1.03
<i>T. portentosus</i> ²	10	0.41	0.43	0.08	5.67	1.76
<i>G. bimaculatus</i> ²	10	0.5	0.95	0.45	2.12	0.95

¹Increase in thickness of harp; ²decrease in area of harp. Details of calculations are given in Table S1.

How physics, physiology and evolutionary history interact to constrain signal evolution

The low-frequency limit to cricket song

We have shown (Fig. 6) that for field cricket species to sing at lower frequencies of 1.5 kHz with a sound radiation efficiency of 1%, their resonators (harps) will have to become 7- to 10-fold larger in area. Given allometric scaling and the high correlation between resonator size and body size, this means that these species would have to be up to 5–6 times larger. *Tarbinskiellus portentosus* is among the largest field crickets (pronotum width about 1 cm) and has a relatively high acoustic radiation efficiency of 2.2% (Table 3): it would have to become over 5 times its size to produce a carrier frequency of 1.5 kHz with the same efficiency. Thus, the constraint imposed by physics (sound radiation efficiency) on singing at lower frequencies is resonator size, and its allometric scaling with body size. The largest extant insects include the giant tree weta (*Deinacrida heteracantha*, an orthopteran, like crickets), goliath and elephant beetles (genus *Goliathus* and *Megasoma*), and a giant cockroach (genus *Megaloblatta*), which can grow up to 10–12 cm in length. Insects appear to be evolutionarily constrained from becoming any bigger, probably because of their tracheal respiratory system, where oxygen supply to tissues occurs by diffusion rather than via a circulatory system (Harrison et al., 2010). The constraint on cricket low-frequency song production is thus imposed by an evolutionary constraint on insect body size.

The high-frequency limit to cricket song

We explored two mechanisms by which crickets could in principle increase the carrier frequency of their songs to 10 and 20 kHz using the clockwork mechanism: increasing the harp thickness whilst keeping the harp area constant, or alternatively, keeping the harp thickness constant and decreasing the harp area. For the first strategy, the increase in resonator mass, together with the number of file teeth being struck, results in an increase in the total energy required for stridulation, which in turn increases with song carrier frequency. For 20 kHz, the extra energy cost was substantial (3.7- to 8.7-fold) and clearly higher for smaller as compared with larger species but this was not the case for a carrier frequency of 10 kHz. Nonetheless, to call at 10 kHz would require a 1.5- to 2.8-fold increase in energy invested for stridulation. Whether this extra energetic requirement constitutes a physiological constraint large enough to limit cricket song carrier frequency to less than 10 kHz over evolutionary time is an interesting question that requires more empirical and comparative studies on the energetics of cricket stridulation. Note that this mechanism maintains the allometric scaling relationship between body size, wing size and resonator area.

The second possible mechanism to increase carrier frequency, which is to keep the harp thickness constant and decrease the harp area, results in more modest increases in the energy required for stridulation at 20 kHz (1.4- to 2.7-fold), and little or no increase in energy for stridulation at 10 kHz. However, the substantial decrease in harp area would significantly decrease the signal intensity and thus impact the effective broadcast area of the call, which is already compromised at higher frequencies as a result of increased excess attenuation during transmission (Römer and Lewald, 1992). In addition, whilst making the calculations for this mechanism, we have assumed that body size for each cricket species remains constant, i.e. we did not maintain the allometric scaling relationship between the harp area and body size shown in Fig. 3 (but we did maintain allometric scaling between harp and wing area). If this allometric scaling relationship acts as an evolutionary constraint,

then the second mechanism may be less likely than the first. It would be interesting to explore allometric scaling between body size, forewing size, resonator area and file length over a much larger number of field cricket species to ascertain how tight this relationship has remained over evolutionary time.

Another plausible reason for the high-frequency limit to field cricket song was recently put forth by Jonsson et al. (2021). As field crickets have symmetrical forewing structures (on the left and right wings), they have two resonant harps, both of which vibrate during stridulation. The presence of two resonators coupled during stridulation allows up to 2-fold amplification of the sound signal by constructive interference, provided the wings oscillate in phase. Jonsson et al. (2021) showed that, for *G. bimaculatus*, with a song carrier frequency of 5.1 kHz, the measured phase differences between the wings ranged from 6 to 79 deg across individuals (corresponding to a time lag of 3–43 μ s), producing amplitude gains of 1.97–1.34. The time lag between wings at which the gain drops below 1 was calculated to be lower for higher frequencies (48 and 33 μ s for 7 and 10 kHz, respectively) and the maximum frequency above which stridulation became inefficient (gain dropped below 1) was in the range 7.8–8.8 kHz, which corresponds to the known high-frequency limit of field cricket song. Jonsson et al. (2021) therefore propose that the high-frequency limit of cricket song is imposed by the limit on song amplification using coupled resonators. In this context, it would be interesting to perform more empirical measurements of wing coupling and signal gain on multiple field cricket species, especially those that produce song frequencies close to the computed limits.

Another useful way to look at the problem is to use a comparative approach: scaly crickets of the Family Mogoplistidae are among the smallest known crickets, with body lengths of 3–5 mm in males of the genera *Cycloptiloides*, *Cycloptilum* and *Micrornebius* (Chopard, 1969). Crickets of these genera produce pure-tone calls similar to those of field crickets, in the frequency range 6–8 kHz (Love and Walker, 1979; Dambach and Gras, 1995; Diwakar and Balakrishnan, 2007), which are remarkably low frequencies given their body size. Indeed, the wing and resonator areas of *C. canariensis* (measured by Dambach and Gras, 1995) are about 5% those of *G. bimaculatus*; yet, they produce relatively low-frequency songs in the same range as those of the bigger field crickets. Dambach and Gras (1995) examined the stridulatory structures of *C. canariensis* and found that the main resonant structure was the mirror, which was 0.2 μ m in thickness and occupied most of the area of the dorsal field of the forewing, though the harp also vibrated (similar to tree crickets: see Mhatre et al., 2012). The mirror had a sharply tuned resonant frequency at 6 kHz, corresponding with the carrier frequency of the song; this, together with the symmetric nature of the forewing stridulatory apparatus on the two wings and the structure of the file, led Dambach and Gras (1995) to conclude that these miniature crickets also use the same clockwork mechanism as field crickets, in spite of the fact that sound radiation efficiency is likely to be greatly compromised, given the ratio of resonator size to song wavelength. It would be interesting to use finite element models of sound production in these tiny crickets to examine where they lie in the evolutionary design space. The fact that they call at relatively low frequencies rather than at high frequencies, which would have much higher radiation efficiency, is an interesting paradox, and suggests a constraint on producing high frequencies using the clockwork mechanism.

Among the true crickets (Family Gryllidae), however, some lebinthine species of the subfamily Eneopterinae have been found to

produce much higher frequency calls (12–26 kHz: Robillard and Desutter-Grandcolas, 2004). Interestingly, investigation into their sound production mechanisms has shown that these differ from the clockwork mechanism used by field crickets (Robillard et al., 2013). High-frequency songs in these species appear to have been enabled by an increased tooth strike rate and exploitation of higher wing resonance modes. These modes are variable over different resonant parts of the forewing and do not exactly match the carrier frequency of the song, which are sometimes of higher spectral bandwidth, suggesting a departure from a clockwork mechanism (Robillard et al., 2013).

In summary, understanding the reasons for the high-frequency limit on field cricket song requires more empirical work in a comparative framework on the energetics of stridulation, allometric scaling between body size and stridulatory structures, and the coupling between resonators to understand the relative importance of constraints from energetics and allometry, and the need for signal amplification.

An additional explanation for the high-frequency limit on field cricket song, apart from physiological constraints, may be that frequencies higher than 10 kHz could overlap with the echolocation call frequencies of bats, which crickets tend to steer away from (Pollack, 2016). This tendency may make it difficult for cricket males to attract females if they use higher frequencies, constraining the evolution of high-frequency songs.

Predictive finite element models and their applications

We have, for the first time, used a finite model as a tool to predict cricket song carrier frequencies, and validated its accuracy: predicted call carrier frequencies were within 7% of the mean measured values for 7 out of 8 species examined and these translate into a deviation of only a few hundred hertz. These are the most accurate predictions to date of cricket or bushcricket song carrier frequency. The best statistical models for bushcricket call frequencies had deviations of between 1 and 2 kHz (Montealegre-Z et al., 2017). It would be interesting to extend finite element models to other groups of crickets and bushcrickets, for which the sound production mechanisms are fairly well understood (Montealegre-Z, 2009) and examine their efficacy as predictive models.

We also found that the ratio of harp thickness to area was a highly reliable predictor of call carrier frequency. This opens up the possibility of obtaining accurate estimates of the song carrier frequency for field cricket species for which only morphological data are available, such as museum specimens. This would be especially valuable for species that are represented only by museum specimens or are rare, extinct or in inaccessible geographical locations, wherein obtaining sound recordings may present a challenge. The requirement for measurements of harp thickness may not, however, allow this model to be applied to fossils where only data on wing and harp area may be available, and one may need to employ statistical models for these instead.

Predictive finite element models could similarly be extended to a number of other sound-producing animal taxa such as mammals, birds and frogs, and other insect groups such as moths and cicadas, which would allow deduction of call features from museum specimens and morphological data. With the increasing application of computed tomography techniques to live and museum specimens across a range of taxa, including insects, such 3D finite element models open up exciting avenues for predicting signal structure from the morphology of sound-producing organs, especially of museum specimens.

Acknowledgements

Ranjana Jaiswara made available the song recordings and some of the specimens of field cricket species. We are grateful to Manjunatha Reddy, Sudhakar Gowda and Kaveri Bittu Rajaraman for help with capture and/or maintenance of field crickets.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: V.G., R.B., R.P.; Methodology: V.G.; Software: V.G.; Validation: V.G.; Formal analysis: V.G.; Investigation: V.G.; Resources: R.B., R.P.; Data curation: V.G.; Writing - original draft: R.B.; Writing - review & editing: V.G., R.P.; Visualization: V.G.; Supervision: R.B., R.P.; Project administration: R.B., R.P.; Funding acquisition: R.B., R.P.

Funding

This project was partially funded by the Department of Biotechnology Government of India DBT-IIISc Partnership Program Ph-II (no. BT/PR27952/1NF/22/212/2018) and Ministry of Electronics and Information Technology (MeitY), Government of India. Ministry of Human Resource Development, Government of India funded the student fellowship of V.G.

Data availability

Data files and codes are available from figshare: <https://doi.org/10.6084/m9.figshare.19069547>.

References

- Bennet-Clark, H. C. (1998). Size and scale effects as constraints in insect sound communication. *Philos Trans. R Soc. Lond. B Biol Sci.* **353**, 407–419. doi:10.1098/rstb.1998.0219
- Bennet-Clark, H. C. (1999). Resonators in insect sound production: how insects produce loud pure-tone songs. *J. Exp. Biol.* **202**, 3347–3357. doi:10.1242/jeb.202.23.3347
- Bennet-Clark, H. C. (2003). Wing resonances in the Australian field cricket *Teleogryllus oceanicus*. *J. Exp. Biol.* **206**, 1479–1496. doi:10.1242/jeb.00281
- Chivers, B. D., Jonsson, T., Soulsbury, C. D. and Montealegre-Z, F. (2017). Structural biomechanics determine spectral purity of bush-cricket calls. *Biol. Lett.* **13**, 151–164.
- Chopard, L. (1969). *The Fauna of India and the Adjacent Countries: Orthoptera*, Vol. 2. Calcutta, India: Baptist Mission Press.
- Dambach, M. and Gras, A. (1995). Bioacoustics of a miniature cricket, *Cycloptiloides canariensis* (Orthoptera: Gryllidae: Mogoplistinae). *J. Exp. Biol.* **198**, 721–728. doi:10.1242/jeb.198.3.721
- Diwakar, S. and Balakrishnan, R. (2007). The assemblage of acoustically communicating crickets of a tropical evergreen forest in southern India: call diversity and diel calling patterns. *Bioacoustics* **16**, 113–135. doi:10.1080/09524622.2007.9753571
- Elliott, C. J. H. and Koch, U. T. (1985). The clockwork cricket. *Naturwissenschaften* **72**, 150–153. doi:10.1007/BF00490404
- Godthi, V. and Pratap, R. (2015). Dynamics of cricket sound production. *J. Vib. Acoust.* **137**, 041019, Paper No: VIB-14-1284. doi:10.1115/1.4030090
- Harrison, J. F., Kaiser, A. and VandenBrooks, J. M. (2010). Atmospheric oxygen level and the evolution of insect body size. *Proc. R. Soc. B* **277**, 1937–1946. doi:10.1098/rspb.2010.0001
- Jaiswara, R., Nandi, D. and Balakrishnan, R. (2013). Examining the effectiveness of discriminant function analysis and cluster analysis in species identification of male field crickets based on their calling songs. *PLoS ONE* **8**, e75930. doi:10.1371/journal.pone.0075930
- Jonsson, T., Chivers, B. D., Robson Brown, K., Sarria-S, F. A., Walker, M. and Montealegre-Z, F. (2017). Chamber music: an unusual Helmholtz resonator for song amplification in a Neotropical bush-cricket (Orthoptera, Tettigoniidae). *J. Exp. Biol.* **220**, 2900–2907.
- Jonsson, T., Montealegre-Z, F., Soulsbury, C. D. and Robert, D. (2021). Tenors not sopranos: Bio-mechanical constraints on calling song frequencies in the Mediterranean field-cricket. *Front. Ecol. Evol.* **9**, 225.
- Kinsler, L. E., Frey, A. R., Coppens, A. B. and Sanders, J. V. (2000). *Fundamentals of Acoustics*, 4th edn New Delhi: Wiley India.
- Koch, U. T., Elliott, C. J. H., Schäffner, K.-H. and Kleindienst, H.-U. (1988). The Mechanics of Stridulation of the Cricket *Gryllus campestris*. *J. Comp. Physiol. A* **162**, 213–223. doi:10.1007/BF00606086
- Leppington, F. G., Broadbent, E. G. and Heron, K. H. (1982). The acoustic radiation efficiency of rectangular panels. *Proc. R. Soc. Lond. A* **382**, 245–271.
- Love, R. E. and Walker, T. J. (1979). Systematics and acoustic behavior of scaly crickets (Orthoptera: Gryllidae: Mogoplistinae) of eastern United States. *Trans. Am. Entomol. Soc.* **105**, 1–66.

- Mhatre, N., Montealegre-Z, F., Balakrishnan, R. and Robert, D.** (2012). Changing resonator geometry to boost sound power decouples size and song frequency in a small insect. *Proc. Natl Acad. Sci. USA* **109**, E1444-E1452.
- Montealegre-Z, F.** (2009). Scale Effects and Constraints for Sound Production in Katyids (Orthoptera: Tettigoniidae): Correlated Evolution between Morphology and Signal Parameters. *J. Evol. Biol.* **22**, 355-366. doi:10.1111/j.1420-9101.2008.01652.x
- Montealegre-Z, F., Windmill, J. F., Morris, G. K. and Robert, D.** (2009). Mechanical phase shifters for coherent acoustic radiation in the stridulating wings of crickets: the plectrum mechanism. *J. Exp. Biol.* **212**, 257-269. doi:10.1242/jeb.022731
- Montealegre-Z, F., Ogden, J., Jonsson, T. and Soulsbury, C. D.** (2017). Morphological determinants of signal carrier frequency in katyids (Orthoptera): a comparative analysis using biophysical evidence of wing vibration. *J. Evol. Biol.* **30**, 2068-2078. doi:10.1111/jeb.13179
- Pollack, G. S.** (2016). Hearing for defense. In *Insect Hearing* (ed. G. S. Pollack et al.), pp. 81-98. Springer International Publishing Switzerland.
- Prestwich, K. N. O'Sullivan, K.** (2005). Simultaneous measurement of metabolic and acoustic power and the efficiency of sound production in two mole cricket species (Orthoptera: Gryllotalpidae). *J. Exp. Biol.* **208**, 1495-1512. doi:10.1242/jeb.01550
- Robillard, T. and Desutter-Grandcolas, L.** (2004). High-frequency calling in eneopterinae crickets (Orthoptera, Grylloidea, Eneopteridae): adaptive radiation revealed by phylogenetic analysis. *Biol. J. Linn. Soc.* **83**, 577-584. doi:10.1111/j.1095-8312.2004.00417.x
- Robillard, T., Montealegre-Z, F., Desutter-Grandcolas, L., Grandcolas, P. and Robert, D.** (2013). Mechanisms of high-frequency song generation in brachypterous crickets and the role of ghost frequencies. *J. Exp. Biol.* **216**, 2001-2011.
- Römer, H. and Lewald, J.** (1992). High-frequency sound transmission in natural habitats: implications for the evolution of insect acoustic communication. *Behav. Ecol. Sociobiol.* **29**, 437-444. doi:10.1007/BF00170174
- Timoshenko, S. and Woinowsky-Krieger, S.** (1959). *Theory of Plates and Shells*. McGraw Hill.

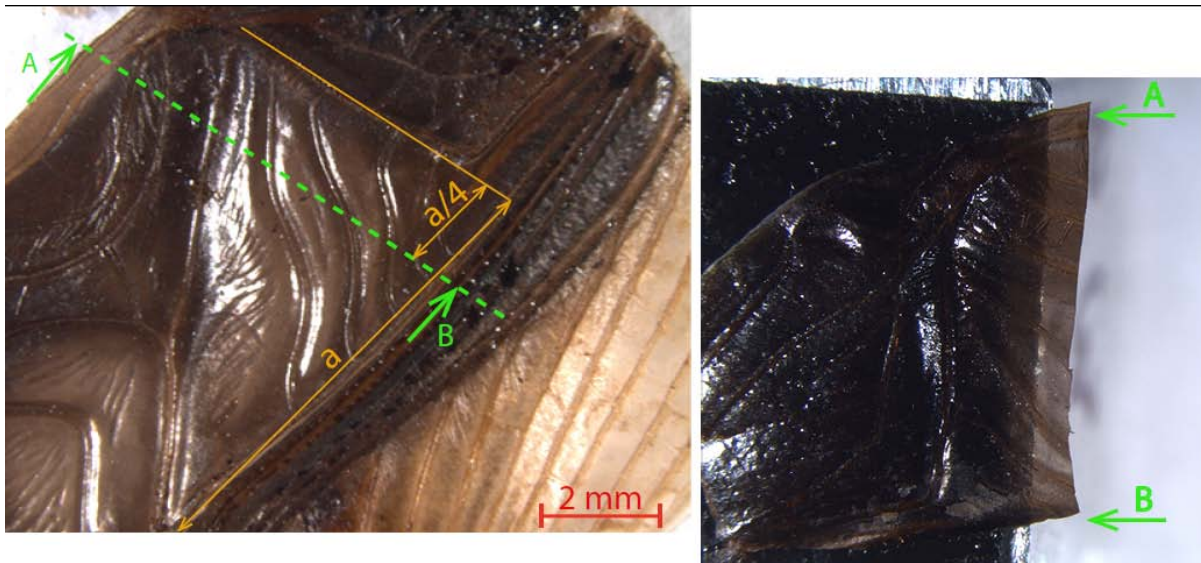


Fig. S1. Details of processing cricket forewings for measurement of harp thickness showing the axis along which the harp was cut.

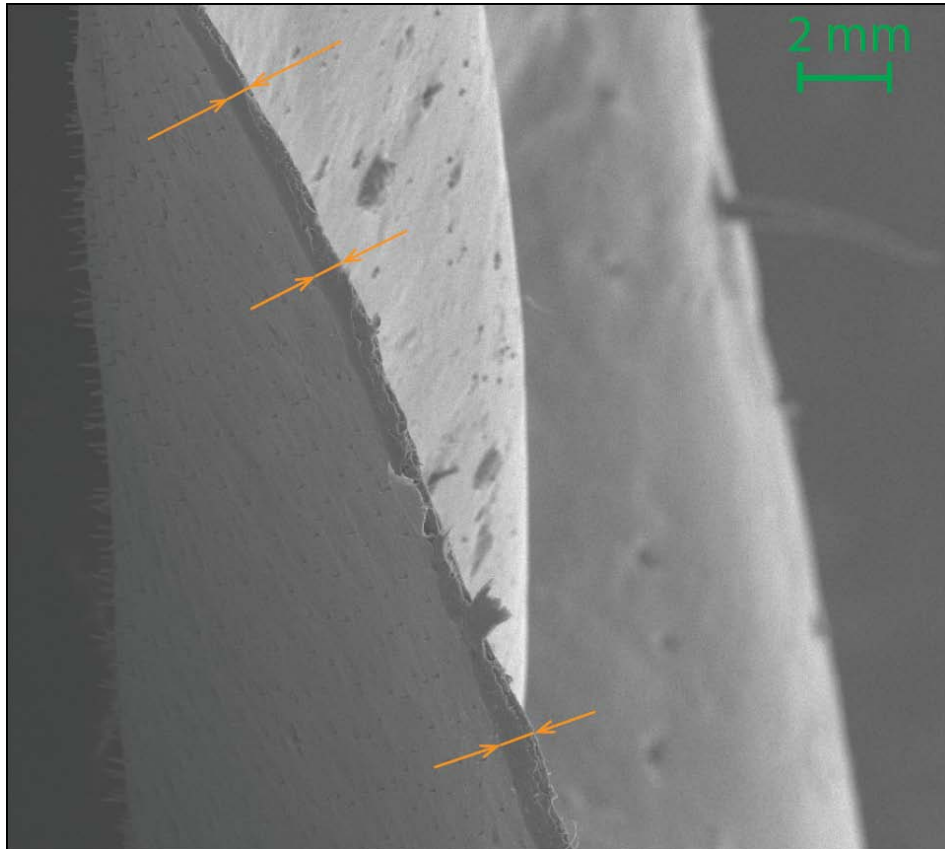


Fig. S2. SEM image of a transversely sectioned harp for thickness measurement.

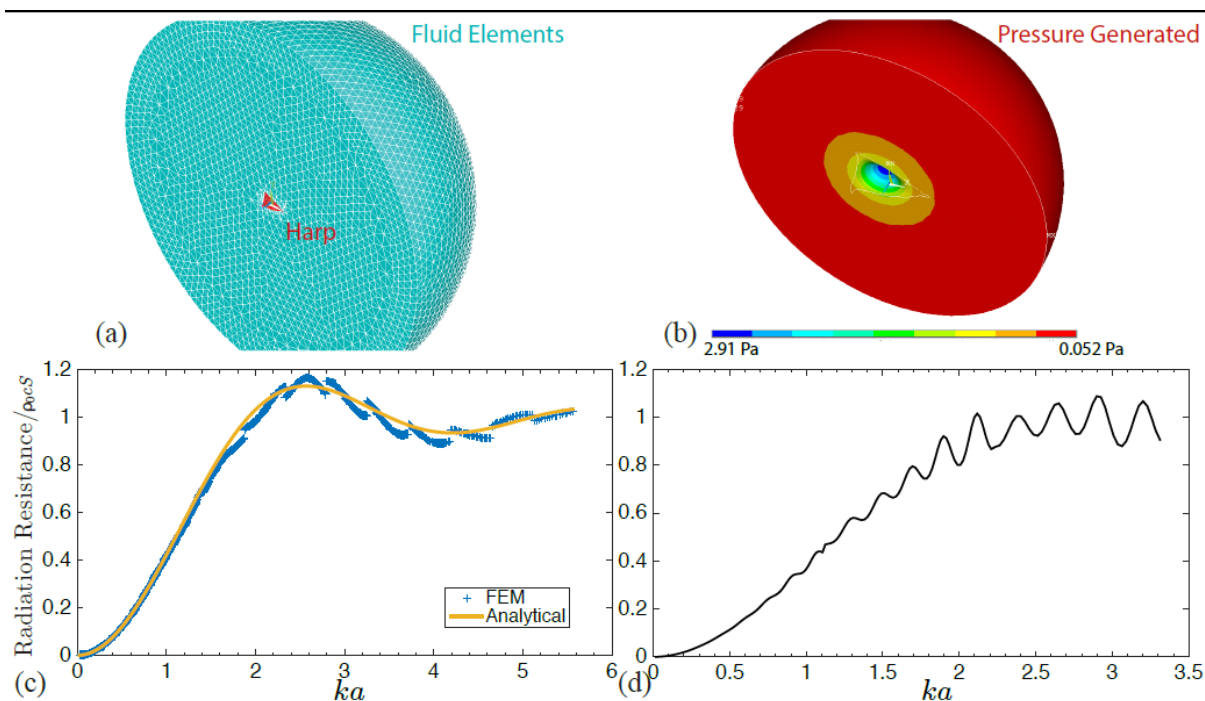


Fig. S3. FEM acoustic simulation: (a) FE model showing the acoustic elements surrounding the harp, (b) simulated sound pressure radiated from the harp, (c) simulated and analytical results of radiation efficiency (radiation resistance/ $\rho_0 c S$) from a circular piston (where, ρ_0 is the density of air, c is the speed of sound in air and S is the area of the radiating source), and (d) simulated radiation efficiency (radiation resistance/ $\rho_0 c S$) from the harp.

Table S1. Stridulation energetics at high frequencies: Details of calculations leading to values shown in Table 4 of manuscript. In these energetics calculations, we have travelled along two extreme directions - one, where we have kept the thickness constant and decreased the harp area and the other where we have kept the harp area constant and increased the harp thickness.

To achieve a song frequency of 20kHz												
Increasing Harp thickness, keeping size constant												
Species	Fold-change in rotational energy	Fold increase in stridulation energy	0.7*rotational energy + 0.3*stridulation energy	Song Frequency	Fold change of thickness = Fold change of mass	Plectrum Speed	Fold change in rotational speed =120 (since this is plectrum speed needed to excite a file with tooth spacing of 12microns at 20kHz)/scaled plectrum speed	Fold change in rotational energy	Tooth spacing	Fold change in stridulation energy (if tooth spacing becomes 12microns from a larger spacing, more teeth need to be struck, proportionately increasing the energy required for stridulation)		
<i>Gryllodes sp.</i>	11.70	1.8	8.73	5.88	3.40	64.7	1.85	11.70	22	1.8		
<i>T. portentosus</i>	1.47	8.8	3.67	4.12	4.85	218	0.55	1.47	106	8.8		
<i>G. bimaculatus</i>	7.19	3	5.94	4.98	4.02	89.7	1.34	7.19	36	3.0		
Decreasing Harp size, keeping thickness constant												
Species	Fold-change in rotational energy	Fold increase in stridulation energy	0.7*rotational energy + 0.3*stridulation energy	Song Frequency	Fold change of Area (current song frequency/10 kHz) = Fold change of mass	Fold change in size (square root of area fold change)	Scaled plectrum speed (due to scaled plectrum radius)	Fold change in rotational speed =120 (since this is plectrum speed needed to excite a file with tooth spacing of 12microns at 20kHz)/scaled plectrum speed	Fold change in rotational energy	Tooth spacing	Scaled file spacing (assuming allometric scaling)	Fold change in stridulation energy (if tooth spacing becomes 12microns from a larger spacing, more teeth need to be struck, proportionately increasing the energy required for stridulation)
<i>Gryllodes sp.</i>	3.44	1	2.71	5.88	0.29	0.54221767	64.7	35.08148315	3.42	3.44	22	11.92878871
<i>T. portentosus</i>	0.3	4	1.41	4.12	0.21	0.45387223	218	98.94414586	1.21	0.30	106	48.11045624
<i>G. bimaculatus</i>	1.79	1.5	1.70	4.98	0.25	0.498999	89.7	44.76021012	2.68	1.79	36	17.96396393
To achieve a song frequency of 10kHz												
Increasing Harp thickness, keeping size constant												
Species	Fold-change in rotational energy	Fold increase in stridulation energy	0.7*rotational energy + 0.3*stridulation energy	Song Frequency	Fold change of thickness = Fold change of mass	Plectrum Speed	Fold change in rotational speed =120 (since this is plectrum speed needed to excite a file with tooth spacing of 12microns at 20kHz)/scaled plectrum speed	Fold change in rotational energy	Tooth spacing	Fold change in stridulation energy (if tooth spacing becomes 12microns from a larger spacing, more teeth need to be struck, proportionately increasing the energy required for stridulation)		
<i>Gryllodes sp.</i>	1.46	1.8	1.56	5.88	1.70	64.7	0.93	1.46	22	1.8		
<i>T. portentosus</i>	0.18	8.8	2.77	4.12	2.43	218	0.28	0.18	106	8.8		
<i>G. bimaculatus</i>	0.9	3	1.53	4.98	2.01	89.7	0.67	0.90	36	3.0		
Decreasing Harp size, keeping thickness constant												
Species	Fold-change in rotational energy	Fold increase in stridulation energy	0.7*rotational energy + 0.3*stridulation energy	Song Frequency	Fold change of Area (current song frequency/10 kHz) = Fold change of mass	Fold change in size (square root of area fold change)	Scaled plectrum speed (due to scaled plectrum radius)	Fold change in rotational speed =120 (since this is plectrum speed needed to excite a file with tooth spacing of 12microns at 20kHz)/scaled plectrum speed	Fold change in rotational energy	Tooth spacing	Scaled file spacing (assuming allometric scaling)	Fold change in stridulation energy (if tooth spacing becomes 12microns from a larger spacing, more teeth need to be struck, proportionately increasing the energy required for stridulation)
<i>Gryllodes sp.</i>	0.86	1.41	1.03	5.88	0.59	0.76681158	64.7	49.61270926	1.21	0.86	22	16.86985477
<i>T. portentosus</i>	0.08	5.67	1.76	4.12	0.41	0.64187226	218	139.928153	0.43	0.08	106	68.03845971
<i>G. bimaculatus</i>	0.45	2.12	0.95	4.98	0.80	0.70569115	89.7	63.30049621	0.95	0.45	36	25.40488142

Table S2. In these energetics calculations, we have investigated an intermediate combination of thickness increase together with decreased harp size to arrive at the energy required to call at 20kHz and 10kHz.

To achieve a song frequency of 20kHz															
Decreasing Harp size, and increasing thickness 2 fold															
	Fold-change in rotational energy	Fold increase in stridulation energy	0.7*rotational energy + 0.3*stridulation energy	Song Frequency	Fold change of thickness	Fold change of Area	Fold change of Mass = Fold change of thickness * Fold change of Area	Fold change in size (square root of area fold change)	Plectrum Speed	Scaled plectrum speed (due to scaled plectrum radius)	Fold change in rotational speed =120 (since this is plectrum speed needed to excite a file with tooth spacing of 12microns at 20kHz)/scaled plectrum speed	Fold change in rotational energy	Tooth spacing	Scaled file spacing (assuming allometric scaling)	Fold change in stridulation energy (if tooth spacing becomes 12microns from a larger spacing, more teeth need to be struck, proportionately increasing the energy need for stridulation)
Grylloides sp.	6.88	1.4	5.24	5.88	2	0.50	1.18	0.766812	64.7	49.61270926	2.42	6.88	22	16.86985477	1.4
T.portentosus	0.81	5.7	2.13	4.12	2	0.41	0.82	0.641872	218	139.928153	0.86	0.61	106	68.03845971	5.7
G.bimaculatus	3.58	2.1	3.14	4.98	2	0.50	1.00	0.705691	89.7	63.30049621	1.90	3.58	36	25.40488142	2.1
Decreasing Harp size 0.6 fold, and increasing thickness															
Grylloides sp.	7.02	1.4	5.34	5.88	2.04	0.60	1.22	0.774597	64.7	50.1164045	2.39	7.02	22	17.04112672	1.4
T.portentosus	0.88	6.8	2.67	4.12	2.91	0.60	1.75	0.774597	218	168.8620739	0.71	0.88	106	82.10724694	6.8
G.bimaculatus	4.31	2.3	3.72	4.98	2.41	0.60	1.45	0.774597	89.7	69.48132123	1.73	4.31	36	27.88548009	2.3
To achieve a song frequency of 10kHz															
Decreasing Harp size, and increasing thickness 1.5 fold															
	Fold-change in rotational energy	Fold increase in stridulation energy	0.7*rotational energy + 0.3*stridulation energy	Song Frequency	Fold change of thickness	Fold change of Area	Fold change of Mass = Fold change of thickness * Fold change of Area	Fold change in size (square root of area fold change)	Plectrum Speed	Scaled plectrum speed (due to scaled plectrum radius)	Fold change in rotational speed =60 (since this is plectrum speed needed to excite a file with tooth spacing of 12microns at 10kHz)/scaled plectrum speed	Fold change in rotational energy	Tooth spacing	Scaled file spacing (assuming allometric scaling)	Fold change in stridulation energy (if tooth spacing becomes 12microns from a larger spacing, more teeth need to be struck, proportionately increasing the energy required for stridulation)
Grylloides sp.	1.29	1.7	1.42	5.88	1.5	0.88	1.32	0.939149	64.7	60.76291122	0.99	1.29	22	20.66126811	1.7
T.portentosus	0.11	6.9	2.16	4.12	1.5	0.62	0.93	0.78613	218	171.3762877	0.35	0.11	106	83.32975459	6.9
G.bimaculatus	0.87	2.8	1.25	4.98	1.5	0.75	1.12	0.864292	89.7	77.52695809	0.77	0.67	36	31.11449823	2.8
Decreasing Harp size 0.75 fold, and increasing thickness															
Grylloides sp.	1.10	1.6	1.24	5.88	1.28	0.75	0.96	0.866025	64.7	56.03184362	1.07	1.10	22	19.05255888	1.6
T.portentosus	0.14	7.8	2.39	4.12	1.82	0.75	1.37	0.866025	218	188.793538	0.32	0.14	106	91.7986928	7.8
G.bimaculatus	0.87	2.8	1.25	4.98	1.51	0.75	1.13	0.866025	89.7	77.68247872	0.77	0.67	36	31.17691454	2.8