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Is significant acoustic energy found in the audible and ultrasonic harmonics in cricket calling songs?

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Abstract

Crickets are known to be inefficient sound producers. When calling, typically less than 1% of their metabolic energy is converted into sound. This low efficiency has been attributed to losses within the insect and to poor acoustic coupling with the environment. A previously uninvestigated factor that might contribute to low efficiency is ultrasonic radiation. If the impacts of the plectrum and file teeth excite vibration in the ultrasonic range, then the sound pressure level meters typically used to measure acoustic power would not accurately detect it. We made audible and ultrasound recordings of the calling songs of a phylogenetically diverse group of 6 cricket species, and, for comparison, 2 katydid species. In most of the cricket species, energy was present well into the ultrasonic region as a series of harmonics of the carrier frequency. However, the energy in these peaks was very small in comparison to the audible-range harmonics. There was no evidence of significant oscillations that were not harmonics of the carrier frequency. In all but one cricket species, over 97% of the total audible and ultrasonic energy was contained in the carrier frequency band.

Keywords

acoustics, spectra, cricket, katydid, efficiency, sound, ultrasound, *Gryllus*, *Anurogryllus*, *Allonemobius*, *Eunemobius*, *Neoconcephalus*, *Scapteriscus*

Introduction

Crickets are seemingly inefficient sound producers. In most of the species studied, it appears that less than 1% of metabolic energy used to produce an advertisement call is converted to audible (<18 kHz) sound (Kavanagh 1987, Forrest 1991, Prestwich 1994, Prestwich & O'Sullivan 2005). This is somewhat surprising given that these calls are commonly characterized as relatively pure tones (Bennet-Clark 1989) with most energy present in a small bandwidth (high Q_{-3dB} Bennet-Clark 1999). The carrier frequency (f_C, defined as the most energetic frequency) is determined by the resonance properties of the coupled tegmina, principally their Cu2 veins and harps (Nocke 1970, Bennet-Clark 2003). Explanations for low sound-production efficiency by these apparently sharply tuned (high-*Q*) resonators have centered on (i) losses associated with stridulation, and (ii) the coupling of the cricket's acoustic radiator (tegminal harps) to the environment (Bennet-Clark 1989, Bailey *et al.* 1993, Prestwich 1994, Prestwich & O'Sullivan 2005).

A not previously considered example of the former (i) would be the excitation of vibrations leading to the radiation of sound at frequencies not measured by the sound pressure level meters used to find acoustic power (Peterson 1980). Recent investigations into the mechanics of stridulation by Bennet-Clark & Bailey (2002) and Bennet-Clark (2003) have revealed what are termed "ticking" sounds at $2f_C$. These authors attribute "ticking" sounds to the catch and release of the tegminal plectrum by the teeth of the contralateral *pars stridens*. This led us (i) to wonder whether the impacts of the stridulatory mechanism might produce significant ultrasound, and (ii) to ask how much energy was actually being radiated at frequencies outside the f_C band. Both questions relate to the efficiency of sound production and the second also relates to the ability of a calling insect to put energy into the frequencies being heard by conspecific females. To answer these questions, we analyzed the calls of a phylogenetically diverse group of 6 cricket species. For comparison purposes, we also performed the analysis on 2 katydid species.

Materials and methods

Recordings.— We made all recordings in the field. *Allonemobius allardi* Alexander and Thomas, *Eunemobius carolinus* Scudder, and *Gryllus pennsylvanicus* Burmeister were recorded in Worcester, MA, USA. *Anurogryllus arboreus* T. Walker, *Scapteriscus borellii* Giglio-Tos, and *Scapteriscus vicinus* Scudder in Gainesville, FL, USA and the katydids *Neoconocephalus robustus* Scudder and *Neoconocephalus ensiger* Davis in New Braintree, MA, USA. Recordings were of 2 types: audible-range biased (below 20 kHz) and broad-band (up to 100 kHz).

For audible-range frequencies, we used a Sennheiser (Wedemark, Germany) ME64 zoom microphone with K-6 preamplifier. According to the manufacturer, this microphone has a broad resonance with its peak response at about 9 to 10 kHz. Relative to 1 kHz, the response is flat to 4 kHz and then increases by 2.5 dB at the 9 to 10 kHz peak. By 20 kHz, the response decreases by 5 dB from the peak (-2.5 dB from the 1 kHz reference). Thus, for the purpose of estimating energy, the ME64 will indicate relatively more energy than a 1 kHz standard, for signals between 4 and 15 kHz and will under-represent sounds above 15 kHz by up to 2.5 dB (http://www.sennheiser.com/sennheiser/icm_eng.nsf/root/03282#).

We made recordings by attaching the powered shotgun microphone to a Marantz (D&M Professional, Itasca, IL, USA) PMD 201 cassette recorder using type II high-bias tape. We located the microphone 0.3 to 1 m from the subject. We digitized our recordings using a 16-bit, 44.1 kHz A/D converter equipped with an anti-aliasing filter under the supervision of Canary 1.2.4 software (Cornell Bioacoustics Workstation, Ithaca, New York, USA). During digitization, the tape was played at half the recording speed to give a digitization rate of 88.2 kHz.

We made our broad-band recordings using a Pettersson Elektronik AB (Uppsala, Sweden) D980 ultrasound (bat) detector. The D980's condenser microphone appears to have an essentially flat response (± 1 dB compared to average) between about 23 and 80 kHz with an approximately 1 dB additional drop-off between 80 and 100 kHz). On the other hand, its response drops off rapidly below about 7.5 kHz and at 2 kHz is nearly 10 dB below the response at 25 kHz. A smaller (-4 dB) trough occurs at about 20 kHz. Thus, the D980 is mainly biased against sounds below about 7.5 kHz with some minor attenuative distortion between 15 and 22 kHz (response curve kindly provided by Lars Pettersson).

The D980 has a time expansion (TE) feature that digitizes 3-s blocks of the microphone's output at 350 kHz with 8-bit resolution. After the D980 obtains and stores the 3-s sample in memory, it constructs and outputs a 1/10 speed analog waveform by stepping through the stored data at a rate of 35 ksamples (kS) s^{-1}. Thus, the output is a 10-fold time expansion of the original sound. We redigitized the expanded signal at 44.1 kHz as described above. The result was an effective digitization rate of 350 kHz. This theoretically allowed us to investigate frequencies up 175 kHz. However, since we only knew the microphone response up to 100 kHz, we used that frequency as the upper limit of our analyses. Please note that our procedure has 2 A/D rates. One is associated with the original digitization of the signal by the bat detector (350 kHz) and the other with redigitizing the time-expanded signal (441 kHz). The useful digitization rate cannot exceed the lower value. The manufacturer recommends this procedure as a means of obtaining spectrograms for bats; we have simply applied it to ensiferans.

To make recordings, we moved the D980's microphone to within 0.5 m of the subject and then adjusted the instrument for the maximum amplitude without over-driving. This distance minimized differential absorption of higher frequencies. Previous measurements of atmospheric attenuation of ultrasound frequencies (Lawrence and Simmons, 1981) range from 0.7 dB/m at 30 kHz to 8 dB/m at 200 kHz.

Pulse selection.—Since *A. allardi*, *A. arboreus*, *S. borellii*, *S. vicinus*, and *N. ensiger* produce continuous, monosyllabic trills of similar pulses, we chose 5 pulses at random for analysis. The continuous chirps of *E. carolinus* are characterized by a repeated pattern of a smaller pulse followed by 6 or 7 similar pulses. Thus, we selected at random 5 smaller pulses and 5 larger pulses. Because *G. pennsylvanicus* produces polysyllabic, discontinuous chirps of 3 to 5 distinct pulses, we chose 5 of its first pulses and 5 of the last pulses at random.

Analysis.— We analyzed these pulses using the Canary software and a Macintosh G4 computer. We applied a digital high-pass filter to all recordings to minimize background noise. We selected cutoff filtering frequencies for this filter so as to reduce the background to at least 20 dB below the peak level for f_C, while also ensuring that the f_C was attenuated by less than 2 dB. From the filtered records, we selected single sound pulses (see above) and we obtained Fourier transform spectra generated using a Hamming window function. These typically had a frequency resolution of 22 Hz.

We identified signal components as peaks on a frequency-domain spectrum that were not present in background spectra. Ideally, the beginning and end of a frequency band was defined by a sharp difference with background. We calculated the power of each peak using Canary's built-in "energy flux density" function. This function determines the total energy for a peak by integration between the upper and lower band limits (Fig. 1). We then subtracted background (which was always insignificant when compared to the peak).

In practice, it was often hard to define exactly where a peak began. In order to obtain a measure of the effect of this uncertainty on the energy flux measurement, we first estimated energy for the band of frequencies that represented our best definition of a particular peak. We then repeated the measurement of energy using a band with the same center, but with twice the bandwidth of the first measurement (Fig. 1). Finally, we subtracted this measurement from the first to gain our estimate of uncertainty. We verified our ability to correctly measure energy flux density by creating a synthetic data set in Microsoft Excel and then analyzing it with the Canary software.

We used the energies of each significant peak in the spectrum to calculate % E f_C, [the energy contribution of the f_C, band as a percentage of the total signal energy]:

Eq. 1 $$\% \, E f_C = \frac{E_{f_c}}{\sum E_f} \times 100$$

where $\sum E_f$ is the sum of the energy flux density of all the animal-produced frequencies.

Results and Discussion

Crickets produce some ultrasound incidental to their advertisement calls. Fig. 2 presents spectra of 4 pulses making up a *G. pennsylvanicus* chirp. The pulses are not all the same. As is well known for this species, the first pulse is shorter (40%) than the next 3 (or 4) and less intense (peak amplitude is about 50% of later pulses). Also, the f_C increases slightly from one pulse to the next (peak at 4.82, 4.95, 5.08 and 5.17 kHz in this example). However, all 4 pulses have the same number of harmonics. These harmonics closely approximate integer multiples of f_C. Some of these are in the ultrasound region, but relative to the f_C and audible harmonics they are very low amplitude. Fig. 3 shows spectra for the final pulses of a chirp for 3 *G. pennsylvanicus*. Once again, all show some, but very little, ultrasound. The locations of the peaks differ among individuals but within each individual they are always harmonics of f_C. This relationship implies that all harmonics are excited by a common mechanism, most certainly the operation of the escapement system on the various vibrational modes of the tegminal oscillator (Elliott & Koch 1985, Koch *et al.* 1988, Fletcher 1992, Prestwich *et al*. 2000, Bennet-Clark 2003).

Similar results are seen with the other cricket species. Fig. 4 shows the spectra for the grylline *A. arboreus*. Fig. 5 shows the spectrum of the nemobine, *A. allardi*, with noticeable peaks at $3f_C$ (about 24 kHz) and $4f_C$ (about 32 kHz). However, another nemobine, *E. carolinus*, shows no peaks in the ultrasonic region (Figs 6 and 7). This difference may be related to *E. carolinus*' lower fundamental (f_C = 4.9 kHz *vs* 8.2 kHz in *A. allardi*). As with *G. pennsylvanicus*, pulses of different amplitude and duration in *E. carolinus* have similar harmonic characteristics (Fig. 7). The spectrum for the single *S. vicinus* for which we obtained an ultrasound recording is shown in Fig. 8. Given this species' tuned acoustic burrow, one might be surprised by the number and comparatively intense (but still weak) harmonics. However, the tuning of the cricket/burrow system, as measured by its $Q_{\text{ln decrement}}$ (see Bennet-Clark 1999), is about 6 (Bennet-Clark 1987, Prestwich & Sullivan 2005) and thus the spectrum is consistent with the *Q*.

Our spectra for the katydids *N. ensiger* (Fig. 9) and *N. robustus*

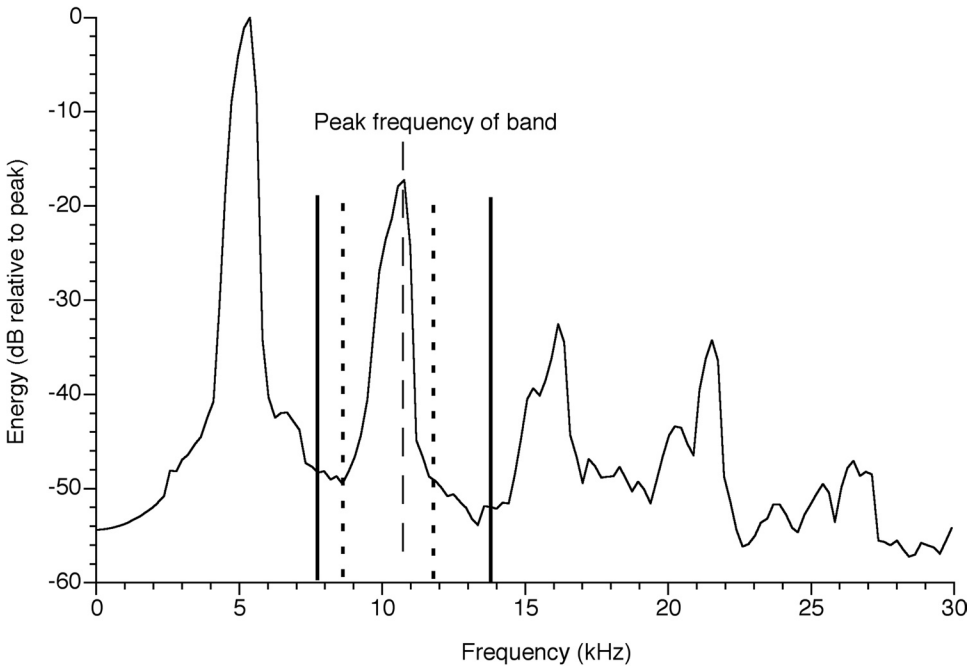

Fig. 1. Determination of the energy for a frequency band (here, the second harmonic). The dashed vertical line shows frequency at the band's energy peak. Dotted lines to either side indicate the observer-judged bandwidth. Integration of energy for each frequency between these limits gives the lower estimate of band energy. The heavy solid lines show the limits defined by the peak energy frequency (central dotted line) ± 2 × the observer-defined half-bandwidth. Integration between these limits gives the second estimate of band energy.

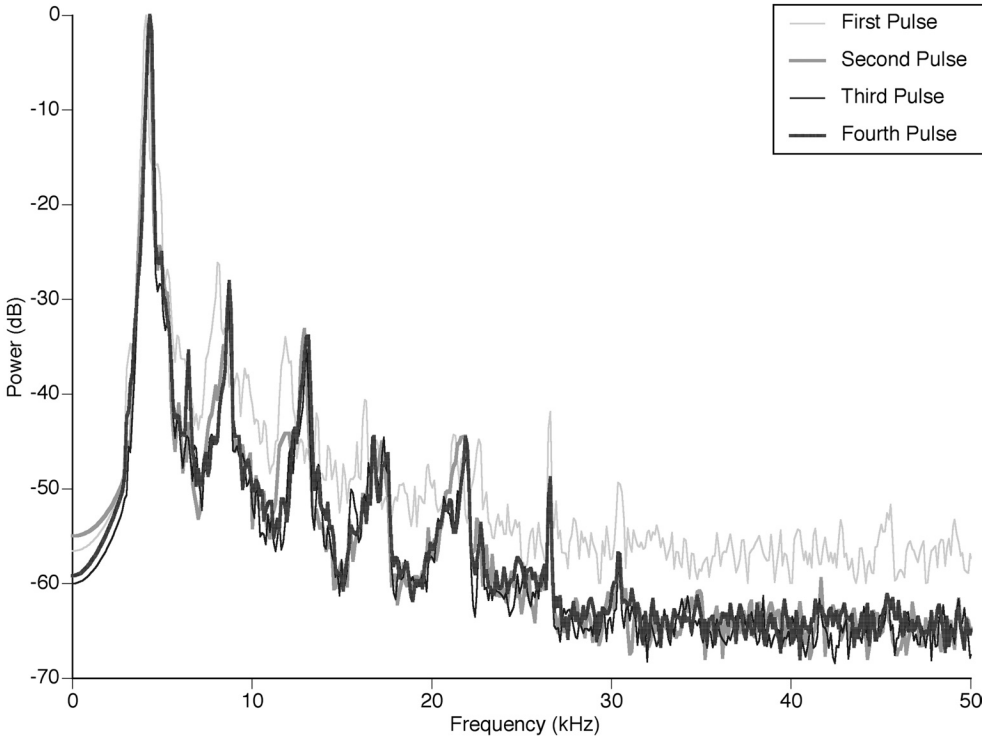

Fig. 2. Spectra for the 4 sound pulses making up 1 chirp by *G. pennsylvanicus*. Each spectrum is normalized to its peak energy. Note the generally close resemblance of the spectra of each sound pulse. Since the first pulse is weaker than the later pulses, there is a smaller difference between the background and the peak. This explains the apparently elevated high frequency background compared to the other records.

(Fig. 10) are similar to those obtained from animals calling in an anechoic chamber (Schul & Patterson 2003). This increased our confidence in our field recordings. The f_C is lower in the very large *N. robustus*. Compared to the cricket species we studied, these 2 katydids had much broader spectral peaks, lower Q_{-3dB} and proportionately more energy in the ultrasound region.

We have shown that there is an ultrasonic component to the calls of most of these crickets and katydids. But do the harmonics of f_C represent a substantial energy loss? Our calculations of % E f_C (see Eq. 1) made from audio-range and ultrasound microphone recordings are given in Table 1. Generally these independent estimates of % E f_C for a given species agree well with each other, even though the ultrasound microphone recordings tend to under-represent the lowest audio-range frequencies. Even so, since nearly all energy is present near the f_C, then moderate under-representations of f_C make little difference to the final estimate of % E f_C. We expect that the most substantial differences between the audible and ultrasound microphone estimates occur in species such as *S. vicinus* that have very low f_C. At these low frequencies, the ultrasound microphone has a decreased response of 5 to 8 dB. This could account for % E f_C of

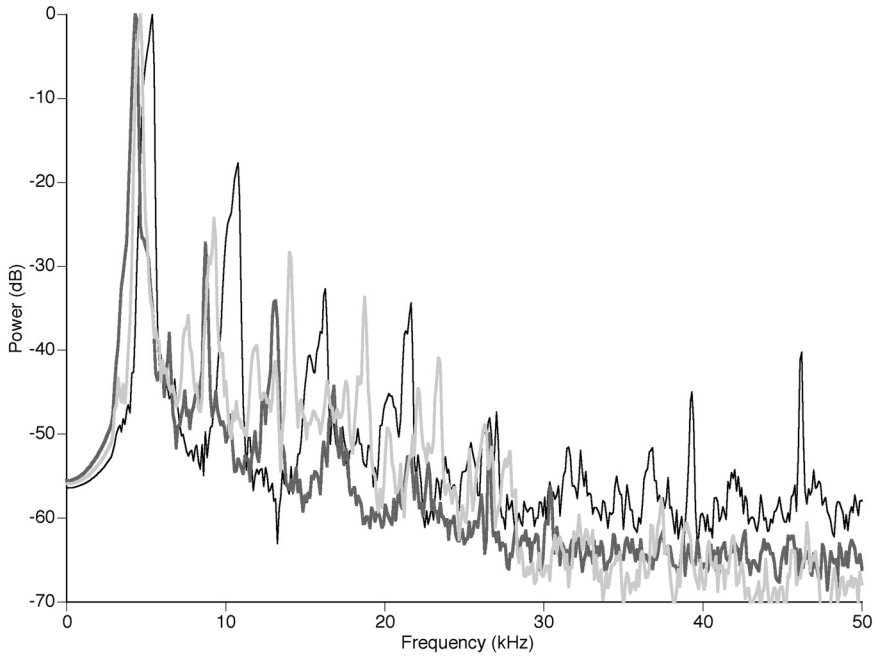

Fig. 3. Spectra for the final sound pulse of chirps made by 3 typical *G. pennsylvanicus*. Although the frequencies differ between individuals, the same harmonics are present. The peaks near 39 and 47 kHz are probably instrument artifacts.

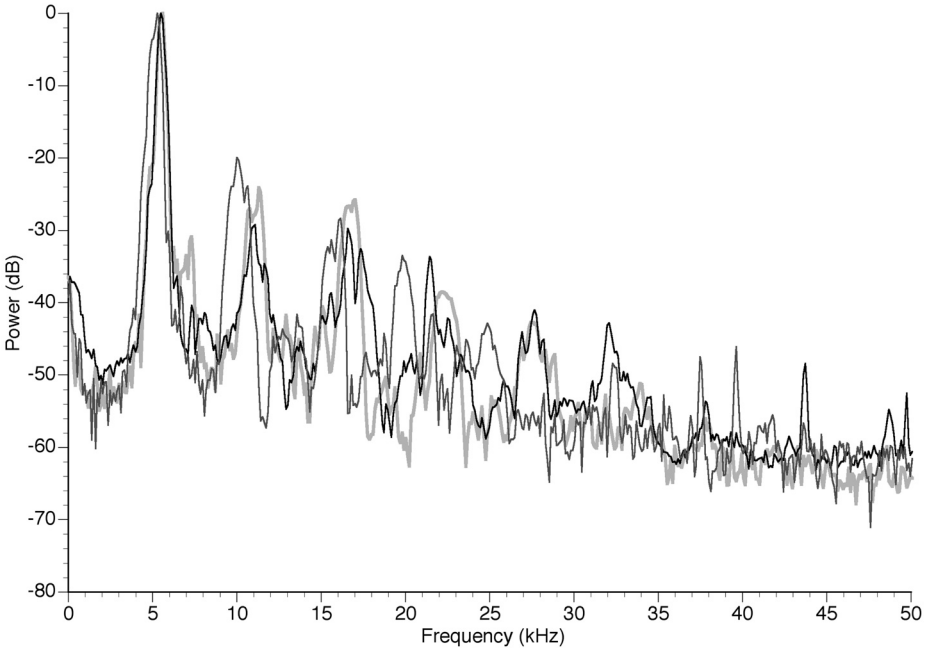

Fig. 4. Spectra for 3 *A. arboreus*.

about 88% *vs* the 99% estimated from the audio-range microphone. Given the low amount of ultrasonic energy in *S. vicinus* (Fig. 8), the audio-range microphone gives the more accurate result. Although we do not have audible-range recordings for the two *Neoconocephalus*, the relatively high values of these species' carrier frequencies and their prominent ultrasound harmonics suggest ultrasound recordings are the most useful measurements. For these 2 species, about 96% of their acoustic energy resides in the audible-range f_C band and the remaining 4% as ultrasonic harmonics. We do not know how significant ultrasound may be for communication in these species but it is certainly not a large component of their acoustic power. While this is almost certainly also true of some other tettigoniids (the pseudophylline *Pterophylla camellifolia*, for example), we hasten to add that these species should not be taken to be typical of all tettigoniids. The f_C of some katydids lies well beyond the audible range; some neotropical species use frequencies from 65 to 128 kHz as their dominant channel of acoustic signaling (Morris *et al.* 1994, Montealegre-Z pers. com.).

We have shown that the ultrasound contribution to acoustic power in a phylogenetically diverse group of crickets is much less than 1% of the total. Ultrasonic radiation is not significant and thus represents neither a significant "misdirection" of energy nor a cause of the low efficiency of audible-range sound production. Moreover, we have quantified the total energy in all harmonics of the f_C. These measurements show that all higher harmonics sum to only a few percent of total radiation energy. Thus, we have put

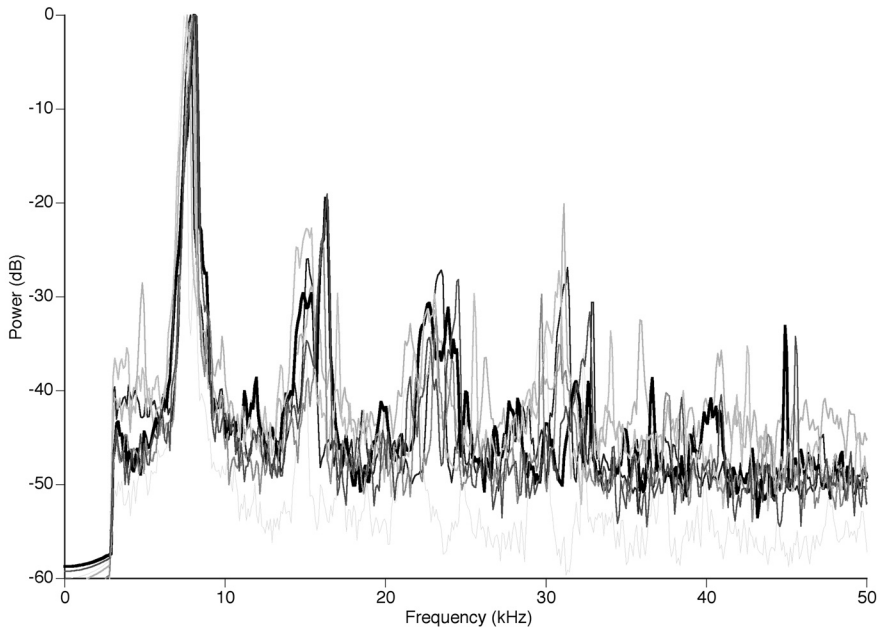

Fig. 5. Spectra for 7 *A. allardi*. Isolated narrow bandwidth spikes seen on several of the records are probably instrument artifacts.

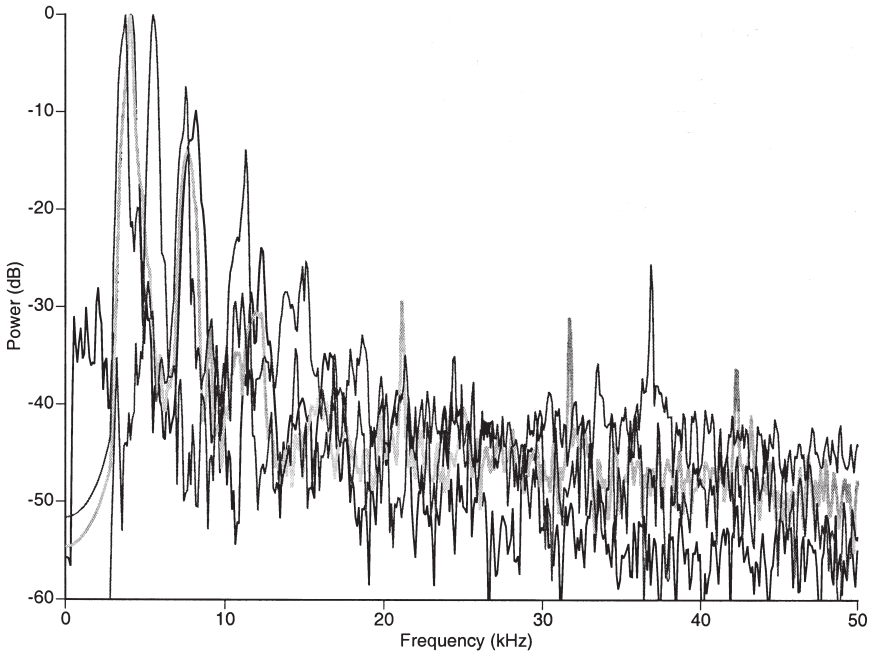

Fig. 6. Spectra for 4 *Eunemobius carolinus*. Note that virtually no energy is present above the audible range. Narrow bandwidth spikes found in the ultrasound are probably instrument artifacts.

a number, if you will, on what is commonly said about crickets based on their spectra — energy is highly concentrated near the f_C and therefore the energy loss to frequencies not used for communication is trivial. The inefficiencies that occur during sound production are thus attributable to the chemo-mechanical chain of energy transfers and to relatively poor coupling of the crickets' harps to its acoustic environment (Bennet-Clark 1989, Bailey *et al.* 1993, Prestwich 1994, Prestwich & Sullivan 2005).

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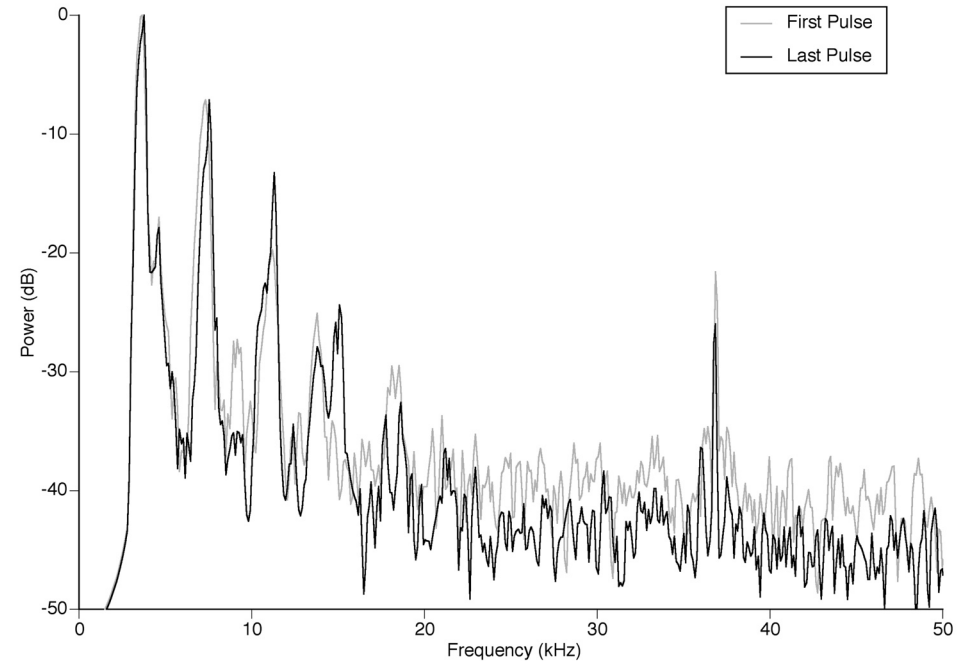

Fig. 7. Comparison of spectral characteristics of the first and last pulses of an *E. carolinus* chirp. Note their close correspondence. The peaks near 37 kHz are probably instrument artifacts.

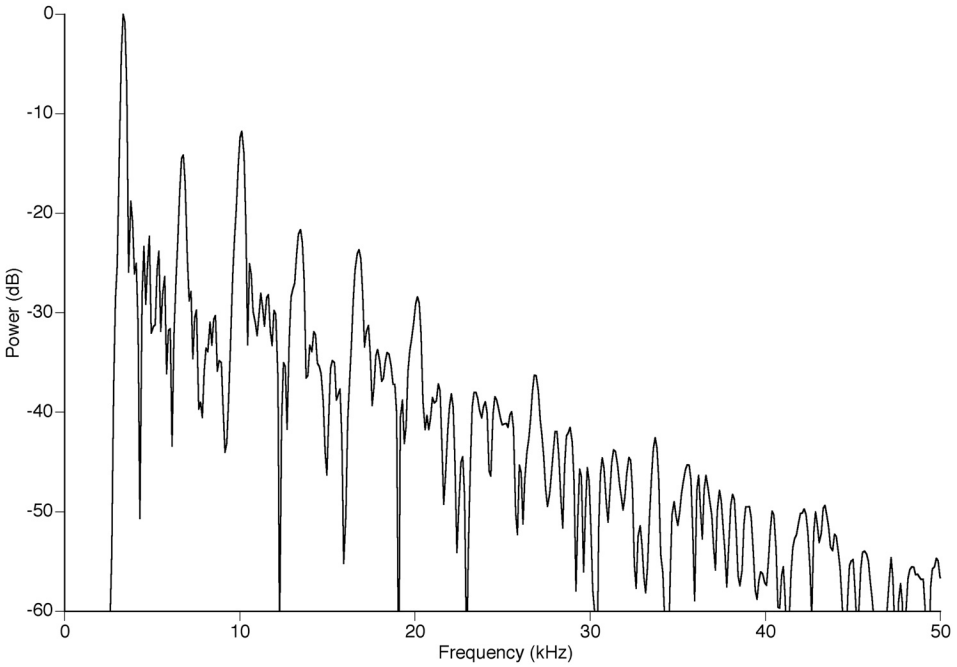

Fig. 8. Spectrum for a single *S. vicinus*.

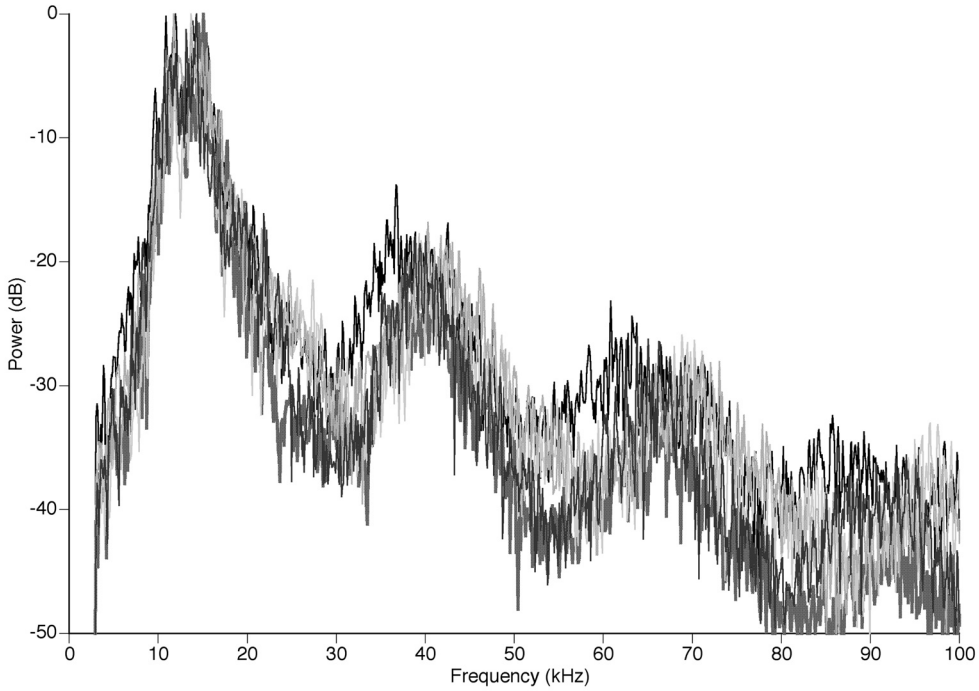

Fig. 9. Spectrum for three *Neoconocephalus ensiger*. Frequency bands are broader than the crickets (lower Q_{-3dB}) and a greater, but still minor, proportion of energy is found in the ultrasound region when compared to crickets.

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Table 1. Mean carrier frequencies, $f_C \pm s_{\bar{x}}$ and sample size (parentheses) and percentage of total acoustic energy in the carrier frequency band (% E f_C) for recordings taken with audio frequency range and ultrasound microphones. % E f_C is given as a range where the lower value is based on the minimal estimate of each harmonic's bandwidth and the higher on a bandwidth twice that (see Methods and Fig. 1). Individuals recorded with the ultrasound microphone were sometimes not the same as those recorded using the audible-range microphone.

	Audio Range Microphone		Ultrasound Microphone	
Species	f_c (kHz)	% E f_c	f_c (kHz)	% E f_c
Allonemobius allardi	8.17 ± 0.49 (10)	99.87 – 99.90 (10)	7.88 ± 0.26 (7)	99.99 – 99.99 (7)
Anurogryllus arboreus	5.44 ± 0.22 (7)	99.25 – 99.28 (7)	5.26 ± 0.31 (3)	98.75 – 98.83 (3)
Eunemobius carolinus	4.89 ± 0.30 (10)	98.62 – 98.79 (10)	4.34 ± 0.73 (4)	99.87 – 99.93 (4)
Gryllus pennsylvanicus	4.93 ± 0.26 (7)	97.43 – 98.29 (7)	4.79 ± 0.53 (3)	99.13 – 99.28 (3)
Scapteriscus borellii	2.81 ± 0.10 (7)	99.93 – 99.94 (7)	--	--
Scapteriscus vicinus	3.14 ± 0.23 (7)	99.76 – 99.80 (7)	3.39 (1)	87.19 – 89.49 (1)
Neoconcephalus ensiger	--	--	13.8 ± 1.14 (5)	95.91 – 97.05 (5)
Neoconcephalus robustus	--	--	7.00 (1)	95.56 _ 96.56 (1)

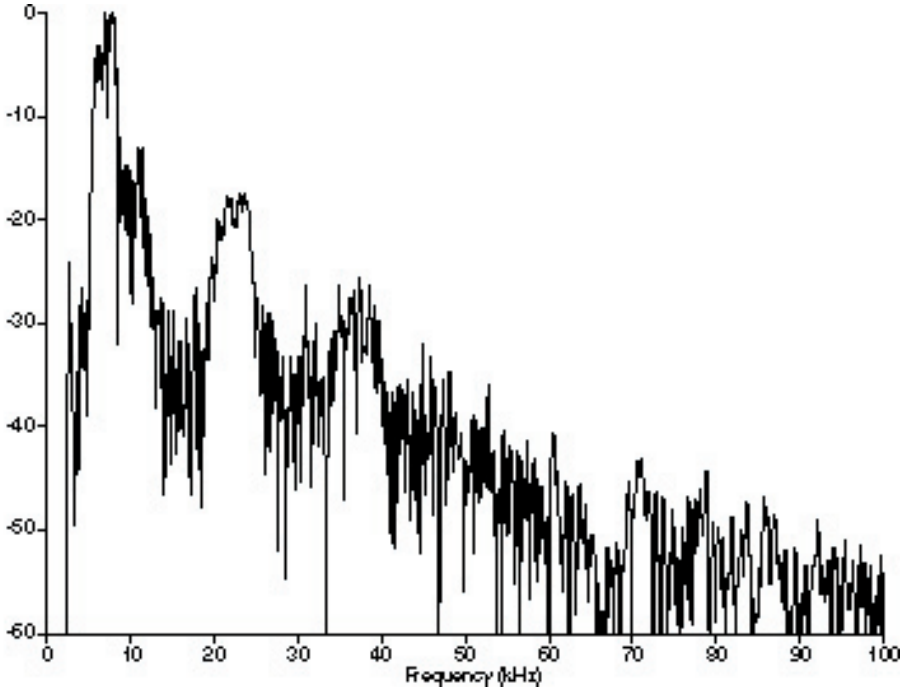

Fig. 10. Spectrum for a single *N. robustus*. As with its congener, the frequency bands are broader than in crickets.