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THE CONTROL OF CARRIER FREQUENCY IN CRICKET CALLS: A REFUTATION OF THE SUBALAR–TEGMINAL RESONANCE/AUDITORY FEEDBACK MODEL

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Summary

The subalar–tegminal resonance/auditory feedback hypothesis attempts to explain how crickets control the carrier frequency (f_C), the loudness and the spectral purity of their calls. This model contrasts with the 'clockwork cricket' or escapement model by proposing that f_C is not controlled by the resonance of the cricket's radiators (the harps) but is instead controlled neurally. It suggests that crickets are capable of driving their harps to vibrate at any frequency and that they use a tunable Helmholtz-like resonator consisting of the tegmina and the air within the subalar space to amplify and filter the f_C. This model predicts that f_C is variable, that call loudness is related to tegminal position (and subalar volume) and that low-density gases should cause f_C to increase.

In *Anurogryllus arboreus*, f_C is not constant and varied by as much as 0.8 % between pulses. Within each sound pulse, the average f_C typically decreased from the first to the last third of a sound pulse by 9 %. When crickets called in a mixture of heliox and air, f_C increased 1.07- to 1.14-fold above the value in air. However, if the subalar space were part of a Helmholtz-like resonator, then its resonant frequency should have increased by 40–50 %. Moreover, similar increases occurred in species that lack a subalar space (oecanthines). Experimental reduction of the subalar volume of singing crickets resulted neither in a change in f_C nor in a change in loudness. Nor did crickets attempt to restore the subalar volume to its original value. These results disprove the presence of a subalar–tegminal resonator.

The free resonance of freshly excised *Gryllus rubens* tegmina shifted by 1.09-fold when moved between air and a mixture of helium and air. Auditory feedback cannot be the cause of this shift, which is similar to the f_C shifts in intact individuals of other species.

Calculations show that the harp is 3.9–1.8 times more massive than the air that moves *en masse* with the vibrating harps. Replacing air with heliox-air lowers the mass of the vibrating system sufficiently to account for the f_C shifts. These results re-affirm the 'clockwork cricket' (escapement) hypothesis. However, as realized by others, the harps should be viewed as narrow-band variable-frequency oscillators whose tuning may be controlled by factors that vary the effective mass.

Key words: cricket, acoustics, carrier frequency, subalar space, resonance, 'clockwork cricket' model, escapement, frequency control, heliox, auditory feedback, tegminal free resonance.

Introduction

Two competing hypotheses have been advanced to explain the control of the carrier frequency (f_C) or pitch of a cricket's call. The escapement or 'clockwork cricket' model (Elliott and Koch, 1985) proposes that the f_C is determined principally by the mechanical resonance of the wing cells that radiate sound. More recently, Stephen and Hartley (1995b) proposed an alternative that we here term the subalar–tegminal resonance/auditory feedback model. It claims that f_C is controlled neurally, not mechanically. We here refute this model.

To produce advertisement calls, male grylloid crickets spread and elevate their tegmina (Fig. 1). This behavior creates a semi-enclosed subalar airspace between the tegmina and body (Fig. 1) which Stephen and Hartley (1995b) claimed has important acoustic properties (see below). A pulse of sound is produced when a cricket closes its tegmina through a small arc (typically several millimeters) while engaging stridulatory structures. These structures, known as the files and plectra, are found on both tegmina. The files are Cu2 veins that differ from typical wing veins in that their lower surfaces are supplied with knobs or teeth. The plectra are heavily sclerotized areas on the anterior medial margin of each tegmen; they are attached to the anterior medial end of each file (see Bennet-Clark, 1989). During typical stridulation, the plectrum of the bottom wing is alternately captured and released by the file teeth on the lower side of the top wing at a rate referred to as the plectrum-to-file impact rate (f_{PFI}). With each capture, the Cu2 vein of each wing is set into vibration – directly in the case of the top wing and *via* the plectrum for the lower wing. Since each wing's Cu2 vein forms one border of a triangular wing cell known as the

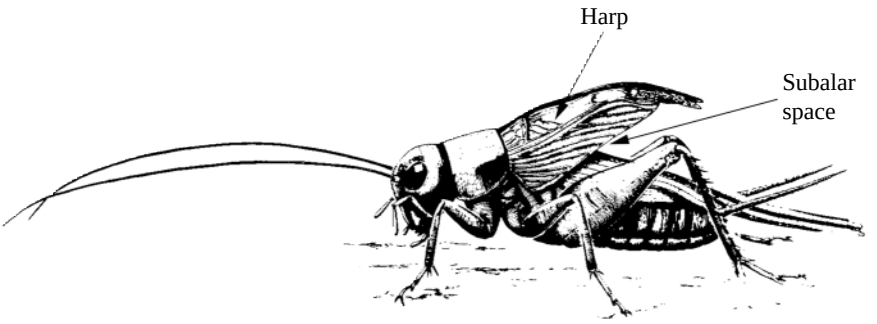

Fig. 1. Typical tegminal position during stridulation in grylloid crickets. The harp (major acoustic radiator) is the small triangular area dissected by several small veins near the anterior of the wing. Stephen and Hartley (1995b) termed the semi-enclosed air space beneath the tegmina and above the body the subalar space. Note the fold in the lateral field of the wing delimited by a long slightly curved vein running anterior to posterior. This tends to make the tegmina tent-like and, according to Stephen and Hartley (1995b), better encloses the subalar space. However, note that the subalar space is largely opened during stridulation except where the wings join the body. The line drawing of the cricket was kindly provided by Professor R. D. Alexander.

harp, vibrations of Cu2 excite the harps to vibrate and radiate sound at the f_{PFI}. Thus, the f_{PFI} equals the f_C of a cricket's call. Pulses of sound alternate with silent periods when the insect reopens its tegmina (see Fig. 6) at what is referred to as the pulse rate or wing stroke rate (f_{WS}) (Walker, 1962).

Nocke (1971) investigated the resonant properties of cricket wings. Resonance occurs when the reactive components of impedance (due to the system's compliance and mass) are equal and opposite. Since reactances are frequency-dependent, it is an easy matter to solve for the resonant frequency f_0:

$$f_0 = \frac{1}{2\pi}\sqrt{\frac{1}{LC}}, \qquad (1)$$

where L (kg) is the system's inertance (the mass, in kg, of the vibrating portions of the harp plus the air in the immediate vicinity) and C ($s^2\,kg^{-1}$) is the harp's compliance (Fletcher, 1992). Nocke (1971) measured L and C for the harps of *Gryllus campestris*; substituting L into equation 1 gave good agreement between the calculated f_0 and the tegminal free resonance (the resonant frequency measured from the harps of isolated wings).

Nocke's (1971) work was utilized by Elliott and Koch (1985), Koch et al. (1988) and Bennet-Clark (1989) to explain how field crickets (*Gryllus* species and their close relatives) manage to maintain a relatively constant f_C regardless of temperature changes. Although the f_C of field crickets changes only slightly with temperature, the f_{WS} shows strong temperature-dependence. From a knowledge of the stridulatory apparatus, one would expect that a change in f_{WS} would alter the f_{PFI} and f_C by a similar proportion.

The 'clockwork cricket' (escapement) model explains this paradox by invoking parallels between escapement clocks and stridulating crickets. Escapements are devices that regulate energy input and motion. In mechanical clocks, they alternately lock and release the mechanism that moves the clock's hands. The rhythm of lock and release is, in turn, controlled by a regulating oscillator such as a pendulum or balance spring. Escapements also provide a means to provide the regulator with discrete amounts of in-phase energy in order to maintain its oscillations (Landes, 1983). In the clockwork cricket analogy, the escapement is composed of the stridulatory structures with the harps acting as the regulating oscillator. (If one wishes to complete the analogy, radiated sound can be viewed as the clock's hands.) Each time a tooth captures the plectrum, they lock together and motion briefly stops. Energy is transferred to the harps in phase with their motion, just as in an escapement clock. A moment later, when the direction of the harp's vibration reverses, the plectrum is released and it skips to the next tooth. The results are that the resonance of the harp determines the f_{PFI} and that the energy to produce sound is provided without disrupting the harp's vibrations. Moreover, closing speed and f_C remain roughly constant (being governed by the harp's resonance) while f_{WS} can change, primarily by altering the silent tegminal opening time.

Stephen and Hartley's (1995b) rejection of the escapement model grew out of spectral measurements of the calls of *Gryllus bimaculatus*. Their data showed that crickets do not keep perfect time and that the harp's oscillations had a number of imperfections that, if found in a watch, would eventually render it useless as a timepiece. For instance, they reported that the sound pulses had two spectral peaks. The most energetic (the f_C) had a mean value of 4.86 kHz, but it varied by up to 3 % from pulse to pulse. They also reported a minor peak (12 dB SPL below the f_C) whose value (5.5 kHz, the tegminal free resonant frequency) was constant from pulse to pulse regardless of experimental conditions. They argued that clocks cannot run at variable frequencies, let alone at two frequencies at once – especially when the minor frequency corresponds to the harp's resonance. They concluded that the f_C was not controlled *via* an escapement mechanism regulated by the harps.

After some additional experiments, Stephen and Hartley (1995b) constructed their alternative subalar–tegminal resonance/auditory feedback model of cricket sound production. It can be summarized as follows. (i) The f_{PFI} (and therefore the f_C) is controlled neurally and can have any value. They believed that information from the auditory system was used to control central neural mechanisms ('auditory feedback') that in turn determined the f_{PFI}. They cited the dual spectral peaks mentioned above in partial justification of this supposition. (ii) They realized that, if the tegmina were driven at f_{PFI} values greatly different from their resonance, the radiated sounds would be weak and would probably contain

energy at a number of additional frequencies. To amplify and filter the tegminal signal, they proposed a tunable resonator consisting of the subalar space and tegmina. As with the f_{PFI}, the tuning of this 'subalar–tegminal resonator' would be controlled by neural mechanisms. This resonator will be described in more detail below. To summarize their scheme briefly, they believed that a cricket listens to its song and then adjusts its f_{PFI} and subalar–tegminal resonance to produce a loud, pure-frequency signal.

Let us consider the proposed subalar space–tegminal resonator in more detail. Bailey and Broughton (1970) speculated that the subalar space (Fig. 1) might act as part of a resonator in bush crickets (Tettigoniidae). Following their lead, Stephen and Hartley (1995b) proposed that a Helmholtz-like resonator operated in gryllids. This resonator would be able to amplify any f_{PFI}, would filter out unwanted frequencies and would tend to entrain the f_{PFI} to its resonant frequency. In many ways, what they proposed resembled the abdominal resonator found in many species of cicada (Young, 1990; Bennet-Clark and Young, 1992).

The physics of Helmholtz resonators is well-understood (Fletcher, 1992). A classic example is a jug or flask. The mass of air in and near the neck is free to move back and forth *en masse* and acts as an inertance whose value is given as:

$$L = \frac{\rho l'}{S} , \qquad (2)$$

where ρ is the density of the air ($kg\,m^{-3}$), l' is the effective length (m) of the neck, which is equal to the physical length plus a correction factor, and S (m^2) is the neck's cross-sectional area. The air in the jug's reservoir acts as a compliance. Since it is contained everywhere except at the neck, if force is applied either from the jug's wall or *via* the air in the jug's neck, the air in the reservoir will be compressed or rarefied but not displaced. This compliance, C ($s^2\,kg^{-1}$) is given as:

$$C = \frac{V}{\rho c^2} , \qquad (3)$$

where V is the volume (m^3) and c is the speed of sound ($m\,s^{-1}$). If we substitute equations 2 and 3 into equation 1, we obtain the resonant frequency of a Helmholtz resonator in terms of its dimensions:

$$f_0 = \frac{c}{2\pi} \sqrt{\frac{S}{l'V}} . \qquad (4)$$

This expression is valid provided that none of the dimensions is large compared with 0.1λ, where λ is the wavelength of f_0 (Fletcher, 1992).

Although Stephen and Hartley (1995b) stated that their proposed resonator was 'Helmholtz-like', there are striking differences. In their subalar–tegminal resonator, the inertance is the mass of some portion of the tegmina, and the air within the subalar space acts as the compliant element. However, note that this air is far from enclosed, and it is hard to imagine how it could be compressed (Fig. 1). Nevertheless, they suggested that perhaps it was sufficiently confined to act as a compliant element. They derived an equation for the resonance of the proposed system essentially by substituting equation 3 (compliance of a volume of air) into equation 1:

$$f_0 = \frac{c}{2\pi} \sqrt{\frac{\rho}{LV}} , \qquad (5)$$

where in this case the inertance, L, is the tegminal mass expressed in acoustic units ($kg\,m^{-4}$). Note that the value of f_0 for both their model (equation 5) and a Helmholtz resonator (equation 4) can be altered by changing the subalar or reservoir volumes. Thus, Stephen and Hartley (1995b) suggested that crickets could simply change the spread and elevation of their tegmina to alter f_0 of the subalar–tegminal resonator.

For reasons that are not clear, Stephen and Hartley used equation 4 (Helmholtz resonator), not the equation they derived for their system (equation 5), to make important predictions about the subalar–tegminal resonator. The most important of these predictions is that f_0 for a Helmholtz resonator will shift if the vessel is filled with gases that have different values of the speed of sound, c. This can be accomplished by filling the chamber with gases of differing densities since:

$$c = \sqrt{\frac{\gamma P_0}{\rho}} , \qquad (6)$$

where γ is the dimensionless ratio of specific heats and P_0 is the pressure in the absence of any sound. Stephen and Hartley (1995b) attempted to use this phenomenon to prove the existence of their proposed resonator by exposing calling *G. bimaculatus* to a mixture of helium, oxygen and room air ('heliox-air'). The f_C of the resulting calls increased by 1.05- to 1.10-fold, far less than the 1.35-fold increase expected if the subalar volume was part of a Helmholtz-like resonator that entrained the f_{PFI} (equation 4). However, instead of rejecting a role for the subalar space, they chose to interpret the smaller-than-predicted f_C shift as being caused by distortions within the auditory system. Paradoxically, they had used this same interpretation previously to explain a decrease in the most energetic frequency produced by a bush cricket calling in heliox (Stephen and Hartley, 1995a). Presumably, they believed that the gas filling the tympana of *G. bimaculatus* was different from that of the general atmosphere, perhaps because of the high levels of metabolic CO_2. In any case, to support their proposed subalar–tegminal resonator, they constructed a model system. However, this model did not resemble the situation in crickets in one critical aspect: it used an essentially closed cavity as an analog to the very much open subalar space (Fig. 1).

For these reasons, the present study set out to test experimentally the major features of Stephen and Hartley's (1995b) model. First, we repeated their investigations of pulse-to-pulse variation in f_C and of f_C shifts in heliox-air mixtures. Next, we compared frequency shifts in the free resonance of

excised tegmina with the f_C shifts of intact individuals. We predicted that, if auditory feedback caused the f_C shifts, then the shifts should not occur in isolated wings. To determine whether a subalar–tegminal resonator was present, we experimentally reduced the subalar volume of calling *A. arboreus* and looked for decreases in song amplitude, compensatory increases in f_C and/or outward movement of the tegmina to restore the original subalar volume.

Materials and methods

Crickets

Most experiments used *Anurogryllus arboreus* T. Walker, a member of the same subfamily (Gryllinae) of crickets (Gryllidae) as *Gryllus bimaculatus* (Otte, 1994; Walker, 1998). Sound production in *A. arboreus* shares a number of features in common with members of the genus *Gryllus*. *A. arboreus* possesses a similar tegminal morphology, including a pre-costal fold (Fig. 1), and when stridulating it holds its tegmina in a similar position, thus producing a subalar space. We also examined two species that lack a subalar space: the tree crickets *Oecanthus celerinictus* T. Walker and *O. quadripunctatus* Beutenmuller. Although members of the Gryllidae (Otte, 1994), the tegmina of oecanthines (which belong to a different subfamily, Oecanthinae) are flatter and are held at a nearly vertical orientation during stridulation. Their stridulatory structures are similar to those of other gryllids, but their f_C has a greater temperature dependence and may be controlled by a different mechanism than in the genera *Gryllus* and *Anurogryllus* (Walker, 1963; Sismondo, 1979; Bennet-Clark, 1989). For our measurements of the effect of air load on tegminal free resonance, we used tegmina isolated from *G. rubens* Scudder, a congener to *G. bimaculatus*.

The calling chamber and gas composition

We recorded calls in a chamber (Fig. 2) similar in design to that used by Stephen and Hartley (1995a,b). The base (0.22 m diameter) consisted of styrofoam covered with acoustical foam. Cut into the base was a port through which to introduce the cricket (filled with foam and sealed when the chamber was in use) and openings for an Electret microphone (Radio Shack 33-3013 or equivalent), a Tygon tube through which heliox or air could be pumped, and a thermocouple to measure temperature. A polyethylene bag was taped to the circumference of the base. When the chamber was filled, the height of the bag reached approximately 0.28 m.

During an experiment, we introduced the cricket (which was free to roam about the chamber) and then slowly pumped in air or heliox (20 % O_2:80 % He), both saturated with water vapor. Final gas concentrations were calculated on the basis of the fraction of the gas that was CO_2 using an Anarad (model AR 50) CO_2 analyzer (500 p.p.m. full scale) and were brought to either 78 % He or <2 % He. Temperature was maintained at 25.2±0.3 °C with *A. arboreus* and 24.3±0.5 °C (means ± S.D.) for the two *Oecanthus species*. In no case were the slight deviations in temperature sufficient to affect stridulation sufficiently to explain the f_C shifts we observed (Prestwich and Walker, 1981). Moreover, there was no consistent pattern to these small variations in temperature. Temperatures might be slightly higher or lower in heliox than in air in different individuals or in replicates of the same individual.

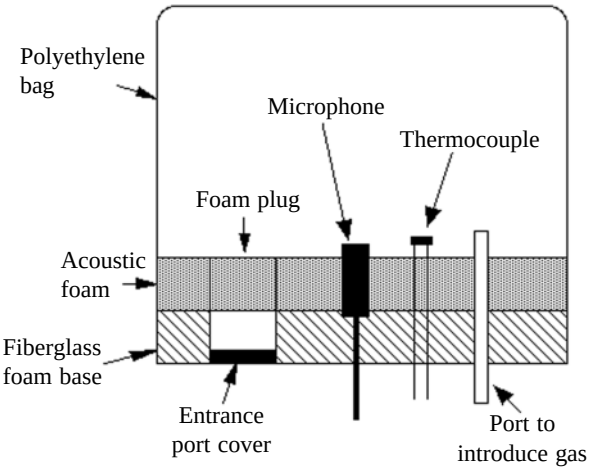

Fig. 2. The chamber used to alter the atmosphere around calling insects and to record the resulting song. The design is similar to that used by Stephen and Hartley (1995a,b).

The apparatus leaked, and after 30 min the concentration of He was typically reduced to near 70 %. Thus, there was always some air in the 'heliox' chambers and we will use the term 'heliox-air' to emphasize that these were mixed atmospheres whose composition varied over time. Crickets usually spontaneously began calling continuously 10–15 min after gas had been pumped into the chamber; if sufficient data were not obtained within 30 min, the chamber was refilled with the appropriate gas. We randomized the order of exposure of individuals to different gases.

We were concerned that reflected sound might badly distort our recordings, especially with the heliox-air mixture because of the large difference in the index of refraction of the gas in the chamber compared with that in the room air. To check for this, we filled chambers with either pure helium (therefore producing an even larger difference in the indices) or with air and then played a 5 kHz tone through a 2.5 cm diameter cone speaker located in the middle of the chamber. Simultaneously, we recorded this sound using the chamber's microphone. Fig. 3 shows a typical result, and statistical analysis showed that that there was no difference in the frequency measured in chambers filled with air or helium-air (P=0.83, N=4, paired t-test).

Sound pressure level

To determine whether the sound pressure level (SPL) changed in heliox-air *versus* air, we placed a Larson-Davis (model 812) SPL meter outside the calling chamber. Its microphone was located 0.5 m from the cricket along a line that originated near the center of the cricket rising towards the anterior at an angle of 45 °. It was not possible to place the microphone in the chamber because of near-field effects.

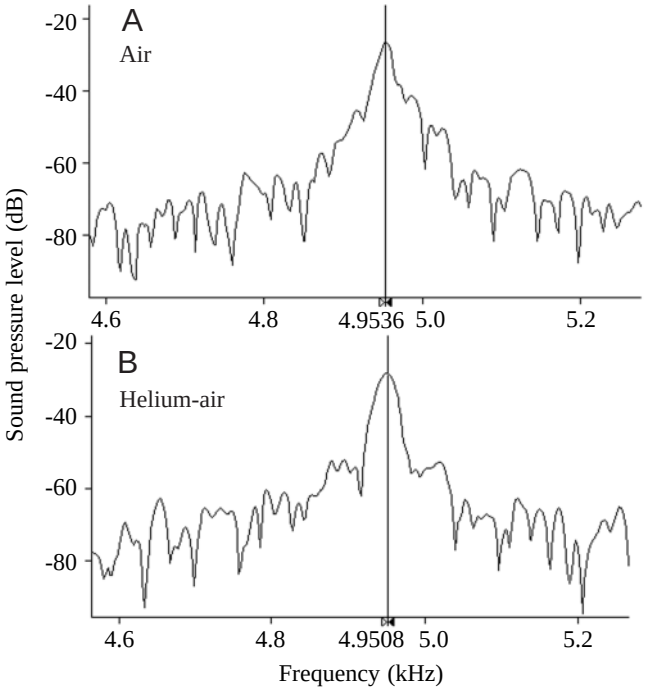

Fig. 3. Recordings made in the chamber shown in Fig. 2 when filled with air (A) or approximately 100 % helium (B). A 5 kHz tone was played through a cone loudspeaker located inside the chamber, recorded using the chamber microphone and analyzed as for insect calls (see Materials and methods). The spectra of the digitized signals showed no difference in peak frequency (vertical line) in air compared with helium. The approximately 50 Hz difference between the synthesized frequency (5 kHz) and the peak frequencies in both air and helium was due to a slight difference in the speeds of the tape recorders used to record and play the signal. This difference was repeatable when the same experiment was performed in the open laboratory. Spectra are referenced against a 120 dB SPL re 20 μPa signal.

Measurements made outside the chamber will suffer some excess attenuation, and it was not possible to achieve precise positioning of the microphone relative to the cricket. Nevertheless, experiments using a speaker in the chamber showed that this arrangement could reliably detect changes of 1–2 dB SPL re 20 μPa.

Tegminal free resonance

To measure the free resonances of isolated wings in air and helium-air, we used apparatus and procedures similar to those of Nocke (1971) and Bennet-Clark (1987). We clipped the basal stalk of freshly isolated tegmina from male *Gryllus rubens* to a flexible wire, put it in an inverted position (the wing is curved), dusted it lightly with charred cork dust and positioned it over an exponential horn loudspeaker. The output of an audio signal generator (Leader Electronics, model LAG 120B) was amplified by a Realistic SA-155 audio amplifier that in turn drove the horn loudspeaker. The harp could be observed with a low-power microscope. We placed microphones for monitoring SPL and frequency near the wing, and then enclosed the entire apparatus except for the signal generator, amplifier and SPL meter in a plastic bag that was sealed with tape. The microscope objective entered the bag *via* a taped opening.

We inflated the bag with either compressed air or helium (which became ‘heli-air’ mixture since the bags leaked) until it was nearly turgid. We calculated the degree to which the helium was diluted using the method described previously for the recording chambers. At the time of the measurements, typical ‘heli-air’ mixtures were 75 % helium:25 % air. The experimental sequence was air, heli-air and then air to establish that there were no changes to the harps during the experiment.

Experiments consisted of varying the frequency of applied sound while looking for harp resonance which could be identified by movement of the cork dust on the vibrating harp. We maintained constant SPL levels (within ± a few tenths of a decibel) regardless of driving frequency. We found the resonant frequency by recording (and analyzing as described below) a sample of the sound that produced the visually determined maximum displacement of the cork dust.

Collection and digitization of sounds

We collected sounds using either the calling chamber’s Electret microphone (Fig. 2) or, in the case of recordings in the anechoic chamber (see below), an Azden ECZ-660 zoom microphone. In all cases, the microphones were attached to a Marantz PMD 201 cassette recorder using type II high-bias tape. We digitized the sounds using 16 bit, 44.1 or 48 kHz A/D converters. Nearly all the energy in our recordings was at frequencies below 6 kHz. The signals lacked any significant energy near the Nyquist limit (22 or 24 kHz) so aliasing was not a problem.

Analysis of sounds

We analyzed sounds using Canary 1.2 sound-analysis software (Cornell Laboratory of Ornithology, Ithaca, New York, USA) and a Macintosh computer. Spectra had a frequency resolution of approximately 22 Hz.

Average carrier frequencies were determined on the basis of 1–2 s of constant calling (40–160 sound pulses, depending on the species and time). We also determined the f_C of individual sound pulses by isolating and placing them in a sound window preceded and followed by 10 ms of silence. Inclusion of the silent periods avoided ‘end effects’ (frequency artifacts in the spectrum when the beginning or end of the signal coincides with the onset or cessation of sound). To check for intra-pulse frequency modulation, we isolated calls as described above and used the software’s spectrograph feature. Since we identified a decrease in frequency with time, we divided single calls into three equal parts, isolated each third as described above, determined its average frequency and then tested the results for statistically significant differences.

We verified our ability to detect frequency changes of the same magnitude as those we observed in our experiments by creating synthetic sounds with known spectral characteristics that resembled those measured from cricket songs. We played

these through a speaker, and recorded, digitized and analyzed them using identical methods to those used for the experimental data. These calibrations showed that we could distinguish between frequencies that varied by as little as 22 Hz. This result was in agreement with the theoretical frequency discrimination limit for our software as we employed it. Moreover, the changes that we observed when crickets called in different atmospheres or the within-pulse modulation of cricket calls (when measured between different thirds or a call) was at least 10 times greater than our discrimination limit. Thus, we were confident in our ability to accurately discern frequency shifts in our experimental subjects.

Reduction of the subalar volume

For these experiments, *A. arboreus* were released in an anechoic room illuminated by low levels of red light. Shortly after a cricket began to sing, we started recording. As we continued recording, we reduced the subalar volume (Fig. 1) of the actively calling cricket by placing wooden dowels, dowels covered with acoustic foam or even fingers into the subalar space. In control experiments, the same objects were placed just outside and anterior or lateral to the subalar space. Unless the crickets were inadvertently touched during these manipulations, they usually remained in one position and continued calling. During all these experiments, the Azden recording microphone was situated at a constant position relative to the cricket in the far field at a distance between 0.25 and 0.5 m.

*Estimation of the quality factor (*Q*) for the advertisement call of* Anurogryllus arboreus

The quality factor (*Q*) for the tegminal resonator is given by:

$$Q = \frac{\pi}{\log_e(\text{decrement})} = \frac{f_0}{BW_{-3\text{dB,SPL}}} = \frac{2\pi f_0 M}{R}, \quad (7)$$

where f_0 is the resonant frequency, $BW_{-3\text{dB,SPL}}$ is the bandwidth at 3 dB SPL re 20 μPa below the peak, $\log_e$(decrement) is the natural logarithm of the rate of decrease of the amplitude of an undriven oscillator, M is the mass of the system and R is the damping (specific acoustic) resistance (Bennet-Clark, 1989). We found Q by using the natural logarithm of the rate of signal amplitude decay at the end of a sound pulse. This portion of the pulse is presumed to be the decay of an undriven system (Bennet-Clark, 1989).

Statistical analyses

In all cases, the threshold for rejecting the null hypothesis was set at $P \leqslant 0.05$. Whenever possible, we used a paired *t*-test to establish statistical significance, although in some cases we were forced to use a less powerful *t*-test which assumes unequal variances or a one-way analysis of variance (ANOVA). To discuss variation, we use the coefficient of variation (CV), defined as 100 times the standard deviation divided by the mean.

Results are presented as means ± S.D.

Results

Frequency variations among whole sound pulses in Anurogryllus arboreus

For any individual, the coefficient of variation (CV) of the mean f_C for whole sound pulses was less than 0.8 %, and in four of the six individuals used, the CV was less than 0.04 % (N=6 individuals, 10 pulses occurring within 2 s analyzed per individual). The mean f_C was approximately 5.60 kHz with an average range encompassing approximately ±40 Hz (maximum of 100 Hz). Similar results were obtained in heliox-air with the exception that the mean frequency was shifted upwards (see below). Calls recorded from the same individuals several days apart at the same temperature had mean whole sound pulse carrier frequencies that were not significantly different for any individual (P=0.62, paired *t*-test), thus showing very little variation over time.

Within-pulse f_C *and amplitude changes*

In *A. arboreus* calling in air, there was a highly significant decrease of approximately 9 % (480 Hz) in the mean f_C from the first to last third of the call (P<0.0001, paired *t*-test, Table 1). Moreover, there were significant decreases in frequency from each third of the sound pulse to the next (P<0.0001, paired *t*-test, Table 1). The pattern was the same in heliox-air (Table 1). Although Stephen and Hartley (1995b) reported that within-pulse f_C remained constant in *G. bimaculatus*, other published spectrograms for *Gryllus* species show the f_C decreases during a pulse (Alexander, 1957; Leroy, 1966; Koch et al., 1988).

Stephen and Hartley (1995b) proposed that the slow decay in the amplitude of a sound pulse in crickets (see Fig. 6), which often begins well before the end of the pulse, is caused by an increasing mismatch between the excitation frequency and f_0 of the proposed subalar–tegminal resonator. Thus, if the tooth strike rate (driving frequency) either remains constant (as they reported) or decreases (present study; Alexander, 1957; Leroy,

Table 1. *Variation in the mean carrier frequency within single pulses in* Anurogryllus arboreus

Portion of pulse	Mean f_C in air (kHz)	Mean f_C in heliox-air (kHz)
First third	5.90±0.02	6.22±0.05
Middle third	5.62±0.04*	5.96±0.05*
Last third	5.42±0.10*	5.64±0.04*

Sound pulses were arbitrarily divided into thirds.

f_C, carrier frequency.

Values are means ± S.D. (N=4 individuals; for each individual at least eight pulses from different times within a calling period were examined).

Asterisks mark significant differences from the value of f_C for the first third of the call (P<0.0001).

Table 2. *Carrier frequencies and wing stroke rates in air and heliox-air for three cricket species*

		f_C (kHz)				f_{WS} (Hz)			
Species	*N*	Air	Heliox-air	*P*	Ratio (heliox/air)	Air	Heliox-air	*P*	Ratio (heliox/air)
Anurogryllus arboreus	5	5.73±0.25	6.51±0.44	<0.001*	1.14	79.0±1.1	78.8±1.2	0.61	1.00
Oecanthus celerinictus	4	4.13±0.05	4.44±0.19	0.01*	1.07	63.1±1.4	61.0±1.0	0.085	0.97
Oecanthus quadripunctatus	3	4.02±0.16	4.53±0.33	0.03*	1.12	41.7±1.6	39.9±1.2	0.015*	0.96

f_C, carrier frequency; f_{WS}, wing stroke rate.
Values are means ± S.D.
Temperatures were 25.2±0.3 °C (mean ± S.D.) for *A. arboreus* and 24.3±0.5 °C for the oecanthines.
Asterisks indicate significant differences between values in air and heliox-air (f_C, one-tailed paired *t*-test; f_{WS}, two-tailed paired *t*-test).

1966; Koch et al., 1988) then, as the tegmina close, f_0 of the proposed subalar–tegminal resonator would increase since the subalar volume decreases (equations 4 and 5). Our examination of thousands of sound pulses from 14 individuals showed that, in most cases, the amplitude reached a maximum early in the call and then decayed slowly for an extended period followed by a rapid fade-out when the animal reversed its wings. However, it was not uncommon to see changes in this pattern within an individual, even over a short period. Most significantly, the calls of *O. celerinictus* and *O. quadripunctatus* showed the same patterns even though these species lack a subalar space.

Carrier frequency and SPL in air and heliox

Table 2 gives the mean f_C and f_{WS} for all three species in air and heliox-air at 25 °C. The values for air agree well with those previously published for the same species (Walker, 1963, 1973; Prestwich and Walker, 1981). Placing *A. arboreus* in heliox-air resulted in a statistically significant average 1.14-fold increase in f_C with no statistically significant differences in f_{WS}. When we determined mean SPL values in air and in heliox-air for each of five individuals (based on 2–4 separate measurements per individual per atmosphere), a paired *t*-test showed no statistically significant differences (P=0.24). The mean SPLs in both atmospheres for each individual were always within ±2 dB of each other; in two cases, the mean SPL in heliox-air was slightly higher than the mean SPL in air, while in the remaining three cases the SPL in heliox-air was slightly lower than in air. Sound pressure level measurements were difficult for technical reasons (see Materials and methods). Some uncertainty is therefore inherent in these measurements, but it is not so great as to undermine the conclusions drawn from these data.

Fig. 4 gives the frequency spectra for representative single sound pulses in air and heliox-air for an individual *A. arboreus*. The principal difference is an upward shift in frequency in heliox-air. The spectra from seven individuals showed minor frequency peaks in addition to the f_C, but these were not consistent from individual to individual. Furthermore, spectra for sound pulses taken from the same individual at different times showed variation in the positions of these frequency peaks. We found no evidence of a consistent frequency peak near the f_C that might be due to a separate resonance (cf. Stephen and Hartley, 1995b).

In the oecanthines, heliox-air induced an increase in f_C similar to that in *A. arboreus* (Table 2). Surprisingly, the sound pulse rate also decreased, although this was only statistically significant in *O. quadripunctatus*. This was not due to temperature: in the singing chamber, the mean temperature (24.3±0.5 °C) never changed by more than 0.6 °C. Usually the change was less than 0.3 °C, and the changes that did occur were not in a consistent direction. A reduction in f_{WS} should result in a reduction in f_C (Walker, 1963). We are unable to explain the reduction in f_{WS}, although we suspect that the paradoxical increase in f_C is the result of changes in the air load acting on the tegmina (see Discussion) leading to excitation of

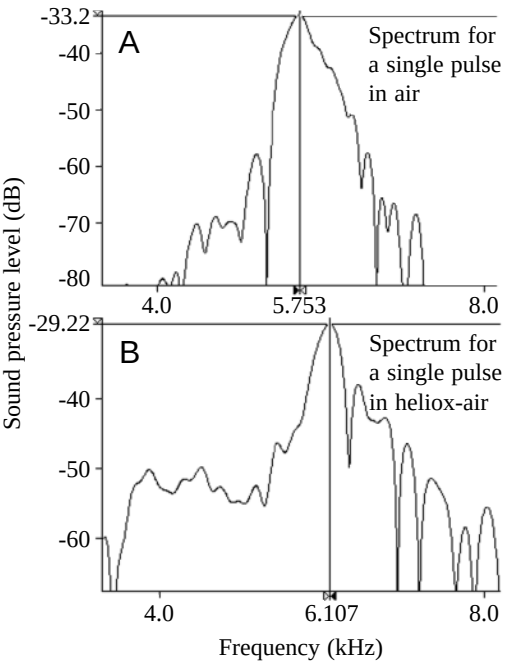

Fig. 4. Typical spectra for *Anurogryllus arboreus* calling in air (A) and in heliox-air (B). These spectra are for single sound pulses made by the same individual recorded approximately 30 min apart at a temperature of 26 °C. The carrier frequency f_C is marked by the vertical solid line. The ratio of f_C in heliox-air to f_C in air is 1.06. Spectra are referenced against a 120 dB SPL re 20 μPa signal.

Table 3. *The effect of experimental reduction of the subalar space on the carrier frequency and wing stroke rate of* Anurogryllus arboreus

Condition	f_C (kHz)	f_{WS} (Hz)
Normal	6.78±0.50	83.2±0.8
Reduced space	6.74±0.41	83.0±2.4

Subalar volumes were reduced by 50–90 %.
f_C, carrier frequency; f_{WS}, wing stroke rate.
Values are means ± S.D. (N=6).
There were no significant effects of reduction of subalar space (one-tailed paired t-test; P>0.3 in both cases).
The mean experimental temperature was 30.4±0.4 °C.

different tegminal resonators (Sismondo, 1979; Bennet-Clark, 1989). Sound pressure level measurements for each individual in each atmosphere were within ±3 dB of each other. As with *A. arboreus*, there was no consistency as to the atmosphere in which the higher SPL occurred.

Alteration of the subalar volume in Anurogryllus arboreus

Table 3 presents the results of a direct test of the subalar–tegminal resonance model of f_C control in *A. arboreus*. When variously sized objects were placed in the subalar spaces of calling individuals such that between 50 and over 90 % of the volume was filled, there were no statistically significant changes in f_C. Upon reducing the subalar volume, f_C might either decrease or increase but in no case was the change greater than 0.8 % of the control f_C. Note that the experiments reported in Table 3 were carried out on generally smaller crickets than those used in other experiments (mean for this experiment 0.279±0.063 g; mean mass for chamber recording experiments 0.4434±0.025 g). Smaller *A. arboreus* have higher f_C than larger individuals (K. N. Prestwich, unpublished data) and this accounts for most of the 18 % difference in control values of f_C (compare Tables 2 and 3). In addition, a small part of the increase in f_C can be accounted for by a higher mean temperature of 30.4±0.4 °C (Prestwich and Walker, 1981). The important point is that the experimental manipulations resulted in no significant changes in f_C compared with control values. Moreover, in two additional experiments at 26 °C, reduction of the subalar volume was accompanied by a slight decrease in f_C in one case and an increase in another (both changes were less than 1 %).

Subalar volume reduction also did not affect the SPL, as can be seen from the constant sound pulse amplitudes in Figs 5, 6. Furthermore, the crickets made no observable adjustments in tegminal position when the subalar volume was reduced (the experimenter was within 0.3 m of the subject and could clearly see the tegmina). The experimental volume reductions were so large that any postural compensations or SPL reduction should have been evident.

Tegminal free resonances in Gryllus rubens

At 23 °C, the mean free resonant frequency of harps isolated

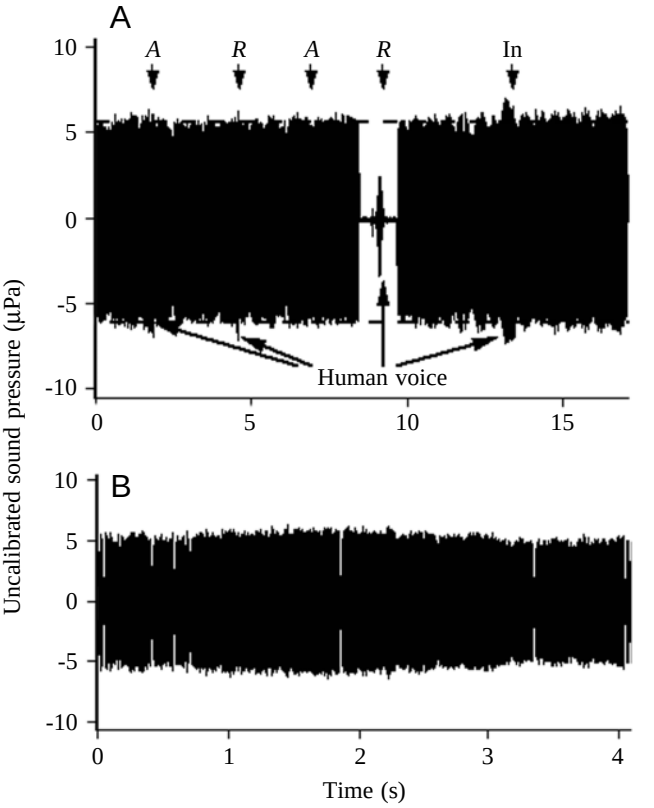

Fig. 5. Low-resolution waveforms recorded during the subalar space reduction experiment at 30 °C. (A) A 17 s calling period. Wooden dowels that occupied 50–90 % of the subalar volume were placed either in control or experimental positions. There were two types of control: 'above' (*A*) means that the dowels were placed immediately above the tegminal harps (not in the subalar space); 'removed' (*R*) is when the dowels were removed totally from the vicinity of the cricket. The experimental treatment ('in') means that the dowels were moved as close to the tegmina and as deeply into the subalar space as possible. Experimenter speech artifacts are indicated; the cricket stopped calling briefly when the dowel touched the tegmina (center). Note that there were no changes in amplitude when the dowel was inserted into the subalar space. (B) A low-resolution view of 5 s of calling during which no experimental manipulation occurred. Note that some changes in amplitude occur as the animal calls continuously.

from *G. rubens* was 5.21±0.41 kHz (N=4) in air and 5.69±0.29 kHz (N=4) in a helium-air mixture containing approximately 75 % helium:25 % air ('heli-air'). This difference was statistically significant (P<0.01, one-tailed paired t-test). The mean ratio of the resonant frequency in heli-air to air was 1.09±0.04 (N=4), similar to that found in intact crickets (Table 2). This indicated that auditory feedback did not cause the frequency shifts in singing animals. Free resonant frequencies in air were higher than the f_C of natural *G. rubens* calls, which we determined to have a mean value of 4.79±0.23 kHz (N=4) at 23 °C.

Measurement of Q *in* Anurogryllus arboreus

The mean Q of *A. arboreus* calls in air was 18±5 (N=3),

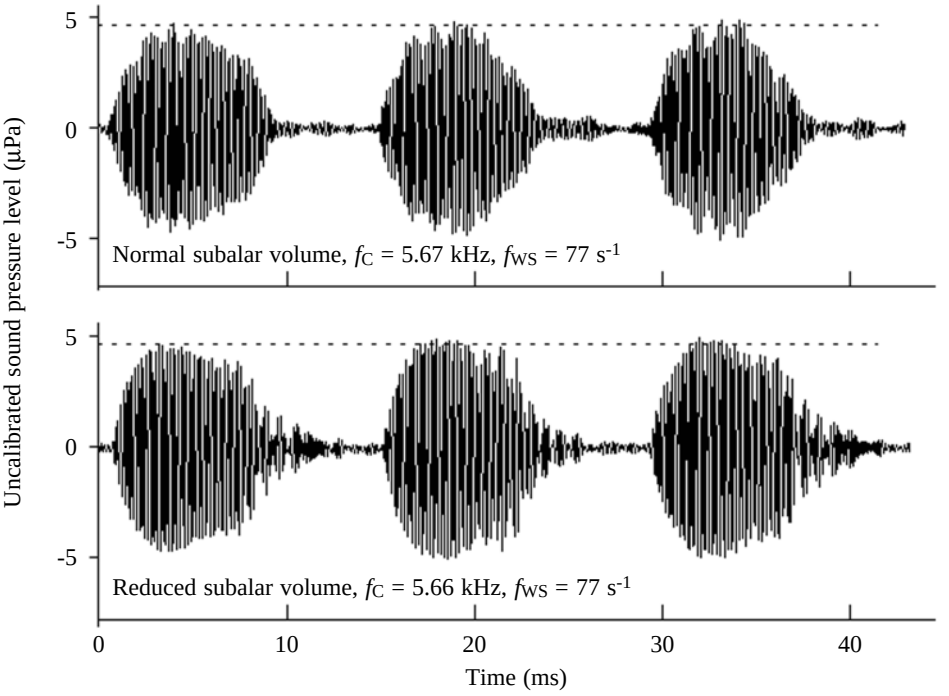

Fig. 6. High-resolution waveforms for an individual *Anurogryllus arboreus* calling before (A) and during (B) the reduction of the subalar volume by 50–90 %. A and B were recorded within 3 s of each other and are for a different individual from that in Fig. 5. The cricket continued to call from the same position relative to the microphone throughout this procedure and did not adjust its tegminal position in response to the volume reduction. Note that the peak and mean pulse amplitudes are the same in A and B. Minor differences in pulse shape occur over time irrespective of whether or not the subalar volume is altered. Identical results were obtained in experiments on five other *A. arboreus*. The recordings were made at 30 °C. f_C, carrier frequency; f_{WS}, wing stroke rate.

based on measurements of 10 pulses for each individual; the CV for each individual was approximately 25 %. This value of Q is similar to that reported by Bennet-Clark (1971), but lower than that reported by Nocke (1971) for isolated *Gryllus campestris* tegmina ($Q \approx 28$).

Discussion

Stephen and Hartley (1995b) regarded the 5–10 % change in f_C that occurred when crickets called in different atmospheres as central evidence for their model of f_C control. Their model predicts that, for crickets with a subalar space, such as *A. arboreus*, calling in heliox-air would cause an increase in the f_{PFI} and therefore an increase in f_C. Presumably, the cricket would attempt to call initially at its normal f_C and would then adjust its call using auditory feedback. Their model also predicts that the subalar volume would need to decrease so as to retune the subalar–tegminal resonator to match and amplify the new f_{PFI}. Failing this adjustment, the amplitude of the new higher-frequency call would decrease.

We found f_C shifts in crickets calling in heliox-air (7–14 % increases; Table 2) similar to those reported by Stephen and Hartley (1995b). However, these occurred regardless of whether the species possessed a subalar space and were accompanied neither by decreases in SPL nor by observable alterations in tegminal position. These results cast doubt on a causal role for the subalar space. But could the f_C shifts have been due to auditory distortion as Stephen and Hartley (1995b) suggest? We did not observe a period of frequency adjustment when a cricket first began to call in a new atmosphere. The f_C of the initial calls in the new atmosphere was already shifted to the same extent as subsequent calls. However, we did record shifts in the free resonance frequency of isolated tegmina from *G. rubens* that were similar to the f_C shifts of intact crickets, even though auditory feedback was impossible. The auditory feedback element of the model is thus disproved.

Our results also show conclusively that the subalar space and tegmina do not form a Helmholtz-like resonator. Direct experimental manipulation of the subalar volume did not affect the call amplitude nor did it result in changes in the f_C or in the position of the tegmina. Moreover, there is no reason to believe, *a priori*, that the subalar space could function as the compliant element of a Helmholtz-like resonator. Fig. 1 shows that the rear of the subalar volume, its largest aperture, is fully open to the environment; the lateral regions are also open. These gaping openings present virtually no impedance to bulk airflow. Any tendency to compress air between the wings and the body is negated by flow out through the sides and the rear aperture. Instead of resembling a Helmholtz resonator, the tegmina and subalar space are analogous to a flask with its bottom broken off. Such flasks do not resonate. We conclude that a subalar–tegminal resonator also does not exist in crickets that stridulate and produce songs similar to those of *Anurogryllus arboreus* and *Gryllus bimaculatus*.

What then caused the f_C shifts in heliox-air? Shifts in the free resonance frequency of excised tegmina were very similar to the f_C shifts observed in living crickets, suggesting that the structures affected by the change in gas composition were the tegminal harps. According to equation 1, f_0 will increase if either the system's compliance C and/or its inertance L decrease. It is possible that compliance would decrease if the tegmina dried when they were exposed to dry gas, such as heliox from a compressed air cylinder. However, humidification of both air and heliox-air had no effect on the f_C or free resonance shifts, thereby ruling out compliance changes as the cause.

The alternative possibility is that the inertance of the resonating system changed. This inertance (L, given as kg) consists of two components in series:

$$L = L_{harp} + L_{gas}, \quad (8)$$

where L_{harp} is the inertance due to the mass of the vibrating portions of the harp and L_{gas} is the inertance due to the mass of the thin layer of gas that is displaced along with the harp. Typically, one ignores the air load when calculating the resonance of a mechanical radiator (e.g. a metal tuning fork) because the vibrating object is far more massive than the air. Stephen and Hartley (1995b) found no change in the free resonance of *G. bimaculatus* tegmina in what they believed (but did not measure) to be a pure CO_2 atmosphere. However, given the amounts of air that entered their (and our) recording chambers, it is likely that their chamber did not contain enough CO_2 to cause an observable shift in the free resonant frequency, especially since a given change in CO_2 will not have as great an effect on resonance as helium.

In addition, it is known that cricket's harps are exceedingly lightweight (Nocke, 1971). Bennet-Clark (1975, 1989) pointed out that harps must be damped by a relatively heavy air load to make them function as good radiators. Therefore, we investigated whether changes in L_{gas} could explain the observed shifts. First, we estimated the relative values of L_{harp} and L_{gas}. Assuming that compliance is constant, we can substitute equation 8 into equation 1 and derive an expression for the ratio of the harp's resonant frequency in heliox-air ($f_{0,heliox\text{-}air}$) to that in air ($f_{0,air}$):

$$\frac{f_{0\ heliox\text{-}air}}{f_{0\ air}} = \sqrt{\frac{(L_{harp} + L_{air})}{(L_{harp} + L_{heliox\text{-}air})}}, \quad (9)$$

where L_{air} and $L_{heliox\text{-}air}$ are, respectively, the inertances (kg) due to the masses of the air and heliox-air displaced by the harps. Since heliox-air is approximately 40 % as dense as air, if we rearrange equation 9 and substitute $0.4L_{air}$ for $L_{heliox\text{-}air}$, we can then find the relative values of L_{harp} and L_{air}. For the observed range of frequency shifts of 1.07–1.14 (Table 2), the harp must be approximately 3.9–1.8 times more massive than the air load.

These air loads were larger than expected from other calculations (Bennet-Clark, 1989). So, at the urging of an anonymous referee, we compared the estimate with a calculation of the air mass (inertance) using published values for *G. campestris*. In *G. campestris*, the area of the harp is approximately 15 μm^2 (Nocke, 1971); if we approximate its shape to a disk (for ease of calculation), it would have a radius of 2.2 mm^2. In this case, the radiator is small compared with the sound's wavelength, and so bulk movement of air occurs to a distance approximating the radiator's radius (Fletcher, 1992). Thus, the volume of the air load on the two sides of the harp is approximately 66 µl, and the total air mass is approximately 78 µg at 20 °C. Nocke (1971) calculated the effective mass of the harp (the inertance due to the mass of the vibrating portion of the harp plus the air load) of *G. campestris* to be 163 µg. For comparison, he reported that the same harp weighed 190 µg. Thus, in *G. campestris*, the air mass makes a substantial contribution to the total system mass, perhaps approaching as much as half of the effective mass (78/163=0.48 µg). This agrees well with our calculated values from the present study, suggesting that the explanation for the f_C shifts does indeed lie in changes in the gas load portion of the total inertance of the vibrating system.

The 'clockwork cricket' hypothesis

When proposing the clockwork cricket model, Koch et al. (1988) clearly realized that crickets do not operate as perfect clocks. For example, their data show that the f_C tended to decrease during a sound pulse, suggesting that the regulator of the f_C was a variable-frequency oscillator. Nevertheless, harps have often been discussed as if they were fixed-frequency devices (probably for the sake of simplicity). This is not a problem unless one reifies this clockwork analogy into an actual clock. This was perhaps the fundamental error made by Stephen and Hartley (1995b).

For instance, they pointed to multiple spectral peaks and stated that no clock could run at two frequencies simultaneously. We also observed minor peaks (Fig. 4) although, unlike those reported by Stephen and Hartley (1995b), these peaks were not in constant locations relative to the principal peak. Accessory peaks are probably due to additional tegminal resonances (Bennet-Clark, 1989) whose values could change with subtle differences in wing position or stridulatory movement. Or, they could be caused by reflections within the recording chamber. Regardless, in both studies, the accessory spectral peaks were of very low amplitude compared with the f_C peak. Any slight effect they may have had on the timing of the movement of the stridulatory structures would only be noticeable over long periods. Crickets do not need to maintain their f_C accurately for long periods: the duration of a sound pulse is generally less than 50 cycles (10 ms).

Stephen and Hartley (1995b) reported up to ±3 % pulse-to-pulse variation in the f_C of *G. bimaculatus*; we found up to ±1 % in *A. arboreus*. In both cases, the variation is far greater than would be found in a useful clock (Stephen and Hartley, 1995b). However, these findings do not disprove the existence of an escapement type mechanism in crickets. Instead, they point to differences in the operation of the controlling oscillators of clocks in comparison with those of crickets. These differences relate to the relative values of Q and to the fact that the cricket's oscillator is a variable-frequency device.

Q is a measure of the range of frequencies over which a system can be driven successfully. Systems with higher values of Q have greater amplitudes at resonance, but this response drops off rapidly as the difference between f_0 and the driving frequency increases (Fletcher, 1992). If accurate timekeeping is the objective, the oscillator needs a high Q, which makes it difficult to operate at any frequency but f_0. Oscillators of mechanical clocks typically have Q values in the range of

several hundred; quartz oscillators have far greater Q values and are far more accurate (Landes, 1983; Fletcher, 1992). In contrast, cricket harps must both control the f_C and act as an effective radiator. To be a good radiator, the harp must be damped by high radiation resistance (Bennet-Clark, 1975, 1989). This reduces Q since it is proportional to the ratio of system mass to the radiation (damping) resistance (equation 7). The low Q (Q=18 in *A. arboreus*) makes it possible to drive the harp over a wider range of frequencies than if it were less damped.

A low Q permits frequency variation, but what mechanism is responsible for producing such variation? Not only does f_C variation occur between pulses but also, in most species, there is pronounced within-pulse frequency modulation. We found a 9 % intra-pulse decrease in f_C in *A. arboreus* (Table 1) similar to other values for gryllids (Alexander, 1957; Leroy, 1966; Koch et al., 1988). Recently, Simmons and Ritchie (1996) showed that the degree of intra-pulse frequency modulation in *G. campestris* depends on the relative dimensions and therefore the masses of the left and right harps. In experiments in which they ablated one or the other harp, their results suggest that the resonance of the left (usually smaller) harp is largely responsible for setting the f_C during the initial third of the pulse. The right harp, which is usually larger, with a lower f_0, then becomes dominant for the remainder of the pulse. These surprising results have recently been replicated in *A. arboreus* (K. N. Prestwich, unpublished data).

Bennet-Clark (1999) believes that these data show that the resonating system's mass increases during the tegminal closure. He argues that the f_C is typically lower than the tegminal free resonance (see, for example, our data for *G. rubens*) and concludes that, when the two harps are coupled together *via* the stridulatory apparatus, mass is added to the system. He cautions that little is known of the exact mechanism, but speculates that the cause is a shift in effective mass caused by changes in the point from which the right harp is excited during a wing stroke. Although the left (lower) harp is driven throughout the tegminal closure from its medial apex *via* the plectrum, the driving point for the right (more massive) harp moves laterally from its medial apex as the contact point with the plectrum skips along the file. If the vibrating mass changes as a function of the relative sizes of the left and right harps and the position of the plectrum on the file, then it is easy to imagine that pulse-to-pulse differences in f_C could be due to differences in the point where the plectrum first contacts the file.

So, it is clear that crickets are not as accurate as fine Swiss watches. However, both watches and crickets are controlled by escapement mechanisms. The workings of a watch are optimized to keep time accurately for human uses. Crickets use an analogous escapement/regulator mechanism, but optimize its operation to make brief loud signals at a frequency as near as possible to the peak auditory sensitivity of conspecific females. Calling males seek to attract mates and make time, not keep time. We might add that watches are also used to attract mates, but the mechanism in this case is different.

List of symbols

$BW_{-3dB,SPL}$	bandwidth at 3 dB SPL re 20 μPa below the peak
c	speed of sound
C	compliance
$f_{0,air}$	resonant frequency in air
f_C	carrier frequency
f_0	resonant frequency
f_{PFI}	plectrum-to-file impact rate
$f_{0,heliox\text{-}air}$	resonant frequency in heliox-air
f_{WS}	wing stroke or sound pulse rate
L	inertance
L_{air}	inertance of air moving *en masse* together with the vibrating harp
L_{gas}	inertance of any gas moving *en masse* together with the vibrating harp
L_{harp}	inertance of the harp
$L_{heliox\text{-}air}$	inertance of heliox-air moving *en masse* together with the vibrating harp
l'	effective length
$\log_e$(decrement)	the natural logarithm of the rate of decrease of the amplitude of an undriven oscillation
M	mass
P_0	pressure in the absence of sound
Q	quality factor
R	damping (specific acoustic) resistance
S	cross-sectional area
SPL	sound pressure level, re 20 μPa
V	volume
γ	dimensionless ratio of specific heats
λ	wavelength
ρ	density

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