

# STRATEGIES FOR HEARING IN NOISE: PERIPHERAL CONTROL OVER AUDITORY SENSITIVITY IN THE BUSHCRICKET *SCIARASAGA QUADRATA* (AUSTROSAGINAE: TETTIGONIIDAE)

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## Summary

The carrier frequency of the call of the Australian bushcricket *Sciarasaga quadrata* is unusually low for tettigoniids at 5 kHz. The sound transmission measured in the habitat of the insect reflects the advantages of producing low- rather than high-frequency signals; attenuation is explained almost entirely by the spherical spreading of sound. The natural vibration frequency of the wings is controlled by size and stiffness. The small tegmina are unusually fleshy, with an order-of-magnitude higher water content than in comparable sagine species. Reduced stiffness allows the insect to call at low carrier frequencies, albeit at lower intensity levels (60 dB SPL at 1 m), than bushcrickets of comparable size (80–90 dB SPL). The responses of the tympanic nerve and a first-order interneurone (omega neurone) in the afferent auditory pathway showed that the hearing system is most sensitive to frequencies of 15–20 kHz, an effective mismatch to the conspecific call resulting in a reduced sensitivity of approximately 20 dB at the carrier frequency of the call. *S.*

*quadrata* can occlude its spiracular opening, which increases the sensitivity of the ear to lower frequencies. Under such conditions, the best frequency of the ear matched that of the carrier frequency of the call. We measured the activity of auditory neurones in the field, noting the ability of the open and partially closed ear to filter out potentially masking calls of congeners. At the same time, the directionality of the system was only slightly reduced in the closed relative to the open spiracle status. We discuss the evolutionary advantages of an insect both calling with a low carrier frequency and having the ability to close down the tracheal system to avoid the effects of masking. In addition, we consider the advantages of such a signalling system in avoiding the most significant predator of the male, the ormine fly *Homotrixa alleni*.

Key words: hearing, noise, bushcricket, *Sciarasaga quadrata*, Tettigoniidae.

## Introduction

For most animals that use sound to communicate between the sexes, there is a match between the pitch, or dominant frequency, of the signal and the hearing sensitivity of the receiver (Ryan and Keddy-Hector 1992). Although there are a number of exceptions to this general rule among the insects (cicadas: Popov, 1981; Huber *et al.* 1990; bushcrickets: Bailey and Römer, 1991; hagdids: Mason, 1991), it can be assumed that sensory matching has been arrived at by reciprocal selection on both signallers and receivers (Endler, 1992).

There are three major sources of selection on call frequency and the best frequency of the auditory system: (i) mate choice (Searcy and Andersson, 1986; Andersson, 1994), (ii) predator detection and avoidance (Endler, 1992), and (iii) prey detection by acoustically orienting predators (Cade, 1975; Wagner, 1995). In many systems, female preference exerts stabilising selection on carrier frequency, and the average tuning of the auditory system matches the mean carrier frequency of the

population. In other systems, females prefer signals with carrier frequencies above or below the population mean, and this constitutes a source of directional selection on the song (e.g. Gwynne and Bailey, 1988; Latimer and Sippel, 1987; Ryan and Keddy-Hector, 1992). In still other systems, predators can be detected by auditory units that are tuned to frequencies distinct from those used for listening to the calls of conspecifics (Moiseff *et al.* 1978; Robert *et al.* 1994; Libersat, 1989). In such cases, the tuning of the ear may be under selection from potentially conflicting forces, mate attraction and predator avoidance (Bailey, 1991). Endler (1992) refers to the complex evolutionary processes that shape the sensory system as 'sensory drive' (Endler and McLellen, 1988), and we argue that such processes may have shaped the phenomenon we describe in the present paper.

As most environments are heterogeneous in time and space, degradation of the signal will, in most cases, occur in an

unpredictable manner (Wiley and Richards 1982; Embleton, 1996), and there will be strong selection on the ability of the receiver to detect a signal against background noise. Background noise may be from the environment itself, such as moving water, disturbed vegetation or sounds made by noisy congeners. Ideally, the signaller should call at optimum times when the habitat is acoustically benign (Wiley and Richards, 1978) and so the signal-to-noise ratio is high. This can be achieved by significant behavioural changes or by shifts in the frequency of the communication channel. Several studies suggest that animals calling within single- and multiple-species aggregations adopt different tactics to avoid being masked by neighbouring animals (Schwartz, 1987, 1994; Römer *et al.* 1989; Greenfield, 1993, 1994).

Narins (1995) suggests that masking interference in frogs may lead to species adopting 'private channels' for intraspecific communication; in other words, the use of a unique band of frequencies for the mixed-species communities. Shifts in either the carrier frequency of the call or the best frequency of the ear as an evolved response to masking or predator detection may lead to an apparent mismatch between sender and receiver (Römer, 1993). A decrease in absolute threshold sensitivity at the carrier frequency of the call may be compensated by a higher signal-to-noise ratio, achieved largely by using a frequency band less used by congeners. In reviewing constraints on the evolution of long-range signalling and hearing in insects, Römer (1993) referred to apparent auditory mismatching in the genus we use in the present study, *Sciarasaga quadrata* (Austrosaginae: Tettigoniidae), which was then referred to as an undescribed species. At 5 kHz, the call of this sagine is remarkably low for tettigoniids (Allen, 1995a) and is well beneath the most sensitive frequency of the ear of 10–20 kHz. In contrast, the calls of sympatric congeneric bushcricket species are typically in this range (there are at least 16 sympatric tettigoniid species in the area studied; Allen, 1995a), which suggests that *S. quadrata* has increased the signal-to-noise ratio by calling outside a frequency range used by species competing for these carrier frequencies.

In the present paper, we describe a case of auditory mismatching in an unusual species of sagine bushcricket. We attempt to relate this phenomenon to behavioural observations both in the field and in the laboratory, where *S. quadrata* altered its auditory system by partial closure of the auditory spiracle. We demonstrate that such a closure brings the system into a matched tuned condition and we test the effects of these changes on auditory sensitivity and masking. Finally, as *S. quadrata* is heavily parasitized by an acoustically orienting parasitoid fly, *Homotrixa alleni*, we speculate that the call of the bushcricket may be under strong selection to be outside the best frequency range of the hearing system of the fly (Lakes-Harlan *et al.* 1995).

## Materials and methods

### *The insect*

*Sciarasaga quadrata* (Orthoptera, Tettigoniidae) is a monotypic genus within the Austrosaginae and is endemic to

restricted coastal heathlands of southwestern Australia (Rentz, 1985). Males are large (3–4 cm total length and pronotum length between 9.8 and 10.3 cm; Allen 1995a), non-saltatorial and brachypterous, emerging as adults in late spring (mid-November) and continuing to call into February. They typically call from deep within dense coastal scrub, which includes species such as *Spyridium globulosum* (height  $1.2 \pm 0.06$  m), *Olearia axillaris* (height  $1.4 \pm 0.05$  m) and *Melaleuca acerosa* ( $0.7 \pm 0.03$  m) (Allen, 1995a). Although dense, the leaves of these sclerophyllous plants tend to be small (less than 1 cm across and less than 3 cm long). Calling commences during mid-to-late afternoon and continues throughout the night. Although males appear to maintain no spatial relationship with calling neighbours, they move frequently and patterns of spacing are extremely dynamic (Allen, 1995a).

The study site for experiments at Cape Naturaliste, Western Australia (33°33'S, 115°01'E) encompassed approximately 8 ha. Field experiments described in this paper were carried out during 1990/1991.

### *Sound transmission*

The sound transmission properties of the coastal habitat were studied in two ways. First, we located individual calling males and recorded their height within the bush. To avoid disturbing the insect, the sound pressure level (SPL) of the call was measured at arbitrary distances from the insect, using a Brüel and Kjaer 1/2 inch microphone (type 3265) fitted to a Brüel and Kjaer sound level meter (type 2209) coupled to an external highpass filter set to 2 kHz. The distance between the insect and the microphone was later measured.

The second technique involved broadcasting pre-recorded male calls (Nagra IV-SJ) through a loudspeaker (Audax TW8 spec.) mounted on a tripod 50 cm from the ground. The intensity of the broadcast signal was adjusted to 80 dB SPL at a distance of 1 m. Although this intensity is approximately 20 dB above that of a calling male at the same distance, we used these higher intensities to achieve higher sound pressure levels, and thus better signal-to-noise ratios, at greater distances. Wind speed varied between 1 and 5 m s<sup>-1</sup> during the time the experiments were conducted, resulting in considerable fluctuations in call intensity. Therefore, five recordings were taken at each distance at times when wind speed was low (<1 m s<sup>-1</sup>).

### *Tegmina*

The natural vibration frequency of insect tegmina is controlled, in part, by their size and also by cuticular stiffness (Bailey, 1970). To test the hypothesis that the frequency of sound production in *S. quadrata* is dependent on the stiffness of the fore tegmina, we removed the wings and compared the water content of the tegmina of *S. quadrata* with that of a sympatric sagine of similar size, *Hemisaga denticulata*. After removal, the tegmina were weighed before and after oven-drying; water content was expressed as a percentage of tegmen mass.

### Neurophysiology

Recordings of neural activity were made in three ways. First, we monitored the activity of an identified auditory interneurone, the omega neurone, in the field (Rheinlaender and Römer, 1986). The omega cell is a local, first-order interneurone in the prothoracic ganglion receiving excitatory input from the array of receptors in the tibial hearing organ of the foreleg (Römer, 1987). The tuning of the cell reflects the broad-band hearing sensitivity typical of most tettigoniids, and the spike response faithfully copies the temporal pattern of an acoustic stimulus. Both the ability of the neurone to follow acoustic events and its accessibility for long-term, extracellular recordings make the cell a suitable target for the study of the masking effects of calls from other species in the field.

Second, we recorded the spike activity from the same interneurone in the laboratory under controlled acoustic conditions. Insects were anaesthetised with CO<sub>2</sub> and mounted ventral side up on a small thin metal sheet with the forelegs oriented perpendicular to the axis of the body. A small flap of cuticle covering the prothoracic ganglion was removed, and the electrode was lowered into the region of the omega neurone. Spike activity was recorded extracellularly using electrolytically sharpened, glass-insulated tungsten electrodes (1–3 M $\Omega$ ). The leg nerve carrying axons of the auditory receptors, contralateral to the recorded neurone, was cut to prevent any side-dependent inhibitory effect on the activity of this neurone. The preparation was placed at the centre of an anechoic chamber at a distance of 50 cm from the speaker (Technics EAS-10 TH400A), which could be rotated in steps of 15 or 30° in the horizontal plane around the insect.

Sound pulses (duration of 30 ms, rise-and-fall time 1 ms, repeated once per second, with different pure-tone carrier frequencies in the range 2–80 kHz) were used to determine the threshold of the neurone. Sound pulses were attenuated in steps of 1 or 10 dB (Akustischer Stimulator II, Burchard). The threshold of the neurone was determined by the procedure described in Rheinlaender and Römer (1980). Sound intensities (SPL re 20  $\mu$ Pa – RMS fast) were measured with a Bruel and Kjaer 1/4 inch microphone (type 4136) through a Bruel and Kjaer sound level meter (type 2209).

Third, we checked the tuning of the ear by recording the activity of the afferent axons in the tympanic nerve. Auditory mismatching may be caused by the omega neurone not integrating all afferent low-frequency fibres from the tympanic nerve. We used a chlorided silver hook electrode under the dissected leg nerve and measured thresholds from averaged summed action potentials over 256 sound presentations (Neurolog Averager NL750). Threshold was reached when there was no detectable summed action potential in response to a sound stimulus.

### The auditory spiracle

The auditory spiracle is a primary route through which sound travels to the inner surface of the tympanic membranes (Lewis, 1974; Seymour *et al.* 1978; Bailey, 1993; Michelsen *et al.* 1994). During field experiments, we noted that *S.*

*quadrata* males closed their auditory spiracle when calling. We brought males (uninfected by the fly parasitoid *Homotrixia alleni*) into the laboratory and filmed them while calling. As in the field, there was partial closure of the auditory spiracle. However, when continuous pure tones at 16 kHz were played at 80 dB SPL measured at the insect (an experiment described more fully elsewhere), we observed the almost total closure of the spiracle. In addition, the insect could close its spiracle when handled. Fig. 1 shows the progressive closure of the auditory spiracle in a male. Females were able to close the spiracle in an identical manner, both in the presence of noise and when handled.

One hypothesis we test in this paper is the extent to which the insect may influence its hearing sensitivity by closing the tracheal system. To determine the contribution of the auditory spiracle to the tuning and sensitivity of hearing, we progressively blocked the spiracle with wax. The area of open spiracle was measured after each experiment by placing the insect beneath a binocular microscope and drawing the opening of the spiracle using a *camera lucida*.

A second, related hypothesis concerns the relationship between the opening status of the auditory spiracle and the ability of the insect to filter the high-frequency sound signals of sympatric species. To test this, we presented calls of conspecific males mixed with calls of heterospecific species through two adjacent loudspeakers, each placed ipsilaterally to the preparation. The SPLs of the calls of conspecific and sympatric species were calibrated at the position of the preparation and adjusted through separate attenuators. Each stimulus was presented 20 times to calculate peri-stimulus-time (PST) histograms of the omega neurone response. The open spiracle was then partially blocked with wax in the manner described above, and the procedure repeated.

## Results

### Sound production and signal transmission

As is typical for tettigoniid Orthoptera, *S. quadrata* produces sound by tegminal stridulation. However, unlike other tettigoniids, males of this species have extremely fleshy wings. The water content of the short tegmina of the male (length 15–17.4 mm; mean  $\pm$  S.D.,  $N=7$ ) was almost an order of magnitude greater than that of *H. denticulata* (*S. quadrata*,  $63 \pm 2\%$ ,  $N=7$ ; *H. denticulata*,  $5 \pm 3\%$ ,  $N=7$ ; mean  $\pm$  S.D.). The length of the strigil on the right wing, which is proportionately as long as the mirror frame of species that have a sound-radiating mirror, was close to 4.8 mm. Without the resonant mirror structures associated with the cubital vein, the tegmina appear to act as poor radiators of sound, primarily because the mechanics of sound production are dependent on both the stiffness of the wings (Young's modulus) and the size of the mirror area (Bailey, 1970). The call, as measured 1 m dorsally, had a mean SPL of 61.7 dB and seldom exceeded 63 dB SPL, with the maximum energy peak at 5 kHz. There is very little energy in the call above 10 kHz (Fig. 2).

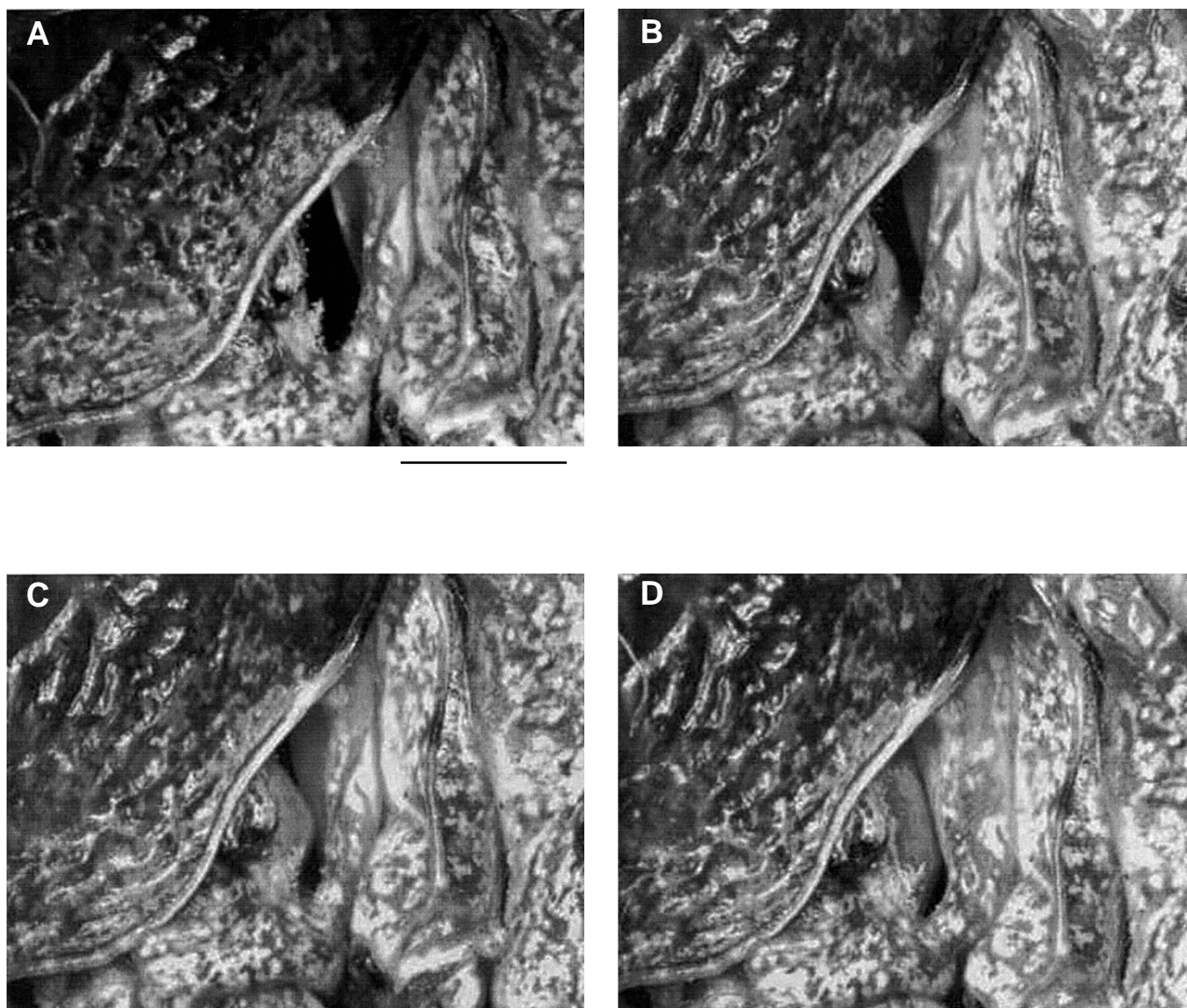


Fig. 1. The closure of the auditory spiracle of *Sciarasaga quadrata*. Progressive single-frame video images showing the closing of the front and rear walls of the spiracle. Left is anterior, top is dorsal. Scale bar, 2.5 mm.

The call of *S. quadrata* is transmitted extremely well through the vegetation. Measurements from both calling males (Fig. 3, lower plot) and from the speaker (Fig. 3, upper plot) show that the variation of the SPL of the call with distance can be explained almost entirely by the spherical spreading of sound (i.e. 6 dB per doubling of distance; dashed lines in Fig. 3). This was particularly true for insects calling low in the scrub where, on the basis of previous studies (see Römer and Lewald, 1992), we expected excess attenuation to be severe.

#### Hearing sensitivity

The hearing sensitivity of *S. quadrata* was studied in the frequency range 3–70 kHz, by monitoring the summed spike discharge of the tympanal fibres and the omega neurone (Fig. 4A). With the spiracle open, the highest sensitivity was consistently found between 10 and 20 kHz, with absolute

thresholds close to 20 dB SPL. The comparison between the tuning of five omega cell preparations and that of tympanal receptors (dashed line in Fig. 4A) reveals a slightly lower threshold determined from the receptor axons at frequencies below 5 kHz, but a good correspondence at higher frequencies. Therefore, the threshold of the omega neurone could be viewed as monitoring the hearing sensitivity of the whole ear.

There is, however, an apparent mismatch between the carrier frequency of the male call at 5 kHz and the frequency of highest sensitivity in the ear from 10 to 20 kHz. At 5 kHz, the ear is approximately 20 dB less sensitive than it is between 10 and 20 kHz.

Hearing sensitivity is dependent on sound reaching the internal surface of the tympanum *via* the auditory spiracle and associated trachea. When sound is prevented from entering through this route by completely blocking the spiracle opening,

the system loses sensitivity over the frequency range from 4 to approximately 70 kHz (Fig. 4A, dotted lines). In the completely closed spiracle condition, the ear is rather broadly sensitive between 5 and 20 kHz. Fig. 4B shows the net gain provided by the tracheal input, i.e. the change of amplitude for sound propagating to the internal surface of the tympana, as measured by the difference in threshold between the blocked and unblocked conditions. At frequencies between 4 and approximately 30 kHz, the trachea appears to provide a high relative gain of up to 30 dB, acting as an effective band-pass filter.

Blocking the spiracle to varying degrees with dental wax mimicked the condition of spiracle closure illustrated in Fig. 1. In each experiment, the open spiracle condition was used as a control. Fig. 4C shows the effect of reducing the area of the spiracular opening to varying degrees on the tuning of the omega neurone. When the spiracle was blocked to 15% or 7% of its opening area, the sensitivity of the ear increased in absolute dB for frequencies below 10 kHz and 7 kHz, and decreased between 8 and 40 kHz by up to 32 dB at 20 kHz by comparison with the open spiracle condition. Clearly, the most significant effect is seen with the partially blocked spiracle, with an increase in sensitivity to frequencies of the conspecific

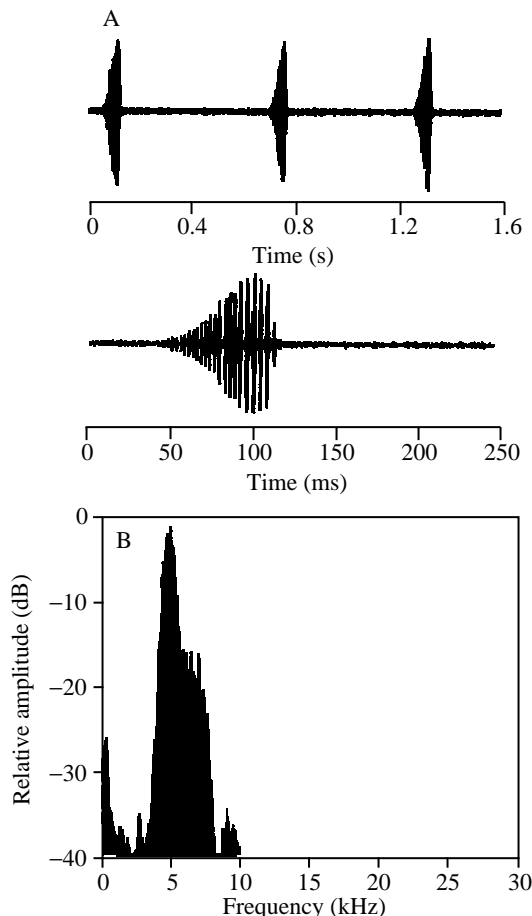


Fig. 2. The temporal pattern pattern shown on two time scales (A) and the spectrum (B) of the calling song of a male *Sciarasaga quadrata*.

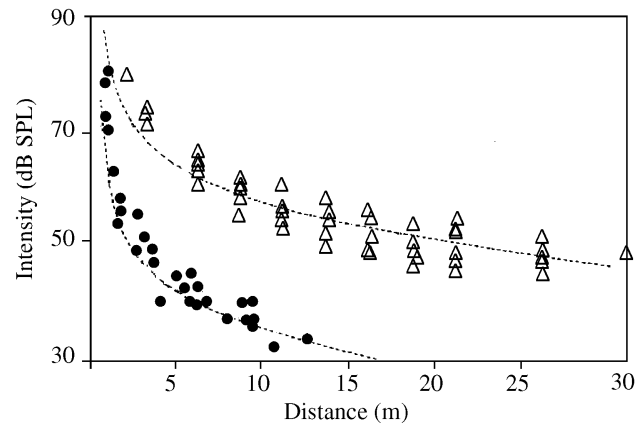


Fig. 3. The sound pressure level (SPL) of the male call at various distances from the source in the natural habitat. The upper curve (open triangles) gives measurements obtained from a speaker broadcasting a male call with an SPL of 80 dB at 1 m. The lower curve (filled circles) gives data from calling males in the same habitat. The dashed lines indicate attenuation of sound due to geometric spreading alone (6 dB per doubling of distance) assuming, at 1 m, an SPL of 80 dB or 60 dB, respectively.

calling song and a decrease at higher frequencies, depending on the extent of spiracle closure. As a result, in the partially closed spiracle condition, the sensitivity to the male call increases by 5 dB ( $N=6$  males).

#### Auditory tuning and masking

Given the degree of mismatch in the open spiracle condition, we predicted that sounds in the environment occupying a frequency range between 10 and 30 kHz would effectively mask the calls of conspecific males. We suggest this for two reasons. Although bushcrickets have auditory receptors tuned to low frequencies (which would be little affected by high-frequency masking sounds), there are no reports of first- or higher-order interneurons ascending and providing tuned information to the brain areas. Rather, there are more or less broadly tuned interneurons, such as ON1 (omega neurone), AN1, AN2 and others (for a review, see Stumpner, 1997). Such neurones would be strongly influenced by masking from the high-frequency signals of other species. We identified two likely candidates with relatively continuous calls that would achieve such masking, namely *Mygalopsis pauperculus* (Copiphorini) and *Metaballus litus* (Tettigoniini). The sagine *Hemisaga denticulata*, which is also sympatric, has a slow extended chirp repeated over several seconds (Römer *et al.* 1989). *M. pauperculus* has a call frequency with acoustic energy in the range 14–25 kHz, the call of *M. litus* has dominant frequencies between 12 and 25 kHz, and that of *H. denticulata* has a broad-band spectrum with a main peak at 12 kHz. Our field recordings indicate that SPLs at the position of the receiving male show that these potential masking sounds often exceed the intensity of calls made by neighbouring conspecifics.

We predicted that, in the natural setting, calls of *S. quadrata*



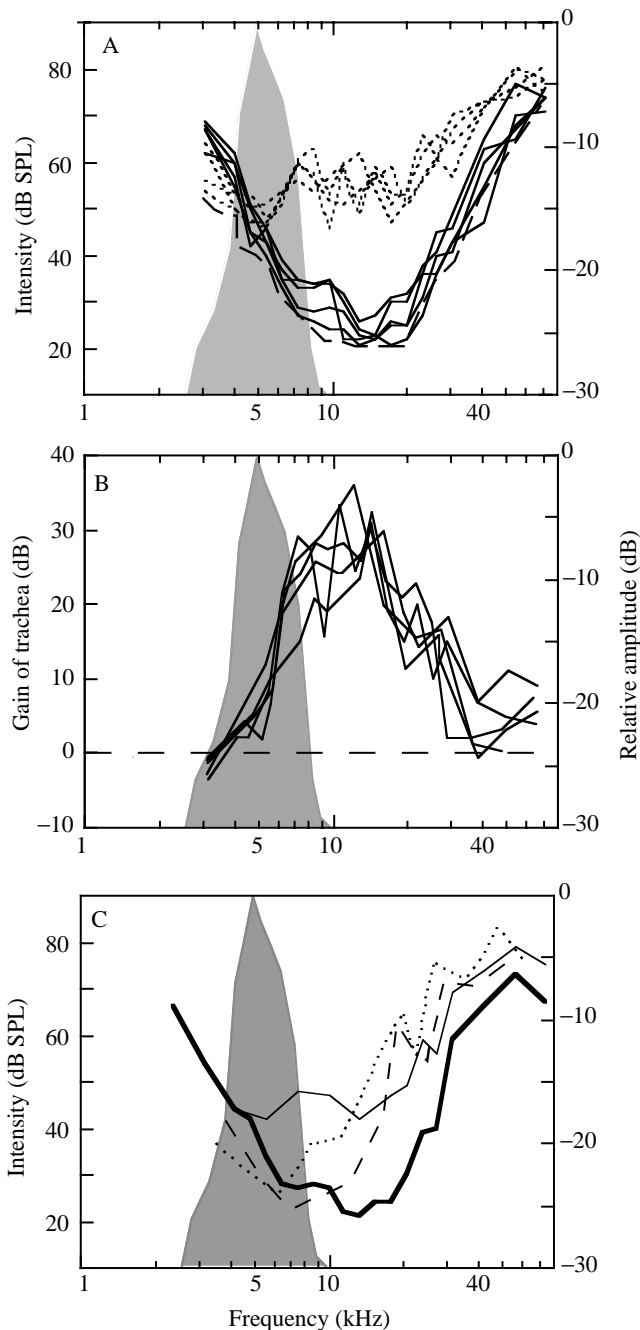


Fig. 4. (A) Tuning of five omega cell preparations with the unmodified, open tracheal system (solid lines) and with the spiracle completely blocked with wax (dotted lines). The dashed line gives the tuning of the ear established from tympanal nerve recordings (mean values for three males and one female). (B) The amplitude part of the gain of the trachea given as the difference in sensitivity between the two tracheal conditions. (C) Tuning of one omega cell preparation with the unmodified, open tracheal system (thick, solid line) and the same preparation with the spiracle blocked with wax to 15% (dashed line), 7% (dotted line) and 0% (complete block; thin solid line). The spectrum of the male call (shaded area) is given for comparison.

would be masked in the presence of calling heterospecifics. We therefore located calling male *S. quadrata* in the field and replaced them with a portable preparation of the omega

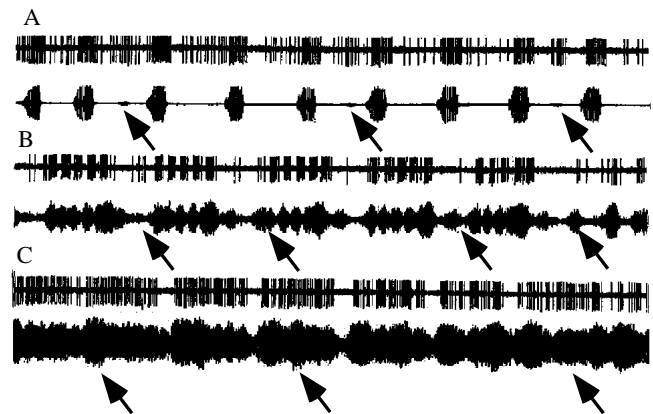


Fig. 5. Masking of the response to conspecific male calls by heterospecific bushcricket species in the field. Recordings of omega cell activity were made at the position of three different *Sciarasaga quadrata* males in the field (A–C; upper lines), and microphone recordings at a distance of approximately 5 cm from the preparation (lower lines). (A) Activity in response to a conspecific male at a distance of 1 m and another male (arrows) 6 m away in the same direction as the first male. (B) The conspecific male (arrows) was within 4 m of the preparation, while a male *Metaballus pauperculus* was 6 m away. The continuous calling of *M. pauperculus* effectively masks the response of the omega cell to the conspecific. (C) The masking effect is even more marked in another situation when *M. pauperculus* is within 3.5 m and another unknown heterospecific is at a distance of approximately 5 m.

neuron. Fig. 5A–C shows three representative examples of omega neuron activity from three different recording positions. The activity shown in Fig. 5A was in response to a conspecific male at a distance of 1 m and a second male 6 m away in the same direction as the first male. There were no other calling insects within a range of at least 10 m. Masking appears minimal under these conditions, except where the calls of the two males overlap. In the case illustrated in Fig. 5B, a conspecific male was within 4 m of the preparation while a male *M. pauperculus* was 6 m away. The continuous calling of *M. pauperculus* effectively masks the response of the omega neuron to the conspecific. The masking effect is even more marked when the heterospecific is within 3.5 m (Fig. 5C).

Such field observations with a ‘biological microphone’ do no more than illustrate the potential for masking by sympatric species. If our assumption that the insect is capable of closing the auditory spiracle under noisy conditions is correct, we would expect males to hear conspecifics under a closed spiracle condition with an improved signal-to-noise ratio. We therefore performed a series of laboratory experiments in which we simulated different masking conditions experienced in the field, again using open and partially closed spiracle conditions.

Fig. 6A shows the results of an experiment where the conspecific call was broadcast in the presence of a potential masking species, *Metaballus litus*. The intensities of both calls were adjusted to 50 dB SPL, which represents a conspecific male calling at a distance of 3–4 m and the heterospecific

calling slightly beyond this distance. In the open spiracle condition, the response to the conspecific is entirely masked when the chirp sequences of *M. litus* temporally overlap the single calls of *S. quadrata*. The magnitude of the response of the omega neurone to the unmasked conspecific was smaller than that to the heterospecific. When the opening area of the spiracle was reduced to 6% by partial blocking, the same stimulation resulted in an increased response to the conspecific call and, at the same time, a strongly reduced response to the masking heterospecific (compare the response of the first syllable in Fig. 6A with that in Fig. 6B). In the closed spiracle situation, the activity of the omega neurone exhibits a discharge pattern showing the conspecific signal without the masking influence of *M. litus*.

We then recorded sounds at the position of a removed focal male in the field, where another conspecific male as well as a number of heterospecifics were calling. The amplitude of the heterospecific call in this recording was approximately 20 dB less than that of the conspecific. When this recording was played to an omega preparation in the laboratory with a peak intensity of 60 dB SPL, the omega neurone responded strongly to the conspecific call as well as to the less-intense background sounds when the spiracle was open (Fig. 7). However, when the spiracle was completely blocked, the response to

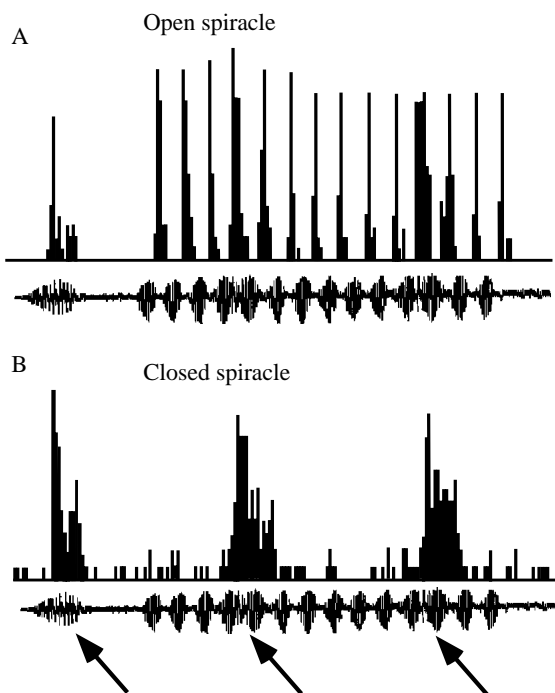


Fig. 6. Activity of an omega neurone in response to a simultaneous broadcast of a conspecific male call (arrows in lower line) and a series of chirps of *Metaballus litus* in the unmodified, open tracheal system (A) and the same preparation with the spiracle partially blocked with wax to 6% (B). Note the increase in response to the conspecific first call and the almost complete cessation of the response to the syntopic species in the partially blocked condition. The histogram is made up of 20 repetitive responses; bin width 2 ms.

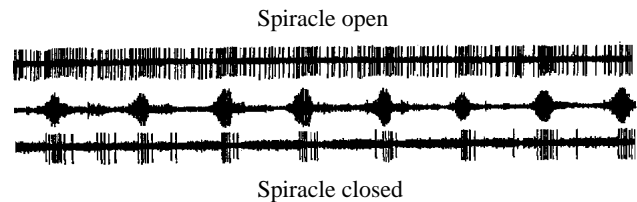


Fig. 7. Activity of an omega neurone in response to sound recordings made in the field at the position of a removed male where another male was calling as well as a number of heterospecifics in the background. The amplitude of the heterospecific calls was approximately 20 dB lower than that of the conspecific. Playback intensity was 60 dB SPL. Note that, in the open spiracle condition (upper recording), the omega neurone exhibits high background activity in response to the less-intense sounds of the syntopic bushcrickets, whereas in the blocked condition (lower recording) there is a clearly detectable response pattern to the species-specific call.

background sounds was much reduced, while there was a consistent and undisturbed response to the conspecific call.

#### Directionality

To examine any effect of spiracle aperture on the directionality of hearing, we measured thresholds of the omega neurone at different stimulus angles of sound incidence. As expected, sounds presented ipsilaterally elicited a response at the lowest threshold (Fig. 8). The steepest increase in threshold with changing stimulus angle was from 30° ipsilateral to 30° contralateral, with a maximum difference of 6 dB. When the

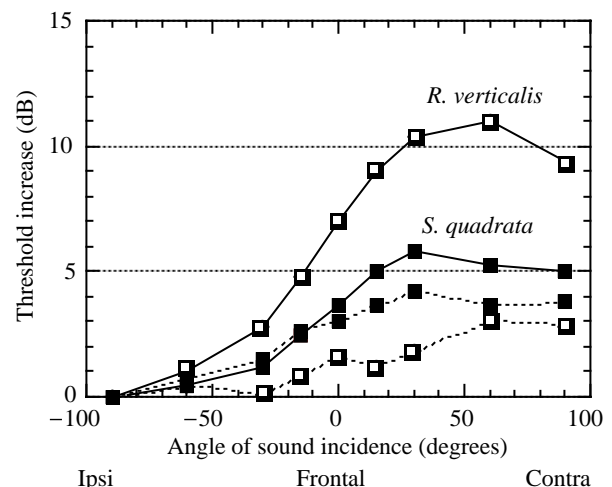


Fig. 8. Directionality of the peripheral auditory system of *Sciarasaga quadrata* in the open (filled squares, continuous line) and completely blocked (filled squares, dashed line) condition. Directionality is given as the increase in threshold of the unilateral omega neurone preparation in response to the conspecific call with changing angle of sound incidence (0° is sound from the front). Values are means of five preparations, s.d.  $< \pm 1$  dB. The results of similar experiments with the bushcricket *Requena verticalis* are given for comparison (open squares). Note that the peripheral directionality in *S. quadrata* is only slightly affected by closing the spiracle (difference 1.5 dB) compared with *R. verticalis* (difference 8.0 dB).

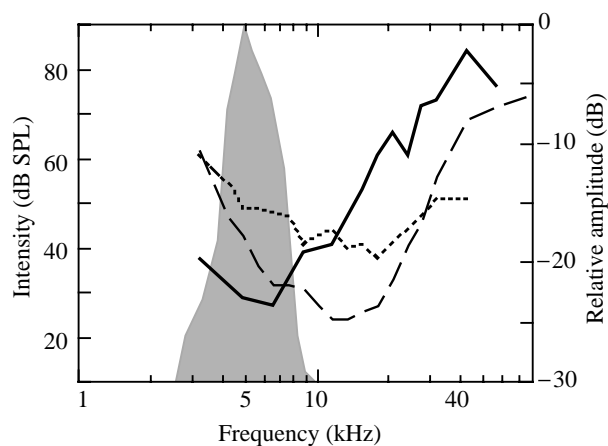


Fig. 9. Hearing sensitivity of *Sciarasaga quadrata* in the open (dashed line) and partially blocked (solid line) spiracle conditions compared with the sensitivity of the ear of its most common predator, the parasitoid fly *Homotrixia allenii* (dotted line; after Lakes-Harlan *et al.* 1995). Note the selective advantage to *S. quadrata* of hearing conspecifics by shifting the carrier frequency of the call to 5 kHz relative to the ability of the fly to detect its prey at this low frequency. The spectrum of the calling song of *S. quadrata* (shaded area) is given.

spiracle was blocked completely, directionality was only slightly reduced in response to a maximum right–left difference of 4 dB. The same experiment performed with the bushcricket *Requena verticalis* (male pronotum length 7–9.5 mm; broad-band spectrum of the call with a maximum at 16 kHz) revealed a much higher directionality of 11 dB with the open spiracle, but a stronger reduction after spiracle closure to a maximum right–left difference of 3 dB.

## Discussion

### *Tuning and sensitivity of the ear*

The hearing system of tettigoniid Orthoptera includes a chordotonal organ (*crista acustica*) linked to a paired tympanic membrane beneath the knee of the fore tibia (Lakes and Schikorski, 1990). The air cavities behind the tympana lead through a single leg trachea to an expanded trachea in the prothorax and then to the outside through the auditory spiracle. The tracheal system is dedicated to sound transmission, and it is through this pathway that most of the sound energy reaches the back of the tympana. The leg trachea itself would appear to contribute little to the tuning characteristics of the system (Michelsen *et al.* 1994), while the expanded trachea or bulla in the thorax acts as a highly tuned system (Nocke, 1974; Lewis, 1974; Seymour *et al.* 1978; Bailey, 1993).

In most, but not all, species of tettigoniids, the auditory spiracle is permanently open (Bailey, 1993). The size of the opening determines the overall sensitivity of the ear, as demonstrated by interspecific comparisons (Nocke, 1975) and also by an examination of intraspecific variation (W. Bailey, unpublished data). Thus, ears with large spiracles are more sensitive than those with smaller ones. In this paper, we show

that the tuning of the open system is to frequencies in the range from 10 to 20 kHz. However, if the ear is modified by full or partial closure, it becomes more sensitive to lower frequencies. These results are in accordance with those of Stumpner and Heller (1992), Heinrich *et al.* (1993) and Kalmring and Jatho (1994), who also found an increased sensitivity for low frequencies (<5 kHz) after blocking the spiracular opening. The degree of opening not only determines the absolute sensitivity of the ears but also the cut-off frequency at which the trachea provides sound energy to the inner surface of the tympanic membranes (see Fig. 4C). Michelsen *et al.* (1994) argued that blocking the tracheal input to the ear may not be an appropriate method for studying the function of the acoustic trachea, since it changes the impedance of the tympanum by reducing the compliance of the closed air space behind the tympanum. The degree of impedance mismatch will depend on the size of the air space behind the tympana and, compared with the species used by Michelsen *et al.* (1994), the tracheal cavity of *S. quadrata* is significantly larger. More importantly, our data show that there is no discontinuity in the tracheal gain as the spiracle is progressively blocked and that the closing behaviour of the insect itself goes through all the stages mimicked in the blocking experiments (Figs 1, 4). The amplitude part of the tracheal gain of approximately 30 dB shown for this species is comparable to that found in a phaneropterine bushcricket using a different method (Michelsen *et al.* 1994), but approximately 10 dB higher than measurements made by Heinrich *et al.* (1993), Kalmring and Jatho (1994) and Hoffmann and Jatho (1995) on other species of bushcrickets. This discrepancy has been attributed to methodological differences by Michelsen *et al.* (1994).

If the tuning and sensitivity of the hearing system are largely determined by the physics of the acoustic trachea and spiracular aperture, and in *S. quadrata* the system shows remarkable sensitivity to a frequency range between 10 and 20 kHz, why do males call at 5 kHz? There are three possible explanations for this apparent anomaly: (i) interspecific competition for free communication channels; (ii) an increase in the efficacy of sound transmission; and (iii) a reduction in predation by tachinid flies.

Masking by heterospecifics is a common phenomenon in acoustic insects (Greenfield, 1988). We have shown in another sagine that masking of a short-duration call by a long-lasting call can lead to complete masking of the conspecific signal and a reduction in nocturnal calling activity (Römer *et al.* 1989). By calling at 5 kHz, *S. quadrata* escapes the interfering calls of a number of nocturnal tettigoniid species and, remarkably, at least in the habitats we have studied, also the calls of crickets that would normally occupy this frequency range. The density of gryllids in these habitats is extremely low (G. Allen and W. Bailey, personal communication) and would provide little or no masking sounds at 5 kHz. Male *S. quadrata* continue singing in the presence of other continuously calling species.

Calling with low frequencies may also favour sound transmission. We show that transmission of sound from within dense sclerophilous bushes from heights ranging from 0.2 to



1.2 m is remarkably efficient. Loss of signal amplitude through excess attenuation for a species calling at 20 kHz may amount to 40 dB over 30 m (Römer and Lewald, 1992), but in this case, for the low-frequency call of *S. quadrata*, there is almost no attenuation in excess of that produced by spherical spreading alone (Fig. 3).

Fullard and Yack (1993) discussed the relationship between the characteristic hearing frequencies of moths and the sonar frequencies of bats. Fullard (1982) provided evidence that selection on hearing sensitivity in the prey, and echolocating frequency in the predator, is a dynamic process whereby moths may gain the advantage by increased tuning to common bat sonar frequencies, while bats may gain by using sonar outside these frequency ranges. One of the primary and spectacular predators of *S. quadrata* is the ormiine parasitoid fly *Homotrixa alleni*. Allen (1995b) reported rates of predation on male *S. quadrata* of 85 % late in the season; flies detect their hosts entirely by male call and females are not parasitised.

Male *S. quadrata* might escape, or at least lessen, these intense levels of predation by shifting the carrier frequency of their call. Lakes-Harlan *et al.* (1995) show that the sensitivity of the ear of *Homotrixa alleni* exhibits a broad-band sensitivity between 10 and 20 kHz and is therefore partially mismatched to the call of *S. quadrata* (Fig. 9, dotted line). In contrast, the hearing sensitivity of the fly almost exactly matches that of *S. quadrata* in the open spiracle condition. A shift to lower frequencies in the call of male *S. quadrata* may reflect an advantage over the fly since the parasitoid becomes less sensitive to its host by approximately 10–15 dB and, at the same time, by closing its spiracle *S. quadrata* becomes more sensitive to the conspecific call (Fig. 9, solid line). In addition, reducing the call to this frequency also decreases call intensity. Most bushcrickets of comparable size have a call intensity of between 80 and 90 dB SPL at a distance of 1 m, whereas that for *S. quadrata* is only 60–63 dB SPL. Reducing call intensity by almost 20 dB adds further to the 10–15 dB advantage over the parasitoid and is presumably adaptive in avoiding predation since louder sounds attract more parasitoids (Cade, 1975). In contrast, selection has taken an alternative route in the phaneropterid bushcricket *Poecilimon veluchianus*, where the sensitivity of its fly predator *Therobia leonidae* exactly matches the call frequency of the host (Stumpner and Lakes-Harlan, 1996).

If calling at lower frequencies is adaptive for the reasons discussed above, we may assume that *S. quadrata* has, over evolutionary time, lowered its call carrier frequency outside the range of noisy sympatric heterospecifics and outside the best sensitivity of the parasitoid fly. (Because low-frequency calls are the rare exception among the tettigoniids, a first-base assumption is that calling with low frequencies is derived.) The mechanics involved in lowering the frequency at which the sound generator can operate are not straightforward, as the natural vibration frequency of the harp (the modified cubital vein surrounding the mirror) of most tettigoniids is controlled by size, density and Young's modulus, which is an index of elasticity (Bailey, 1970). Furthermore, because the wings of

most tettigoniids are remarkably similar in terms of structure, particularly the elasticity of the veins, size becomes the most significant determinant of call frequency (Bennet-Clark, 1989); there is a strong correlation between harp size and the frequency of the call (Bailey, 1970). Small wings produce high frequencies, and call frequency is strongly correlated, in a linear manner, with the area of the mirror and harp. *S. quadrata* does not have a 'mirror' area, but its frame length (which may be considered close to the 'mirror' length used to calculate the correlation) fits the expected size for a tegmen producing a natural vibration frequency of 5 kHz. Its ability to achieve these low frequencies is enhanced by the relatively low elasticity of the tegmen.

An alternative, although not necessarily independent, way of achieving a reduction in call carrier frequency is to alter the Young's modulus of the wing, i.e. the elasticity and density of the sound-generating system. Early studies of sound generation in bushcrickets established that the natural vibration of the wings was affected by water content: isolated wings increased their natural vibration frequency as they dried out (Bailey, 1968). *S. quadrata* has peculiarly fleshy wings with the water content of the fore tegmen an order of magnitude higher than that of a related sagine of similar size (63 % compared with 5 % in other sagines). We suggest that the exceptionally low frequency produced by this species is achieved by having soft tegmina with a low Young's modulus. One consequence is that the peak energy of the call is also lowered to levels beneath that of bushcricket species of comparable size.

#### *Lowering the tuning of the receiver*

One part of sensory drive theory implies a tension between the evolved characters of the emitter and the context under which both signaller and receiver operate (Endler, 1992). For example, where a signal is under strong selection through female choice, females may prefer louder sounds of longer duration or brighter, more gaudy colours. At the same time, these exaggerated signals could increase the risk of predation, and an evolutionarily stable condition will develop that will be a compromise between traits used for female attraction and those less likely to attract predators. In the case of *S. quadrata*, we suggest that a trade-off exists between three conflicting directions: escape from masking sounds of heterospecifics; exposure to predation; and hearing the call of conspecifics. Where there are clear selective arguments for shifts in call frequency and a reduction in call intensity, we may expect sexual selection to act on the receiver to increase its sensitivity to the conspecific call. Females best able to differentiate between the calls of males should be able to choose between males, and males most able to hear the calls of conspecifics would be better able to outcompete them, thereby gaining a greater mating advantage.

One feature of the ear of many tettigoniids is the input through the auditory spiracle (Bailey, 1993). Recent comparisons between two species of phaneropterine bushcricket, *Poecilimon thessalicus* and *P. laevis*, show the same phenomenon (Stumpner and Heller, 1992; Michelsen

*et al.* 1994). Every study of the tettigoniid tracheal system so far confirms a gain at high frequencies (>10 kHz). Given this contribution of the spiracle and trachea, it would seem that the most obvious way to reduce the operating frequency of the ear is to close down the tracheal input.

We found that reducing the input, by partially occluding the aperture of the spiracle, achieves this in *S. quadrata*. The overall high-frequency sensitivity is lost, and the ear may even increase its sensitivity at the carrier frequency of the call. Bioacoustical measurements with probe microphones confirmed a cut-off frequency for the gain of the trachea at approximately 5 kHz in six species of bushcricket (Hoffmann and Jatho, 1995). Partial closure of the spiracle selectively increases sensitivity to the conspecific call, while reducing sensitivity to heterospecifics, thus increasing the signal-to-noise ratio in a noisy environment. Given the increased efficiency of sound transmission, the distance over which effective communication occurs is scarcely less than that of other sagines calling at much higher intensities at high sonic or ultrasonic frequencies (Rheinlaender and Römer, 1986; Römer and Lewald, 1992).

Bailey (1990) observed that the auditory trachea of a related sagine *Pachysaga australis* could be closed by collapsing the anterior wall of the trachea lining. If closure is caused by muscular and hydrostatic changes in the prothorax, it might be expected that the response of the system would be slow, allowing the hearing system to arrive at an 'optimal' condition over several seconds. Therefore, given proprioceptive control on sound output (an assumption we make from studies of crickets; e.g. Dambach *et al.* 1983; Elliot and Koch, 1983), it may not be unreasonable to expect a similar degree of adjustment to occur to the input, particularly when the acoustic environment is highly variable. The result of playback experiments in the laboratory using high-frequency tones confirms that such a mechanism exists in *S. quadrata* (Fig. 1).

Finally, why should the ear not be permanently closed? More substantial long-term evolutionary changes have occurred within the Tettigoniidae, leading to dramatic cases of sexual dimorphism in hearing structures and significant between-species shifts in spiracle and hearing sensitivities (Bailey and Römer, 1991; Stumpner and Heller, 1992). In the case of *Kawanaphila nartee*, the male spiracle is almost completely closed, while the female maintains a more normal opening. If selection is so strong on tuning within this species, it is reasonable to question why evolution has not similarly shut down the tracheal system of *S. quadrata*. Counterselective forces would include the advantage of hearing with a high sensitivity over a wide range of frequencies (the condition of open spiracle) and allowing either sex to detect approaching predators both during the day and at night.

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## References

- ALLEN, G. R. (1995a). The calling behaviour and spatial distribution of male bushcrickets (*Sciarasaga quadrata*) and their relationship to parasitism by acoustically orienting tachinid flies. *Ecol. Ent.* **20**, 303–310.
- ALLEN, G. R. (1995b). The biology of phonotactic parasitoid, *Homotrixa* sp. (Diptera: Tachinidae) and its impact on survival of male *Sciarasaga quadrata* (Orthoptera: Tettigoniidae) in the field. *Ecol. Ent.* **20**, 103–110.
- ANDERSSON, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.
- BAILEY, W. J. (1968). Studies in the mechanics of sound production in *Homorocoryphus nitidulus vicinus* (Scopoli) and allied species. Doctoral thesis, University of London.
- BAILEY, W. J. (1970). The mechanics of stridulation in bush crickets (Tettigoniidae, Orthoptera). I. The tegminal generator. *J. exp. Biol.* **52**, 495–505.
- BAILEY, W. J. (1990). The anatomy of the tettigoniid hearing system. In *The Tettigoniidae: Biology, Systematics and Evolution* (ed. W. J. Bailey and D. C. F. Rentz), pp. 217–245. Bathurst, NSW: Crawford House Press.
- BAILEY, W. J. (1991). *Acoustic Behaviour: an Evolutionary Approach*. London: Chapman & Hall.
- BAILEY, W. J. (1993). The tettigoniid (Orthoptera: Tettigoniidae) ear: Multiple functions and structural diversity. *Int. J. Insect Morph. Embryol.* **22**, 185–205.
- BAILEY, W. J. AND RÖMER, H. (1991). Sexual differences in auditory sensitivity: mismatch of hearing threshold and call frequency in a tettigoniid (Orthoptera, Tettigoniidae: Zaprochilinae). *J. comp. Physiol. A* **169**, 349–353.
- BENNET-CLARK, H. C. (1989). Songs and the physics of sound production. In *Cricket Behaviour and Neurobiology* (ed. F. Huber, T. E. Moore and W. Loher), pp. 227–261. Ithaca, London: Cornell University Press.
- CADE, W. H. (1975). Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science* **190**, 1312–1313.
- DAMBACH, M., RAUSCHE, H.-G. AND WENDLER, G. (1983). Proprioceptive feedback influences the calling song of the field cricket. *Naturwissenschaften* **70**, 417–418.
- ELLIOT, C. J. H. AND KOCH, U. T. (1983). Sensory feedback stabilising reliable stridulation in the field cricket *Gryllus campestris* L. *Anim. Behav.* **31**, 887–901.
- EMBLETON, T. F. W. (1996). Tutorial on sound propagation outdoors. *J. acoust. Soc. Am.* **100**, 31–48.
- ENDLER, J. A. (1992). Signals, signal conditions and the direction of evolution. *Am. Nat.* **139**, S125–S153.
- ENDLER, J. AND McLELLAN, T. (1988). The processes of evolution: towards a newer synthesis. *A. Rev. Ecol. Systematics* **19**, 395–421.
- FULLARD, J. H. (1982). Echolocation assemblages and their effects on moth auditory systems. *Can. J. Zool.* **60**, 2572–2576.
- FULLARD, J. H. AND YACK, J. E. (1993). The evolutionary biology of insect hearing. *Tree* **8**, 248–252.
- GREENFIELD, M. D. (1988). Interspecific acoustic interactions among katyids (*Neoconocephalus*): inhibition-induced shifts in diel periodicity. *Anim. Behav.* **36**, 684–695.
- GREENFIELD, M. D. (1993). Inhibition of male calling by

- heterospecific signals. Artifact of chorusing or abstinence during suppression of female phonotaxis? *Naturwissenschaften* **80**, 570–573.
- GREENFIELD, M. D. (1994). Cooperation and conflict in the evolution of signal interactions. *A. Rev. Ecol. Systematics* **25**, 97–126.
- GWYNNE, D. T. AND BAILEY, W. J. (1988). Mating system, mate choice and ultrasonic calling in a zaprochiline katydid (Orthoptera: Tettigoniidae). *Behaviour* **105**, 202–223.
- HEINRICH, R., JATHO, M. AND KALMRING, K. (1993). Acoustic transmission characteristics of the tympanal tracheae of bushcrickets (Tettigoniidae). II. Comparative studies of the tracheae of seven species. *J. acoust. Soc. Am.* **93**, 3481–3489.
- HOFFMANN, E. AND JATHO, M. (1995). The acoustic trachea of tettigoniids as an exponential horn: theoretical calculations and bioacoustical measurements. *J. acoust. Soc. Am.* **98**, 1845–1851.
- HUBER, F., KLEINDIENST, H.-U., MOORE, T., SCHILDBERGER, K. AND WEBER, T. (1990). Acoustic communication in periodic cicadas: neuronal responses to songs of sympatric species. In *Sensory Systems and Communication in Arthropods* (ed. F. G. Gribakin, K. Weiss and A. Popov), pp. 217–228. Basel: Birkhäuser.
- KALMRING, K. AND JATHO, M. (1994). The effect of blocking inputs of the acoustic trachea on the frequency tuning of primary auditory receptors in two species of tettigoniids. *J. exp. Zool.* **270**, 360–371.
- LAKES, R. AND SCHIKORSKI, T. (1990). Neuroanatomy of tettigoniids. In *The Tettigoniidae: Biology, Systematics and Evolution* (ed. W. J. Bailey and D. C. F. Rentz), pp. 166–190. Bathurst, NSW: Crawford House Press.
- LAKES-HARLAN, R., STUMPNER, A. AND ALLEN, G. R. (1995). Functional adaptations of the auditory system of two parasitoid fly species, *Therobia leonidei* and *Homotrixa spec.* In *Nervous Systems and Behaviour. Proceedings of the Fourth International Congress on Neuroethology* (ed. M. Burrows, T. Matheson, P. L. Newland and H. Schuppe), p. 358. Stuttgart: Thieme.
- LATIMER, W. AND SIPPEL, M. (1987). Acoustic cues for female choice and male competition in *Tettigonia cantans*. *Anim. Behav.* **35**, 887–900.
- LEWIS, D. B. (1974). The physiology of the tettigoniid ear. II. The response characteristics of the ear to differential inputs: lesion and blocking experiments. *J. exp. Biol.* **60**, 821–869.
- LIBERSAT, F. (1989). Neuroethological aspects of bat-avoidance behavior in Tettigoniidae. *Israel J. Zool.* **36**, 173.
- MASON, A. C. (1991). Hearing in a primitive ensiferan: the auditory system of *Cyphoderris monstrosa* (Orthoptera: Haglidae). *J. comp. Physiol. A* **168**, 351–363.
- MICHELSSEN, A., HELLER, K.-G., STUMPNER, A. AND ROHRSEITZ, K. (1994). A new biophysical method to determine the gain of the acoustic trachea in bushcrickets. *J. comp. Physiol. A* **175**, 145–151.
- MOISEFF, A., POLLACK, G. S. AND HOY, R. R. (1978). Steering responses of flying crickets to sound and ultrasound: Mate attraction and predator avoidance. *Proc. natn. Acad. Sci. U.S.A.* **75**, 4052–4056.
- NARINS, P. (1995). Frog communication. *Scient. Am.* **273**, 62–67.
- NOCKE, H. (1974). The tympanal trachea an integral part of the ear in *Acripeza reticulata* Gukrin (Orthoptera: Tettigoniidae). *Z. Naturforsch.* **29**, 652–654.
- NOCKE, H. (1975). Physical and physiological properties of the tettigoniid ('Grasshopper') ear. *J. comp. Physiol.* **100**, 25–57.
- POPOV, A. V. (1981). Sound production and hearing in the cicada, *Cicadetta sinuatipennis* Osh. (Homoptera, Cicadidae). *J. comp. Physiol.* **142**, 271–280.
- RENTZ, D. C. F. (1985). A *Monograph of the Tettigoniidae of Australia*, vol. I, *The Tettigoniinae*. Melbourne: CSIRO.
- RHEINLÄNDER, J. AND RÖMER, H. (1980). Bilateral coding of sound direction in the CNS of the bushcricket *Tettigonia viridissima* L. (Orthoptera, Tettigoniidae). *J. Comp. Physiol. A* **140**, 101–111.
- RHEINLAENDER, J. AND RÖMER, H. (1986). Insect hearing in the field. I. The use of identified nerve cells as 'biological microphones'. *J. comp. Physiol. A* **158**, 647–651.
- ROBERT, D., READ, M. P. AND HOY, R. R. (1994). The tympanal hearing organ of the parasitic fly *Ormia ochracea* (Diptera, Tachinidae, Ormiini). *Cell Tissue Res.* **275**, 63–78.
- RÖMER, H. (1987). Representation of auditory distance within a central neuropil of the bushcricket *Mygalopsis marki*. *J. comp. Physiol. A* **161**, 33–42.
- RÖMER, H. (1993). Environmental and biological constraints for the evolution of long-range signalling and hearing in acoustic insects. *Phil. Trans. R. Soc. Lond. B* **340**, 179–185.
- RÖMER, H., BAILEY, W. AND DADOUR, I. (1989). Insect hearing in the field. III. Masking by noise. *J. comp. Physiol. A* **164**, 609–620.
- 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.
- RYAN, M. J. AND KEDDY-HECTOR, A. (1992). Directional patterns of female mate choice and the role of sensory biases. *Am. Nat.* **139**, S4–S35.
- SCHWARTZ, J. J. (1987). The function of call alternation in anuran amphibians: A test of three hypotheses. *Evolution* **41**, 461–471.
- SCHWARTZ, J. J. (1994). Male advertisement and female choice in frogs: recent findings and new approaches to the study of communication in a dynamic acoustic environment. *Am. Zool.* **34**, 616–624.
- SEARCY, W. A. AND ANDERSSON, M. (1986). Sexual selection and the evolution of song. *A. Rev. Ecol. Systematics* **17**, 507–533.
- SEYMOUR, C., LEWIS, D. B., LARSEN, O. AND MICHELSSEN, A. (1978). Biophysics of the ensiferan ear. II. The steady-state gain of the hearing trumpet in bushcrickets. *J. comp. Physiol.* **123**, 205–216.
- STUMPNER, A. (1997). Vergleichende Analyse der Lauterkennung und ihrer neuronalen Grundlagen bei Orthopteren. Habilitation thesis, University of Göttingen.
- STUMPNER, A. AND HELLER, K.-G. (1992). Morphological and physiological differences of the auditory system in three related bushcrickets (Orthoptera: Phaneropteridae, Poecilimon). *Physiol. Ent.* **17**, 73–80.
- STUMPNER, A. AND LAKES-HARLAN, R. (1996). Auditory interneurons in a hearing fly (*Therobia leonidei*, Ormiini, Tachinidae, Diptera). *J. comp. Physiol. A* **178**, 227–233.
- WAGNER, W. E. (1995). Convergent song preferences between female field crickets and acoustically orienting parasitoid flies. *Behav. Ecol.* **7**, 279–285.
- WILEY, R. H. AND RICHARDS, D. G. (1978). Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.* **3**, 69–94.
- WILEY, R. H. AND RICHARDS, D. G. (1982). Adaptations for acoustic communication in birds: Sound transmission and signal detection. In *Acoustic Communication in Birds* (ed. D. E. Kroodsma, E. H. Miller and H. Quillet), pp. 131–182. New York: Academic Press.