

BIOACOUSTICS OF A MINIATURE CRICKET, *CYCLOPTILOIDES CANARIENSIS* (ORTHOPTERA: GRYLLIDAE: MOGOPLISTINAE)

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Accepted 6 October 1994

Summary

Male crickets, *Cycloptiloides canariensis* (body length 5 mm), stridulate with their forewings, which are hidden during rest under the large shield-like pronotum. The wings are opened into the stridulatory position by bending the body between the pro- and mesothorax. The song is a 2 s trill composed on average of 260 pulses (syllables) with a carrier frequency of about 6 kHz. The sound-emitting structures on the wings have been studied by laser vibrometry and particle dusting. A distinct membrane area, which includes a prominent mirror cell, acts as a resonator, amplifying the fundamental carrier frequency

produced by interactions between the file and plectrum. The resonating membrane is extremely thin (mirror cell thickness 0.2 μm), which is a physical requirement for maintaining the carrier frequency in the cricket-specific range. Covering the wings after singing is probably an adaptation to protect these delicate structures from damage by mechanical contact during social interactions, especially mating.

Key words: *Cycloptiloides canariensis*, cricket, sound production, stridulation, resonator.

Introduction

The basic principles of sound communication in Orthoptera have mainly been studied in a few suitable species. In cricket bioacoustics, for example, *Gryllus*, *Teleogryllus* and *Gryllotalpa* have dominated the investigation of biophysical, neurosensory and behavioural processes. Such approaches have yielded fascinating results, but comparative studies, including work on highly specialized forms, must also be carried out. Our bioacoustic studies on *Cycloptiloides canariensis* were undertaken with such comparative intentions.

Gryllidae and Tettigoniidae use the elythro-elytral method for stridulation, in which each contraction of the 'song' muscles is converted into vibrations of a higher frequency. In crickets, during the closing stroke of the forewings (tegmina), a file (pars stridens) on the ventral side of a modified vein (Cu₂) of the right (upper) tegmen moves over the plectrum (scraper), situated on the inner edge of the left tegmen (Pierce, 1948; Davis, 1968; Kutsch, 1969; Nocke, 1971; Bennet-Clark, 1989). The sound is amplified and radiated by resonant vibration of specialized areas on the male tegmina, namely the harp and the mirror cell. In *G. campestris*, also, the harp on each forewing is the relevant sound-radiating structure. Its vibratory resonance is tuned to the primary tooth impact frequency of 4–5 kHz (Nocke, 1971).

For physical reasons, effective stridulation in crickets is limited by body size. The size of the sound-generating structures, the physical properties of the skeletal material, the

properties of the sound-propagating medium (air) and the sound frequency are variables whose interdependence is governed by physical laws (Michelsen and Nocke, 1974; Bennet-Clark, 1989). To emit sound effectively, the diameter of the sound-radiating structure must be large relative to the sound wavelength. This means that when the frequency is held constant, the sound radiator cannot be made continually smaller, because the intensity of the radiated sound will be gradually reduced by acoustic short-circuiting (Bennet-Clark, 1989; Olson, 1957). This can be compensated in part if only a limited wing area serves as a sound radiator and the remaining area acts as a flat baffle. There is also a limit on the minimum size of the oscillating membrane. In order to maintain a given resonance frequency, a smaller membrane must also be thinner (Pierce, 1948; Morse, 1948), but reduction in thickness has mechanical limits. As *C. canariensis* is one of the smallest stridulating crickets with well-defined sound-generating structures, it is especially attractive for comparative bioacoustic studies. The present publication deals with the sound-generating structures and the general acoustic behaviour of this species.

Materials and methods

Animals

The genus *Cycloptiloides* comprises eight species, four of which are found in Africa (Chopard, 1968). Only one species of this genus (*C. americanus*) has been described for the

Western Hemisphere (Love and Walker, 1979). The species of our study, *Cycloptiloides canariensis* Bolivar 1914 (described as *Ectadoderus canariensis*), is endemic to the Canary Islands. Bolivar (1914), Willemse (1949/1950), Chopard (1954) and Gangwere *et al.* (1972) reported this species on the main island Tenerife.

C. canariensis is a small cricket (body length 5–7 mm, females slightly larger than males) with a depressed body and hindlegs well developed for jumping. The brown body pigmentation is located in minute scales, which cover nearly all exposed surfaces. The term ‘scaly crickets’ has therefore been proposed as a common name (Love and Walker, 1979). The females are wingless. The males lack hindwings, but bear stridulatory forewings which, during rest, are hidden under the large pronotum. There is only one tympanal membrane on the antero-lateral side of each foreleg (Michel, 1979).

An initial laboratory culture was established from a gravid female, caught in 1977 on Gran Canaria. A second culture was started in 1991 from 23 specimens collected in La Palma. Animals were held in groups in small plastic containers, with hiding places, at 27 °C under a 13 h:11 h light:dark regime. Food consisted of dry dog food (‘Bonzo Komplett’ Latz GmbH) and lettuce. The containers had a water dispenser and a jar with moist tissue-paper for egg laying.

Morphology

Morphometry

The form and size of the tegmina and of the resonating fields were documented by microphotography or by using the wing itself as a negative in a photographic enlarger. Areas were measured with a planimeter. The lengths of files and their number of teeth were determined from *camera lucida* drawings and scanning electron micrographs.

Scanning electron microscopy (SEM)

For a detailed study of wing surface structures (veins, file, hair fields), SEM was used. Males were isolated just before the imaginal moult to avoid contamination with debris and loosened scales. About 1 day after moulting, entire animals were fixed and dehydrated with ethanol and diethyl ether. The isolated tegmina were then dried in air, mounted on aluminium sample holders and coated with gold. The specimens were photographed using a Hitachi S-520 scanning electron microscope.

Transmission electron microscopy (TEM)

The membrane thickness of the resonating fields and of veins was measured from TEM sections. Males were fixed in Karnovsky’s solution (diluted 1:2) just after the imaginal moult. The dissected wings were embedded in Spurr’s (1969) epoxy resin. Sections were photographed in a Zeiss EM9 S-2 electron microscope, and a transect from the file to the apical frame of the mirror cell was reconstructed. Thickness measurements were made from representative sections.

Behavioural and sound analyses

For detailed inspection of unrestrained animals during

stridulation and mating, a lightweight stereoscopic viewer was used (Binoskop, magnification 9×, 12×; Eschenbach Optik, Nürnberg).

Sound recordings were performed in a sound-isolated room [background noise level about 15 dB(A)] using an audio tape recorder (Uher Report 4200 IC) with different microphones. For detailed studies of song variables and for measuring the sound pressure level (SPL), an SPL meter (Brüel & Kjær, type 2209) with a 2.5 cm condenser microphone (Brüel & Kjær, type 4145) was used. The a.c. output signal of the SPL meter was recorded at 19 cm s⁻¹ on the AM channel of a tape recorder (Racal Store 7 DS).

For laser Doppler vibrometry (Michelsen and Larsen, 1978), a freshly decapitated male was mounted with wax on the tip of a toothpick, and the pronotum was elevated at right angles to the abdomen, i.e. into a position similar to the natural singing posture. The lower tegmen was fixed onto the abdomen so that a laser beam could be focused onto the mirror cell of the exposed tegmen. Pure tones with frequencies of 1–15 kHz and a constant SPL of 70 dB near the preparation were presented through a high-fidelity loudspeaker positioned 34 cm from the preparation. The vibrations were recorded in the Doppler vibrometer mode, with a 5 mV He–Ne laser (Disa 55 x). The reflected beam was transformed to an output signal proportional to vibration velocity, which was converted into a measure of amplitude.

Horizontally mounted wings were particle-dusted on the upper surface and then excited with pure tones. Movement of the particles was observed with a binocular microscope. The small dimensions of the membranes required that the mass of loaded particles was kept as small as possible, because the resonance was considerably reduced if the added mass became large relative to that of the vibrating membrane. It was difficult to find a sufficiently light powder with discrete particles of equal size. Cork and talcum powders formed flocks, which rendered spatial resolution more difficult. The best materials proved to be *Lycopodium* spores or fine emery powder. *Lycopodium* spores were of equal size (diameter about 34 µm), but they tended to adhere to the wing surface by electrostatic or adhesive forces. The emery powder did not adhere, but the grains were relatively heavy and of irregular form and size (average diameter 70 µm). In a sound-isolated room, a fresh preparation was mounted with one tegmen in a horizontal position and excited with pure tones of frequencies from 2 to 20 kHz in ascending and descending succession and at sound pressure levels of 115 dB. As the frequency altered, the particles, either *Lycopodium* or emery, suddenly began jumping and migrated to the margins, indicating that the membrane was vibrating in resonance.

Results

General behaviour

Under favourable conditions, much stridulation occurs in a population of *C. canariensis*. There is only one type of song, which consists of a series of ungrouped pulses, named a trill

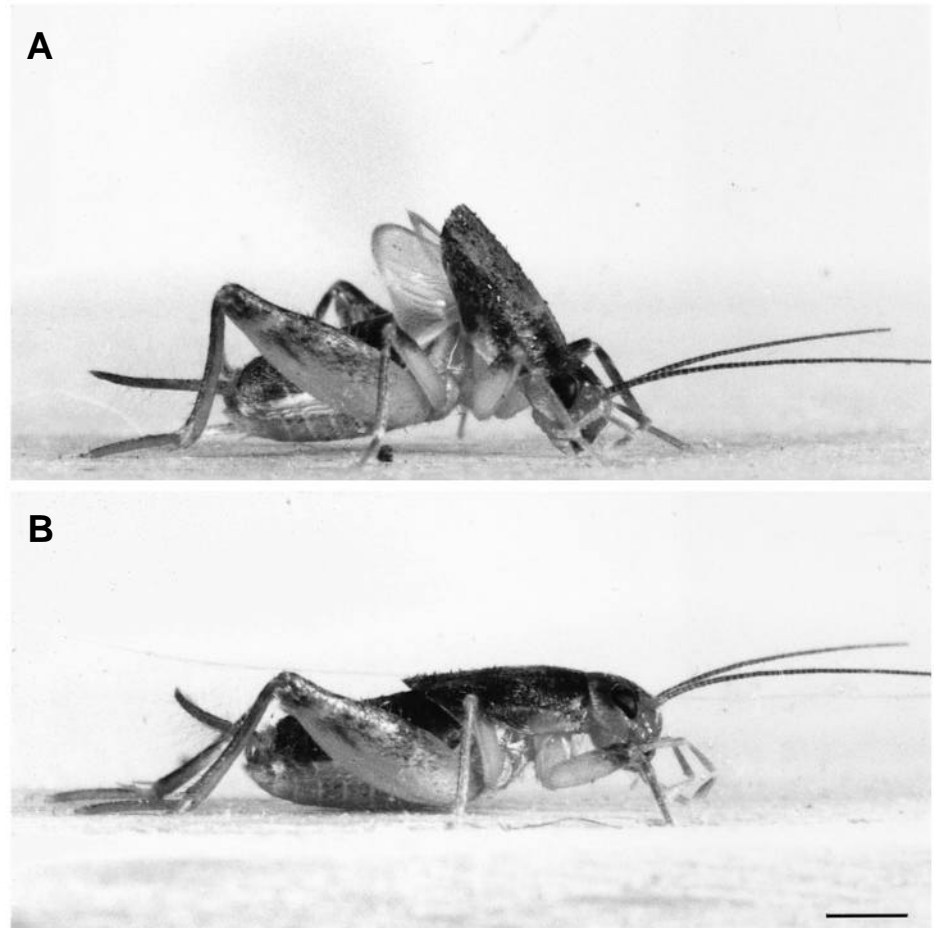


Fig. 1. Male *Cycloptiloides canariensis*. (A) Stridulatory position. The pronotum is elevated by bending of the body between the pro- and mesothorax, and the delicate forewings (tegmina) are exposed. (B) Resting position. The forewings are concealed by the large pronotum. Scale bar, 1 mm.

(Alexander, 1962). When a male comes into antennal contact with a female, he begins to stridulate, while adopting an unusual posture: the body is bent between the pro- and mesothorax so that the pronotum is elevated to an angle of about 70° , and the tegmina are extended into a stridulatory position (Fig. 1). After the trill, with a delay of 0.5–2.5 s, the pronotum and the tegmina are turned down into the resting position. The stridulatory posture enables extension of the tegmina. Males usually stridulate only near females or other males. Sexually unreceptive females move away from stridulating males, whereas receptive ones remain motionless or respond within a specific interval by bobbing their abdomen. During the pre-mating phase, the trills are repeated at intervals of about 10 s. The trill and bobbing interactions usually end with the pair facing head-to-head. The male then turns suddenly, lowers his abdomen, slips backwards under the female and hooks his pair of paraproct processes onto the female's subgenital plate (Dambach and Beck, 1990).

Song characteristics

Temporal pattern

A trill sounds like a faint buzzing that increases in volume and ends abruptly (maximum intensity 30 dB SPL at 1 m). The trill is composed of a train of pulses (syllables) produced at a uniform rate but continuously increasing in amplitude (Fig. 2).

The intervals between successive trills are variable. According to the general principle of cricket stridulation, every pulse is produced by the interaction between the file and plectrum during a single closing of the wings. The wingstroke rate therefore determines the pulse rate, whereas the tooth-strike rate, in interaction with the vibration of the sound radiator, determines the carrier frequency (Bennet-Clark, 1989). At 27°C , trill durations of 2.1 ± 0.3 s (mean \pm s.d.) were measured (8 individuals, 10 trills each). Each trill was composed of 261 ± 39 pulses, which gives a mean pulse rate of 124 pulses s^{-1} (mean pulse period 8 ms). The pulse duration (pd), the number of cycles of the carrier frequency per pulse and the pulse amplitude (pa) increase continuously during a trill (pd from about 1 to 7 ms; number of cycles from about 9 to 30; pa, 10 dB rise ratio). Carrier frequency (see below) and pulse period (pp) remain constant.

Carrier frequency

The file-and-plectrum mechanism and tuned sound radiator (see below) emit tone pulses of a nearly pure frequency. Because of its predominant character, the fundamental frequency can easily be calculated by counting the cycles from an oscillogram (film speed 8 m s^{-1}). For five animals, every successive tenth pulse within a trill (recorded at 27°C) was analysed in this way. The pulses may differ in amplitude

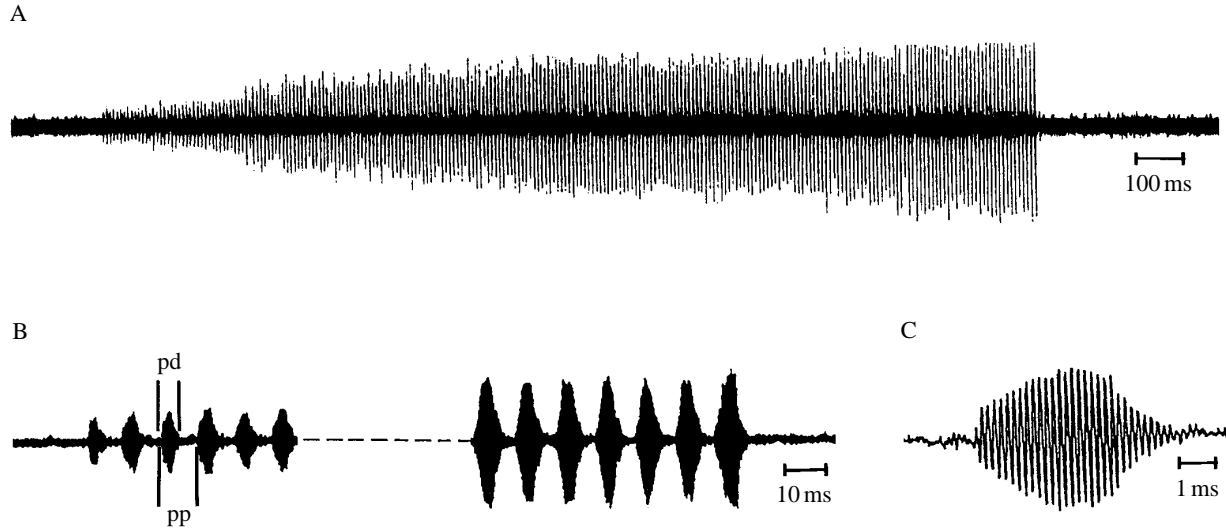


Fig. 2. Records of the song of *Cycloptiloides canariensis*. (A) A complete trill, containing 245 pulses. (B) Pulse sequences from the beginning and end of the trill. The duration and amplitude of pulses increase during the trill. pd, pulse duration; pp, pulse period. (C) A single pulse from the end of the trill on a more expanded time scale.

(Fig. 2A) but their frequency does not. Nevertheless, each individual had its own characteristic frequency within the range 5.7 ± 0.1 kHz ($N=25$ pulses) to 6.1 ± 0.2 kHz ($N=27$ pulses).

Sound-generating structures

Orientation of the tegmina

Crickets generally stridulate with their wings in the right-over-left position. The males of *Gryllus campestris* have completely mirror-imaged tegmina, but in about 98% of specimens the right forewing covers the left during rest and stridulation (Stärk, 1958; Möss, 1971). The males of *C. canariensis* also have mirror-imaged tegmina but they are used with random overlap, as in the mole cricket (*Gryllotalpa australis*) (Kavanagh and Young, 1989). 55% of *C. canariensis* males ($N=56$) had the left-over-right tegminal position. Preliminary studies were performed to establish whether each individual was permanently disposed to be a right- or left-stroker, or whether this occurred by chance at the moment of imaginal moulting, when the forewings expand into the overlapped position.

Observations of isolated, stridulating males over a period of days revealed that they changed their wing overlap at irregular intervals. Macro-binoculars were used to determine the wing position at the end of each trill, when the tegmina rested in the stridulatory position for about 1 s. When the tegmina were inverted artificially, the males stridulated in the new position for as long, and as well, as they did after a normal spontaneous change.

The file and resonating membranes

The venation and partition into membrane cells is reduced to the minimum necessary for effective stridulation, namely a file, a plectrum and a mirror cell plus the surrounding membranous areas (Fig. 3). The stridulatory file of crickets

consists of a regularly spaced row of teeth on the ventral side of a cubital vein (Cu2) (Fig. 4). In *C. canariensis*, the teeth have an approximately circular sharp edge and are oriented obliquely, pointing inwards, in the direction of stridulatory movement. The left and right files are equal in length and bear the same number of teeth. The right file has a mean length of 0.48 ± 0.02 mm ($N=13$) and the left file has a mean length of 0.48 ± 0.03 mm ($N=14$). The number of teeth was 36 ± 2 ($N=13$) on the right file and 36 ± 3 ($N=14$) on the left file. For comparison, in *Gryllus bimaculatus* the mean file length is 4.3 mm with 135 teeth on both sides (Stärk, 1958). There is a

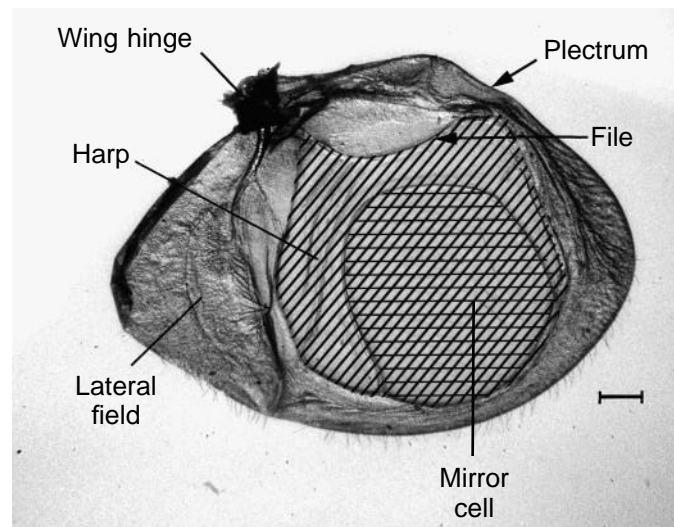


Fig. 3. Photograph of a right forewing, ventral side. The stridulatory equipment consists of the file, the plectrum and the translucent resonator area (hatched), which includes the mirror cell (cross hatched), the harp and a membrane field between the mirror and file. Left lateral side represents the morphological anterior side of the wing. Scale bar, 0.2 mm.

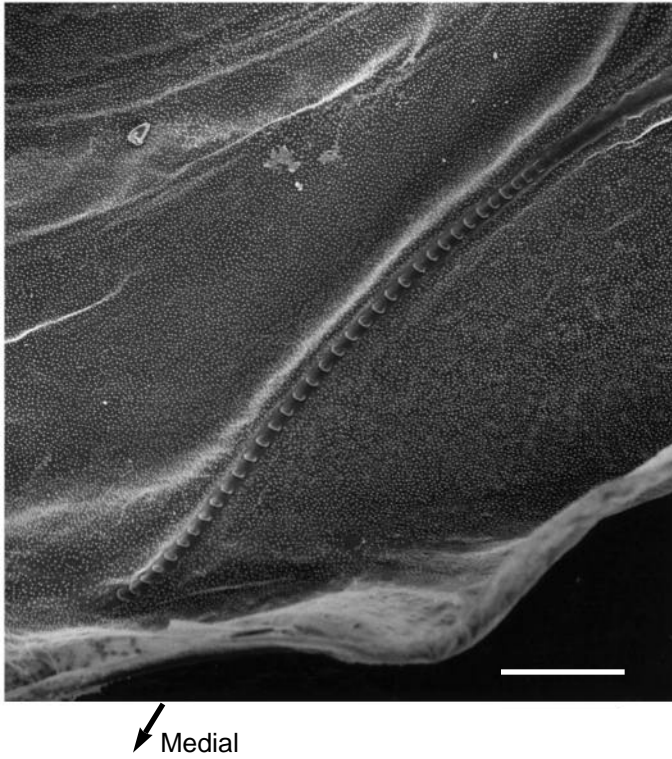


Fig. 4. Scanning electron micrograph of the file on the underside of the right forewing. The teeth are oriented obliquely, pointing forwards in the direction of stridulatory movement (medial). Scale bar, 100 μm .

continuous increase in the pulse duration from about 9 to 30 cycles per pulse, indicating that the portion of the file actively involved in stridulation increases within the trill from 25 % to 83 %.

The most remarkable features of the tegmina in *C. canariensis* are their minute size (Fig. 5, Table 1) and fragility.

Table 1. Comparison of forewing dimensions in *Cycloptiloides canariensis*, *Gryllus campestris* and *G. bimaculatus*

Forewing characteristics	<i>Cycloptiloides canariensis</i>	<i>Gryllus bimaculatus</i>
		and <i>G. campestris</i>
Area of whole forewing (mm^2)	3.2	141.4
Harp area (mm^2)	–	17.7
Vibrating field area (mm^2)	1.3	–
Mirror diameter (mm)	0.9	3.4
Vibrating field diameter (mm)	1.3	–
Cuticle thickness of mirror cell (μm)	0.2	2.5*
Cuticle thickness of harp (μm)	–	6*
Cuticle thickness between mirror and file (μm)	0.52	–
Vein thickness (μm)	5	16*

*Nocke (1971).

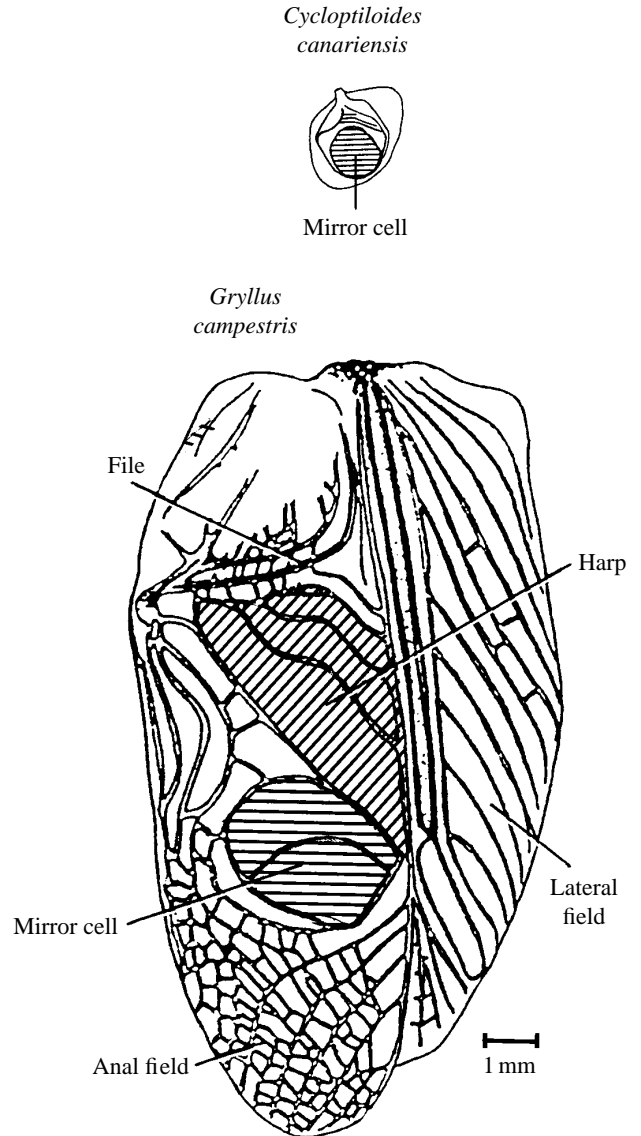


Fig. 5. The difference in size and form of male forewings in stridulating crickets. Comparison of *Cycloptiloides canariensis* and *Gryllus bimaculatus* (drawn to same scale). Right tegmina, viewed from above.

The width of a tegmen is about 2.3 mm and the length about 1.7 mm. The whole wing area of *C. canariensis* is smaller than either the mirror cell or the harp of the tegmen in *Gryllus campestris*, but the areas and fields typical of the forewings in male Gryllidae are still identifiable in *C. canariensis* (Figs 3, 5). The small lateral field is folded ventrally; the anal field is practically absent; and the harp area is reduced and divided by only two oblique veins, with its largest cell 'folded' around the mirror cell. The most prominent area of the wing is the circular mirror cell, which is relatively large (about 25 % of the wing area) and slightly corrugated. Its iridescence and susceptibility to damage indicate that it must be extremely thin. The size, form and position of the mirror cell suggested that it may function as a resonator, which amplifies and radiates the stridulatory sound. Resonance measurements, however,

demonstrated that it acts as part of a somewhat larger area including the surrounding membrane cells (see below). Physically, the vibrating membrane area can be regarded as a circular clamped plate whose fundamental frequency is determined by its geometrical dimensions (diameter, thickness) and its material properties (density, elasticity). The thickness of the mirror and the surrounding membrane cells was measured for comparison with other membranes and for calculation of the resonance frequency.

Membrane thickness

Cross sections of the mirror cell and the area between mirror and file revealed a double membrane with a thick upper layer and a thin lower layer. The mirror cell is wavy and covered by microsculptures of denticles on both sides of the membrane. Thickness was measured at the points of nine troughs and at four dorsal peaks of the waves. The mean value of the thick sections (peaks) was $0.3\ \mu\text{m}$ and of the thin ones (troughs) $0.1\ \mu\text{m}$, which gives an overall mean value of about $0.2\ \mu\text{m}$. Membrane thickness between mirror and file was $0.5\ \mu\text{m}$, and vein diameter approximately $5\ \mu\text{m}$.

To obtain comparable values for tegminal membranes of other species, we used the same method for measuring the middle of the three distal cells in the tegmen of *Oecanthus pellucens* (specimen preserved in 70% ethanol). This membrane, which also had a wavy appearance, ranged in thickness between 1.2 and $1.9\ \mu\text{m}$ (mean, $1.6\ \mu\text{m}$). The thickness of the membranes in the harp and mirror cell of *Gryllus campestris* was $2.5\ \mu\text{m}$ (Nocke, 1971), and that of the mirror cells of the right (lower) forewings of five tettigoniid species ranged between 3.4 and $8.4\ \mu\text{m}$ (Pierce, 1948).

Resonance measurements

A laser beam was focused on the mirror cell of an exposed tegmen and pure tones of constant sound pressure were presented by a loudspeaker to vibrate the membrane. The amplitude of vibration was plotted as a function of the excitatory frequency to give typical resonance curves, with a sharp peak at the resonant frequency. Fig. 6 shows the resonance curve of a fresh preparation. The sharp peak at $6\ \text{kHz}$ corresponds to the carrier frequency of the stridulatory sound. The resonance frequencies measured from four different preparations ranged from 6 to $9\ \text{kHz}$. With increasing exposure duration, the resonant frequency increased to higher values, near $9\ \text{kHz}$, probably because of increasing stiffness resulting from desiccation.

The sharpness of a resonant tuning can be characterized by the Q factor (quality factor), which can be calculated from a resonance curve by determining the bandwidth at $3\ \text{dB}$ intensity decay:

$$Q = F_0 / (F_2 - F_1),$$

where F_0 is the resonance frequency and $F_2 - F_1$ is the bandwidth at $3\ \text{dB}$ intensity decay (see Fig. 6).

A large Q factor means that the excitation of resonance can be reached only within a narrow frequency band and that the

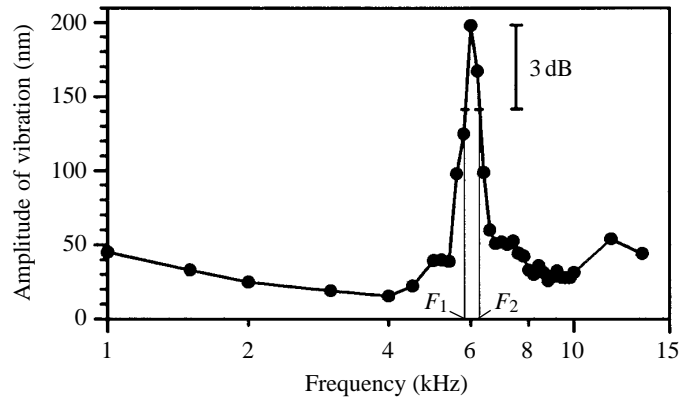


Fig. 6. Resonance in the tegminal membrane measured by laser vibrometry. The wing was acoustically excited with distinct frequencies at $70\ \text{dB SPL}$. The laser spot was focused on the mirror cell. F_2 minus F_1 gives a measure of the bandwidth at $3\ \text{dB}$ intensity decay.

amplitude of an oscillation decays slowly when the excitation is stopped. Q values of cricket wing membranes range from 10 to 20 (Bennet-Clark, 1971, 1989; Bennet-Clark and Young, 1992). Nocke (1971) gives values of up to 28 for isolated tegmina of *G. campestris*. On the basis of three resonance curves from laser vibrometry, a mean Q value of 15.4 ± 3.2 was calculated for *C. canariensis*, which indicates that the vibrating area acts as an effective mechanical sound-emitting resonator.

Tegminal vibration pattern

The mirror cell is the most prominent membrane field of the wing, but it was not clear whether it represents the primary resonator alone or in combination with the surrounding membrane areas. This could not be clarified with laser vibrometry because the laser spot was too large to scan the relevant surfaces. We therefore used the particle-dusting method for visualizing the vibration patterns on the tegmina.

When exciting the preparation at frequencies between 2 and $20\ \text{kHz}$, it was not the mirror cell alone that resonated. Instead, the mirror cell vibrated as part of a larger area consisting of the mirror itself, the lateral harp and a frontal membrane strip between the mirror cell and file (hatched area in Fig. 3). Particle translocation on the tegminal surface started at about $4\ \text{kHz}$ with increasing frequencies and at about $5.4\ \text{kHz}$ when using decreasing frequencies. In addition, there was at least one higher mode of vibration of the mirror cell alone between 15 and $20\ \text{kHz}$. Within this range, depending on the particle load, the mirror cell resonated separately from the inactive surrounding areas.

The observation that, in the particle experiments, the fundamental resonance was 0.5 – $2\ \text{kHz}$ below the carrier frequency of the song ($F_0 = 6\ \text{kHz}$) may be explained by the additional mass from the particle load. The reduction of resonance frequency caused by a varying number of particles on the vibrating surface is difficult to quantify. In a rough approximation, in which only one emery particle is fixed on the resonance area to act as a damping mass, the frequency

would be suppressed to $F=0.8F_0$. (Average particle mass m is 0.31×10^{-3} mg; the mass of resonating membrane M is 0.71×10^{-3} mg, calculated from membrane cell area, membrane thickness and vein volumes, all with an assumed density d of 1.2 mg mm^{-3} . For the formulae, see Nocke, 1971; Dambach, 1972.)

Discussion

Tegminal orientation

According to their general body plan, pterygote insects have mirror-imaged right and left wings. In species whose wings overlap horizontally at rest, a positional asymmetry arises. Two folding alternatives may occur: right-over-left or left-over-right. Field crickets (Gryllidae) generally hold their forewings and stridulate in the right-over-left position (right-strokers), whereas Tettigoniidae are left-strokers (Stärk, 1958; Masaki *et al.* 1987). *G. campestris* has completely mirror-imaged tegmina (Stärk, 1958) but behaves as an obligatory right-stroker (Kutsch, 1969; Möss, 1971; Elliott, 1983). In *G. campestris*, a forced inversion is corrected immediately after the next few chirps by a characteristic 'wing-spreading' (Elliott and Koch, 1983). For mole crickets (*Gryllotalpa vulgaris*) stridulation on both sides was first reported by Regen (1903), and this phenomenon was analysed in detail by Kavanagh and Young (1989) for the Australian mole cricket *G. australis*. Males of this species have approximately mirror-imaged stridulatory equipment on their forewings, and there is no significant difference between calling songs produced in the right-over-left and left-over-right wing arrangements.

C. canariensis also has mirror-imaged tegmina with complementary venation and equal numbers of file teeth. Its wings overlap randomly at rest and during stridulation, and artificial inversion is not corrected. A special set of sensory hairs that control wing orientation in *G. campestris* (Elliott and Koch, 1983) was not found in *C. canariensis*. The 'ambidextrous' mole cricket possesses such an array of hairs, but they are shorter and more sparse (Kavanagh and Young, 1989). *C. canariensis*, therefore, is a cricket with morphological and functional symmetry, and sound production is identical in either wing position.

It can be supposed that, from an evolutionary point of view, all true crickets began with symmetrical stridulatory equipment. Specialization at the neuronal and muscular levels then led to a stable positional asymmetry, as in *G. campestris*, and further to morphological asymmetry. The left (hidden) tegmen may become thinner and less pigmented and may have a reduced number of teeth on the file (Masaki *et al.* 1987). All other types of morphological wing asymmetries (e.g. glands on the upper wing, size reduction of the lower wing) are regarded as secondary derivations (Otte, 1992).

Files, membranes and sound frequencies

Crickets produce pure tones whose fundamental frequencies are within a relatively narrow range (tettigoniids reach ultrasound and use broader frequency bands). The carrier

frequencies range from 1.6–3.4 kHz in mole crickets (Bennet-Clark, 1989; Kavanagh and Young, 1989) to 10 kHz in small Nemobiinae (Bennet-Clark, 1989). Small species of the subfamily Mogoplistinae also produce these higher frequencies. Love and Walker (1979) presented audiospectrograms of 17 species of *Cycloptilum*, revealing frequencies from 6 to 8 kHz. The relatively low frequency in mole crickets is probably an adaptation to their singing in burrows (Bennet-Clark, 1989), whereas higher frequencies may be a consequence of the small size of the singers. The physical basis of pure tone generation is the stridulatory equipment: a file with regularly spaced teeth cooperates with a sharply tuned (high Q value) resonator membrane. In the ideal case, the carrier frequency is identical to the tooth impact frequency, i.e. there is a 1:1 ratio. A direct test of this relationship would be to excise a number of teeth and to correlate the modified pulse with the position of the gap on the file (Nocke, 1971; Sismondo, 1979). This treatment is not practicable in *C. canariensis* because of the small size and delicacy of the wings. The existence of a 1:1 ratio, however, could be concluded indirectly by comparing the number of cycles of the carrier frequency in the song pulse with the number of teeth on the file. In *C. canariensis*, at most 83% of the available teeth are active during one stroke, which is even more than in *G. campestris* (maximum 70%; Bennet-Clark, 1989) for which a 1:1 relationship was proved. Koch *et al.* (1988) offered a convincing model that describes the stridulation mechanism in *G. bimaculatus* as functioning in a way that is analogous to a clockwork mechanism with an escape system. The vibrating harp acts like a pendulum, releasing the file–plectrum connections tooth by tooth with each period; i.e. there is mechanical feedback between the oscillating membrane and the progression of tooth impacts. One of the functional advantages of the clockwork principle is that the carrier frequency is kept constant at different temperatures. The structural requirements for the clockwork model are a sharply tuned sound radiator in close mechanical connection to the file.

The laser experiments revealed the existence of a sharply tuned resonator (with a high Q factor), which is one of the requirements of the clockwork model. The particle experiments further demonstrated that a large part of the tegminal area resonates at the fundamental frequency. The resonator includes nearly the whole translucent tegminal area, which is circular in shape and includes the prominent mirror cell. The resonating membrane, therefore, is not a homogeneous plate but, instead, consists of several cells of different size framed by veins. The mirror cell itself vibrates with one, or possibly more, higher mode(s) whose frequency is superimposed on the fundamental vibration, and therefore produces the higher harmonics of the song.

Problems of size

C. canariensis has a body length of only 5–7 mm. Species of similar size are known from the related mogoplistine genus *Cycloptilum*, the morphology and songs of which have been studied by Love and Walker (1979). The subfamily Nemobiinae (ground crickets) also comprises such tiny singers.

The tendency to small size is probably an ecological adaptation. Nevertheless, reduction of body and wing size, together with maintenance of stridulation, has some physiological and acoustical consequences. First, the muscle power available for stridulation is reduced. Second, there is a problem of sound radiation. If the radius of the vibrating membrane remains below 33% of the wavelength, the radiating resistance will be low and sound emission becomes poor (Bennet-Clark, 1989). This problem could be overcome by physically shifting to higher frequencies (smaller wavelengths), but this is not done in dwarfs such as *C. canariensis*. On the contrary, the cricket-specific frequency is maintained but with the disadvantage of ineffective sound radiation (low SPL). In species that live in groups, such as *C. canariensis*, short-distance acoustic communication is obviously sufficient. If a resonant membrane becomes smaller in diameter, it must also be reduced in thickness to maintain a particular frequency. Such delicate membranes are extremely vulnerable. During copulation, when the female is mounting the male, they could easily be perforated if they were exposed. This problem is solved by keeping the tegmina under the pronotum, and swinging them out only during stridulation. Whether the giant pronotum, with its concave underside and vertical positioning during stridulation, also improves sound radiation has still to be studied.

We thank Beate Mardini for providing us with specimens of *C. canariensis* from La Palma. We are very much indebted to Dr Barbara Schmitz, University of Konstanz, for introducing us to laser vibrometry. We also thank Drs Heribert Gras, Hans-Ulrich Kleindienst and Hans Scharstein for critical comments and Marlies Grosman for help with TEM techniques.

References

- ALEXANDER, R. D. (1962). Evolutionary change in cricket acoustical communication. *Evolution* **16**, 443–467.
- BENNET-CLARK, H. C. (1971). Acoustics of insect song. *Nature* **234**, 255–259.
- 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.
- BENNET-CLARK, H. C. AND YOUNG, D. (1992). A model of the mechanism of sound production in cicadas. *J. exp. Biol.* **173**, 123–153.
- BOLIVAR, I. (1914). Dermápteros y Ortópteros de Marruecos. *Mem. R. Soc. esp. Hist. Nat.* **8**, 157–238.
- CHOPARD, L. (1954). Insectes orthoptéroïdes récoltés aux îles Canaries par M. H. Lindberg. *Comm. Biol. Soc. Fenn.* **14**, 1–15.
- CHOPARD, L. (1968). Gryllides. In *Orthopterorum Catalogus*, pars 12, *Mogoplistinae* (ed. M. Beier), pp. 215–242. s-Gravenhage: Junk.
- DAMBACH, M. (1972). Der Vibrationssinn der Grillen. I. Schwellenmessungen an Beinen frei beweglicher Tiere. *J. comp. Physiol.* **79**, 281–304.
- DAMBACH, M. AND BECK, U. (1990). Mating in the scaly cricket *Cycloptiloides canariensis* (Orthoptera: Gryllidae: Mogoplistinae). *Ethology* **85**, 289–301.
- DAVIS, W. J. (1968). Cricket wing movements during stridulation. *Anim. Behav.* **16**, 72–73.
- ELLIOTT, C. J. H. (1983). Wing hair plates in crickets: physiological characteristics and connections with stridulatory neurones. *J. exp. Biol.* **107**, 21–47.
- ELLIOTT, C. J. H. AND KOCH, U. T. (1983). Sensory feedback stabilising reliable stridulation in the field cricket *Gryllus campestris*. *Anim. Behav.* **31**, 887–901.
- GANGWERE, S. K., MORALES MARTIN, M. AND MORALES AGACINO, E. (1972). The distribution of the Orthopteroidea in Tenerife, Canary Islands, Spain. *Contr. Am. ent. Inst. (Ann Arbor)* **8**, 1–40.
- KAVANAGH, M. W. AND YOUNG, D. (1989). Bilateral symmetry of sound production in the mole cricket, *Gryllotalpa australis*. *J. comp. Physiol. A* **166**, 43–49.
- KOCH, U. T., ELLIOTT, C. J. H., SCHÄFFNER, K.-H. AND KLEINDIENST, H.-U. (1988). The mechanics of stridulation of the cricket *Gryllus campestris*. *J. comp. Physiol. A* **162**, 213–223.
- KUTSCH, W. (1969). Neuromuskuläre Aktivität bei verschiedenen Verhaltensweisen von drei Grillenarten. *Z. vergl. Physiol.* **63**, 335–378.
- LOVE, R. E. AND WALKER, T. J. (1979). Systematics and acoustic behavior of scaly crickets (Orthoptera: Gryllidae: Mogoplistinae) of eastern United States. *Trans. Am. ent. Soc.* **105**, 1–66.
- MASAKI, S., KATAOKA, M., SHIRATO, K. AND NAGAHARA, M. (1987). Evolutionary differentiation of right and left tegmina in crickets. In *Evolutionary Biology of Orthopteroid Insects* (ed. B. M. Baccetti), pp. 347–357. New York: Ellis Howard.
- MICHEL, K. (1979). Ein neuer Typ eines Grillenohrs: Konstruktion und Ultrasrtuktur von *Cycloptiloides canariensis* (Bolivar) (Mogoplistinae, Gryllidea). *Zool. Anz. Jena* **203**, 139–150.
- MICHELSSEN, A. AND LARSEN, O. N. (1978). Biophysics of the ensiferan ear. I. Tympanal vibrations in bushcrickets (Tettigoniidae) studied with laser vibrometry. *J. comp. Physiol.* **123**, 193–203.
- MICHELSSEN, A. AND NOCKE, H. (1974). Biophysical aspects of sound communication in insects. *Adv. Insect Physiol.* **10**, 247–296.
- MORSE, P. M. (1948). *Vibration and Sound*. New York: McGraw Hill.
- MÖSS, D. (1971). Sinnesorgane im Bereich des Flügels der Feldgrille (*Gryllus campestris* L.) und ihre Bedeutung für die Kontrolle der Singbewegung und Einstellung der Flügellage. *Z. vergl. Physiol.* **73**, 53–83.
- NOCKE, H. (1971). Biophysik der Schallerzeugung durch die Vorderflügel der Grillen. *Z. vergl. Physiol.* **74**, 272–314.
- OLSON, H. F. (1957). *Acoustical Engineering*. New York: Van Nostrand.
- OTTE, D. (1992). Evolution of cricket songs. *J. orthopt. Res.* **1**, 24–46.
- PIERCE, G. W. (1948). *The Songs of Insects*. Cambridge: Harvard University Press.
- REGEN, J. (1903). Neue Beobachtungen über die Stridulationsorgane der saltatoren Orthopteren. *Arb. Zool. Inst. Univ. Wien* **14**, 359–422.
- SISMONDO, E. (1979). Stridulation and tegminal resonance in the tree cricket *Oecanthus nigricornis* (Orthoptera: Gryllidae: Oecanthinae). *J. comp. Physiol. A* **129**, 269–279.
- SPURR, A. R. (1969). A low viscosity epoxy resin embedding medium for electron microscopy. *J. Ultrastruct. Res.* **26**, 31–43.
- STÄRK, A. (1958). Untersuchungen am Lautorgan einiger Grillen- und Laubheuschrecken-Arten, zugleich ein Beitrag zum Rechts-Links-Problem. *Zool. Jb. Anat.* **77**, 9–50.
- WILLEMSE, C. (1949/1950). Second addition to the knowledge of the Dermaptera and Orthoptera of the Canary Islands. *Tijdschr. Ent.* **92**, 248–250.