SEXUAL SIGNALLING IN BLADDER GRASSHOPPERS: TACTICAL DESIGN FOR MAXIMIZING CALLING RANGE

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Summary

Pair formation in the bladder grasshopper (*Bullacris membracioides*) is by duetting and male phonotaxis. Low-frequency stridulatory signals are emitted by an abdominal resonator in the male and are answered by females using a species-specific time delay. Acoustic transmission in the natural environment was studied using playback of sexual signals over distances of 450 m under two atmospheric conditions (day and night). Upward-refracting sound conditions and a sound shadow zone beyond approximately 50 m prevailed during the day. Acoustic enhancement was demonstrated at night when downward-refracting temperature inversions created a tunnel effect with sound caught between the ground and zones of different temperatures. Transmission conditions are almost ideal at night when the species actually calls; calling distances of 150 m for the male signal in the afternoon increased to 1.5–1.9 km at night, arguably the largest calling distance yet reported for insects. In contrast, female calls transmit over a maximum of 50 m, signifying a marked discrepancy in the active space of sex-specific signals. Transmission distance may, however, be profoundly affected by levels of masking noise. Adaptations to increase the signal range may variously be found in the signal itself, in behaviour patterns or in the sensory system. Here we demonstrate aspects of the first two types of adaptation in the sexual signalling system of a grasshopper in which maximizing the calling range appears to be the major selection pressure, with lesser effects imposed by inter- and intraspecific pressures and by the transmission channel.

Key words: *Bullacris membracioides*, grasshopper, acoustic signalling, transmission distance, meteorology.

Introduction

Recent attention has focused on the characteristics of natural transmission channels and the effects of physical factors on acoustic signals, and has generated considerable debate over whether the maximum range of detection is in fact the primary selection pressure on animal vocalizations (Michelsen, 1978; Richards and Wiley, 1980; Römer, 1997; Wiley and Richards, 1978, 1982). Constraints imposed by acoustic characteristics of the habitat are important in that they provide the framework within which other selection pressures must operate. Yet the generality of any 'rule' is questionable owing to the multiplicity of local factors affecting sound propagation, our relative ignorance of strategic design in many taxa, and the fact that the signal itself is not an evolutionarily independent trait. Signal, sensory systems and behaviour are functionally related (Endler, 1992), and adaptations to increase signal range may be found in any, or all, of these areas.

In the context of intraspecific communication, natural selection to maximize broadcast range favours characteristics that maximize the received signal relative to background noise and that minimize signal degradation. Female preference for the more intense of two or more competing signals found in empirical studies on a variety of insect taxa indicates a strong selection to maximize calling range (Bailey and Yeoh, 1988; Bailey *et al.* 1990; Forrest, 1983; Forrest and Green, 1991; Latimer and Sippel, 1987; Partridge *et al.* 1987; Shuvalov and Popov, 1973; Thorson *et al.* 1982). Moreover, selection to increase sound output has favoured the development of a variety of behavioural mechanisms including the use of amplifying burrows (Bennet-Clark, 1987), baffles (Prozesky-Schulze *et al.* 1975), resonators (Young and Hill, 1977), temporal sound windows (Gogala and Riede, 1995; Moore *et al.* 1989; Narins, 1995) and preferred signalling sites (Arak and Eiriksson, 1992; Paul and Walker, 1979). The use of spatial sound windows and atmospheric controls on long-distance animal vocalizations has rarely been considered, however, particularly with respect to insects. Enhanced transmission of signals between 1.6 and 2.5 kHz indicated a ground-level sound window for this frequency range in forest habitat (Morton, 1975). Waser and Waser (1977) suggested that canopy monkeys in tropical forests give their long-distance vocalizations primarily in the few hours after sunrise when the advantageous temperature gradient for sound transmission is likely to be best developed above the canopy. Similarly, the early evening peak in elephant social activity and infrasound
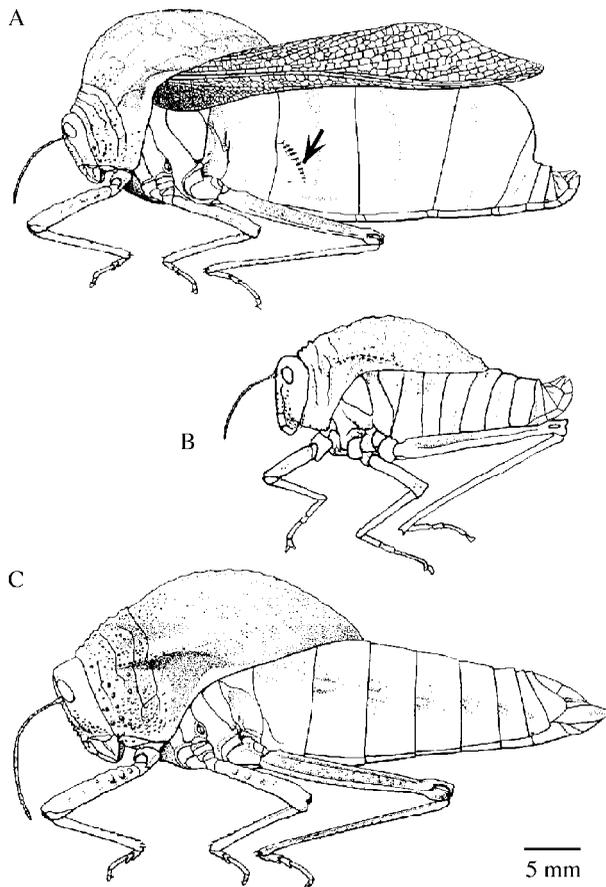
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Fig. 1. Trimorphism in *Bullacris membracioides*. (A) Adult male with strongly inflated abdomen; stridulatory file arrowed. (B) Apterous 'alternative' male which lacks the anatomy for sexual stridulation. (C) Typically acridid-shaped micropterous adult female. All morphs have a pair of hearing organs attached laterally in the first abdominal segment, but frank tympana are absent. A and C are taken from Dirsh (1965) with permission; copyright Natural Resources Institute, UK.

vocalization corresponds with optimal sound transmission conditions created by the formation of a thermal inversion 1–2 h after sunset (Garstang *et al.* 1995).

This study focuses on the tactical design (Guilford and Dawkins, 1991) of long-distance acoustic signals in bladder grasshoppers (Orthoptera, Pneumoridae), a taxon for which spectacular auditory signalling is a defining characteristic, but for which our knowledge of natural history in general, and the communication system in particular, is meagre (Alexander, 1992; Lewis, 1891; Péringuey, 1916; Thunberg, 1775; van Son, 1958). The family is endemic to southern Africa, where it occurs in a patchy distribution primarily within the coastal belt. The conspicuous nocturnal calls of males are audible to humans over several kilometres, but in all other respects the taxon is cryptic (Dirsh, 1965). Females are micropterous and typically acridid-shaped; however, males can function as a flighted, stridulating adult with a strongly inflated abdomen or may mate as an apterous 'alternative' morph (Fig. 1) without

the anatomy or behaviour for sexual stridulation (Alexander and van Staaden, 1989).

Here we examine properties of acoustic signals and signalling behaviour that maximize calling range in *Bullacris membracioides* (Walker). We characterize the sexual signals and the mechanisms by which they are produced, measure acoustic transmission distances directly in the natural habitat under two different atmospheric conditions, and assess the behavioural strategies by which adult males minimize or eliminate factors producing sound attenuation in excess of that due to geometrical spreading.

Materials and methods

Study site

Field experiments were performed in February of 1994–1996 in undisturbed habitat at Inchanga (KwaZulu-Natal, 29.74346° S, 30.67759° E), 814 m above sea level and approximately in the centre of the species' range. The area is characterized by steep-sided valleys, high humidity levels and vegetation that is essentially tropical in affinity, comprising a mixed mosaic of bush and grassland. The latter is C4 grassland with *Themeda*, *Tristachya*, *Trachypogon* and *Aristida* spp. the most prominent components. Average grass height is 50 cm, with approximately 60 % ground cover. An anemometer (type 260 P/D; Kroneis) was positioned 2 m above ground in open grassland, and electronic temperature sensors (type NTC; Kroneis) encased in open-ended aluminium sleeves were mounted at heights of 1, 5 and 10 m. Wind speed and temperature measurements were registered every 5 s and averaged over 5 min periods on a datalogger, providing a continuous weather profile. Humidity readings were taken at a height of 1.5 m using a stick hygrometer (Hanna Instruments, Hi 8565) at the start of each transmission experiment.

Sound recording, signalling mechanisms and laser vibrometry

Bullacris membracioides were hand-caught, and nymphs were raised to adulthood in groups of 5–10 individuals in the laboratory. The natural calling songs of adult males and females were recorded dorsally at a distance of 1 m in wire-mesh cages, using a sound level meter (Bruel & Kjaer, model 2009, 1/2 inch condenser microphone, type 2540 Larson & Davis; A weighting; RMS fast). Songs were digitized at a sampling rate of 44 kHz on an Apple Macintosh Powerbook 520 computer *via* the built-in 16-bit A/D sound board, edited (Macromedia, SoundEdit 16) and stored digitally. Measurement of female response time to playback calls of males was performed in wire-mesh cages using the same experimental set-up as for sound transmission (see below). Playback intensity at the position of the female was 85 dB SPL. Mechanisms of sound production were determined in the laboratory using a combination of laser vibrometry and scanning electron microscopy with standard preparative techniques.

Vibration of the air-filled abdomen of males was measured

with a laser vibrometer (Polytech OFV-3000, with measurement head OFV 501), which enables sound-induced vibrations of cuticular structures to be measured without contact (reviewed in Lewin *et al.* 1990). The animal was attached to a holder by its ventral thorax using dental wax, with the air-filled abdominal cavity left free to vibrate. Since the quality of the laser measurement depends strongly on the amount of light reflected from the cuticular vibrating surface, signal-to-noise-ratio was considerably enhanced by attaching up to five small retro-reflecting glass spheres (approximately 0.2 µg each, Scotchlite no. 7610, OM company) to the pleura of the third abdominal segment, where all measurements were made. The preparation was placed in the centre of an anechoic chamber such that echoes at the position of the preparation were more than 40 dB less intense than the signal. Pure tone stimuli were broadcast through a wide-band amplifier (Realistic 80W) and speaker (TW8 special) mounted on a holder at a distance of 45 cm. Sound pulses with different pure tone carriers between 800 Hz and 12 kHz (duration 1 s; repetition rate $0.5\,\mathrm{s}^{-1}$) were generated to study the vibration velocity of the cuticle.

Sound transmission

The transmission distances of sexual signals were measured along a 450 m straight-line transect in essentially flat, open grassland, with markers at 5, 10 or 50 m intervals to aid placement of the microphone and sound level meter. The majority of experiments were conducted during the normal calling time of 22:00–24:00 h, under environmental conditions in which temperature varied from 18.5 to 24 °C and relative humidity from 74 to 100 % between experiments. For comparative purposes, transmission distances for the male call were also measured between 10:00 and 17:00 h. To obtain transmission data unconfounded by variable wind conditions, night measurements were performed only when there was essentially no wind, and in no case did wind speed during the day exceed $1\,\mathrm{m\,s}^{-1}$. In the windless conditions under which measurements were performed, the background noise level excluding other calling insects was usually below the sensitivity of the microphone at night (27 dB SPL) and varied from 32 to 46 dB SPL during the day. In the latter case, most of the background noise was at frequencies below 500 Hz as a result of traffic on a highway at a distance of approximately 1 km.

Playback stimuli for sound transmission measurements were typical male and female calls (see Fig. 2), amplified by a custom-made wide-band amplifier driven by a car battery and broadcast at a rate of $0.5\,\mathrm{s}^{-1}$ through a speaker (Siemens RL 101 G4). The mean height of the song post and receiver was 2 m (M. J. van Staaden and H. Römer, personal observation); hence, the speaker was placed on a pole at a height of 2 m and calls were broadcast at typical sound intensities of 98 dB SPL for male calls and at 60 dB SPL (at 1 m) for female calls. Sound pressure levels (SPLs) were determined at 5 or 10 m intervals using a portable sound level meter (Bruel & Kjaer, model 2009; 1/2 inch condenser microphone, type 2540 Larson &

Davis; A weighting; RMS fast reading). The microphone was separated from the sound level meter by a 3 m extension cord fixed on a pole at a height of 2 m and directed towards the loudspeaker. SPLs are expressed in dB re 2×10^{-5} Pa. Because of the variability of SPL observed with RMS-fast readings, we recorded levels for three consecutive sounds at each test distance and then calculated the mean, after converting SPL into pressure units. The transmitted male call was simultaneously recorded using an Aiwa JS215 cassette recorder for later spectral analysis of sounds recorded on the transect.

Results

Sexual signalling behaviour

Pair formation of *B. membracioides* females and primary males is achieved by duetting and male phonotaxis. Under calm conditions, males broadcast a high-intensity calling song (Fig. 2A) from approximately 22:00 h until shortly before daylight. Calling is at irregular intervals from a stationary position high up in the vegetation, usually taking advantage of high bushes and trees, and males may move distances of up to 500 m between successive calls in the absence of a female response. Receptive females, including virgins, respond with a low-intensity call (Fig. 2A) within 860 ms of the end of the male call (range 720–860 ms; mean ± S.D. 788.5±44.9 ms; N=13) when the SPL of the male call at the position of the female was kept constant at 86 dB. Auditory response induces the development of a duet and male phonotaxis, such that he makes a short flight and moves up to a high point on the vegetation before calling again, reorienting and repeating the procedure until the female is contacted. As the male approaches the responding female, his calls become softer and less resonant. Orientation is extremely direct and accurate (an estimated 30 cm vertically and horizontally) once the male is within hearing range of a female's response or an acoustic model in the field, suggesting a high degree of directionality of hearing in an open-loop situation which merits further examination. No courtship song or complex premating behaviour have been noted.

Pair formation calls are simple and highly stereotyped in this species. The male call is relatively invariant in form, comprising five short, 'noisy' syllables and a sixth long, resonant syllable centred around 1.7 kHz (range 1.58–2.05 kHz; mean ± S.D. 1.73±0.12 kHz; N=22; Fig. 2A). First and second harmonics occur at approximately 3.4 and 5.1 kHz (see Fig. 7A), attenuated by approximately 20 dB at 3.4 kHz and by approximately 30 dB at 5.1 kHz relative to the carrier frequency. An additional 'noisy' syllable occurs prior to 16 % (N=446) of calls. The SPL of the short introductory syllables is attenuated by 20–25 dB relative to the final syllable.

The female call has a narrow frequency spectrum (3–11 kHz) with maximum energy between 5 and 7 kHz, a short duration (range 130–175 ms; mean ± S.D. 155±13.6 ms; N=15) and is produced in a series of 1–8 syllables (Fig. 2A,C). The male response to a crude model of the female call, in which
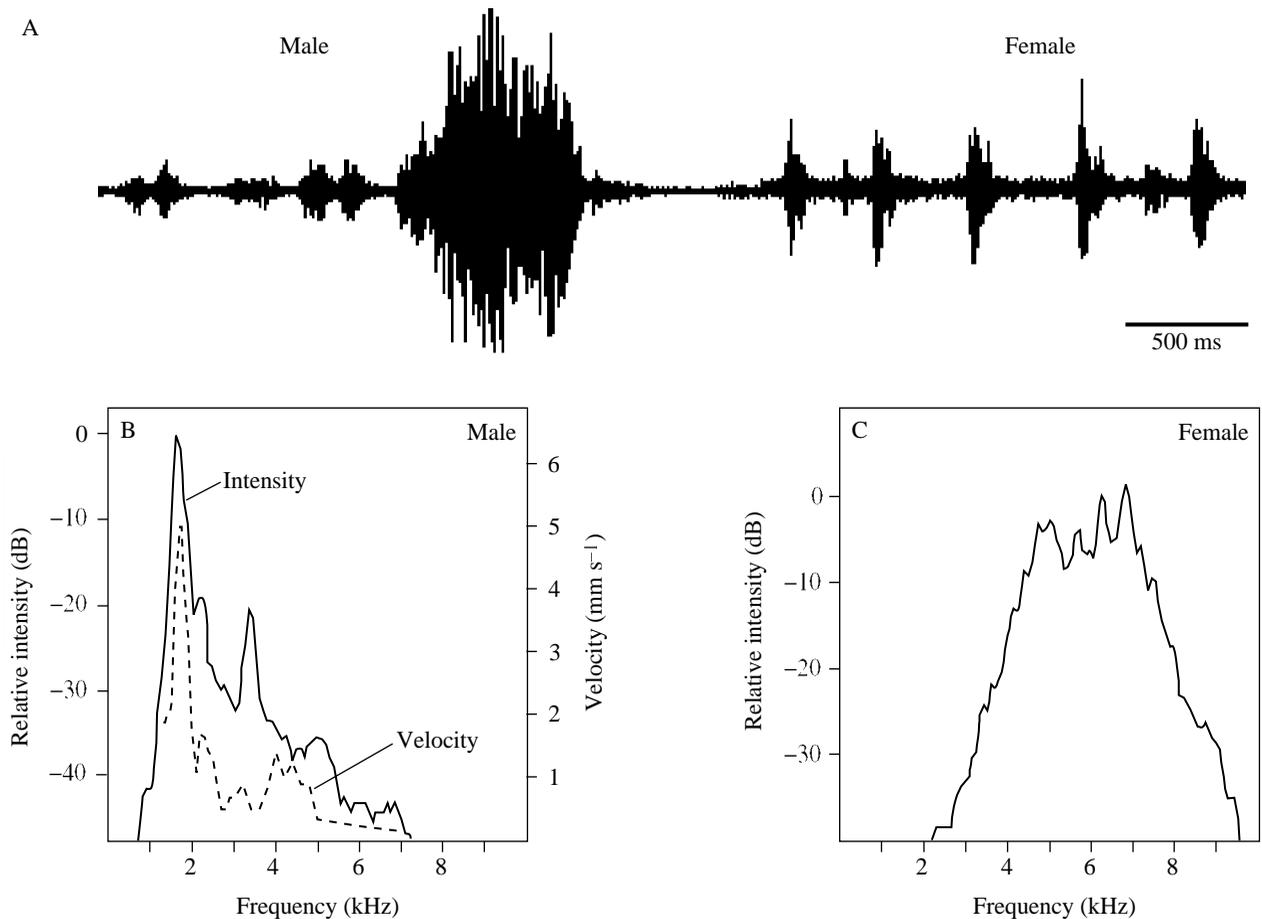
Fig. 2. Oscillograms (above) and power spectra (below) of adult *Bullacris membracioides* pair formation calls recorded in captivity at a distance of 3 m. (A) Call form is a stereotyped six syllables in males, but variable from 1 to 8 syllables in females. The mean latency of the female response is 788.5±44.9 ms (mean ± S.D.; N=13) after the end of the male call. (B) Male power spectrum and laser-Doppler vibrometry for vibration velocity of the inflated abdomen in response to acoustic stimulation with pure tones at an SPL of 86 dB, recorded laterally on the third abdominal segment. The maximal vibration velocity at 1.7 kHz (range 1.6–2.1 kHz) corresponds with the carrier frequency of male calls (range 1.58–1.96 kHz). (C) Female power spectrum.

the frequency range was not well reproduced but which was faithful to the temporal pattern and to the latency relative to the males' last syllable, indicates that a broad-band sound alone is sufficient for pair formation and that the frequency characteristics of the female call are relatively unimportant.

Sound production mechanisms

Sexual signals are produced by abdominal–femoral stridulation in males and abdominal–wing stridulation in females. In males, a short scraper consisting of a high carina with a small row of strong, transverse ridges (range 18–25; mean ± S.D. 21±2.4; N=20) on the proximal side of the hind femur (Fig. 3B), is moved along a file of nine (range 8–9; mean ± S.D. 8.9±0.3; N=20) strongly sclerotized ridges on the second abdominal tergite (Fig. 3A). Both elements are highly symmetrical. At the final larval instar, the abdomen expands dramatically, forming a permanently inflated bladder. Laser vibrometry indicates that maximal vibration velocity occurs at frequencies of approximately 1.7 kHz (range 1.6–2.1 kHz;

Fig. 2B). The impact of file and scraper is spread across the large surface of the resonating abdomen, producing a sound output of 98 dB SPL at 1 m for the last syllable.

The female response, which averages 60 dB SPL at 1 m (N=13), is produced by rubbing teeth-bearing veins on the ventral margins of the wings (Fig. 3D) across raised pegs in a differentiated region of the tergum beneath the resting wing (Fig. 3C). Ablation experiments confirm that the elytra play no part in the production of the female sexual signal.

Sound transmission in the field

Meteorological measurements revealed that super-adiabatic conditions, in which temperature drops rapidly with height above the hot ground surface, prevail from mid-morning to mid-afternoon (Fig. 4A; values for 5 m were between those for 1 and 10 m). This gradient (between 1.5 and 4.5 °C at a depth of 9 m) results in moderately turbulent mixing and the development of significant surface wind (wind speed greater than 7 m s^{-1}) as the ground warms (Fig. 4B). In contrast,
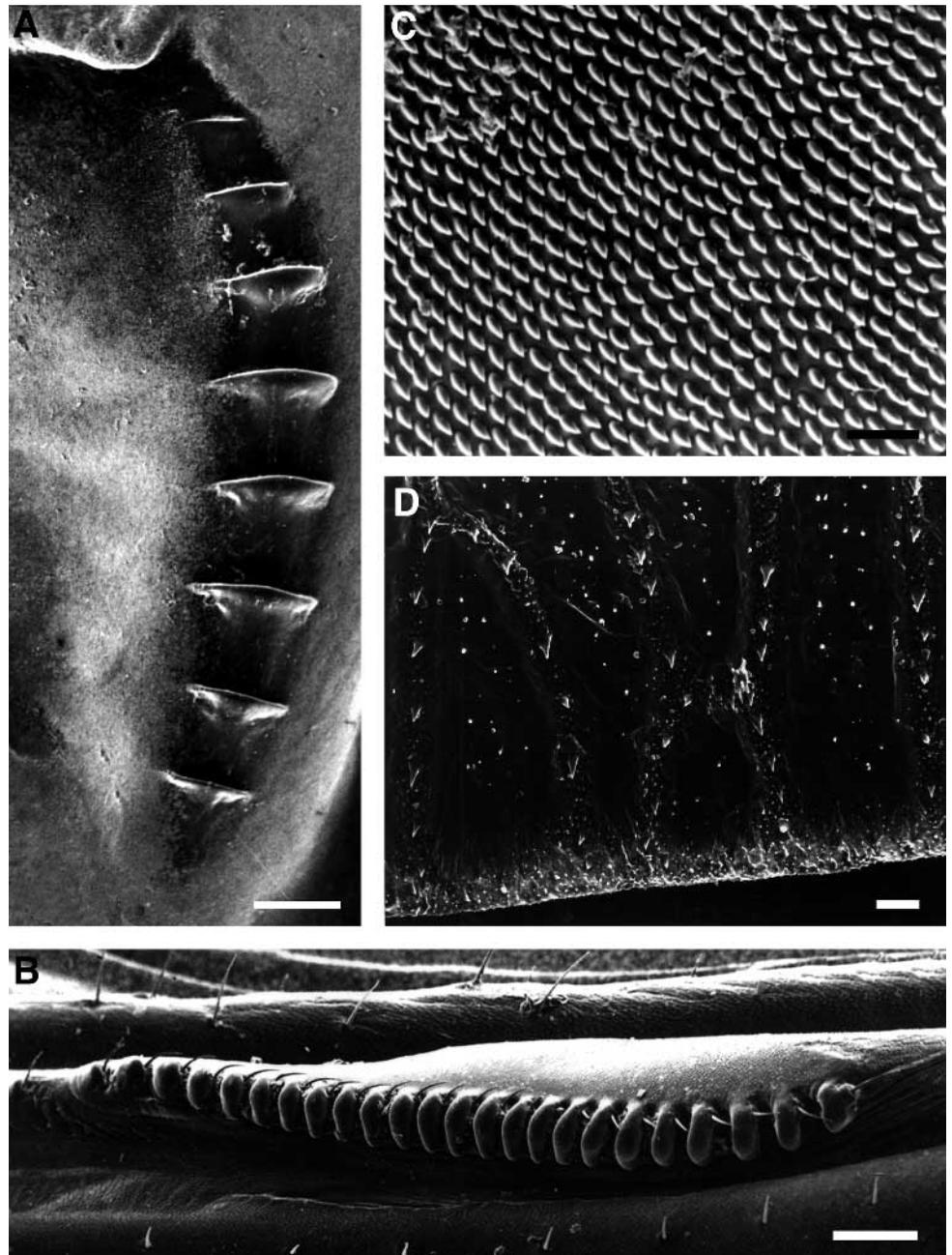
Fig. 3. Scanning electron micrographs of adult stridulatory mechanisms. (A) Sclerotised file on pleura of male second abdominal segment. Scale bar, 400 μm. (B) Scraper on proximal surface of male hind femur. Scale bar, 100 μm. (C) Stridulatory pegs in differentiated region of female abdominal tergite. Scale bar, 25 μm. (D) Ventral surface of female wing showing stridulatory teeth on veins. Scale bar, 200 μm.

temperature increases with height from the ground at night. The strong temperature inversions that form at the surface shortly after sunset (1.2 °C over 9 m) and decay with sunrise are accompanied by calm wind conditions (less than 2 m s^{-1}) during early to late evening.

Measurements of SPL for male calls played back during the day showed substantial variability (Fig. 5A; open circles) which increased with distance from the sound source. Almost all values fell below the theoretical ideal (6 dB per doubling of distance; solid line) beyond 50 m and were below the masking noise beyond 100 m. In contrast, at night when *B. membracioides* actually communicates acoustically, the male call suffers little excess attenuation (Fig. 5A; filled circles). Under a wide variety of environmental conditions (Fig. 5A),

the variability in SPL of played-back calls is lower compared with daytime conditions, and attenuation approaches values according to geometrical spreading of sound for distances up to 450 m. Variability increases little with distance, but over the entire 450 m for which sound pressure levels were directly measured, the range does not deviate from the theoretical ideal.

Broadcast area is defined as the area within which the SPL of a call exceeds the auditory threshold of a receiver (Brenowitz, 1982). Neurophysiological recordings from the afferent nerve carrying the axons of fibres of the hearing organ in abdominal segment A1 indicated that the hearing threshold of females to conspecific male calls averages 33.3±3.6 dB SPL (mean ± s.D.; *N*=18; Römer and van Staaden, 1996). Extrapolating the male call transmission trajectory until the
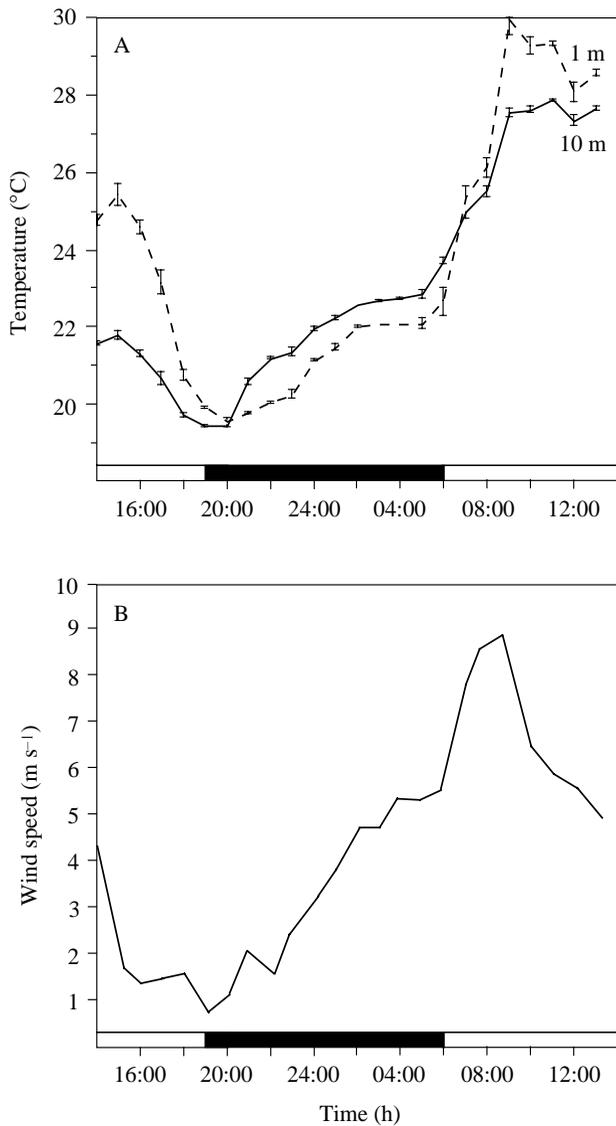
Fig. 4. Weather profile recorded over 24h in open grassland at Inchanga (elevation 814 m) on 12–13 February 1996. Time is in Local Solar Time with sunrise at approximately 06:00 h and sunset at approximately 19:00 h. (A) Thermal profiles for sensors at 1 m (broken line) and 10 m (solid line) height above ground. Values are shown at 30 min intervals and are the mean of 60 measurements over a 5 min period. Error bars show s.d. (B) Wind speed (anemometer height above ground 2 m). Velocity and temperature measurements were registered every 5 s and averaged over 5 min periods. The profile shown is typical of the summer weather pattern in this area, although the absolute values of thermal gradients are usually higher than occurred in 1996.

SPL of the transmitted call intersects the hearing threshold (Fig. 5C) gives a potential transmission distance for the male call to conspecific females ranging between 1500 and 1900 m. If we assume a male *B. membracioides* is an omnidirectional sound source and that homogeneous transmission occurs in all directions, the corresponding area over which a female would be able to detect the call would vary between 7.1 and 11.3 km².

Under a comparable range of environmental conditions, the female call also suffers little or no excess attenuation (Fig. 5B). However, the broadcast SPL of the female call is considerably lower at 60 dB (at 1 m), which results in an estimated effective detection distance by the male of only 50 m, given the male hearing threshold of 29.1±4.9 dB SPL (mean ± s.d.; N=13; H. Römer and M. J. van Staaden, in preparation) to the female response. The corresponding broadcast area would be limited to 0.078 km². Thus, there is a more than 100-fold difference in the maximum broadcast areas of male and female calls.

Estimation of the maximum transmission distances for male and female calls (Fig. 5) assumes the absence of masking noise in the field that might otherwise interfere with the detection of conspecific calls. Potential masking sounds for acoustic communication between male and female *B. membracioides* are primarily produced by a variety of nocturnal crickets with call power spectra ranging from 2 to 6 kHz (Fig. 6) and song duty cycles of 15–90 % depending on the species. These calls could interfere with the detection of *B. membracioides* signals since the sensitivity of the hearing organ of the latter is centred at 4 kHz (Römer and van Staaden, 1996). We therefore analyzed the level and frequency spectrum of background noise for night-time transmission conditions. The distribution of heterospecific cricket males on the transect was patchy in time and space, with most crickets calling in the early to late evening. As a result, the background noise level was neither uniform in time nor uniform over the whole area of the transect. Fig. 7 shows a series of spectra analysed from night-time recordings of a male call on the transect, at distances ranging from 100 to 400 m. The sensitivity of the hearing organ in abdominal segment A1 of a typical young female is superimposed on the spectra to demonstrate the effect of sound transmission and background noise on the detection of the male call. At a distance of 100 m (Fig. 7A), the SPL of the recorded male call was 60 dB, and both the carrier frequency of the call at 1.9 kHz and the frequency components including the first harmonic at approximately 3.8 kHz contribute to detection at this distance. At 250 m, the SPL was 54 dB, but there was also some background noise close to 5 kHz from a distant cricket, which potentially interferes with the hearing sensitivity of a female at this position, despite the energy of the cricket call being 20 dB lower than that of *B. membracioides* (Fig. 7B). A much better detection situation was found at a distance of 400 m and an SPL of 52 dB, although there was a cricket calling at approximately 6 kHz (arrows in Fig. 7B,C). This is, however, outside the hearing sensitivity of *B. membracioides* females.

Discussion

Long-distance acoustic signalling in bladder grasshoppers involves a complex of anatomical and behavioural adaptations that together result in the longest effective transmission distance yet recorded among insects. While the abdomino-femoral stridulatory mechanisms and a concentration of air spaces in the thorax and abdomen are not unique to pneumorids
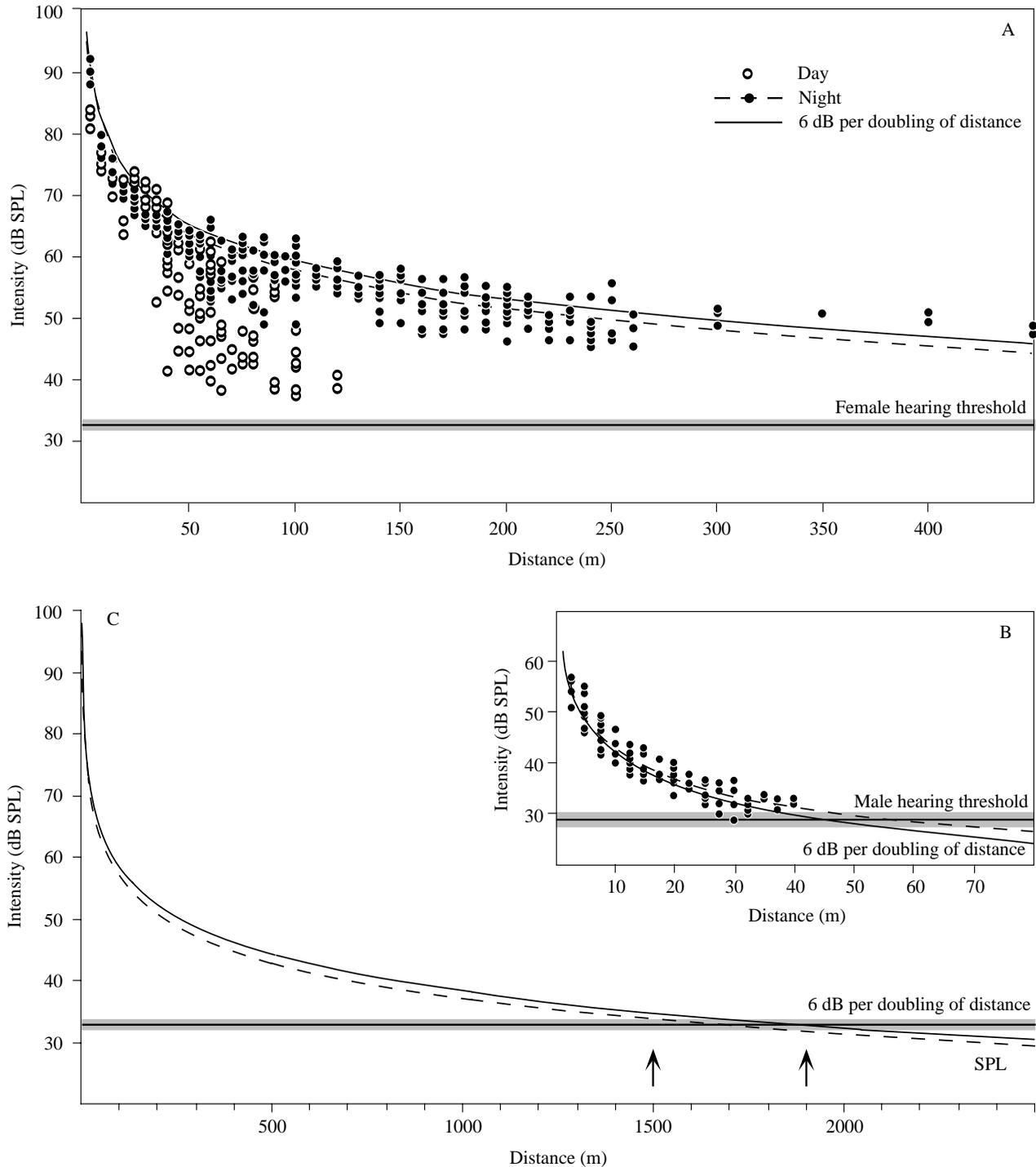
Fig. 5. Transmission of (A) male and (B) female sexual signals in natural habitat at increasing distance from a speaker broadcasting at a constant SPL (males 98 dB; females 60 dB SPL; height of speaker above ground 2 m). Sound pressure levels were measured at a height of 2 m during the day (open circles) and night (filled circles) in February 1994–1996. Each data point represents a mean for three consecutive sounds at each test distance; for A yielding 320 data points at distances less than 100 m, 108 points for distances between 100 and 200 m, and 51 points for distances greater than 200 m. A logarithmic curve was fitted to the night-time data (broken line, $y=96.2746-19.7915\log x$; $r^2=0.902$). For comparison, the theoretical transmission with attenuation due only to geometrical spreading (6 dB per doubling of distance) is shown (solid line). The shaded areas indicate the hearing sensitivity of insects of the opposite sex receiving the signal (mean ± S.D.). (C) Proposed transmission distance (between arrows) of the male call based on field measurements over a distance of up to 450 m and the mean sensitivity of female hearing to this signal.
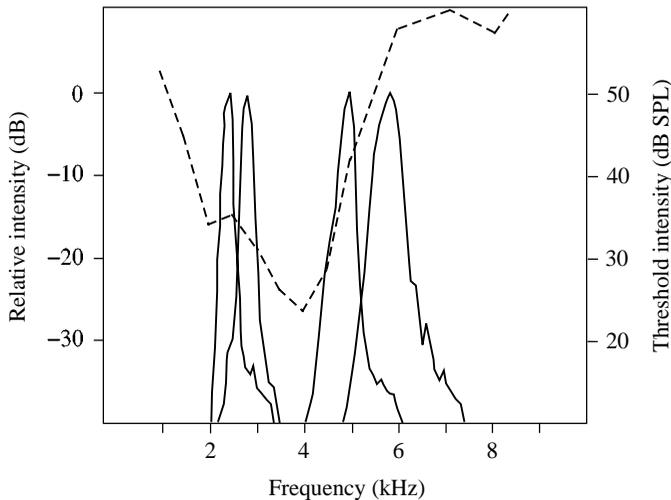
Fig. 6. Power spectra of four species of cricket recorded at or near the transect where the transmission of *Bullacris membracioides* calls was examined. The carrier frequencies of the calls range from 2.3 and 2.5 kHz for the two *Oecanthus* species (left) to 5.0 and 5.9 kHz for two other unidentified cricket species. The potential masking effect of these signals is demonstrated by superimposing on the spectra the averaged female tuning curve (*N*=9) for the hearing organ in abdominal segment A1 (broken line).

(Bennet-Clark, 1994; Field, 1978), the trend reaches its highest point of specialization in the inflated bodies and sound output levels of this taxon. Our data suggest that the efficiency of male pneumorid signal transmission may be a function of both increased sound output and exploitation of weather conditions. This is the first such demonstration for insect auditory signalling and is consistent with results of empirical studies of sound propagation outdoors (Canard-Coruna *et al.* 1990; Piercy *et al.* 1977) and on calculations of atmospheric effects on low-frequency communication in African elephants (Garstang *et al.* 1995).

Atmospheric control on transmission distance

Our results suggest that the distance over which pneumorid males transmit their calls increases more than tenfold at night. Optimum conditions occur 1–2 h after sunset on warm, misty and calm nights, and at these times ranges in excess of 1.5 km are likely. Sound waves are refracted when they meet a change in the acoustic impedance of the medium, e.g. volumes of air differing in temperature, humidity or wind velocity (for reviews, see Embleton, 1996; Larom *et al.* 1997). Vertical gradients in temperature occur regularly in natural habitats. Lapse conditions during the day, in which atmospheric temperature decreases with height from the ground, reduce the speed of sound with height and cause sound waves to bend upwards. Reduced sound levels near the surface thus create shadow zones beyond a certain distance from the source where no direct sound can penetrate. Indeed, our measurements during the day (Fig. 5A) indicate a sudden drop in SPL of the broadcast male call starting at distances of approximately 40 m,
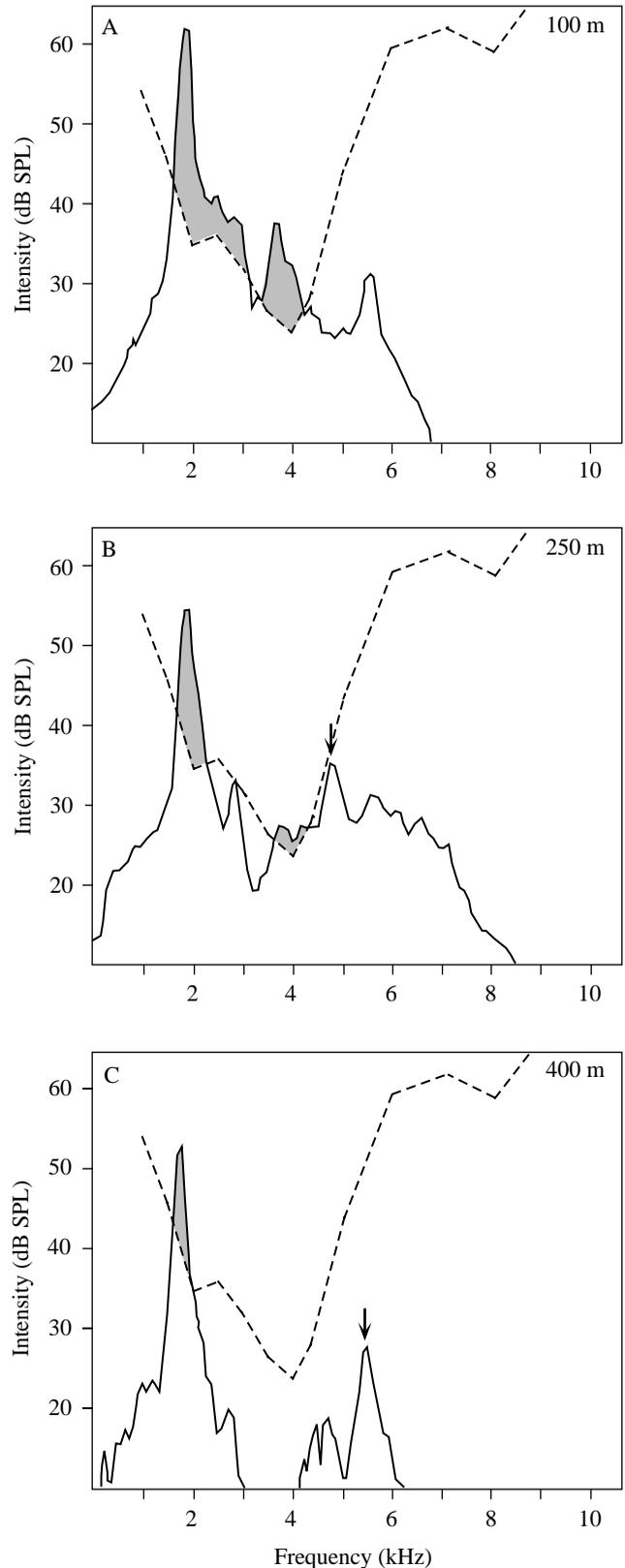

Fig. 7. Power spectra of night recordings of *Bullacris membracioides* male calls on the transect over various distances. Superimposed on the spectra is the averaged female tuning curve (*N*=9) for the hearing organ in abdominal segment A1 (broken line). For further explanation, see the text.

which is consistent with the existence of a shadow zone. Thus, ignoring masking background noise levels (see below), a male calling in the afternoon would at best reach a potential female at distances of only 100–150 m.

Night-time cooling creates temperature inversions, such that temperatures increase with height. Consequently, air is stratified, resulting in calm conditions with reduced wind noise near the ground and downward-reflecting sound waves. The latter give rise to an acoustic enhancement (the opposite of excess attenuation) and, thus, an increase in the SPL at some distance from the source relative to the 6 dB per doubling of distance relationship. These so-called ground-level inversions contrast with elevated inversions, where temperature gradients develop at some height above the ground (tens or hundreds of metres) and therefore do not have the same enhancing effect for sound signals broadcast near the ground (Larom *et al.* 1997). Calculations based on tethered balloon measurements of temperature inversions over African savanna predict an enhancement of 12–15 dB, given a 5 °C inversion strength, for the infrasound frequencies of 15–30 Hz used in elephant communication (Garstang *et al.* 1995). Our experimental data for night-time transmission show only a small amount of evidence for a direct enhancement of the call (see values over 300 m; Fig. 5A). However, the measured SPL at each distance is the additive effect of all enhancing and attenuating conditions experienced by the sound wave, and excess attenuation due to high grass vegetation on the transect is most likely to have negated the enhancing effect of temperature inversions. Moreover, compared with the infrasound frequencies on which the calculations of Garstang *et al.* (1995) and Larom *et al.* (1997) are based, enhancement effects should be reduced at the higher frequencies of *B. membracioides* calls. In this context, it is singularly interesting that a sound window in the same frequency range has been found in forest environments (Morton, 1975).

Although the data illustrated in Fig. 4 demonstrate the temperature inversion occurring at the experimental site, they are not representative of the most common situation for sound transmission in this species. More extreme thermal inversions would normally prevail than are indicated by recordings in the unusually cool and wet 1996 field season. This is true for both the strength of the inversion (the difference in temperature at 10 m relative to ground level) and more particularly for wind speed conditions. In 1995, when the majority of sound transmission experiments were performed, windless conditions for several hours after sunset were the rule rather than the exception. In 1996, in contrast, wind speed at the transmission site was rarely below 1 m s^{-1}. Hence, thermal gradients and temperature inversions during the 1995 measurements were stronger than those shown in Fig. 4, and our measurements of transmission area are thus conservative. For example, an increase in inversion strength from 0.5 to 2 °C was calculated to result in a tenfold increase in broadcast area from 30 km^2 to approximately 300 km^2 (Larom *et al.* 1997).

Topography and wind conditions are other important variables for sound transmission and are clearly more important at greater distances (km) than at shorter distances (Embleton, 1996). However, at present, we know very little about the effect of topography on the formation of shadow zones in the pneumorid frequency range. In general, wind moving up or down a ridge results in up-slope enhancement and down-slope degradation, respectively, and a numerical study demonstrated strong acoustic shadows behind ridges which were downwind of a source (Robertson *et al.* 1989). In KwaZulu-Natal, prevailing nocturnal winds are predominantly down-valley (Preston-Whyte and Tyson, 1988) so that the effects of ground topography on the transmission distance of mating calls are expected to be reflected in the overall patterns of population genetic structure.

The above consideration has neglected the effects of masking noise for the detection of male calls, which potentially limits communication distance. Levels of masking noise are known to be relatively high in certain habitats and may result in temporal or spatial segregation, call inhibition and other behavioural responses (Gogala and Riede, 1995; Greenfield, 1988; Narins, 1995; Römer *et al.* 1989). A particular problem with respect to masking in the pneumorid communication system is the fact that male and female hearing is mismatched to the male call; the ear is approximately 15 dB less sensitive at the male carrier frequency of 1.7 kHz than at its best frequency of 4 kHz (see female tuning curves in Fig. 7). Thus, any heterospecific sounds at frequencies near 4 kHz would have a strong masking effect on the detection of the male call. Recorded calls of crickets on the transect (Fig. 7) have carrier frequencies ranging from 2.3 kHz to approximately 5.9 kHz and could potentially interfere with detection of the signal (Fig. 6). However, the distribution of calling crickets was found to be patchy in time and space at the usual signalling times of *B. membracioides*, so that it very much depends on the location of the receiver (microphone or female) relative to the masking source whether interference takes place. For instance, there was no relevant masking noise at a distance of 400 m, since the low-intensity cricket song at 6 kHz was outside the average hearing sensitivity of a female, whereas at 250 m the SPL of the cricket call (Fig. 7B, arrowed) was just subthreshold at a signal-to-noise ratio of 20 dB. The same masking noise level at a distance of 1.4 km would equal the signal level at that distance and probably render the detection of the male call impossible. The same limitation would occur at a distance of only 400 m, however, if the SPL of the cricket were 20 dB higher. It is evident, then, that female detection of the male call can be strongly influenced by any cricket calling nearby (since the female is largely immobile), resulting in a large variation of transmission distances from an ideal of approximately 2 km to only 100 or a few hundred metres. Males, in contrast, could potentially avoid nearby masking sounds simply by flying to another receiver position.

This study determined pneumorid communication distances by extrapolating from transmission measured directly to 450 m, until the SPL curve intersected the hearing threshold (as determined by neurophysiological techniques). While extrapolating beyond measured data points is not ideal, in this

instance it does provide a reliable and conservative means for estimating a very large sound field. Locally unstable temperature lapses and wind fluctuations generally preclude sufficiently steady readings for accurate, direct measurement of sound fields at large distances outdoors (Embleton, 1996).

Signal design and the importance of context

Design features of the pneumorid communication system are concordant with all expectations of natural selection to maximize broadcast range while avoiding predation and intraspecific competition (Endler, 1992). The received male signal is maximized relative to background noise by repetition of a highly stereotyped signal, increased broadcast amplitude resulting from the abdominal resonator, increased transmitted amplitude using optimal meteorological conditions, and (for an insect) extremely sensitive hearing (H. Römer and M. J. van Staaden, in preparation). In addition to the effect of maximizing broadcast range, the temporal segregation in which calling is restricted to calm, misty conditions may also contribute to avoidance of nocturnal vertebrate predators such as the microchiropteran *Nycteris thebaica* (P. Taylor, personal communication). High-frequency echolocating calls of bats suffer strong absorption at high humidity ($>3\,dB\,m^{-1}$ for sounds above $100\,kHz$ at $25\,°C$ and $50\,\%$ humidity; Lawrence and Simmons, 1982), whereas the absorption coefficient for pneumorid signals is minimal, estimated to be approximately $0.2\,dB$ per $100\,m$ ($1.7\,kHz$ at $20\,°C$ and $90\,\%$ humidity; Harris, 1966).

Sexual selection and differences in active space

Pneumorids exhibit striking sexual differences in transmission distance of mate location signals, such that females may detect calling males ideally at a distance of 1–$2\,km$, but males detect responding females from a maximum of only $50\,m$. This discrepancy in transmission distance results largely from differences in absolute signal intensity, since there is little difference in overall attenuation rates of male and female calls (Fig. 5). If active space is defined as the area in which a signal is above the threshold to elicit a *behavioural* response, however, then maximum transmission distance may not translate into effective communication distance. Moreover, any asymmetry in behavioural response threshold would profoundly affect (counteract or magnify) the observed asymmetry in transmission distance.

Sexual differences in signalling strategies are frequently attributed to differences in relative parental investment (Thornhill, 1979). The energetic and endangerment costs of calling and phonotaxis in *B. membracioides* are, however, completely unknown. Conceivably, the excessive costs for male calling are more apparent than real. Slender cursorial hindlegs and the abdominal resonator may minimize the energy expenditure of calling, and the risks of male flight may be no more than those of females exposed on top of the bush producing a locatable sound. The existence of alternative mating strategies (Alexander and van Staaden, 1989) does, however, imply a substantial fitness differential between winner and loser males, and highlights the potential importance of sexual selection.

The sex ratio of nymphal *B. membracioides* is approximately equal, but food-plant specificity, male dimorphism and differential mortality produce a low-density, patchy distribution, and behavioural observations indicate substantial opportunity for females to exercise choice (M. J. van Staaden, unpublished observations). Evolution through sexual selection may thus have forced males to produce an increasingly intense signal. Since the decrease in SPL of the male calling song is rather flat at large distances, a small increase in effective transmission results in a relatively large increase in broadcast range. Larger active calling ranges reach more females, and selection is therefore expected to act on males to produce increasingly loud signals until the benefit of increased loudness is balanced by (energetic or predation) costs. Certainly in species with more vagile females, differential attraction to louder male calling songs is quite common (for a review, see Ryan and Keddy-Hector, 1992), and field studies of mole crickets have demonstrated that males calling $2\,dB$ below the loudest male attracted fewer females than the average male (Forrest and Green, 1991). It is also conceivable that loud calling in *B. membracioides* acts as a sensitizer for the female response.

At present, we cannot exclude intrasexual selection and a possible second function for the complex male call. Loud calling may space out males, allowing each to broadcast their signal within a zone free from competing conspecifics. The use of sound to maintain range separation and to minimize competition for resources is relatively common and has been shown to increase the ability of males to attract females (bushcrickets, Arak *et al.* 1990). Although it is often difficult to make a clear distinction between inter- and intrasexual selection, spatial genetic analyses may provide a means of distinguishing the adaptive value of sexual differences in transmission distance (M. J. van Staaden and H. Römer, in preparation).

Despite so-called phylogenetic and environmental constraints, the maximum range of detection does appear to be a primary selection pressure on at least some animal vocalizations. Evolutionary explanations for exaggerated signals are generally in terms of runaway sexual selection and honesty in signalling good genes, but the problem may also be recast as one of signal detection and female preference; part of the 'psychological landscape' of the receiver (Guilford and Dawkins, 1991). For a signaller, the situation is exactly the same whether receivers fail to respond to signals because of environmental attenuation or because of 'neural attenuation' resulting from high thresholds or narrow filters for response (Wiley, 1994). Whereas male pneumorids produce spectacular acoustic signals with high inherent detectability and minimal environmental attenuation, females do not. The question of neural attenuation is the subject of a subsequent paper.

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