Bioacoustics: The International Journal of Animal Sound and its Recording
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tbio20

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To cite this article: FRIEDERIKE LANG (2000): ACOUSTIC COMMUNICATION DISTANCES OF A GOMPHOCERINE GRASSHOPPER, Bioacoustics: The International Journal of Animal Sound and its Recording, 10:4, 233-258

To link to this article: http://dx.doi.org/10.1080/09524622.2000.9753437

Bioacoustics
The International Journal of Animal Sound and its Recording, 2000, Vol. 10, pp. 233–258
0952-4622/00 $10

ACOUSTIC COMMUNICATION DISTANCES OF A GOMPHOCERINE GRASSHOPPER

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ABSTRACT

I studied in the laboratory and in the field the communication distance of the gomphocerine grasshopper *Chorthippus biguttulus*, which lives close to the ground in stony, short grass habitats. Using sound measurements and behavioural tests, I examined the frequency dependent attenuation and temporal degradation of the song pattern. Sound measurements (2-40 kHz) in the field revealed that excess attenuation increases with increasing frequency. Close to the ground, excess attenuation reaches 18 dB/m. On the basis of (i) excess attenuations, (ii) tympanic receptor threshold curves and (iii) song spectra, perception distances of female tympanic receptors for male songs and vice versa were calculated. Behavioural tests revealed that, especially in short and stony grass vegetation, the typical habitat of *Ch. biguttulus*, the temporal song pattern is strongly degraded. Thus, in the laboratory and in tall grass vegetation, sound attenuation was found to limit the communication distance. In contrast, in short grass vegetation, degradation of the temporal pattern was found to limit the communication distance of males listening to female songs. I argue that the exploitation of fast amplitude modulations for song recognition restricts the acoustic communication of grasshoppers to short distances (1-2.2 m). In this respect it seems adaptive to stridulate at low intensities.

Keywords: grasshoppers, field studies, acoustic communication distance, sound attenuation, temporal degradation

INTRODUCTION

The middle European grasshoppers of the subfamily Gomphocerinae perform an elaborate acoustic communication which follows fixed inherited stridulatory motor patterns and song recognition patterns. The typical sound signals produced by gomphocerine grasshoppers are soft, non-resonant, broad-band signals with a sound pressure of 62-67 dB SPL (rms, measured at 15 cm distance). They are composed of a low frequency component between 5 and 10 kHz and a broad ultrasonic component between 20 and 40 kHz (Meyer and Elsner 1997). The frequency content of the signals was found to be important

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in recognition of sex: male songs contain far more ultrasonic frequencies than female songs (Helversen and Helversen 1997). The temporal patterns of the songs, with their fast amplitude modulations, differ strongly among species and represent an important cue for species-specific signal recognition (Helversen 1972, 1984, Helversen and Helversen 1987, 1994, Helversen 1986, Stumpner and Helversen 1994).

Most of the neurophysiological and behavioural data on the acoustic communication of gomphocerine grasshoppers have been obtained in the laboratory in a more or less ideal sound field. However, gomphocerine grasshoppers live in grassland habitats with different vegetation heights and densities, where they often sit close to the ground while singing or perceiving the songs of conspecifics. Thus, they place themselves in an acoustic environment (Figure 1) which differs from the sound field in the laboratory in many respects. Due to absorption, reflexions, refraction and diffraction the soil surface, the vegetation and the atmosphere alter the amplitude, frequency content and temporal structure of their sound signals (Embleton 1997, Michelsen 1978, Michelsen and Larsen 1983, Forrest 1994, Michelsen and Rohrseitz 1995, 1997). As a result of such environmental conditions the acoustic communication distance for conspecifics may be strongly reduced. The influence may be due to: (i) attenuation (signal detection), (ii) frequency filtering (signal detection/recognition), (iii) degradation of the temporal pattern (signal recognition), and (iv) loss of directional cues (signal localization).

Using sound measurements and behavioural studies as experimental tools, the present paper addresses the question as to how amplitude, frequency content and temporal pattern of a grasshopper's song are influenced by the natural environment. On the basis of these data the influence of different physical parameters on the communication distance of *Chorthippus biguttulus* in the habitat is demonstrated. I then discuss how the acoustic communication, i.e. the signals and/or the signalling behaviour, might be adapted to the properties of the natural acoustic environment.

METHODS

Definitions

The following terms are used in this paper: *Communication distance*: the maximal distance over which a grasshopper is able to *perceive* the song of a mate *and* to *recognize* its temporal pattern. *Perception distance*: the distance at which the sound energy of a mate's song starts to exceed the perception threshold of the most sensitive tympanic receptors, and at which a grasshopper is able to *perceive* the

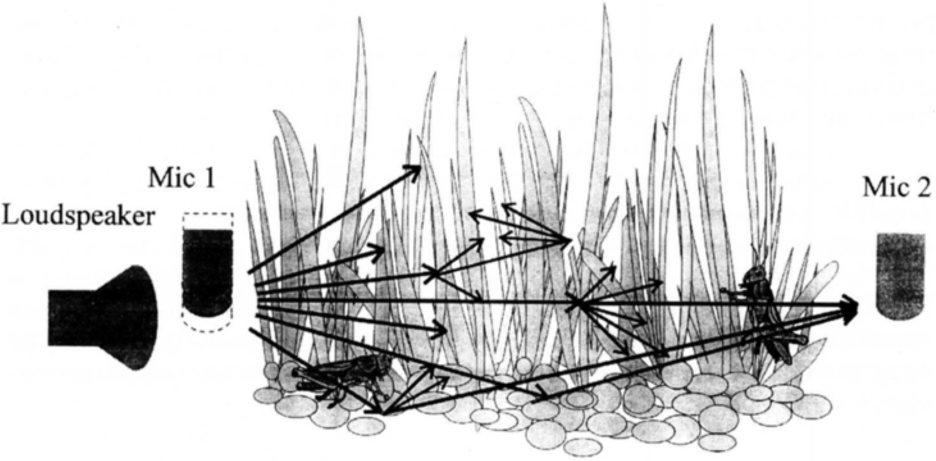

Figure 1. Schematic illustration of the experimental set-up in the field. In typical grasshopper habitats, sound signals were broadcast by a loudspeaker. A reference signal was picked up by mic 1 at 15 cm distance, and – after travelling through the habitat for distances of between 30 cm and 10 m – the attenuated signal was recorded by mic 2. In order to detect possible ground reflexions, mic 1 was placed in different vertical positions in front of the loudspeaker (+/– 3 cm). The arrows indicate transmission, reflexion and scattering of the sound waves.

song of a mate. *Recognition distance*: the distance at which a grasshopper is able to recognize the temporal pattern of a mate's song.

Animals

Males of *Chorthippus biguttulus* which were tested in the behavioural studies were caught as adults in stony, short grass habitat near Göttingen on the "Kerstlingeröder Feld". In the laboratory they were held in cages, separated from the females.

Measurement sites

Sound measurements and behavioural studies were made in different habitats typical of gomphocerine grasshoppers. Sound measurements were taken exactly at those sites which had been chosen for behavioural studies: (i) in habitats with short, stony grass vegetation typical for *Ch. biguttulus* and (ii) in habitats with tall, dense grass vegetation which are populated by *Ch. parallelus*, *Ch. albomarginatus*, *Omocestus viridulus* and some *Ch. biguttulus* (all on the "Kerstlingeröder Feld"). (iii) In parallel, all experiments were also performed in the laboratory in an arena of 1 × 6 m, the sides and the bottom of which were damped by cloth. Performing the behavioural studies under laboratory conditions as well as under natural conditions permitted comparisons with previous behavioural tests and provided data to compare with the field data.

In tall vegetation the sound measurements were taken at different heights above the ground (5-30 cm), corresponding to the possible positions of the animals. In short vegetation and in the laboratory, sound was only measured at 5 and 2 cm above the ground. The microphones were always positioned at the same height as the loudspeaker. The behavioural studies and the sound measurements were made only under climatic conditions which were favourable to song activity of gomphocerine grasshoppers. These were temperatures above 20°C and little wind.

Sound production

Digitized sound signals were played back from a field computer (PC 80386) which had been modified to 12 V DC power input. The signals were D/A-converted on an AD/DA-board (Denner) with a rate of 130 kHz. The signals were amplified (Denon DCA 450) and broadcast via a loudspeaker (Dynaudio DF21/2). This high frequency coil-loudspeaker has a linear frequency characteristic from 2-40 kHz. Its directivity pattern for several frequencies is plotted in Figure 2. The amplifier and loudspeaker had a linear intensity characteristic up to the maximally applied voltage of 10 V. The frame of the loudspeaker had a diameter of 11 cm. For the sound measurements taken at 5 and 2 cm above the ground it had to be dug in the ground. As the membrane itself, in the centre of the frame, only has a diameter of 25 mm, it remained above the ground and sound emission was not disturbed by this.

Sound signals

For the measurement of frequency-dependent signal attenuation, frequency-modulated sweeps of 7.8 ms duration and a frequency content of 2 to 40 kHz were synthesized and played back (Figure 3A, B). For the measurement of signal degradation, songs of a *Ch. biguttulus* female (see below) were played back in the field at high sound intensities (Figure 3C).

Sound measurements

Sound pressure of grasshopper songs: The calling songs of *Ch.*

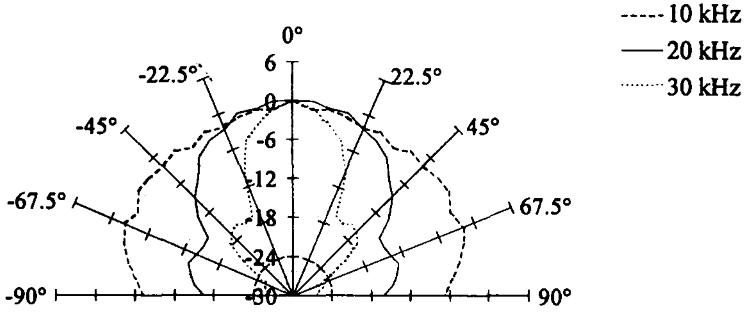

Figure 2. Directivity pattern of the loudspeaker (Dynaudio DF21/2) at 10, 20 and 30 kHz. The axis is scaled in dB.

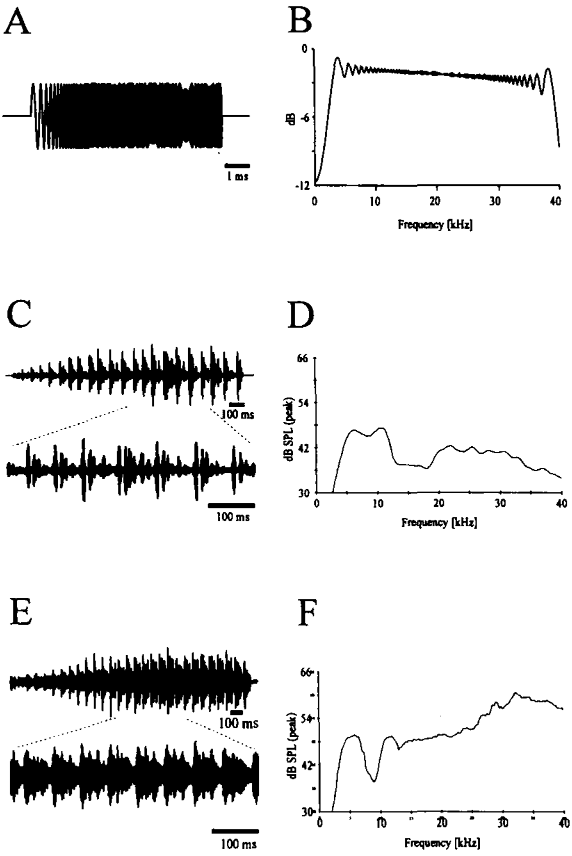

Figure 3. Frequency modulated sound signal (sweep) (A) with corresponding sound spectrum (B); oscillogram of female song of *Ch. biguttulus* at 69 dB SPL peak at 15 cm (C) with song spectrum (D), and oscillogram of male song at 82 dB SPL peak at 15 cm (E) with song spectrum (F). The dotted lines in (D) and (F) are threshold curves of tympanic low frequency and high frequency receptors of males (D) and females (F).

biguttulus males and the response songs of females were recorded with a ½ free-field microphone (Brüel & Kjaer 4133) at a distance of 15 cm (Figure 3C, E). As the temporal pattern of grasshopper songs contains fast amplitude modulations, their sound pressures were measured as "peak"-intensities ("peak" as indicated on a Brüel & Kjaer measuring amplifier 2610, which means a rising time of 1.7 dB/μs), instead of "fast rms" (which for the amplifier means an averaging time of 250 ms). This resulted in peak sound pressures which were at least 15 dB higher than found by rms-measurement: for a female song 69 dB SPL (peak) compared to 52 dB SPL (rms), and for a male song 82 dB SPL (peak) compared to 67 dB SPL (rms).

Sound attenuation and sound degradation: The sound signals were measured with two 1/4″ pressure microphones (Brüel & Kjaer 4136), which were placed perpendicular to the sound waves. The frequency characteristic of these microphones is linear between 1 and 40 kHz. The microphone signals were highpass filtered at 1 kHz, amplified (Brüel & Kjaer 5935), and stored in a portable DAT-recorder (Pioneer D-C88), which records at a frequency span between 5 Hz and 44 kHz (A/D conversion rate of 96 kHz on two channels). During these measurements mic 1 (reference microphone) was kept at a fixed distance of 15 cm from the loudspeaker, while mic 2 was mounted at different distances between 30 cm and 10 m from the loudspeaker (Figure 1). In order to detect possible ground reflexions at the reference microphone, the reference signal was measured from different vertical positions within the beam of the loudspeaker. The sound spectra at the different vertical positions were compared afterwards, and, if necessary, averaged.

Frequency analysis

The recorded signals were digitized and analyzed for their frequency content by means of a signal analyzer HP3567A. The digitization rate was 130 kHz, and the analyzer was equipped with a 50 kHz anti-aliasing low-pass filter. The frequency was analyzed in intervals of 128 Hz. The spectral analysis of the male and female songs, which had been recorded at a distance of 15 cm, was made with a FFT-window size of 7.8 ms. The maximal values of all frequency lines were stored. Subsequently, the spectra were calibrated with a 94 dB, 1 kHz signal (Brüel & Kjaer calibrator 4230) (Figure 3D, F). For the calculation of sound attenuation, for each measurement site the spectra of 100 sweeps at the two microphones were averaged and the frequency response between the two spectra was calculated (Figure 4A).

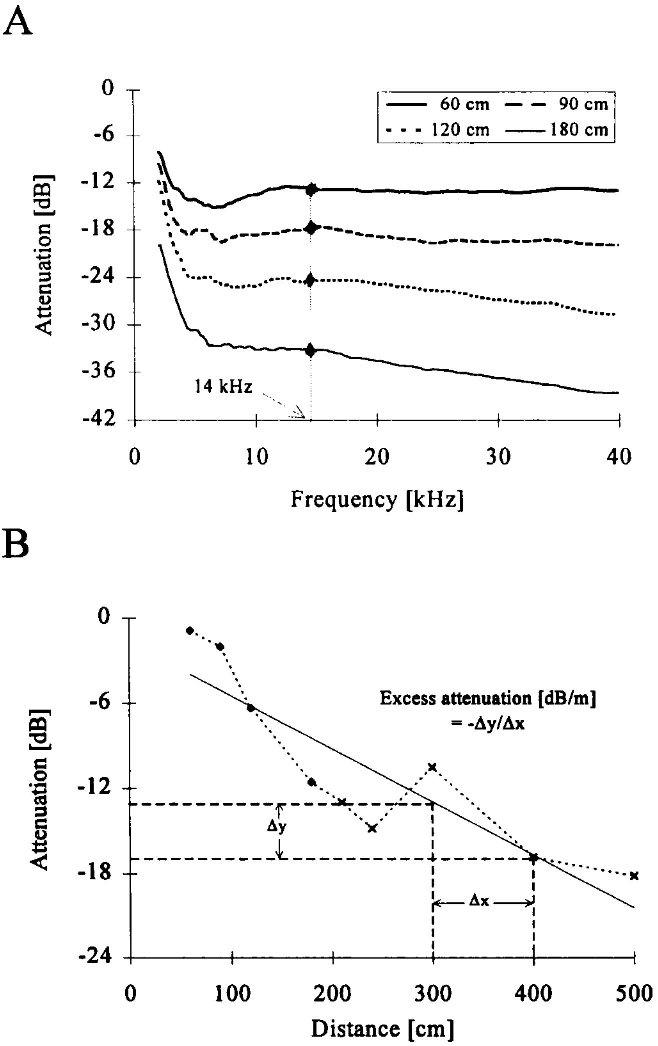

Figure 4.
(A) Spectra of sweeps recorded with mic 2 at different distances from the sound source in the field.
(B) Calculation of excess attenuation for 14 kHz, the frequency marked in (A). Excess attenuation in dB/m equals the slope of the regression curve adapted to the relation between distance and sound pressure (attenuation due to geometric spreading is already subtracted). The filled rhombs mark those values illustrated in (A).

Calculation of sound attenuation

The spectra of the sweeps which had been recorded in different habitats at varying distances from the loudspeaker were analyzed with respect to sound attenuation. On the basis of these data, the excess attenuation for frequencies between 2 and 40 kHz was calculated. Excess attenuation is the attenuation exceeding that caused by geometric spreading of sound (6 dB/ doubling distance (dd) in the far field). The frequency response between the signals of the two microphones was calculated for each distance in each habitat, indicating the attenuation between mic 1 and mic 2. Subsequently, the attenuation due to geometric spreading was subtracted. The resulting excess attenuation of each frequency (in steps of 128 Hz) with the distance from the loudspeaker was plotted (Figure 4B) and a regression curve was fitted to the data. The slope of each regression curve describes for the particular frequency the excess attenuation per distance (in dB/m). The data for the excess attenuations of all frequencies (i.e. the slopes of all particular regression curves) are combined in Figure 6, together with the 190% confidence intervals of the regression coefficient for each frequency. When calculating the regression curves, the excess attenuation was tested for a linear or logarithmic correlation with the distance from the sound source, i.e. either being attenuated in dB/m or in dB/dd. The analysis of these measurements yielded a better correlation with a linear regression between sound attenuation (in dB) and distance than with a logarithmic regression.

Calculation of perception distances by means of hearing threshold curves and song spectra of *Ch. biguttulus*

The perception distance is here defined as the distance at which the song of a mate starts to excite a tympanic receptor above its threshold. In order to calculate the perception distance in the different habitats, (i) the values of the measured excess attenuations, (ii) the song spectra of males and females and (iii) the hearing threshold curves of females and males were combined. The threshold curves of tympanic nerves and single tympanic receptors in *Ch. biguttulus* have previously been obtained by Meyer (1994) and Stumpner (unpubl.).

Male and female songs

The spectra of the male's calling song and the female's song in *Ch. biguttulus* (Figure 3F, D) at low frequencies have a sound pressure maximum at 6-7 kHz with similar energy. The calling song of males additionally contains a broad ultrasonic component, the energy of which is far larger than that of the narrow low frequency component. This large ultrasonic part is missing in the female song

(Meyer 1994, Meyer and Elsner 1996, 1997, Helversen and Helversen 1997).

The male songs (Figure 3E) consist of chirps of 1.2-5 s duration, with slightly increasing sound intensity (77-82 dB SPL peak, measured at 15 cm distance). The intensity of female songs (Figure 3C) during the shorter chirps rises to a maximum of 65-69 dB SPL (peak) at 15 cm distance. The maximum song intensities were taken as a basis for further calculations and were also used in the behavioural tests for the communication distance.

Hearing thresholds

The tympanic threshold curves of *Ch. biguttulus* (dotted lines in Figure 3D, F) have a maximum sensitivity between 5 and 7 kHz. A second broad range of enhanced sensitivity has its maximum around 30 kHz, and thus corresponds well to the spectra of the songs (Meyer 1994, Meyer and Elsner 1996).

For the calculation of perception distances of the auditory system, it is crucial to extricate the excitation of the most sensitive single receptors which form the sensory input to the system at threshold. The calculation of perception distances was therefore performed on the basis of the threshold curves of the most sensitive low frequency and high frequency receptors, which determine the threshold curve of the tympanic nerve. Intracellular receptor recordings and simultaneous extracellular nerve recordings show that the curves of very sensitive receptors correspond well with the whole nerve threshold (Stumpner, unpubl.).

Broad tuning of tympanic receptors

The tympanic receptors of grasshoppers – like other Acridids – have broad threshold curves (grasshoppers: Stumpner, unpubl.; locusts: Michelsen 1971, Römer 1976, Jacobs et al. 1998). It therefore has to be taken into consideration that it is not only the sound energy at the best frequency of a receptor that contributes to its excitation: every other frequency component of the sound signal contributes, depending on the particular sound pressure ratio between signal and receptor threshold curve (Figure 5). For every frequency the calculation of this sound pressure ratio results in a dB-value relative to the receptor threshold curve. All particular sound pressure ratios between signal and threshold curve add to the receptor excitation, which can thus be calculated by linear integration of the pressure ratios over the whole frequency range (Figure 5).

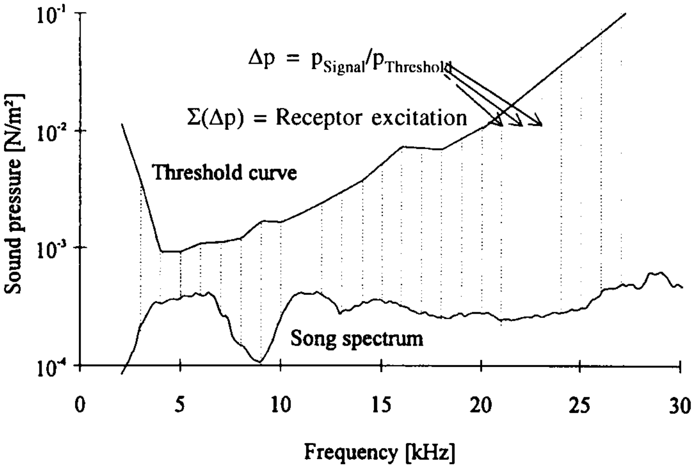

Figure 5. Calculation of receptor excitation from the receptor threshold curve and a given song spectrum. All particular sound pressure ratios (Δp) between signal (song spectrum) and threshold curve add to the receptor excitation, which can be calculated by the linear integration of the Δp over the whole frequency range.

Behavioural tests for communication distance

In the behavioural context, the male repetitively calls, a receptive female responds. If the male has recognized her song, it performs an abrupt turn towards the female, walks or jumps for some distance and continues calling (Helversen 1972). This turning reaction of *Ch. biguttulus* males was taken as an indicator of successful perception and recognition of a species-specific female song.

In this way, *Ch. biguttulus* males were tested with respect to their communication distance in the laboratory and in the field. During these playback experiments unmodified female songs at natural intensity (Figure 3C) were presented to the males at distances between 30 cm and 4 m. For each male, the longest observed distance at which it performed a turning reaction towards the sound source was discarded. The second furthest distance for each male was taken as its individual communication distance. The median value and the corresponding quartile range of all individual communication distances were calculated for each particular habitat (Table 1).

Behavioural tests for degradation of the temporal pattern

In order to measure degradation of the temporal pattern of a song, *Ch. biguttulus* female songs were played back and measured in different habitats at varying distances from the loudspeaker and at different heights above the ground. The recorded signals (as an example: Figure 9), degraded to different extents, were later modified in the following way before being played back in behavioural studies: the envelope of every signal was filled with band-pass filtered noise (4–10 kHz, the most attractive frequency range for a male). In the laboratory these modified female songs were played back to the males from a distance of about 30 cm, at optimal intensities (60-70 dB SPL). The attractiveness of the songs, which had been recorded at different distances in different habitats, was tested with the described behavioural paradigm. The individual perception distance was found in the same way as for the communication distance. The evaluation method was also the same.

The sampled data for the individual communication distances and perception distances were tested for normal distribution. As they were mainly not normally distributed, the median and, correspondingly, the quartile range (the range of the median 50% of data) were used for statistical description. Furthermore, U-tests were employed in order to test for differences between the samples of different habitats and/or different behavioural tests.

RESULTS

The aim of this paper is to demonstrate how the physical properties of the habitat influence the communication distance of *Ch. biguttulus*, which lives in grass habitats close to the ground. The experiments were divided in 3 parts: The first part is concerned with the *communication distances* of males towards female songs in the natural habitat compared to the laboratory situation. In order to explain the dramatic differences in communication distance between field conditions and laboratory experiments, in the second part sound attenuation and sound filtering in the habitat are examined and their consequence for the *perception distance* of males towards female songs and vice versa is demonstrated. As it is not only changes in the frequency domain that have to be taken into account, the third part is concerned with the degradation of the temporal pattern of female songs and the resulting *recognition distance* of males towards female songs.

Communication distance

In behavioural studies in the laboratory and in the short, stony vegetation habitat, *Ch. biguttulus* males were tested for their communication distances. In these tests female songs (Figure 3C) were played back at an intensity of 69 dB SPL (peak, measured at 15 cm distance). The maximal distance at which the males performed turning reactions towards the loudspeaker, was measured for 45 males in the laboratory and 39 males in short vegetation with the loudspeaker at 5 cm above the ground.

In the laboratory, on average the males turned towards the loudspeaker up to 187 cm away, (quartile range 168-197 cm). In the short vegetation, the communication distance was found to be only 107 cm (quartile range 90-128 cm) (Table 1). For the tall dense vegetation, only few data exist, indicating an even shorter communication distance than in the short vegetation.

Perception distance

Measurement of frequency-related excess attenuations of sound in typical grasshopper habitats

Frequency dependent sound attenuation was studied at different heights above the ground in the same habitats in which the behavioural tests concerning communication distance had been performed. Figure 6 shows frequency-related excess attenuations at the different measurement sites and at different heights above the ground. In the laboratory at 5 cm above the ground only a slight excess attenuation of 1-3 dB/m was found, which increased to 3-6 dB/m at 2 cm above the ground. In a stony habitat with short, sparse grass vegetation at 5 cm above the ground, the mean excess attenuation slightly increased with increasing frequency from 1-5 dB/m. When the microphones were placed closer to the ground (at a height of 2 cm), excess attenuation dramatically increased, especially at high frequencies, and reached 18 dB/m at 35 kHz. In dense, tall grass vegetation, the excess attenuation also increased with decreasing height above ground. At 30 cm above the ground, the values increased from 1 dB/m at the lowest frequencies to 6 dB/m at 35 kHz. The relation between excess attenuation and frequency was more obvious closer to the ground; at 5 cm above ground the values continuously increased to 15 dB/m with increasing frequency.

Habitat-dependent changes in the song spectrum

The changes in a song spectrum (recorded at near distance) with respect to its amplitude and frequency content due to filtering in the habitat was calculated on the basis of the measured excess attenuations. Figure 7 illustrates the calculated attenuation of a male song in short (A) and tall (B) vegetation at 5 cm above the ground. In short vegetation the main change is in song amplitude. In the tall vegetation there is a conspicuous change in spectral composition of the male song due to strong attenuation in the ultrasonic range, whereas the low frequencies are only slightly affected.

Perception distances

In order to determine how a song is perceived by a given receptor, the sound pressure differences between song spectrum and threshold curve were integrated over the whole frequency range. By setting a song spectrum, filtered by the habitat, in relation to the threshold curve of a receptor, it is thus possible to determine the distance at which the sound pressure of the signal exceeds the threshold of the receptor (Figure 5; for further explanation see methods).

Male receptors and female songs

The following results were found for the tympanic receptors of a male (Figure 8A). Because of its low ultrasonic portion, a female song is generally detected by a male's low frequency receptors over much longer distances than by its high frequency receptors. Thus, in an undisturbed sound field the perception distance of a low frequency receptor would lie at about 340 cm. In the laboratory, because of the action of excess attenuation, this distance only lies at 226 cm at 5 cm above the ground and at 162 cm at 2 cm above the ground. In short vegetation excess attenuation acts stronger, thus reducing the perception distance of low frequency receptors to 185 cm at 5 cm above the ground and to 115 cm at 2 cm above the ground. In tall vegetation the perception distance also strongly depends on the height above ground: close to the ground, at 5 cm, it amounts to 127 cm, and it rises with rising height (30 cm) to 227 cm. The distance at which the high frequency receptors are excited lies between 45 and 75 cm under all conditions. Therefore, because of its low ultrasonic portion a female song will always be detected first by a male by means of its low frequency receptors. Thus, the reduced communication distance, as observed in the behavioural tests (Table 1), can partly be explained by the reduced perception distance compared to the laboratory conditions. However, in the low vegetation the calculated perception distance still is significantly longer than the communication distances found in the behavioural tests. The question of whether signal attenuation is sufficient to explain the reduced communication distances in the field, or whether other processes contribute to this, is discussed later in this paper.

Female receptors and male songs

Generally, the high frequency receptors are excited much stronger in a female listening to a male song (Figure 8B) because of the strong ultrasonic component in the male song. In the undisturbed sound field the perception distance of high frequency receptors would be distinctly longer (750 cm) than that of the low frequency receptors (343 cm). In the laboratory, excess attenuation already leads to a strong reduction in perception distance to 270 cm compared to 210 cm for the high

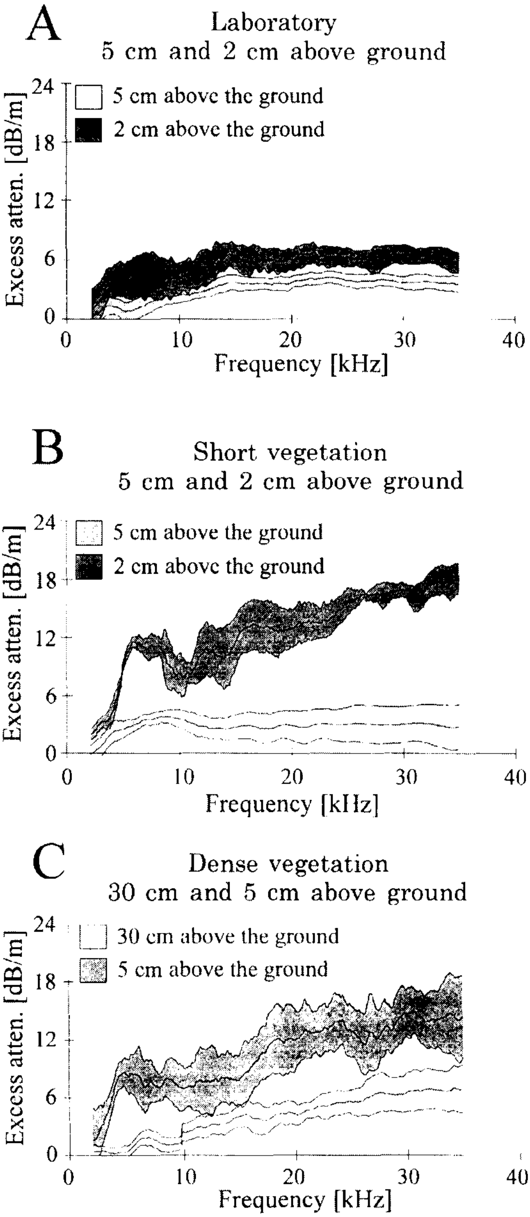

Figure 6. Excess sound attenuation (A) measured in the laboratory at 5 cm (lower graph) and 2 cm above the ground (upper graph), (B) measured in short stony grass vegetation, typical of *Ch. biguttulus*, at 5 cm (lower graph) and 2 cm above the ground (upper graph), and (C) measured in tall dense grass vegetation typical of *Ch. parallelus* and *O. viridulus* at 30 cm (lower graph) and 5 cm above the ground (upper graph). The 90% confidence intervals for the excess attenuation are shaded.

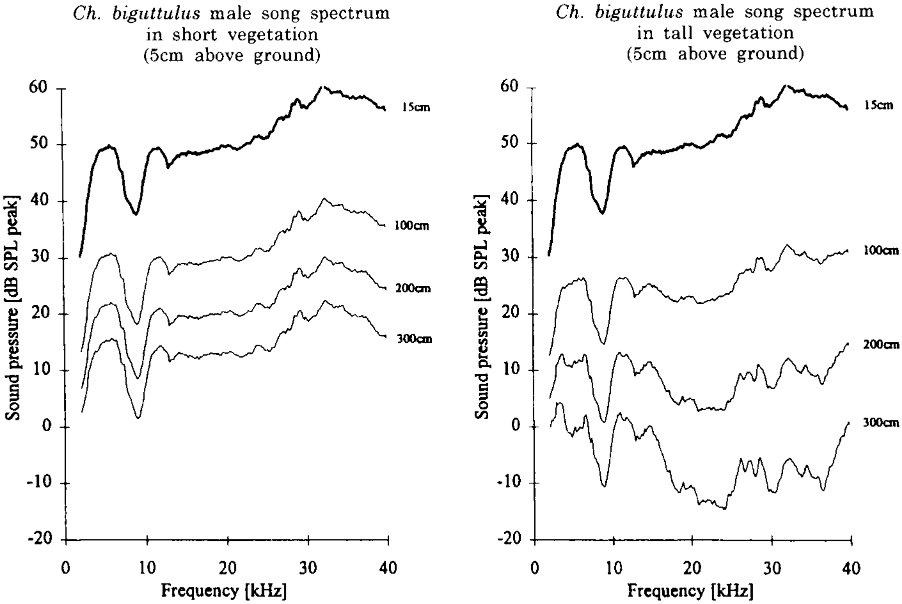

Figure 7. A spectrum of a male song at different distances from the singer when travelling through short vegetation (A) and tall vegetation (B) at 5 cm above the ground, illustrating that a song is not only attenuated, but that, depending on the habitat, its spectral composition changes. The song was recorded at 15 cm from the animal (bold curve), the other data were calculated on the basis of measured frequency dependent sound attenuations.

frequency receptors (5 cm compared to 2 cm above the ground). In the field, however, the reduction of the perception distance is even stronger, especially for the high frequency receptors, because of the ultrasonic attenuation close to the ground (short vegetation: 240 cm; dense vegetation 127 cm). The perception distances for the low frequency receptors resemble those of the male receptors for female songs (compare Figure 8A).

The results illustrate that in the field excess attenuation leads to a strong reduction in perception distance of the high frequency receptors of a female towards a male song. Thus, the difference between perception distances for high and low frequency receptors is clearly smaller than it would be in an undisturbed sound field. This means that in the undisturbed sound field a female would detect a male song with its high frequency receptors first. In contrast, in the laboratory and in the field, especially in dense and high vegetation, the same song is detected by low and high frequency receptors at similar short distances.

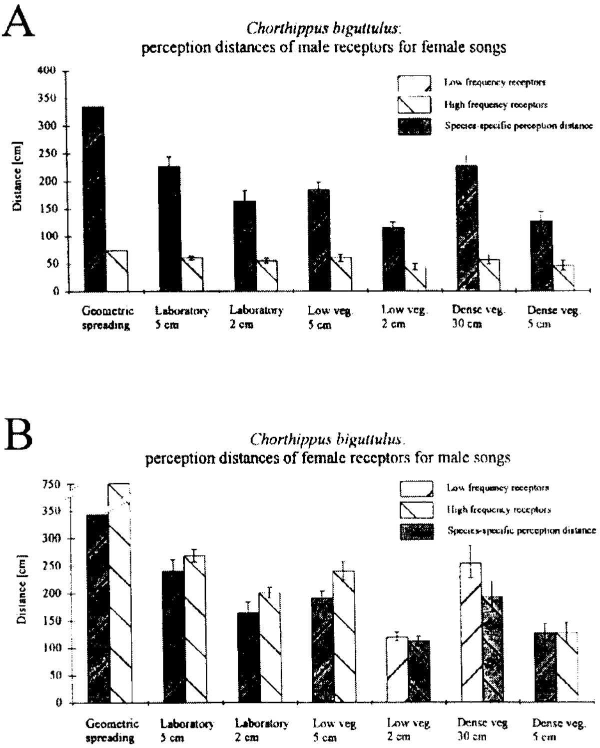

Figure 8. Calculated perception distances of male receptors for female songs (A) and of female receptors for male songs (B) in different habitats. The dark accentuated bars indicate the sex-specific perception distance (the distance at which all those receptors are excited, which are necessary for recognition of the frequency content of a mate's song). For the males this is represented by the low frequency receptors, for the females this is represented by the excitation of the two receptor groups (see discussion).

Recognition distances

Degradation of temporal patterns

Degradation of temporal parameters is caused by reflexions and reverberations (Embleton 1997). In order to find out whether temporal degradation of the song pattern might play a limiting role for communication distances, behavioural studies with *Ch. biguttulus* males were performed. The stimuli used in these laboratory tests were female songs, the temporal pattern of which was degraded in a habitat-specific and distance-specific way. The habitat changes not only the temporal pattern of the signal, but also its frequency content. All test signals were given the same frequency content (see methods).

TABLE 1

Perception distances, recognition distances and communication distances of males for female songs in different habitats. The data for the perception distance of male receptors towards female songs were taken from Figure 8A. The data for the recognition distances and the communication distances are the median values of the individual maximal distances of all tested animals. For the calculated perception distances the 90% confidence intervals are shown; for the recognition distances and the communication distances quartile ranges are shown.

Habitat	Calculated distances (cm)	Behavioural distances (cm)	
	Perception distance	Recognition distance	Communication distance
laboratory	**226 (211-244)**	300 (270-330) (n=20)	187 (168-197) (n=45)
short veg. 5 cm	185 (172-196)	**120 (90-150) (n=26)**	107 (90-128) (n=39)
tall veg. 5 cm	**127 (110-144)**	300 (250-400) (n=24)	< 100 (n=4)

Males performed turning reactions towards female songs which in the laboratory had been recorded at distances up to 300 cm from the loudspeaker (Table 1). Female songs which had been recorded in short stony vegetation were only attractive when they had been recorded within a distance of 120 cm from the loudspeaker, whereas those recorded in tall dense vegetation elicited turning reactions when they had been recorded up to 300 cm from the loudspeaker.

In the laboratory and in tall vegetation the song could be recognized over distances which were longer than the tested communication distance and the calculated perception distance. The difference between recognition distance and communication distance is highly significant for the laboratory experiments. In short vegetation the temporal pattern of the signal is more affected. In this habitat the recognition distance is 65 cm shorter than the perception distance. Correspondingly, recognition distance and communication distance are about equal for these experiments (not significantly different).

Vertical positions of the animals

In both habitats (short and tall vegetation) the vertical position of the animals was monitored. The animals did not show a preference for the height above ground before singing. Instead, a great variation was observed, with a tendency for the females to sit closer to the ground than the males. The males avoided singing positions very close to the ground, climbing the grass or a stone, but they did not consistently choose the most elevated positions for singing or listening, which would enable them to enlarge their communication range.

DISCUSSION

The questions which were addressed in this paper concern the limitations that the physical properties of the habitat exert on the acoustic communication distance of the gomphocerine grasshopper *Chorthippus biguttulus*. Correspondingly, the different influences of the habitat on male and female songs and the resulting communication distances are discussed. The data are compared to findings about communication distances in other orthopteran insects.

In the first series of experiments, it was demonstrated that in the field the communication distance of a *Ch. biguttulus* male is distinctly shorter than under laboratory conditions (Table 1). Subsequently, it was studied whether changes in the frequency domain or changes in the temporal domain of the songs are responsible for the demonstrated reduction in communication distance. Changes in the frequency domain of the species-specific sound signals, due to frequency dependent sound attenuation, influence the perception distance of a song. Changes in the temporal domain of the songs, caused by reflexions and reverberation, influence the recognition distance of a song.

Limitations due to the physical properties

Frequency dependent sound attenuation

Sound attenuation can be brought about by different physical properties of the habitat. Correspondingly, the relation between distance from the sound source and sound attenuation can vary. The measured sound pressures, close to the ground, were found to have mainly a linear correlation with distance, which is caused by absorption in the atmosphere and especially in the vegetation. The frequency-related atmospheric absorption alone amounts to 0.1-0.4 dB/m at 10 kHz and 1.8-2.7 dB/m at 40 kHz (Griffin 1971, Embleton 1997). A logarithmic correlation would be mainly brought about by diffraction from the vegetation (Michelsen 1978).

Sound measurements showed that frequency dependent sound attenuation especially plays an important role very close to the ground: whereas in the short grass vegetation at 5 cm above the ground signal attenuation ranges about 3 dB/m, at 2 cm above the ground it is strongly frequency dependent and increases to 18 dB/m at 35 kHz. Almost the same values were found in tall dense grass vegetation at 5 cm above the ground whereas at 30 cm above the ground, excess attenuation is clearly lower. Also, under laboratory conditions, excess attenuation increases to 6 dB/m very close to the ground (2 cm above the ground, Figure 6), indicating that, generally, very close to the ground the physical properties are unfavourable for sound communication. The increase in sound attenuation very close to the ground – which has been observed in the field and also in the laboratory – is probably due to sound absorption at the ground. For the measurement in the field it has additionally to be taken into account that the surface is not ideally flat, which might result in shadow zones behind an irregularity.

Perception distance

The calculations of perception distances were based on the measured sound attenuations, the tympanic receptor thresholds and the song spectra of males and females. They resulted in distinctly shorter values for the habitat than for the undisturbed sound field (Figure 8A, B). These results clearly demonstrate that living close to the ground – as gomphocerine grasshoppers do – means exploiting a very unfavourable acoustic environment for sound communication. The fact that the grasshoppers do not climb the top of the vegetation can be explained in terms of predator avoidance. Generally, the calculated communication distances (ca. 1-2.5 m) are short compared to many other orthopteran insects which communicate in a similar frequency range. In contrast to the findings that the grasshoppers sit close to the ground or inside the vegetation while singing, other orthopteran insects, like many bushcrickets, take advantage of elevated singing positions with far better acoustic properties (Römer and Bailey 1986).

The acoustic situation of gomphocerine grasshoppers also differs in other respects from that of other sound producing insects: they sing softly, producing non-resonant, broadband signals with extremely fast amplitude modulations. In contrast, many other singing insects like crickets, bushcrickets, cicadas and, recently found a single species of the orthopteran family Pneumoridae, produce loud, partially or completely resonant songs. The pneumoridan species, *Bullacris membracoides*, performs a very specialized form of long-distance communication with communication distances in the range of km (von Staaden and Römer 1998). In a typical bushcricket habitat (bushes) for a frequency of 40 kHz excess attenuations of 18 dB were measured at 10m from the sound source and about 2m above ground and 24 dB at 10 cm above the ground. Römer and Lewald (1992) found the excess attenuation to be composed of a linear part caused by absorption, dominant at low frequencies (at 5 kHz, 0.35 dB/m), and a logarithmic part caused by scattering at higher frequencies (for 10-40 kHz, 4.6-10 dB/dd) (data recalculated after Römer and Lewald 1992). With the Omega-cell of *Tettigonia viridissima* as a biological microphone they found perception distances of 20-40 m. These data show that, besides the higher sound energy which is radiated by bushcrickets, choosing an elevated singing perch strongly decreases sound attenuation and subsequently increases the communication distance. For crickets living in scrub, sound measurements in the habitat were taken by

Popov et al. (1974). They also demonstrated that excess attenuation increases with increasing frequency. These measurements yielded results that match the data presented in this paper (5 cm above the ground: 0.6 dB/m at 4 kHz, 1.3 dB/m at 8 kHz and 2.3 dB/m at 16 kHz). Moreover they showed the excess attenuation to be much greater very close to the ground than on top of the vegetation (2 cm above the ground: 11 dB/m at 4 kHz and at 16 kHz, data recalculated after Popov et al. 1974).

Recognition distance

The temporal pattern with its extremely fast amplitude modulations is known to be an important cue for song recognition in gomphocerine grasshoppers (Helversen 1972, Helversen and Helversen 1994). The behavioural tests on the recognition distance illustrate that degradation of the temporal pattern of female songs is an important parameter limiting the distance for song recognition. The results show that, generally, the recognition distance does not exceed 3 m. This might therefore be looked at as the upper limit of sound communication in this species.

In detail, it is shown that – counterintuitively – the recognition distance of songs recorded in short, stony vegetation is much shorter than that recorded in the laboratory and in tall, dense grass vegetation close to the ground (Table 1). In short vegetation the distance at which a female song can be perceived is clearly larger than the distance at which it can be recognized as species-specific. This indicates that the degradation of temporal parameters limits the sound communication in this habitat.

In the laboratory and in dense vegetation, the recognition distance far exceeds the calculated perception distances, demonstrating that degradation of temporal parameters is not the limiting parameter under these conditions. However, in the laboratory, the calculated perception distance is somewhat longer than the communication distance found in the behavioural tests. A possible explanation for this discrepancy is that the males need a suprathreshold excitation in the auditory system. In this case, an excitation of 2 dB above perception threshold would result in a perception distance of 190 cm, which equals the results of the behavioural tests. For the dense vegetation on this basis a communication distance of ca. 120 cm would be expected.

The high level of temporal degradation in short vegetation can be explained by the scattering and reverberations that are caused by reflecting surfaces like the ground and stones, which are prominent in this habitat. In contrast, the high level of sound absorption and diffraction that takes place within tall, dense vegetation greatly attenuates a sound signal, but only weakly disturbs its temporal pattern. This is illustrated in Figure 9, which indicates that in short

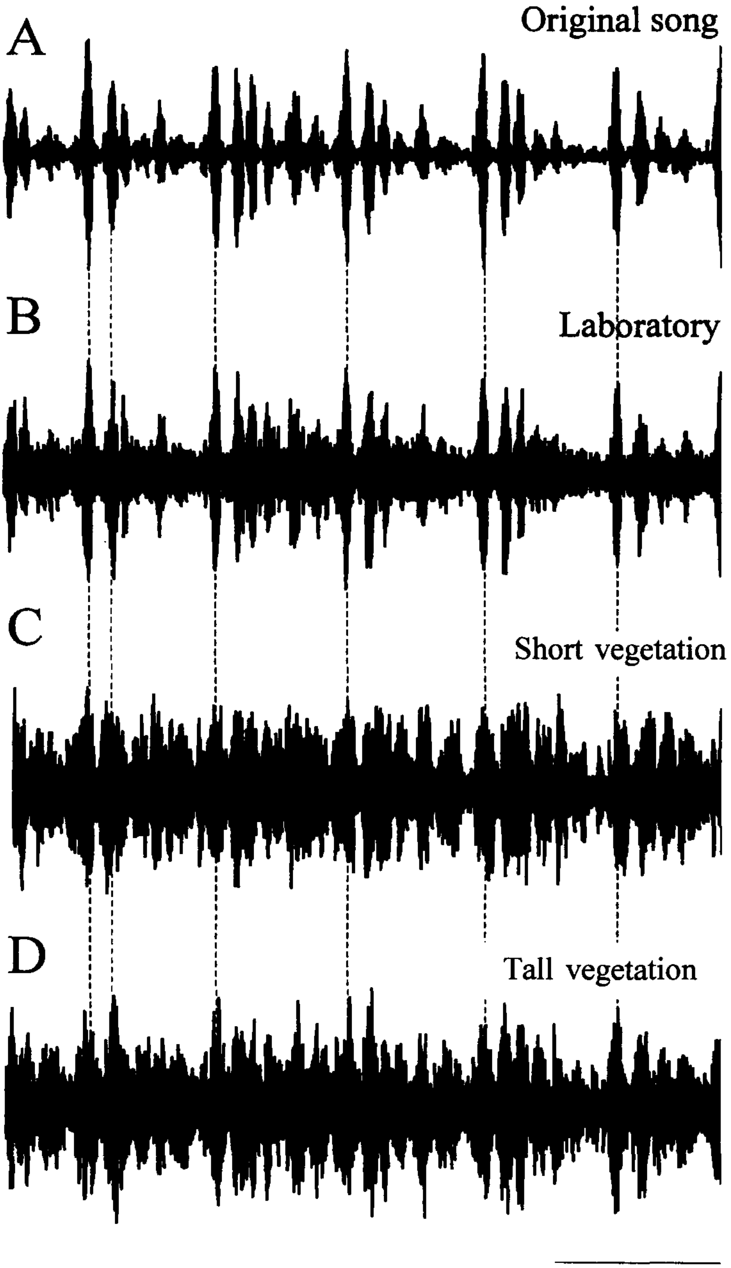

Figure 9. Temporal pattern of a *Ch. biguttulus* female song (A), recorded at 210 cm from the loudspeaker at 5 cm above the ground in the laboratory (B), in short vegetation (C) and in tall vegetation (D).

vegetation the beginning of each syllable and the pulse pattern in general is less pronounced than in the other habitats.

Under field conditions, reverberation greatly changes the temporal pattern of many gomphocerine grasshopper songs, because they contain very fast amplitude modulations up to several hundred Hz. Behavioural and electrophysiological studies showed that the auditory system is able to recognize impulse intervals down to 2 ms. From work by Hill (1983) it was deduced that a locust tympanic receptor should have an integration time of 5-10 ms. Recent studies by Tougaard (1996) of the A1 tympanic receptor of two species of moths corrected these long integration times which are somewhat contradictory to the behavioural findings. These studies revealed an integration time of about 3 ms, which corresponds well to my own studies at locust receptors and interneurons (Lang 1996). Furthermore, it was shown that gomphocerine grasshoppers probably make use of receptor synchronization in order to detect small intervals (Ronacher and Römer 1985, Ronacher and Stumpner 1988). The information about these fast amplitude modulations have been shown to be exploited in terms of song recognition (Helversen and Helversen 1994).

It appears that the gomphocerine grasshoppers have driven their auditory system to the limit with respect to recognition of temporal patterns, thus preventing long distance communication. So the conclusion might be drawn that it would be useless for these animals, living within the grass, to evolve louder songs or more sensitive ears, because the fragile temporal pattern is distorted at greater distances.

In contrast, it might be argued that all those species which have evolved loud resonant songs have specialized in long distance communication, and either avoid using such fast amplitude modulations or live in better acoustic environments. As a contradiction to this argument, Simmons (1988) showed in behavioural studies with ground living crickets that they react very sensitively to degradation of the temporal parameters of their resonant songs, which restricted their communication distance to 2 m. Römer and Lewald (1992) show – on the basis of the variability of responses of an auditory interneuron of a bushcricket – that the degradation is negatively correlated with the bandwidth of the presented sound signal, i.e. a broadband signal is more stable with respect to degradation than a pure tone.

Male and female communication distances

In many gomphocerine grasshopper species, as in *Ch. biguttulus*, the songs of males and females differ with respect to their high frequency content: the male songs contain a strong ultrasonic component which is almost missing in the female songs (Meyer 1994, Meyer and Elsner

1996, 1997 Helversen and Helversen 1997). Behavioural studies (Helversen and Helversen 1997) showed that males of *Ch. biguttulus* react only weakly to artificial female songs with an additional ultrasonic part. They strongly prefer female songs exclusively consisting of frequencies below 10 kHz. Thus the conclusion might be drawn that only the excitation of low frequency receptors leads to a positive phototaxis in this behavioural context, whereas the excitation of high frequency receptors leads to an inhibition. In contrast to males, females prefer male songs which contain both low and high frequencies; songs with only low or only high frequencies (below 10 kHz or above 10 kHz) are much less attractive. In this case it may be concluded that only excitation of both low and high frequency receptors leads to female response behaviour.

The calculations presented here show that in males the perception distances of female songs for low frequency receptors are far longer than those for high frequency receptors (Figure 8A). This means that, while approaching from the distance, the males perceive the female songs only with their low frequency receptors. They consequently recognize the song and react with positive phonotaxis. The resulting species-specific perception distance is marked by dark shaded bars in Figure 8A. Only when close to the female (< 45-75 cm), is there is a range in which both low and high frequency receptors are excited by the female song. Accordingly, in addition to the attractive effect, the animal now has to deal with a repelling effect. Behavioural studies show that this negative effect of the excitation of high frequency receptors is compensated by the massive excitation of all low frequency receptors which occurs at this short distance (D. von Helversen, pers. comm.).

For females listening to a male song, Figure 8B illustrates that, in the undisturbed sound field, the perception distance for high frequency receptors would significantly be longer than that for low frequency receptors. In contrast, in the natural habitat the perception distances for low and high frequency receptors do not differ significantly. Taking into account the behavioural findings that females preferentially react when both low and high frequency receptors are excited, the species-specific perception distance equals the perception distance of the receptor group with weaker excitation (in Figure 8B marked with dark accentuated bars).

In this respect, it seems a plausible mutual adaptation of male song frequencies and female receptor sensitivities that within the vegetation low and high frequency receptors of the females are about equally excited. Furthermore, the comparison of males and females with respect to their species-specific perception distances (Figure 10) shows that these distances in the respective habitats are about equal, i.e. females recognize the calling song of males from the same distance as males recognize the softer responses of the females. This again may

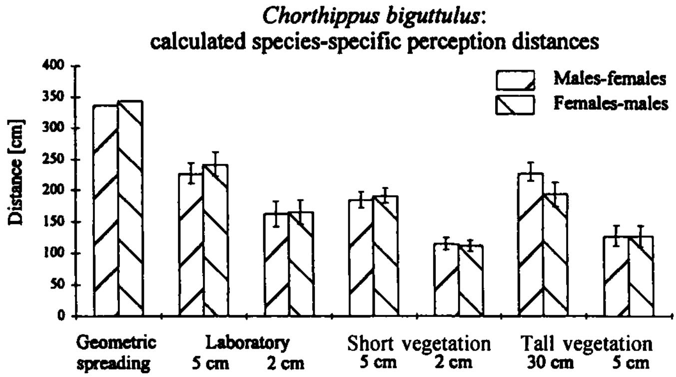

Figure 10. Sex-specific perception distances in *Ch. biguttulus* males for female songs and in females for male songs in different habitats (for explanation see legend of Figure 8).

represent a mutual adaptation of the respective sender and receiver in both directions.

For females listening to male songs, it is still unclear whether or not temporal degradation also could limit the communication distance. In *Ch. biguttulus* the recognition of male songs is somewhat different to that of the female songs: females prefer male songs without fast amplitude modulations within the syllables, only being critical about the accentuation of the syllable beginnings and the syllable/pause-ratio within the verse (Balakrishnan, pers. comm.). Whether these parameters are more resistant to temporal degradation in the habitat than those of the female songs will be subject of further behavioural tests.

ACKNOWLEDGEMENTS

I am grateful to J. Meyer and A. Stumpner for providing data about hearing thresholds and to J. Schul in Erlangen for making available knowledge and software for the stimulation device. I thank A. Stumpner, F. Gilbert, R. Lakes-Harlan, N. Elsner, A. Michelsen and an anonymous referee for their valuable comments on this paper. This study was supported by a grant given to N. Elsner by Deutsche Forschungsgemeinschaft (DFG EL 35/18-1).

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Received 27 March 1998, revised 25 November 1998 and accepted 16 January 1999