Signals and Sex-Specific Active Space in a Duetting Insect (Orthoptera: Phaneropteridae: Poecilimon affinis)

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Signals and sex-specific active space in a duetting insect (Orthoptera: Phaneropteridae: *Poecilimon affinis*)

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Abstract

Members of the family Phaneropteridae are well known for their acoustical duetting behaviour, used for locating and meeting a mate. In *Poecilimon affinis*, typically the male approaches a responding female phonotactically. A set of behavioural experiments, bioacoustic and neurophysiological measurements (some with a relatively low sample size, but not repeatable under the same circumstances) indicates the following system: the male song (92 dB SPL_{peak} at a distance of 1 m) is about 10 dB louder than the female song. The females respond to male signals only if these are ~15-20 dB above their hearing threshold. The males start a phonotactic approach towards a stationary, responding female only if she is no more than ~12 m away. Females, on the other hand, may respond to singing males up to a distance of 28m, and to more distant males with softer signals than to closer ones. A possible function of these weak signals, inaudible for the duetting male, may be to attract eavesdropping males. The communication system will work at densities as low as 0.003 females or 0.0005 males per m^2.

Key words

acoustic communication, duet, hearing, stridulation, female response, population density, Tettigonioidea

Introduction

Many signals in insect communication are used to meet a mate faster, safer or more reliably and to get the best available partner. This is true for all three sensory categories or modalities: chemical (by pheromones), mechanical (by sound or/and vibrations) and visual (for a review see Greenfield 2002). Usually members of one sex send signals and those of the other sex respond by approaching. However, mainly in two sensory channels (the mechanical and the visual), communication systems evolved with an exchange of signals between both partners. This has happened many times independently, and the reasons for the evolution of duetting behaviour are likely found in changing costs for searching and calling in terms of energy and risk (*e.g.*, McCartney *et al.* 2012; for a review see Bailey 2003). Reducing the costs to meet a mate also increases the options to choose from among several physically contacted mating partners.

Acoustic duets by air-borne sound in insects are known from Orthoptera and cicadas. Among Orthoptera they are found in several groups of Caelifera and Ensifera, in the latter in tettigonioids, but not in crickets (Gryllodea) (Bailey 2003). The group with the highest number of duetting species is the bush-cricket family Phaneropteridae (often treated as subfamily Phaneropterinae) with more than 2500 species (Eades *et al.* 2012). All of its winged species have females with tegminal stridulatory organs, and in a few species with completely reduced female tegmina, these organs are lost.

The duetting behaviour has been studied in many species worldwide, first in North America (Spooner 1964, 1968) and later in Europe (Zhantiev & Dubrovin 1977), Australia (Bailey & Field 2000) and Asia (Tauber & Pener 2000). The pair forming strategies were reviewed by Zhantiev and Korsunovskaya (1986) and Spooner (1995), who both described several types of male-female interactions. In some, the female approaches a singing male and starts to respond only when she is quite close to him. There are also species with a complete role reversal of the typical tettigonioid/gryllid situation; in *Leptophyes (albovittata* Zhantiev & Korsunovskaya 1986, *punctatissima* Robinson *et al.* 1986) and *Poecilimon ornatus* (Heller & Helversen 1986) the males approach the stationary female phonotactically, contrasting to the 'typical' situation where only the females move.

While there are quite a number of studies describing the behaviour of males and females, it is poorly known how large the ranges of the signals actually are or what kind of information the animals use to make their decision whether to approach or to respond and when to switch between these two types of reaction. As already mentioned by Spooner (1968, 1995) the loudness of the signals may be very important. However, among the more than 50 species whose duets have been studied, for only one species have these intensities been published (Zimmermann *et al.* 1989).

To understand the selective forces working on the communication system, it is insufficient to measure signal intensities and hearing thresholds: one also needs information about the ranges of the signals in the habitat. Such ranges have been measured in tettigonioid species with uni-directional communication (*e.g.*, Römer & Bailey 1986), crickets (Mhatre & Balakrishnan 2006) and in duetting Caelifera (Van Staaden & Römer 1997, Lang 2000) with quite interesting and partly surprising results, revealing huge ranges and large differences between the sexes. After having determined the signal ranges, it is necessary to find out how many partners are reached by a signal. This approach will allow an estimation of the intersexual and intrasexual competition and hence help understand sexual selection.

Here we present data of the phaneropterid species *Poecilimon affinis* (Frivaldsky, 1867) coping with all these aspects. Some of the data are based on rather low sample sizes. Due to the early passing of Dagmar and Otto von Helversen, however, it is not possible to repeat them under identical conditions. Since they present a unique data set not available for any other duetting species so far, they are

presented here anyway in the hope of encouraging other researchers to perform similar experiments in other duetting species.

In this species males sing, receptive females reply and males perform phonotaxis. Highly motivated females, however, may start phonotaxis towards the male as well (Helversen *et al.* 2012). In principle, the ranges of male and female signals, which are not necessarily identical, can either be estimated when intensity of the signal, sound attenuation in the biotope and the sensitivity of the receiver are known, or it can be measured directly: for the male by determining the maximal distance over which a male signal will release a female answer, and for the female by measuring the probability of male phonotaxis as a function of distance to the female, always tested in animals ready to mate. We employed both approaches: the first to calculate the acoustic range on the basis of physical and physiological properties, and the second to confirm this estimation under those conditions in which acoustic communication normally takes place, with all the unpredictable factors concerning behaviour of the animals in their normal environment with the typical background noise, the conditions of this specific biotope including acoustic attenuation properties of the vegetation, humidity, wind, temperature and its vertical gradients (Michelsen 1978). For the acoustic range we will use the term "active space", introduced by Bossert and Wilson (1963) for chemical communication and now used also in acoustical communication (*e.g.*, in birds: Lohr *et al.* 2003, dolphins: Janik 2000, insects: Van Staaden & Römer 1997). We will not present data on (alternative) acoustical strategies of males and females (*e.g.*, Greenfield & Shelly 1985), which also exist in this species.

The current study is from the same site at which the mating behaviour of *P. affinis* (Heller 1990, 1992; Heller & Helversen 1991) together with other aspects of the acoustic behaviour have also been studied (Heller & Helversen 1993, Helversen & Wendler 2000, Helversen *et al.* 2012).

Methods

The species.—*Poecilimon affinis* is a relatively large, nearly exclusively phytophagous bush-cricket (mean body mass: females 2.1 g, males 1.4 g), which is active mainly at night. It occurs in large areas of the Balkan peninsula (see distribution map in Chobanov & Heller 2010). The field experiments were performed in the Vernon Mountains near Pisoderion (Northern Greece, N. Florina; 40°46′N, 21°14′E) from 1988 to 1990. The species is found in plots bare of trees, especially in clearings held open by grazing sheep and goats. Typical are meadows with a large number of herbs (*e.g.*, *Thymus*) and an additional sparse shrub-like vegetation of thistles, *Verbascum* and *Urtica*. For song recordings, animals from other Greek populations (Pieria Mts) were used.

Test 1: The sound signals.—For characterizing male and female signals, song recordings were made with a Racal store 4-D tape recorder using microphones Brüel & Kjær 4133 and 4135 (frequency response flat up to 40 and 70 kHz respectively). After digitising the songs on a PC or an Apple computer, oscillograms and sound analyses were made using the programs Turbolab (Bressner Technology, Germany) and Amadeus II (Martin Hairer; http://www.hairersoft.com). Wing movements were registered by an opto-electronic device (Helversen & Elsner 1977, modified as in Heller 1988).

Song terminology.—Calling song: song produced by an isolated male. Syllable: the sound produced by one complete up (opening) and down (closing) stroke of the wing. Impulse: a simple, undivided, transient train of sound waves (here, the highly damped sound impulse arising as the impact of one tooth of the stridulatory file).

Intensity of the song was determined using a Brüel & Kjær 2209 sound level meter equipped with a 1/2" B & K 4133 microphone and using the "Peak hold" function. Low frequencies were filtered out by a custom-made 2.6 kHz high pass filter. Males [n = 11, 3-23 (mean 10) measurements per male] were measured in the field sitting head-down at a height of 0.4 m on a thistle with the microphone placed at a distance of 1 m in the same height, thus picking up the sound dorso-anteriorly. The song intensity decreased with distance due to spreading loss, atmospheric attenuation and effects of the vegetation. Therefore, song intensity of three males was measured at distances between 1 and 8 m in the same way as described before. Females (n = 4) were measured in an anechoic room at a distance of 1 m as well. The female songs were responses to a synthesized male song (Vuko VKS 22-16 transient recorder), the intensity of which could be varied using an external amplifier/attenuator. Intensities between 51 and 75 dB SPL were tested in 3 dB steps. Each of the females was only tested with some of the intensities, each intensity presented 12 to 38 times. For 60 and 63 dB SPL, two females were tested.

All measurements are given as dB SPL (ref. 20µPa) peak reading.

Test 2: Neuronal hearing threshold.—Neurophysiological measurement of hearing thresholds were performed in males (n = 3) and females (n = 2; for details see Stumpner & Heller 1992) at the tympanic nerve with a suction electrode. Starting at a high intensity, which elicited a clear response coupled to the stimulus, the minimum intensity (in dB SPL ref. 20µPa) eliciting a detectable response was determined acoustically via earphones and visually via an oscilloscope. The digital attenuator (lab made with a logarithmic attenuator chip AD7128 – Analog Devices, USA) allowed attenuation in 6 dB steps and in 0.375 dB steps. This method has repeatedly proven to be reliable within ± 2 dB, typically even within ± 1 dB (see Stumpner & Heller 1992, for references). Stimuli, intermediate in duration between male song and female response (35 ms with 1.5 ms rising and falling flank and at a rate of 2 Hz), consisted of band filtered white noise (± 200 Hz around a center frequency; Kemo VBF8). Stimuli were given from ipsilateral (as referred to the tympanic nerve recorded from), frontal and contralateral for comparison.

Test 3: Behavioural hearing threshold.—The behavioural threshold of females was determined using a synthesized model of the male song (same equipment as used for female intensity measurements) at different intensities. The female's behavioural threshold was defined as that intensity at which 50% of the presentations released a reply leading to 11 separate data sets from 6 different females (n per set 98-624; n_{total} = 4481 tests).

Test 4: Active space.—Test 4a: To measure the range of the male song under field conditions, a singing male was placed on a "portable" thistle (a cut plant placed in a pot). The thistle with the male was moved away (typically during the silent intervals in the male song) from a responding female, which was also sitting in a height of 0.4 m on another thistle. Female answering was checked visually (by observing movement of tegmina) and with the aid of an ultrasound-converter ("bat-detector") for at least 10 male syllables. When the female ceased to answer, the male was brought nearer again to be sure that the female was still ready to respond. For the experiments, running over 15 days, seven males, but only two virgin females (collected as subadult nymphs) were used. The number of tests per day was variable, depending on weather conditions, but

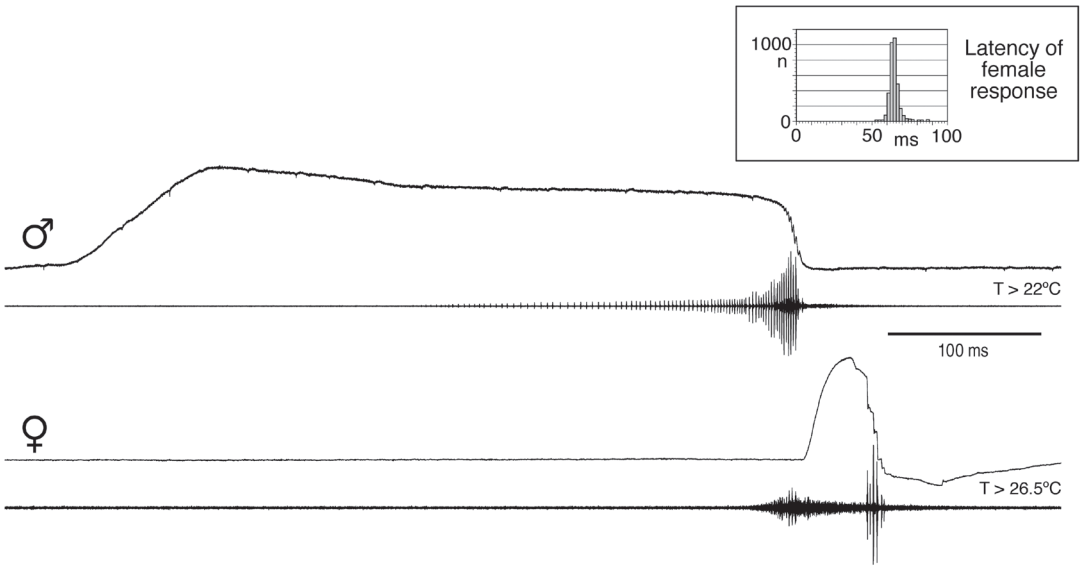

Fig. 1. Oscillograms of male calling song and female response song [synchronous registration of left tegmen movement (upper line; upward deflection represents wing opening, downward wing closing) and sound (lower line); male (ex Vernon Mts.) and female (ex Pieria Mts.) not recorded synchronously]. In the female sound track the male sound can also be seen. Inset: Latency of female response measured from end of male song (data from Helversen & Wendler 2000).

never exceeded three.

Test 4b: A similar experimental design was used to measure the range within which a male would start a phonotactic approach to a responding female. A singing male (n = 6 males) was placed on a "portable" thistle (see above) at a certain distance to a responding female (distance 2-14 m in 2 m intervals, starting distance chosen randomly in the lower half of the range). He was allowed to receive at least 50 answers from the female. If he had failed to start phonotaxis up to the 50th reply, the next nearer distance was tested. When he jumped or moved downwards and maintained direction to the female, phonotaxis was assessed as positive. The male then was replaced on the thistle and the next run from another distance was started. Putting the male back on a plant did not seem to disturb his behaviour – he resumed singing typically within one minute after being set back.

Test 5: Number of receivers.—The number of receivers of the signal of one partner of a duet depends on the range of its signal and the number of animals of the opposite sex within this range. This latter value can be derived from the mean population density. However, such calculation will apply only for infinite, homogeneous populations.

Fortunately, a more precise measure of population data is available from a population studied in the same area by Heller & Helversen (1991). In this study, nearly all animals had been marked and all positions (distance and direction) were registered every third day in reference to a matrix of fixed points. From these data, a map with the positions of all animals was prepared and then individual density information was calculated by means of a custom-made program. We calculated the number of males and females within circles of different sizes (in 1 m steps up to 10 m, in 5 m steps from 15 m on) around each animal and present mean and modal value from these data. Since not all marked animals were recovered during each check, the calculated numbers are slightly underestimated (recapture probability 97%). For comparison with other studies, we have also calculated the nearest neighbour distances.

Results

Test 1: The sound signals.—The sound signals of 11 males and 4 females differed quite distinctly in amplitude modulation and were also produced by different movement patterns (Fig. 1; see also Heller 1984, 1988). Males sang spontaneously in intervals of 20-30 s (see Table 1 in Heller & Helversen 1993), opening the tegmina without any sound and emitting a crescending series of impulses during closure (see also Heller 1988). We never observed isolated impulses, which may imitate a female response, after the end of the syllable as observed in many other Barbitistini species (*e.g.* Stumpner & Meyer 2001). Females ready to mate responded immediately after the song of a male. They opened their tegmina silently, sometimes starting this movement during the male song, and closed the tegmina shortly afterwards, producing a short series of impulses. This series of impulses started very regularly with a latency of about 60 ms after the end of the male song (see Fig. 1, inset; data from Helversen & Wendler 2000). Spontaneous singing in females was not observed.

Although males and females differed clearly in tegmen length (Fig. 2; length of that part which is not covered by pronotum: 4-8 mm in males, 0.5-1 mm in females; Harz 1969), the spectrum of the song showed no major sex specific differences (Fig. 3). In the male, the peak of the broad spectrum was at 18.2 ± 0.9 kHz (band-width 10 dB below peak 10.5 ± 1.9 kHz, center frequency 18.6 kHz; n = 6 males) and in the female at 20.6 kHz (band-width 10 dB below peak 14.5 kHz, center frequency 17.9 kHz; n = 1 female).

The intensity of the male song in the field was 92.0 ± 1.2 dB SPL_{peak} (grand mean; at 1 m), corresponding to measurements in the laboratory, when an attenuation of 6 dB/ doubling distance is assumed (laboratory: 112 dB SPL_{peak} at 10 cm; n = 5) (Heller & Helversen 1993). The variation between males was quite small. Sound propagating laterally and caudally is reduced by 3 to 4 dB and 6 to 7 dB respectively (OvH & KGH, unpublished data). For a better comparison, the mean song intensities of the three males at 1 m (88.6, 91.1, 92.3 dB SPL) were all set to 92 dB and the other values shifted accordingly (Fig. 4). From the curves in fig. 4, the one

Fig. 2. Male (left) and female (right) *Poecilimon affinis.* Note the different sizes of the tegmina.

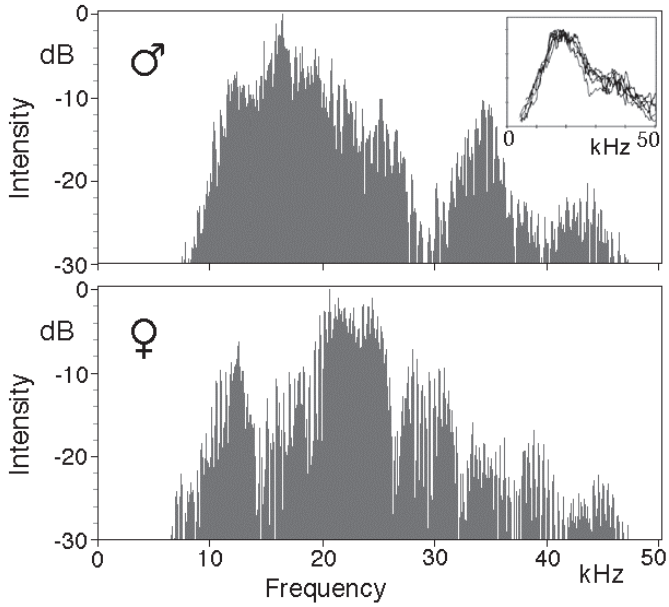

Fig. 3. Spectrum of male (ex Vernon Mts.) and female (ex Pieria Mts) song of *Poecilimon affinis* (Inset: Variability of 5 different males, all ex Vernon Mts).

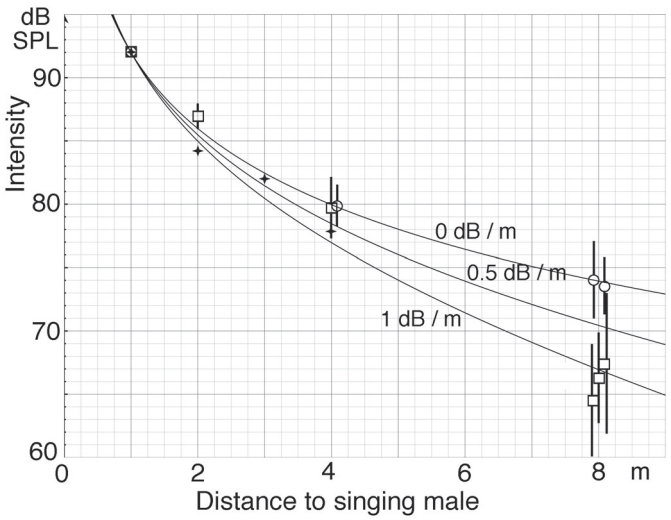

Fig. 4. Intensity of male *Poecilimon affinis* song with distance (mean ± SD; three males, 14 tests at different distances, n per test 5-20, n_{total} = 203 measurements). The three curves indicate the expected song intensity for a song of 92 dB SPL at 1 m, spreading loss of 6 dB per doubling distance and for linear excess attenuations of 0, 0.5 and 1 dB / m. In one male, the variation in intensity at any distance was so small (SD 0.1-0.2 dB) that the SD cannot be seen in the figure.

representing an excess attenuation of 0.5 dB / m results in the best fit being intermediate between the extremes. The intensity of the female songs differed in two aspects from that of the males: 1) Even the loudest female songs were about 10 dB softer than the average male; 2) The intensity was quite variable, surprisingly depending on the perceived loudness of the male song. The less loud the male signal was, the less loud was also the female response (Fig. 5). A distribution of female song intensity with two maxima (Fig. 5B) may indicate that two different types of response can be triggered. All four females tested both at high and low intensities produced softer intensities in response to softer male songs. Females reacted at even lower male song intensities than shown, observable by their wing movement, but the answer could not be measured as it was at noise level of the dB-meter.

Test 2: Hearing – Neurophysiology.—The ears are most sensitive to frequencies between 8 and 20 kHz with lowest thresholds of the five individuals between 29 and 33.5 dB SPL (rms; corresponding to about 32 to 36.5 dB SPL_{peak}; Fig. 6). Responses were measured with ipsilateral, frontal and contralateral stimulation (with reference to the tympanic nerve). Those with frontal stimulation (Fig. 6) correspond best to behaviour during phonotaxis and showed the least interindividual variability. In the most sensitive hearing range, between 8 and 20 kHz, ipsilateral hearing thresholds were on average by 2.6 ± 2.7 dB lower than frontal thresholds (3 males, 2 females, n = 21 pairs of values). Males and females showed very similar threshold functions and did not consistently differ at any (3-35 kHz) frequency tested (mean difference between individual males and females 1.5 dB ± 1.2 dB; 3 males and 2 females, n = 60 comparisons; each male threshold measured at 10 frequencies was compared to each female threshold at the same frequencies). These data show that at least some females have the same hearing thresholds as some males and indicate that no principal difference exists in the hearing of the sexes, although statistical tests for significance cannot reasonably be performed with just two females.

Test 3: Hearing – Behaviour.—The mean threshold of the 6 females tested was 49.8 dB SPL_{peak} with single females ranging from 43 to 58 dB SPL_{peak} (Fig. 7). Surprisingly, reaction curves of one and the same female measured on different days (or even the same day) showed a quite high variability. For a comparison to the neurophysiological data (*ca* 30 - 35 dB SPL at 20 kHz, range 27.5 – 40 dB SPL,

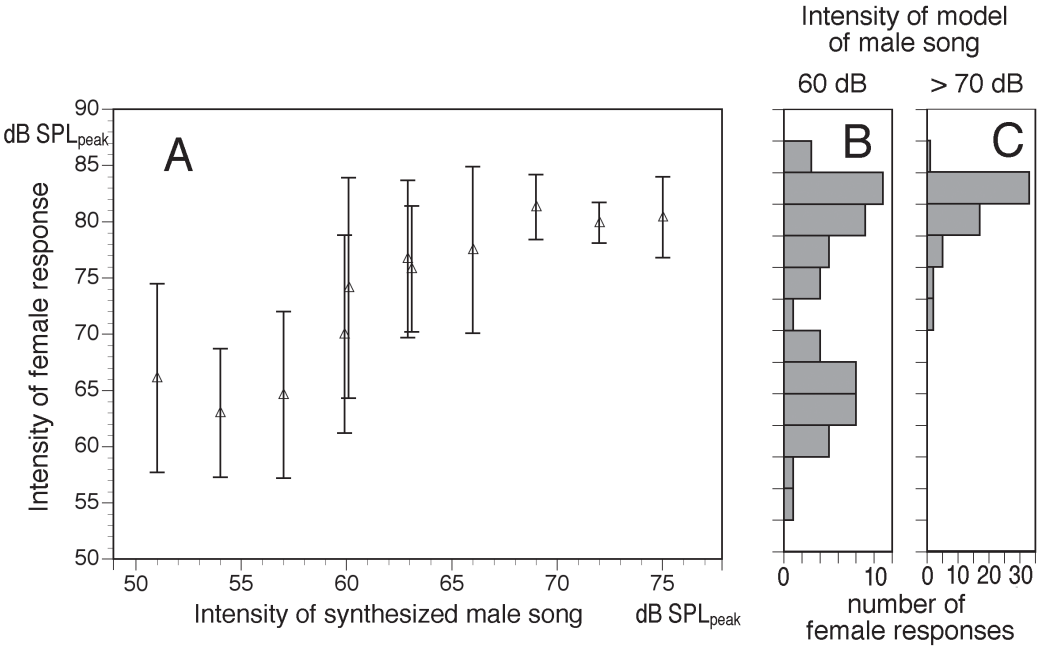

Fig. 5. Intensity of female responses in dependence of the intensity of a synthesized male song. A: Mean intensity values as a function of the intensity of a synthesized male song (mean ± SD; one point per female and intensity with 12-38 measurements each; 4 females); B, C: Distribution of intensities of female responses to synthesized songs with intensity of 60 dB SPL (B) and 72-75 dB SPL (C).

depending on individual and direction), it has to be remembered that the male song is not of constant intensity and that females respond only to songs with a soft beginning and a loud ending (OvH & KGH, unpubl. data).

Test 4: Active space.—For both sexes the effective range of the communication system was tested separately in field experiments. The tested females responded to all singing males up to a distance of 10 m quite regularly. At larger distances the mean response rate decreased more or less linearly (Fig. 8A). The probability that a male starts a phonotactic approach towards a responding female decreased slightly with increasing distance to the female between 2 and 10 m, but dropped abruptly at larger distances, so that none of the 6 males tested moved towards females further away than 12 m (Fig. 8B).

Test 5: Number of receivers in active space.—We calculated the number of males and females within circles of different sizes around each animal and present mean and modal results from these data (Fig. 9).

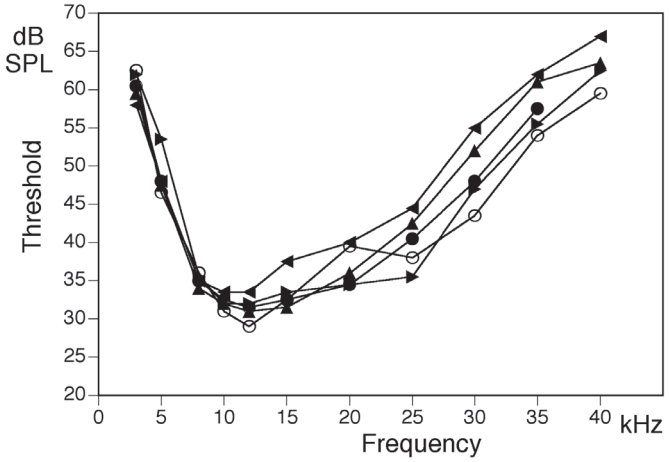

Fig. 6. Hearing thresholds measured as summed recordings from the tympanic nerve to standard stimuli (35 ms). Results of three males (triangles) and two females (circles) with frontal stimulation are shown.

Obviously in this dense population very many receivers / potential duet partners are available for most of its members even at a range of 10 m. In addition, it has to be remembered that at the beginning of the season the number of animals might have been as much as double the size of the measuring period (see Fig. 1, Heller & Helversen 1991). Above a distance of 10 m, edge effects and the finite population size result in distinctly different estimates for homogeneous density and realistic distributions due to the exponentially increasing area size. Interestingly, at distances below 5 m the modal values are much lower than the mean values, indicating some high density clusters. However, the distribution of the partner numbers in the active space varied considerably (see Fig. 9, males around female, 9 and 10 m). Nearest neighbour distances were lowest for male to female (mean 0.7 m, median 0.4 m; n=420; same dates as in Fig. 9) and highest for female to female distances (mean 1.1 m, median 0.8 m; n=403) with the other combinations in-between.

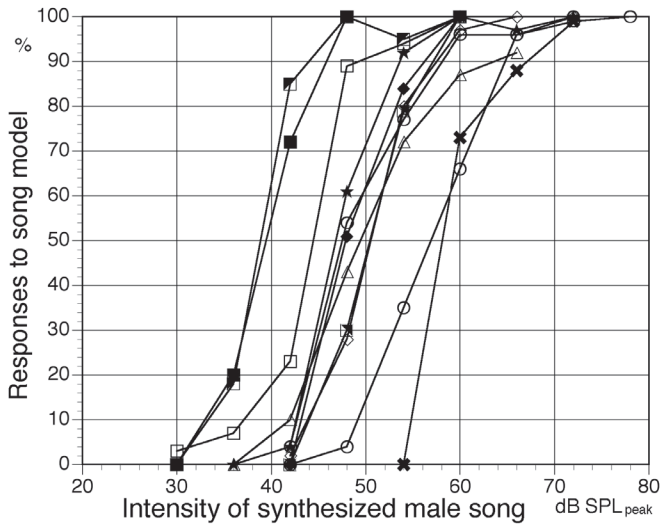

Fig. 7. Percentage of female responses depending on intensity of a synthesized male song (11 curves of 6 different females; n per curve 98-624; n_{total} =4481 tests; different lines with symbols of the same shape represent responses of one female in different tests).

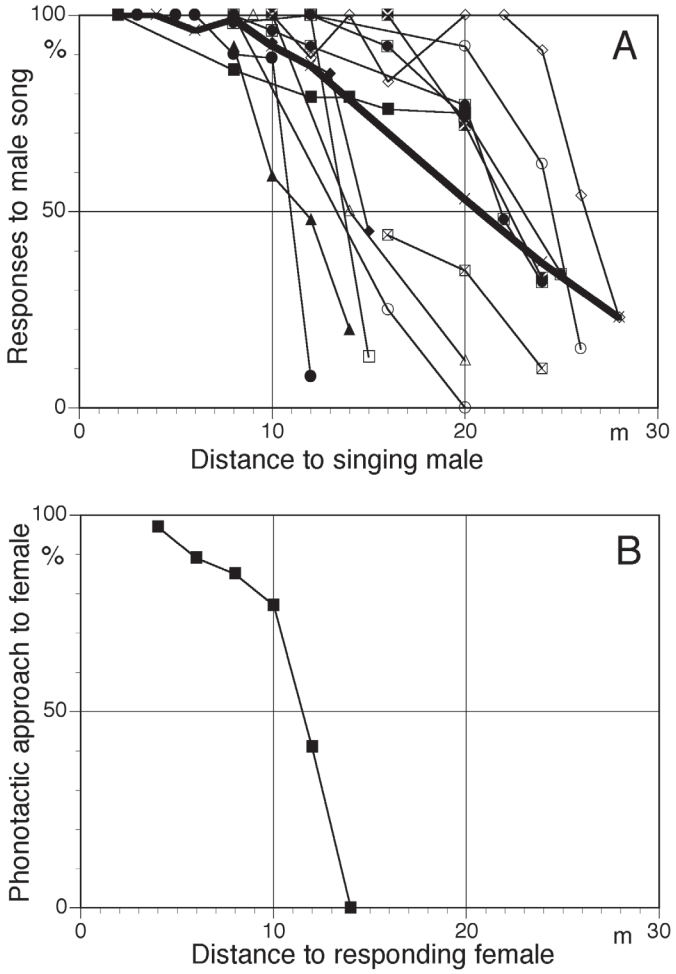

Fig. 8. Communication range of males and females in the field. A: Percentage of answered male signals with distance (n_{total} = 2710 tests from two females responding to songs of 7 males; each line reaction to another male, thick line: mean, calculated from all tests at the respective distance). B: Percentage of 6 males starting a phonotactic approach towards a responding female with distance (n_{total} = 161 tests; n with increasing distance: 38, 9, 47, 22, 39, 6).

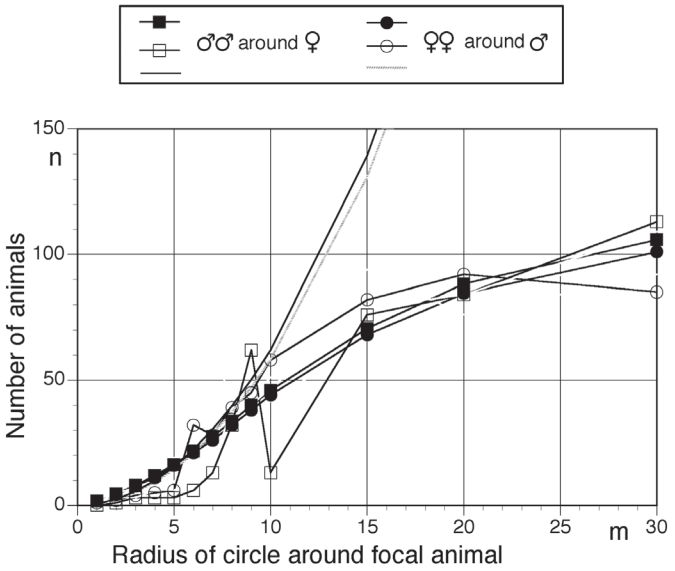

Fig. 9. Number of members of the opposite sex in dependence of distance to the focal animal (solid symbols: mean value, open symbols: modal value, lines calculated from mean population density; position data from 23.7., 26.7., 29.7. and 1.8.1988 combined, together 420 males and 403 females; average population density calculated for 23.7.).

Discussion

Duetting in Phaneropteridae.—The duetting behaviour of *P. affinis* shows an intermediate level of complexity when compared to other phaneropterid species. On the one end there are species with very simple male song structure like in the genus *Leptophyes* and in *P. ornatus*, where the female responds quite indiscriminately to the beginning of any acoustic signal (*e.g.*, Zhantiev & Korsunovskaya 1986, Heller *et al.* 1997a), in some cases possibly only after having evaluated previous songs. On the other side there are species with complicated male songs, where the females react only at particular moments in the song (*e.g.*, trigger syllables) often after having heard a number of male syllables with a characteristic pattern (see Bailey & Hammond 2003 for a review). In *P. affinis*, the calling song consists of only one syllable, presented at an interval of several seconds. After a crescending beginning of the syllable a loud final part follows which may serve as a trigger for the female response. The amplitude modulation is similar to that of several other, mainly allopatric species of the *P. ornatus* group (see Chobanov & Heller 2010). Considering the syllable structure it is not surprising that the latency of the female response has been found to be constant relative to the end of the male syllable (Helversen & Wendler 2000). The spectra of the male and female songs are quite similar despite the existing large differences in the size of the tegmina. On the one hand, this is not surprising considering similar results in other species (*e.g.*, in *Barbitistes* species, Stumpner & Meyer 2001). Moreover, it fits well to the very similar hearing in both sexes (see below). On the other hand, this is certainly not a universal pattern (see *Ancistrura nigrovittata*, Dobler *et al.* 1994; Thai phaneropterids, Heller *et al.* 1997b). The differently sized tegmina of males and females would indicate different song frequency maxima, if the same relationship between body size with corresponding tegmen size and song frequency were true, as found in an interspecific comparison of *Poecilimon* species (Heller *et al.* 2006). So either properties of the tegmina common to both sexes or some kind of other selective forces seem to be involved.

Song intensity, hearing thresholds and communication distance.— Doubtlessly song intensity is very important for the duetting behaviour as it was most obvious in the experiments on the female responses (Fig. 7). As Wiley and Richards (1978) and Michelsen and Larsen (1985) have pointed out, in the natural habitat the broadcast range of an acoustic signal is extremely dependent on the type of vegetation, on the sender's height above the vegetation and many other factors. Therefore we restricted our measurements to a typical situation: the animal sat on a thistle head downwards at a perch height of 40 cm above ground and intensity was measured at the same height. We had chosen optimal conditions for the signal propagation insofar as no plants or other obstacles were between sender and receiver. These were, nevertheless, natural conditions, as both males and females tend to climb up in the vegetation and are often found to sing in plants emerging over the vegetation surface.

Obviously, males and females are under pressure to produce loud songs. The intensity decreases with distance due to the spread-

Table 1. Intensities of songs of phaneropterid species.

Species	Intensity of song in dB SPL at 1 m distance		Reference
	male	female	
Poecilimon affinis	92	81	this paper
Ancistrura nigrovittata	69	61	Stumpner, unpublished
Barbitistes constrictus	67	66	Meyer, Stumpner, unpubl
Barbitistes serricauda	79	70	Meyer, Stumpner, unpubl
Isophya taurica	85	no data	Zhantiev & Dubrovin 1977
Isophya stepposa	72	no data	Zhantiev & Dubrovin 1977
Isophya modesta rossica	89	no data	Zhantiev & Dubrovin 1977
Isophya stysi	80	no data	Zhantiev & Dubrovin 1977
Isophya sp.	75	no data	Zhantiev & Dubrovin 1977
Isophya brunneri	105	no data	Zhantiev & Dubrovin 1977
Isophya gracilis	85	no data	Zhantiev & Dubrovin 1977
Leptophyes punctatissima	90	65	Zimmermann *et al.*, 1989
Holochlora nigrotympana	96	86	Heller *et al.*, 1997b
Stictophaula ocellata	98	93	Heller *et al.*, 1997b
Elephantodeta nobilis	ca. 80	no data	Bailey & Field 2000
Phaneroptera nana	54	<54	Tauber *et al.*, 2001

ing loss, but also due to atmospheric attenuation and effects of the vegetation. These latter factors become stronger with increasing carrier frequency, so low frequency songs should be favoured, if long distance of the song is important (see *e.g.*, Römer & Lewald 1992, Heller *et al.* 2010 for discussions of this well-known problem). As a consequence, both sexes should use frequencies as low as they can produce efficiently. In *P. affinis* the male song is about 10 dB louder than that of the female. With 92 dB SPL at 1 m distance it is in the middle of the broad range known from the few phaneropterid species studied in this respect (Table 1). Only *Phaneroptera nana* seems to produce distinctly softer songs. In all species studied the female songs are weaker than those of the males (Table 1), so the song of the males should have a larger range if, as in *P. affinis*, males and females have the same sensitivity (see Fig. 5). The auditory thresholds are similar to those found in other duetting phaneropterids (Zhantiev & Dubrovin 1977, Forrest *et al.* 2006).

Theoretically one should be able to calculate signal ranges from threshold data and song intensities. For these calculations, only the neuronal threshold data for frontal stimulation were used. They give slightly higher than minimal values, but may represent the typical situation of a male approaching a female; in any case they give the more conservative value preventing an over-estimation of active space. Using the same calculation as below, a female should hear a male up to a distance of 40 m, and a male should hear a female up to 25 m. However, the situation is more complicated. For the females it has to be considered that the male song contains softer parts which are necessary for recognition, so the difference in range may not be as prominent as expected. On the other hand, the female song consists of clearly separated impulses not as densely packed as in the male song. Depending on the integration time in the nervous system, the threshold of such signals may be higher than of male signals with the same peak sound pressure values. Hearing thresholds were determined from the auditory organ with standard stimuli of intermediate duration between male and female songs. This allows the conclusion that hearing in males and females does not differ and therefore is not specifically adapted to the partner's song intensity. For determining neurophysiological thresholds directly comparable to behaviour, one would have to record the activity of relevant interneurons, which would first have to be identified (see Ostrowski & Stumpner 2010 for *Ancistrura nigrovittata*).

Female response behaviour.—A further complication results from the surprising finding that the female responds with soft signals if the signal she receives is soft as well. If the female is able to modulate song intensity at all, one would have expected the opposite behaviour. A female that receives a weak signal from a distant male should produce a loud, far reaching signal. In *Leptophyes punctatissima*, the intensity of the female response was also described as quite variable between females (range of 30 dB; Zimmermann *et al.* 1989) without information on intraindividual variability. In a species of the genus *Caedicia*, Bailey and Hammond (2004) found a weak, but significant effect of song intensity on the number of clicks the female produces. The louder the male signal, the fewer clicks she emits. However, the effect is very weak and the authors doubt its biological significance. Part of a possible explanation for the unusual behaviour of *P. affinis* females might be that they reduce the risk of eavesdropping in case of large distance to a singing male (see below).

To come closer to the actual range of the signal, we tested females with synthesized male songs, which had different intensities. Within a range of *ca* 10 dB, the females increased their response rate from very low to very high percentages (Fig. 7). While they were quite consistent within one experiment, different females and even the same female in different tests showed an unexpected high variability. At present, we must assume unknown changes in their motivational status. In any case, a mean response threshold of 50 dB SPL would be around 15 to 20 dB above their maximum hearing threshold at 10 to 15 kHz. In the closely related species *Ancistrura nigrovittata* this difference between receptor neurons and behaviour is only around 10 dB (Dobler *et al.* 1994). As mentioned above, it is conceivable that the soft parts in the song of *P. affinis*, which must be perceived by the female, account for the larger difference between hearing threshold and behavioural threshold in *P. affinis*.

Signal ranges in theory.—Using the data described above, a rough calculation of the signal range in *P. affinis* seems possible. The male signal should be perceived by a female up to a distance of about 28 m corresponding to a female behavioural threshold of 50 dB SPL, intensity of male song of 92 dB SPL at 1 m, a spreading loss of 6 dB per doubling distance and an excess attenuation of 0.5 dB/m. Our result for the last factor corresponds well with the data obtained by Römer and Lewald (1992) for 20 kHz at 2 m above ground. At

ground level the attenuation is much stronger (own unpublished data; see also Römer & Lewald 1992). So it was not uncommon to observe that during a phonotactic approach the male lost acoustical contact after he had left his singing position. After having moved some distance he climbed up another plant again for orientation. Unfortunately there are no behavioural threshold data for *P. affinis* males. Assuming the same threshold as for a female, one would obtain a maximal range of 15 m (female song 81 dB SPL at 1 m). However, since the structure of the female song is much simpler than that of the male, a male might hear a female over larger distances, *e.g.*, 25 m with a male threshold of 40 dB SPL. On the other hand, the female song is much shorter, containing less energy than the male song, which might increase the neuronal threshold by 5 dB or even more, in turn decreasing the hearing range (see Faure & Hoy 2000). Moreover, for the male it is not only the intensity of the female signal which is important, but also its latency. Signals which arrive at his ears later than 170 ms after the end of his song are neglected. Taking into account a female latency of 60 ms, only 110 ms remain for travelling of the signal from the male to the female and back. Within 110 ms the sound travels about 37.4 m (speed of sound 340 m/s), so responses from females further away than about 20 m will not be responded to by a male since these responses arrive outside its sensory time window.

Communication distance in the field.—The predictions made above were tested in field experiments (Fig. 8). It is quite obvious that males did not start a phonotactic approach if the female was further away than 12 m (Fig. 8B). This would correspond relatively well with the lowest estimate for the female song range, assuming insensitive males and/or female signals were weaker than predicted from peak data. Since response latency does not seem to limit the communication range, the active space should become smaller in habitats where the excess attenuation is stronger. Compared to other duetting species studied so far the communication range is relatively large, as can be expected for a large species. The much smaller species *Leptophyes punctatissima* has a range of only ~4 m at maximum with both intensity and latency limiting (Zimmermann *et al.* 1989), while *Barbitistes* species seem to reach 8 m (Stumpner & Meyer 2001). Acridid grasshoppers duet only at distances just above 2 m (Lang 2000). Pneumoridae, however, are able to cover much larger distances (Van Staaden & Römer 1997). The response of *P. affinis* females was quite variable (Fig. 8A). Up to a male distance of 10 m they responded to more than 80 % of the males' syllables (in one exception with 60%). However, there was a high variability in response rates to males singing at larger distances. Quite a number of males were responded to although further away than 20 m, when the males definitely could not hear the female reply. Either the females were not able to correctly estimate the distance to a singing male from the intensity of the male song and did not stop responding for this reason, or they followed another strategy (indicated by the bimodal distribution of song intensity). They might have intended to advertise their presence to other, non-singing and eavesdropping males nearby. In such a situation the use of soft signals would make sense, since males, which must hear the faint signal of a distant male for eavesdropping, should be relatively close. Eavesdropping of duetting pairs is known from other phaneropterids (Hammond & Bailey 2003, Bailey *et al.* 2006) and was also observed in *P. affinis* (own unpublished observations).

Interestingly, this asymmetry between females responding to quite distant males and a restricted range of male phonotaxis was also observed in species of the closely related genera *Isophya* (Zhantiev & Dubrovin 1977) and *Barbitistes* (Stumpner & Meyer 2001). Under the assumption that the largest distance for a successful duet is 10 m, a male can locate a responding female in an area of about 300 m^2. So the species should be able to successfully reproduce at densities of 0.003 females / m^2 without the necessity of applying special search strategies for mate finding. Low densities have also been assumed to be an important factor in the evolution of duetting in ephippigerine bush crickets (Hartley *et al.* 1974). *P. affinis* females could even accept lower densities, since they can hear a male from a distance of 25 m (corresponding to a density of 0.0005 males/m^2). Of course, at such low distances they would have to walk more than half the way towards the male before a male could hear their response song, a situation similar to that observed in females of the genus *Isophya* (Zhantiev & Dubrovin 1977). Indeed, *P. affinis* females are also able to make a phonotactic approach (Helversen *et al.* 2012), although it is typically the task of the male in this species.

In our test population the densities were much higher than these limiting values. Even in the middle of the season, when many animals already have died, there were on average nearly 50 members of the opposite sex available for each specimen for a successful duet (Fig. 9). Under these conditions even artificially muted females were as successful in obtaining matings or spermatophores as intact females (Helversen *et al.* 2012). It is quite obvious that duetting systems did not evolve under such conditions. Instead, duetting may even secondarily be reduced, as indicated by the recent discovery of a closely related, geographically restricted species with mute females (Chobanov & Heller 2010). On the other hand, it can be expected that at such high densities every animal interested to mate will find a partner as long as anyone from the opposite sex ready to mate is available. The mating frequencies may not be limited by search efforts, but probably by the production rates of spermatophores and potentially eggs. The efficiency of the acoustical communication is also demonstrated by the observation that the same high mating frequencies were observed even at densities of 0.03 animals / m^2, less than one tenth of that described here (Helversen *et al.* 2012).

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References

Bailey W.J. 2003. Insect duets: Underlying mechanisms and their evolution. Physiological Entomology 28: 157-174.

Bailey W.J., Field G. 2000. Acoustic satellite behaviour in the Australian bushcricket *Elephantodeta nobilis* (Phaneropterinae, Tettigoniidae, Orthoptera). Animal Behaviour 59: 361-369.

Bailey W.J., Hammond T.J. 2003. Duetting in insects - does call length influence reply latency? Journal of Zoology (London) 260: 267-274.

Bailey W.J., Hammond T.J. 2004. Female reply strategies in a duetting Australian bushcricket, *Caedicia* sp. (Phaneropterinae: Tettigoniidae: Orthoptera). Journal of Experimental Biology 207: 803-811.

Bailey W.J., MacLeay C., Gordon, T. 2006. Acoustic mimicry and disruptive alternative calling tactics in an Australian bushcricket (*Caedicia*; Phaneropterinae; Tettigoniidae; Orthoptera): does mating influence male calling tactic? Physiological Entomology 31: 201-210.

Bossert W.H., Wilson E.O. 1963. The analysis of olfactory communication among animals. Journal of Theoretical Biology 5: 443-469.

Chobanov D.P., Heller K.G. 2010. Revision of the *Poecilimon ornatus* group (Orthoptera: Phaneropteridae) with particular reference to the taxa in Bulgaria and Macedonia. European Journal of Entomology 107: 647-672.

Dobler S., Stumpner A., Heller K.G. 1994. Sex-specific spectral tuning for the partner's song in the duetting bushcricket *Ancistrura nigrovittata* (Orthoptera: Phaneropteridae). Journal of Comparative Physiology A 175: 303-310.

Eades D.C., Otte D., Cigliano M.M., Braun H. 2012. Orthoptera Species File Online. Version 2.0/4.0. available on http://Orthoptera.SpeciesFile.org (May 2012).

Faure P.A., Hoy R.R. 2000. Neuroethology of the katydid T-cell. I. Tuning and responses to pure tones. Journal of Experimental Biology 203: 3225-3242.

Forrest T.G., Dawn R.L., Dawn C. 2006. Calling songs, duets, and auditory tuning in two cryptic katydids (Tettigoniidae: Phaneropterinae: *Amblycorypha*). Annals of the Entomological Society of America 99: 978-987.

Greenfield M.D. 2002. Signalers and Receivers: Mechanisms and Evolution of Arthropod Communication. Oxford University Press, New York.

Greenfield M.D., Shelly T.E. 1985. Alternative mating strategies in a desert grasshopper: evidence of density-dependence. Animal Behaviour 33: 1192-1210.

Hammond T.J., Bailey W.J. 2003. Eavesdropping and defensive auditory masking in an Australian bushcricket, *Caedicia* (Phaneropterinae: Tettigoniidae: Orthoptera). Behaviour 140: 79-95.

Hartley J.C., Robinson D.J., Warne A.C. 1974. Female response song in the ephippigerines *Steropleurus stali* and *Platystolus obvius* (Orthoptera, Tettigoniidae). Animal Behaviour 22: 382-389.

Harz K. 1969. Die Orthopteren Europas. Series Entomologica 5. The Hague, Dr. W. Junk. 749 p.

Heller K.-G. 1984. Zur Bioakustik und Phylogenie der Gattung Poecilimon (Orthoptera, Tettigoniidae, Phaneropterinae). Zoologische Jahrbücher, Systematik 111: 69-117.

Heller K.G. 1988. Bioakustik der europäischen Laubheuschrecken. J. Margraf, Weikersheim.

Heller K.G. 1990. Life history and communication in phaneropterid bushcrickets. In: Gribakin F.G., Wiese K., Popov A.V. (Eds) Sensory Systems and Communication in Arthropods. Birkhäuser, Basel, Boston, Berlin, pp 204-208.

Heller K.G . 1992. Risk shift between males and females in the pair-forming behavior of bushcrickets. Naturwissenschaften 79: 89-91.

Heller K.G., Helversen D. v. 1986. Acoustic communication in phaneropterid bushcrickets: species-specific delay of female stridulatory response and matching male sensory time window. Behavioral Ecology and Sociobiology 18: 189-198.

Heller K.G., Helversen D.v. 1991. Operational sex ratio and individual mating frequencies in two bushcricket species (Orthoptera Tettigonioidea *Poecilimon*). Ethology 89:211-228.

Heller K.G., Helversen D.v. 1993. Calling behavior in bushcrickets of the genus *Poecilimon* with differing communication systems (Orthoptera: Tettigonioidea: Phaneropteridae). Journal of Insect Behavior 6: 361-377.

Heller K.G., Helversen O.v., Sergejeva M. 1997a. Indiscriminate response behaviour in a female bushcricket: sex role reversal in selectivity of acoustic mate recognition? Naturwissenschaften 84: 252-255.

Heller K.G., Korsunovskaya O.S., Sevgili H., Zhantiev R.D. 2006. Bioacoustics and systematics of the *Poecilimon heroicus*-group (Orthoptera: Phaneropteridae: Barbitistinae). European Journal of Entomology 103: 853-865.

Heller K.G., Ostrowski T.D., Hemp C. 2010. Singing and hearing in *Aerotegmina kilimandjarica* (Tettigoniidae: Hexacentrinae), a species with unusual low carrier frequency of the calling song. Bioacoustics 19: 195-210.

Heller K.G., Schul J., Ingrisch S. 1997b. Sex-specific differences in song frequency and tuning of the ears in some duetting bushcrickets (Orthoptera: Tettigonioidea: Phaneropteridae). Zoology (Jena) 100: 110-118.

Helversen D.v., Helversen O. v., Heller K.G. 2012. When to give up responding acoustically in *Poecilimon* bush-crickets: a clue to population density. Articulata 27: 57-66.

Helversen D.v., Wendler G. 2000. Coupling of visual to auditory cues during phonotactic approach in the phaneropterine bushcricket *Poecilimon affinis*. Journal of Comparative Physiology A 186: 729-736.

Helversen O.v., Elsner N. 1977. The stridulatory movements of acridid grasshoppers recorded with an opto-electronic device. Journal of Comparative Physiology 122: 53-64.

Janik V.M. 2000. Source levels and the estimated active space of bottlenose dolphin (*Tursiops truncatus*) whistles in the Moray Firth, Scotland. Journal of Comparative Physiology A 186: 673-80.

Lang F. 2000. Acoustic communication distances of a gomphocerine grasshopper. Bioacoustics 10: 233-258.

Lohr B., Wright T.F., Dooling R.J. 2003. Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. Animal Behaviour 65: 763-777. doi:10.1006/anbe.2003.2093.

McCartney J., Kokko H., Heller K.G., Gwynne D.T. 2012. The evolution of sex differences in mate searching when females benefit: new theory and a comparative test. Proceedings of the Royal Society B 279:1225-1232. doi: 10.1098/rspb.2011.1505

Mhatre N., Balakrishnan R. 2006. Male spacing behaviour and acoustic interactions in a field cricket: implications for female mate choice. Animal Behaviour 72: 1045-1058.

Michelsen A. 1978. Sound reception in different environments. In: Ali M.A. (Ed.) Sensory Ecology. Plenum Press, New York, pp 345-373.

Michelsen A., Larsen O.N. 1985. Hearing and Sound. In: Kerkut G.A., Gilbert L.I. (Eds) Comprehensive Insect Physiology, Biochemistry and Pharmacology. Pergamon Press, Oxford, pp 496-556.

Ostrowski T.D., Stumpner A. 2010. Frequency processing at consecutive levels in the auditory system of bush crickets (Tettigoniidae). Journal of Comparative Neurology 518: 3101-3116.

Robinson D.J. 1990. Acoustic communication between the sexes in bushcrickets. In: Bailey W.J., Rentz D.C.F. (Eds) The Tettigoniidae: Biology, Systematics and Evolution. Crawford House Press, Bathurst, pp. 112-129.

Robinson D.J., Rheinlaender J., Hartley J.C. 1986. Temporal parameters of male female sound communication in *Leptophyes punctatissima*. Physiological Entomology 11: 317-324.

Römer H., Bailey W.J. 1986. Insect hearing in the field II. Male spacing behavior and correlated acoustic cues in the bushcricket *Mygalopsis marki*. Journal of Comparative Physiology A 159: 627-638.

Römer H., Lewald J. 1992. High-frequency sound transmission in natural habitats: implications for the evolution of insect acoustic communication. Behavioral Ecology and Sociobiology 29: 437-444.

Spooner J.D. 1964. Comparative study of the acoustic behaviour of Phaneropterinae (Orth. Tettigoniidae). Unpublished Ph.D. Dissertation. Univ. of Florida, Gainesville.

Spooner J.D. 1968. Pair-forming acoustic systems of phaneropterine katydids (Orthoptera, Tettigoniidae). Animal Behaviour 16: 197-212.

Spooner J.D. 1995. Pair-forming phonotaxic strategies of phaneropterine katydids (Tettigoniidae: Phaneropterinae). Journal of Orthoptera Research 4:127-129.

Stumpner A. 1997. An auditory interneurone tuned to the male song frequency in the duetting bushcricket *Ancistrura nigrovittata* (Orthoptera, Phaneropteridae). Journal of Experimental Biology 200: 1089-1101.

Stumpner A., Heller K.G. 1992. Morphological and physiological differences of the auditory system in three related bushcrickets (Orthoptera, Phaneropteridae, *Poecilimon*). Physiological Entomology 17: 73-80.

Stumpner A., Meyer S. 2001. Songs and the function of song elements in four duetting bushcricket species (Ensifera, Phaneropteridae, *Barbitistes*). Journal of Insect Behavior 14: 511-534.

Tauber E., Cohen D., Greenfield M.D., Pener M.P. 2001. Duet singing and female choice in the bushcricket *Phaneroptera nana*. Behaviour 138: 411-430.

Tauber E., Pener M.P. 2000. Song recognition in female bushcrickets *Phaneroptera nana*. Journal of Experimental Biology 203: 597-603.

Van Staaden M.J., Römer H. 1997. Sexual signalling in bladder grasshoppers: Tactical design for maximizing calling range. Journal of Experimental Biology 200: 2597-2608.

Wiley R.H., Richards D.G. 1978. Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. Behavioral Ecology and Sociobiology 3: 69-94.

Zhantiev R.D., Dubrovin N.N. 1977. Sound communication in the genus *Isophya* (Orthoptera: Tettigoniidae). Zoologicheskii Zhurnal 56: 38-51 (in Russian).

Zhantiev R.D., Korsunovskaya O.S. 1986. Sound communication in bush crickets (Tettigoniidae: Phaneropterinae) of the European part of the USSR. Zoologicheskii Zhurnal 65: 1151-1163 (in Russian).

Zimmermann U., Rheinlaender J., Robinson D. 1989. Cues for male phonotaxis in the duetting bushcricket *Leptophyes punctatissima*. Journal of Comparative Physiology A 164: 621-628.