

FINDING THE RIGHT PLACE: CONTRIBUTION OF SPACING TO THE ATTRACTIVENESS OF MALES IN AN INSECT AGGREGATION

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Abstract. In many acoustically communicating insect species males attempt to attract females by calling songs. In natural populations, males differ in their source levels and louder signalling males are known to attract a higher proportion of mating partners compared to softer signalling males, investigated in two-choice situations. Another, but related reason for an increased attractiveness of louder than average males is thought to be a larger broadcast area, in which their signals are detectable by receivers. Therefore, a male density often found in aggregations facilitates competition for available broadcast area and suggests broadcast area as an important male resource.

In the current simulation study the influence of the spatial arrangement of signallers in such aggregations was investigated concerning a correlation of source level and the accrued broadcast area. In addition, the attractiveness of signallers differing in their source levels was investigated by simulation of female phonotaxis, which is based on a passive attraction to the louder of competing sound sources. This was investigated in three different spacing scenarios: (1) Random spacing, in which signallers exhibit random inter-agent distances. (2) A natural spacing in which the nearest neighbour is perceived at a sound level of 65 dB. (3) An ‘optimised spacing’, which is the result of an evolutionary optimisation algorithm aiming to maximise the perceived sound level in an aggregation.

Simulating *Mygalopsis marki* bushcricket aggregations, in which males signal from elevated positions and inter-male distance fulfils 65 dB spacing criteria, resulted in a significant correlation between the source levels of males and the percentage of accrued broadcast area. Nevertheless, louder males in simulated *M. marki* aggregations did not succeed in attracting a higher number of females, although such a correlation was found in ‘optimised aggregations’ of the same senders.

1 Introduction

Insect acoustic communication serves two main functions: Attraction of a potential mating partner and establishment of territory, [50, 29]. One important call parameter constitutes signal intensity, a trait associated with mate attraction; confirmed in choice situations in which females showed a preference of the louder of two competing conspecific sounds (*Gryllus integer*, [8], *Scapteriscus borellii* and *S. vicinus*, [13, 19], *Conocephalus upoluensis* and *Requena verticalis*, [4], *G. lineaticeps*, [47]).

Signalling at higher amplitudes results in a larger ‘broadcast area’ [33], defined as that area where a signal can be detected by receptive mates, usually females. In this context Marten and Marler [24] used a different term, namely the ‘active space’ of a signaller. In addition to the study of animal behaviour, computer simulations constitute an important tool for a proper investigation of male spacing strategies and the strategies females use in order to select among individual senders in male assemblages (e.g. [16, 25, 31]). Some results of these studies have shown that inter-male distance can have a dramatic influence on the broadcast area of senders with overlapping acoustic territories and suggests the spatial distribution of senders to be of importance in the context of mate attraction, [12]. According to this, more powerful singers should always increase their mating success in an aggregation, [15, 16].

Signalling at higher amplitude or at a higher rate may result in a higher number of matings, which in turn increases reproductive success (e.g. [9]). A higher calling effort (calling at a higher rate and/or intensity) on the other hand results in higher energetic costs associated with sound production, [37], and suggest this trait as an honest indicator of male quality [54]. In *Mygalopsis marki* (*M. marki*), an Australian bushcricket species, larger males are louder, [39], and females selecting among males according to sound level cues may choose males of better quality (larger ones). Many communication systems suffer from eavesdroppers exploiting the signals of acoustically communicating insects, e.g. passive listening bats or parasitoids (e.g. flies) homing in on signallers. In this context it was shown that katydid males that signalled at a higher calling effort more often became the host of parasitoid flies, [23].

An alternative strategy that results in an increased broadcast area can be found in various insect species. Here males singing from elevated positions increase their calling broadcast area up to 14 times over calling on the ground (short-tailed crickets: [33]). *M. marki* males increase their active space twice by calling from the top of the vegetation, [39]. A drawback resulting from singing from more exposed positions comes with a higher risk

of predation. This often results in an optimum height that maximises broadcast area and minimises the risk of predation, [39, 48, 2, 1]. Therefore, some insects lower their signal redundancy or signal from protected positions inaccessible to predators that locate prey by exploiting sound signals generated by them, [6]. Both of these counter strategies constitute a primary defence against bat predation and was documented for acoustically communicating insects in the neotropical rainforest.

Several studies of singing insects and frogs revealed spacing of singing males to be related to the intensity of the male calling songs (insects: [11, 5, 42, 39]; Frogs: [52, 38]). Males in some bushcricket aggregations were found to space themselves differently from random so that individuals perceived nearest neighbours at a certain sound level (about 65 dB SPL) (*M. marki*: [39], *Mecopoda elongata*: [32]). This strategic male spacing results in a situation in which the broadcast area of individual signallers strongly overlaps and receivers often perceive more than one signaller at a certain position. In computer simulations Forrest and Raspet [6] have shown that silent signallers should stay far from loud ones in order to increase their broadcast area. A '65 dB spacing' of males may therefore allow individual signallers to maintain a certain broadcast area in male assemblages. A tight spacing goes along with a higher competition among signallers in a male assemblage and is thought to result in a conflict of interests between sexes, [12]. Male signallers tend to increase inter-male distances in order to increase their broadcast areas, in contrast male aggregations save female search effort for males of better quality.

Females in search for a mating partner localize males by their acoustic signals, a behaviour that is termed phonotaxis, [36]. Receivers need to discriminate conspecific from heterospecific signals and in addition they need to select among conspecifics of different quality, [18]. In doing so females need to localize sound sources whereby Orthopterans (crickets and katydids) rely on pressure gradient ears that exhibit an intrinsic directionality, [21, 26]. This type of ears suppresses the neuronal representation of a sound source in auditory afferents belonging to the contralateral hemisphere of the insect. This mechanism leads to a contrast enhancement between both ears and allows the allocation of a sound signal to one hemisphere of a receiver. A neuronal mechanism found in crickets and katydids results in a selective representation of the loudest of competing sound sources, [34, 40]. According to this selective attention mechanism a male should increase the area in which he is perceived louder than any rival in order to attract potential mating partners more efficiently.

The drawback of quieter sound sources in dense aggregations is well known from behavioural studies (e.g. [12]) as well as from computer simulations of small male aggregations, [16, 31]. According to this, a dense spacing is more costly for less powerful singers. Therefore, the question arises if softer signalling males in dense aggregations may compensate their obvious drawback by signalling at a position that maximises their own broadcast area, or minimizes the broadcast area of louder signallers.

A multi-agent based computer model was used in the current study for the investigation of the influence of spacing in two dimensions on the accrued broadcast area of individual signallers differing in their source level. The impact of the spacing of senders on the accrued broadcast area and on female encounter rates was investigated in three different spacing scenarios: Inter-male distances of males are random, or males keep a distance to the nearest neighbour, so that this neighbour is perceived by a sound level of about 65 ± 4 dB SPL (termed '65 dB aggregation' simulated after Römer and Bailey [39]). Males signalling in aggregations in which the broadcast area of individual senders strongly overlap should keep inter-male distances that are ideal with respect to the transformation of source level into accrued broadcast area, in which their signal level exceeds all other signals produced in an aggregation. This follows the idea that signals are more easier detectable and locatable when perceived at high signal-to-noise ratio. This was simulated in a third aggregation scenario, which is the outcome of an evolutionary optimisation procedure aiming to maximise loudness (perceived signal level) at any given location in an aggregation achieved through sender arrangement (termed 'optimised aggregation'). The strength of competition for broadcast area in simulated male aggregations was varied by simulation of four different sender densities and by simulation of senders signalling from elevated positions. Finally female encounter rates of senders simulated after real insect aggregations (*M. marki*) were investigated concerning its robustness against perceived sound level fluctuations, minimally discernable sound level differences (required for a proper sound source discrimination) and turning errors occurring during phonotaxis.

2 Methods

A computer model was developed in the multi-agent simulation environment Netlogo 4.03 (<http://ccl.northwestern.edu/netlogo>) simulating senders that produce signals suffering from attenuation due to spherical spreading and excess attenuation that is found for a pure tone of a carrier frequency of 10 kHz transmitted in a natural habitat, [41]. This frequency is often found as the dominant carrier frequency of broadband calling songs of katydids. In an initiation procedure every sender (male) was assigned to a certain sound level taken from one of 75 values that show a Gaussian distribution with a mean of 88 dB SPL and a standard deviation of 4 dB SPL. These values represent source levels of males similar to what was found in a natural population of real males in the field (described for large males of the katydid species *Mygalopsis marki* in Römer and Bailey [39]).

2.1 Simulation of signal broadcast

The simulation arena consisted of 150 x 150 patches, whereby each patch represents a dimension of 1 x 1 m. Equation 1 simulates spherical spreading of sound considering an excess attenuation that was found for insects producing their sounds on the ground, [41]. The sound field of insects producing their calling songs at an elevated position of 2 m above ground was simulated according to equation 2. This results in a signal broadcast similar to what was found for sound attenuation solely caused by spherical loss, [41, 51].

Simulation of acoustic signal broadcast already takes receiver psychology of females into account and provides the basis for a rapid simulation of females attracted to a sound source (phonotaxis). This includes a fixed hearing threshold of 40 dB SPL and a minimal difference of perceived sound levels (signal loudness) that is necessary for a proper localisation of a signaller (2 dB). Hearing thresholds of bushcrickets and field crickets are quite high compared to humans and known from various neurophysiological studies. In the current model hearing thresholds of receivers was fixed to 40 dB SPL, a value that lies between the hearing thresholds determined for bushcricket and crickets.

The loudness of individual senders perceived at a certain distance was calculated according to equation 1 or equation 2 and was stored in the patch array variable *perceived_level* as soon as it exceeded the hearing threshold of receivers. In addition with saving the *perceived_level*, the sender ID was stored in the array variable *potential_owner* for determination of the dominant sender of every patch afterwards (see ‘calculation of the dominant sender’ below). Fluctuations of perceived sound levels were simulated by use of a random normal distribution with a mean of *perceived_level* and a standard deviation of *SD_level_fluct*.

$$perceived_level = sender_level - (14.179 * \ln(distance) - 0.9809) \quad (1)$$

$$perceived_level = sender_level - (10.054 * \ln(distance) - 0.8649) \quad (2)$$

Signals broadcast from different senders do not interfere with each other in any way. This simulates a temporal segregation of signals broadcast from individual senders. Because temporal relationship plays no role in the current simulation, a group of sender in this study was termed ‘aggregation’ instead of ‘chorus’.

2.2 Calculation of the dominating sender

After calculation of the *perceived_level* and the *potential_owner* for all patches in the broadcast area of all senders, a procedure was started which determined the dominating sender for a given patch according to the following rules: When only one sender exceeded hearing threshold, then this patch belongs to it and patch colour changed into the colour of the dominant sender. As soon as two or more senders were perceived suprathreshold, only that sender was considered dominant exhibiting a loudness Δ dB higher compared to all others. In the case that sound level differences on a given patch were in the range of Δ dB, the ownership of that patch was left undefined (‘zone of ambiguity’ shown in blue colour).

A sound level difference of two dB was used in the standard simulation setting corresponding to a sound level difference, insects are able to discriminate when background noise level is low, [45]. Furthermore, a two dB louder sound source attracted a significantly higher proportion of female mole crickets, [15] and *Hyla cinera* frogs exhibited a preference for the louder of two moderately loud sound sources differing by only 3 dB, [17].

2.3 Simulation of sender spacing

‘Random aggregations’: A routine positioned agents to randomly chosen positions by fulfilling the following criteria: All senders need to keep at least 1 empty patch between two senders and all agents were positioned in a square located in the middle of the simulation arena. The dimension of this square (termed ‘habitation square’) and the number of signalling agents on it determined the density of simulated males in an aggregation.

‘65 dB aggregations’: Agents were successively positioned at randomly chosen patches that fulfilled the following criteria: The nearest neighbour needs to be perceived at a sound level of 65 ± 4 dB SPL and the patch needs to be located in the habitation square. This spacing simulates the spacing of real *Mygalopsis marki* males and was determined in the field by Römer and Bailey [39]. In an Indian chirping *Mecopoda elongata* species (bushcricket) the mean SPL of males at the position of nearest neighbours was 71.6 ± 8.1 dB [32].

‘Optimised aggregations’: In this spacing scenario agents had to position themselves in the habitation square in a way so that the perceived maximum sound level accumulated on all patches is maximised. For a proper approximation of this optimisation problem a nested evolutionary optimisation procedure with isolation was used. The x and y coordinates of males in four ‘random aggregations’ represent four parent generations, which were successively mutated (shifted by a maximum of ‘mutation stepsize’ = 0.3 m) and recombined (mated). The four best of seven offspring aggregations were selected and compared in their fitness function with another parallel mutated and recombined population. This optimisation cycle was repeated 200 times and resulted in a

male spacing in which softer males are spaced more densely than louder ones and loud males preferably occupied the margin of the habitation square.

2.4 Virtual female phonotaxis

After finishing the calculation of the signal broadcast area of all senders, the phonotactic approach of virtual females was simulated. Real males in the field never know where females are, unless they respond to the calling songs of males. Therefore, the starting positions of females in the computer model were randomly chosen in a square that exceeds the side length of the habitation square by 60 m. The approach of females to a sound source was simulated by taking the turn angle response of *Tettigonia cantans* females (bushcricket) towards a sound source as a basis [37].

Simulated females do not discriminate between individual signallers; instead they are passively attracted to that signaller that is perceived Δ dB louder than any competing one, [34, 43, 44]. This was simulated by roughly turning towards the direction of a sound source, unless the sound source impinges on a receiver from frontal or from behind (345 - 15 degrees or 165 to 195 degrees relative to the current heading). In this case a virtual female turns by a random turn angle of ± 50 degrees. This was necessary because in a frontal range of ± 15 degrees frogs and insects were unable to correctly turn towards a speaker playing back conspecific signals, [20, 37].

Individual females obeyed the following rules in locating a sound source: In the case a female reaches a patch that is owned by a given sender (a dominant sender is perceived Δ dB louder than any other) and the sound is not perceived from frontally or behind, then she turns towards this sender (*turn_angle*) limited by a maximum turn angle of 35 degrees. The turn angle was taken from a normal distribution with a mean of *turn_angle* and a standard deviation of *turn_angle_error*. After the turning manoeuvre females walked one patch. In the case a patch at the female position was not owned by any sender or the level of competing senders are similar at this position ($< \Delta$ dB), females turned by a random angle (± 50 degrees) in relation to here current heading. After turning she moved one patch ahead. As a result of this, females showed a kind of random walk. According to these rules 1000 individual female phonotactic approaches were successively simulated and the percentage of females attracted to individual senders was correlated with the source level of individual senders.

The values of all simulation parameters used in the standard simulation are summarized in table 1.

2.5 Calculation of parameter correlations

The correlation of sender source levels and the percentage of accrued broadcast area as well as the correlation of sender source level and the percentage of female encounter rate were calculated by a Pearson product-moment correlation (equation 3). With the exception of the source levels of senders a data transformation was necessary in order to achieve normal distributed data sets required for the calculation of Pearson correlation. Data transformation was performed by calculating the logarithm of basis 10 of each data value. The validity of this transformation was controlled in SigmaPlot® 11.0 (SPSS inc.) using Shapiro-Wilkinson test for normality.

A positive correlation between two measurement parameters was considered significant, when r (Pearson correlation coefficient) was equal or higher than 0.65. For 20 simulated sound sources this level of Pearson's r corresponds to a non-directional error probability of 0.0019 and 0.0001 for 30 males, respectively.

$$r = \frac{1}{n-1} \sum_{i=1}^n \left(\frac{X_i - \bar{X}}{S_X} \right) \left(\frac{Y_i - \bar{Y}}{S_Y} \right) \quad (3)$$

X and Y represent two parameters that are investigated for a correlation. S_X and S_Y denotes the standard deviations of each parameter.

2.6 Calculation of the regularity of inter-male distances

The regularity (R) of male spacing was calculated by use of equation 4 resulting in an $R=1$ for randomly spaced individuals, an $R<1$ for an aggregated spacing and an $R>1$ for a regular spacing (for details see: [10, 27]).

$$R = \frac{\left(\frac{\sum_{n=1}^N NN_dist}{N} \right)}{\left(\frac{1}{2 * \sqrt{density}} \right)} \quad (4)$$

NN_dist denotes the distance of a focal male to his nearest neighbour. ‘density’ stands for the actual density of males in an aggregation ($N / \text{area of habitation square}$).

| Parameter | Value | unit |
|--------------------------|------------|---------|
| <i>sender_level</i> | 88 ± 4 | dB SPL |
| <i>hearing_threshold</i> | 40 | dB SPL |
| ΔdB | 2 | dB |
| <i>turn_angle_error</i> | 30 | degrees |
| mutation stepsize | 0.3 | m |
| <i>SD_level_fluct</i> | 0 | dB |

Table 1. Standard simulation parameters

3 Results

3.1 Simulation of senders signalling on the ground

Only a maximum of 50 % of simulated aggregations consisting of randomly spaced males showed a positive correlation of sender source level and the broadcast area accrued by each sender (male). However, the existence of such a correlation strongly depends on the number of males occupying a given habitation area (male density) and the minimum perceived level difference of competing sound signals a receiver is able to distinguish (ΔdB) (Table 2). Increasing ΔdB in medium and low density aggregations even reduced the likelihood of loud males to accrue a larger portion of broadcast area. Simulating an aggregation density that was found in the katydid species *Mygalopsis marki* (density: 0.00256, [46]) no more than 26 % of all simulated aggregations exhibited a significant positive correlation of source level and the area garnered by individual senders ($\Delta dB = 2$). However, it needs to be emphasized that even in high density aggregations those males signalling at a higher intensity more likely accrued a larger broadcast area in comparison to softer signalling males. However, in ‘random aggregations’ this does not constitute a general rule because even loud males may garner only a very small broadcast area, a fact that depends on spacing. Two prerequisites for a large broadcast area of senders have been observed: a high nearest neighbour distance and soft signalling neighbours.

In all simulated aggregations a significant correlation exists between the broadcast area of individual senders and female encounter rate (mean $r = 0.86$). This emphasizes the importance of the broadcast area of a sender for his attractiveness and suggests a random spacing of males to be costly, especially for louder ones.

| male density [N/m ²] | ΔdB | sign. correlation [%] | no correlation [%] |
|-------------------------------------|-------------|-----------------------|--------------------|
| 0.001 | 1 | 57 | 43 |
| 0.001 | 2 | 42 | 58 |
| 0.001 | 3 | 22 | 78 |
| 0.0015 | 1 | 38 | 62 |
| 0.0015 | 2 | 42 | 58 |
| 0.0015 | 3 | 12 | 88 |
| 0.0026 | 1 | 50 | 50 |
| 0.0026 | 2 | 26 | 74 |
| 0.0026 | 3 | 19 | 81 |
| 0.0034 | 1 | 22 | 78 |
| 0.0034 | 2 | 31 | 69 |
| 0.0034 | 3 | 25 | 75 |

Table 2. Percentage of aggregations in which randomly positioned males showed either a significant correlation or no correlation between source level and the proportion of accrued broadcast area. Males signalled on ground level.

A random spacing of ground singing males can result in a reduction of the broadcast area of loud males (Fig. 1, left aggregation). This is in contrast to what was found for optimised aggregations in which louder signalling males preferably occupied the border of the habitation area and silent singing males are more densely packed. In ‘65 dB aggregations’ males are more aggregated when signalling on ground which leads to a reduction of the total broadcast area in such male assemblages.

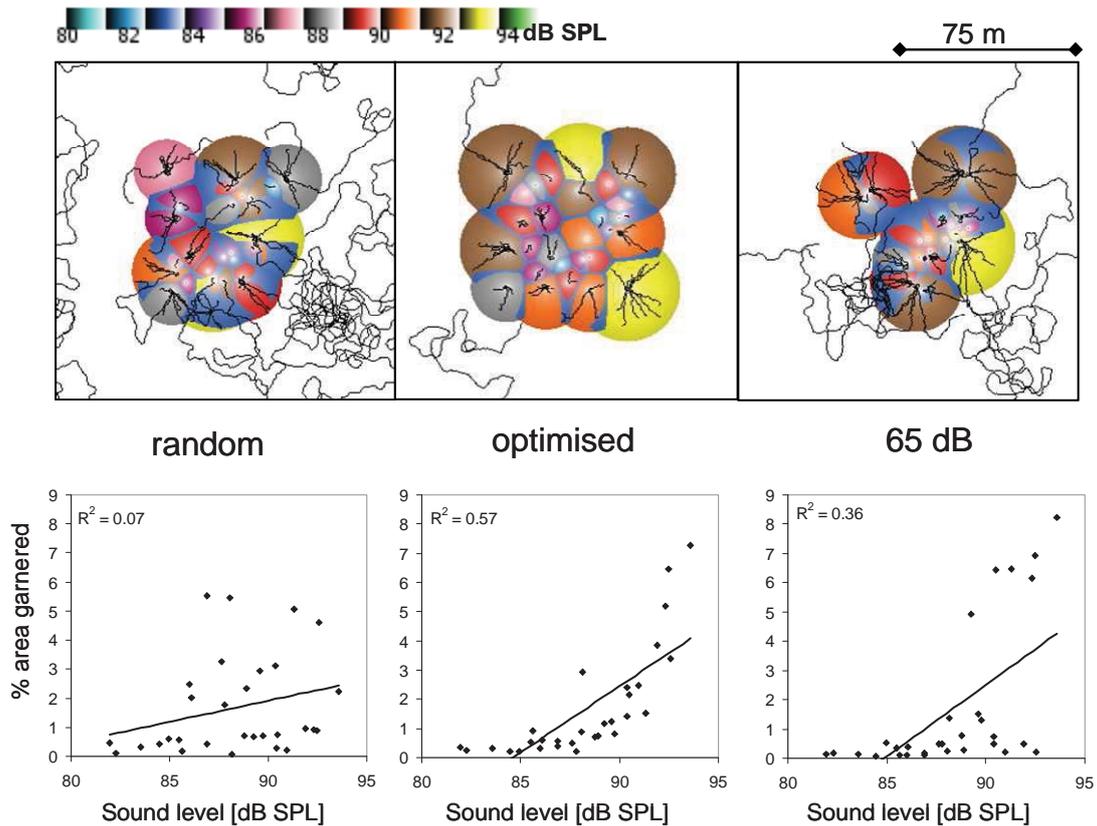


Figure 1. Simulation of the broadcast area of 30 senders arranged in three different spacing scenarios and the phonotactic walking paths of simulated females. 30 senders signalling on ground were arranged in three different manners: randomly (left), optimally (middle) or in a way that the nearest neighbour was perceived at a sound level of 65 ± 4 dB SPL (right). The phonotactic walking paths of 70 females are overlaid in each graph (black traces). Zones in which the sound level of two neighbouring signallers are perceived at a similar sound level (≤ 2 dB) are shown in blue. Colours correspond to the source levels of individual signallers (see above legend). Note that as soon as females leave the simulated world at one side, they reappeared on the opposite side. In the graphs below the sender levels of males are plotted against the percentage of accrued broadcast area. R^2 : Coefficient of determination; Male density: 0.0026 N/m^2 ; Dimension of simulation arena: $150 \times 150 \text{ m}$.

The results obtained from 12 different aggregations each simulated at four different densities revealed that a significant positive correlation ($r \geq 0.65$) between source level of ground signalling senders and the accrued broadcast area as well as a correlation of sender level and female encounter rate was restricted to ‘optimised aggregation’ scenarios (Fig. 2). Here, both correlations gradually decreased at higher male densities. In “65 dB aggregations” a positive correlation between the source level of senders and the accrued broadcast area was sometimes found, but a significant positive correlation between source level and female encounter rate was absent. A random inter-male spacing resulted neither in a significant correlation between source level and broadcast area nor in a correlation between source level and female encounter rate.

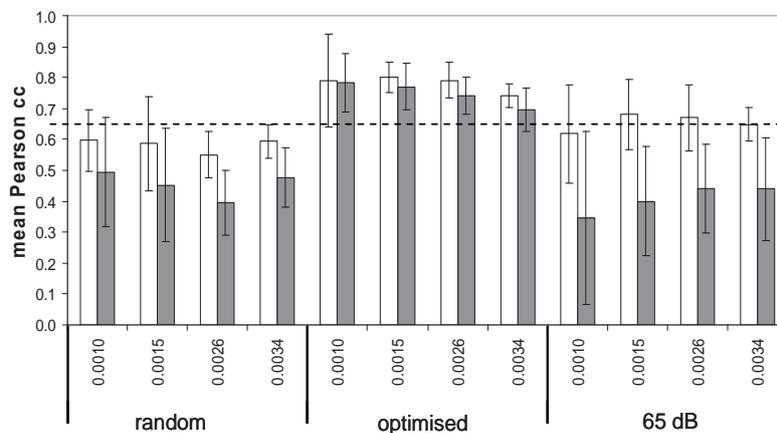


Figure 2. Influence of sender level on the accrued broadcast area as well as on sender attractiveness. Mean Pearson cc of the sound level of senders located on the ground and the

percentage of the accrued broadcast area. Pearson cc were measured in three different spacing scenarios exhibiting different male densities (blank bars). In addition the Pearson cc between sender level and the percentage of females attracted to signallers are shown (grey bars). Numbers below bars denote male density values (N/m^2). Data represent mean \pm SD of Pearson cc obtained from 12 different aggregations.

More aggregated male assemblages as a result of ‘65 dB spaced’ senders signalling on ground were accompanied by large zones in which the signals of different senders were perceived at a similar level (Δ dB \leq 2). In these zones virtual females perform a pseudo-random walk and this lowers the probability of any sender to attract a higher number of females compared to his competitors. Nevertheless, louder senders in ‘65 dB aggregations’ often accrued larger broadcast areas, but when surrounded by competitors, this need not be the case and then loud males are no better than softer signalling males in accruing broadcast area.

As a result of an evolutionary optimisation strategy applied to male spacing a significantly higher regularity (R) was found ($p < 0.001$, $N = 12$, t-test) in comparison to random aggregations and ‘65 dB aggregations’ (Fig. 3). However, increasing density in ‘optimised aggregations’ resulted in a gradual decrease in the regularity of male spacing. Exactly the opposite trend was found in ‘65 dB aggregations’ of signallers located on the ground in which R values slightly increased at higher densities.

The total walking path length accumulated within 1000 female phonotactic runs was significantly higher in ‘65 dB aggregations’ compared to any other spacing scenarios ($p < 0.001$, $N = 12$, t-test). The shortest average female walking path length was found in ‘optimised aggregations’ independently of sender density.

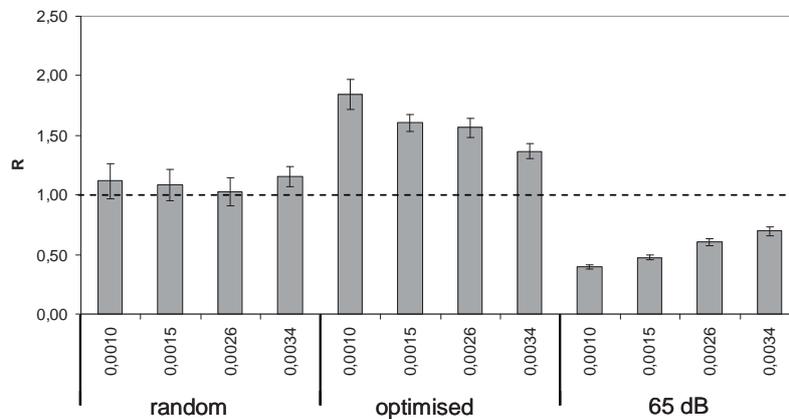


Figure 3. R values (measure of regularity) of senders determined in three different spacing scenarios in which all senders were located on the ground. Numbers below bars denote density values.

3.2 Simulation of male *Mygalopsis marki* aggregations

In a real population of *Mygalopsis marki* (*M. marki*), male spacing was found to be quite regular (mean $R = 1.3$), [46], whereby regularity is known to be achieved by maintaining a ‘65 dB distance’ to the nearest neighbours, [39]. Because, this insect species stridulate from more elevated positions, equation 2 was used in order to simulate signal transmission more realistically. Simulation of such *M. marki* aggregations at a realistic aggregation density ($0.0026 N/m^2$) resulted in a quite regular inter-male spacing (mean $R = 1.19 \pm 0.07$, $N = 12$ aggregations) with an average inter-male distance of about 10 m. Signalling from more elevated positions suffers from less excessive attenuation and in turn increases inter-male competition for broadcast area (Fig. 4C). This strong competition resulted in a situation in which loud senders accrued a major portion of the total broadcast area. Therefore, a significant correlation between source level and the percentage of garnered broadcast area was found (mean Pearson $cc = 0.70 \pm 0.096$, $N = 12$ different aggregations). Nevertheless, loud males in simulated *M. marki* aggregations did not succeed in attracting a higher number of females compared to softer signalling males (Pearson $cc = 0.576 \pm 0.093$, $N=12$), although such a correlation was found in optimised aggregations simulating a male density and sound transmission typical for *M. marki* (mean Pearson $cc = 0.68 \pm 0.13$, $N=12$). This result is a direct consequence of an increased zone in which signals belonging to different senders are perceived at equal loudness (± 2 dB) (blue region in Fig. 4). This zone of ambiguity was increased to about 6 – 14 times when signals were broadcast from elevated positions compared to the ground signalling situation. Simulating female phonotactic approaches from randomly chosen starting positions located at the border of the simulation arena even further reduced the correlation coefficient determined for sender source levels and the percentage of attracted females in ‘65 dB *M. marki* aggregations’ (mean Pearson $cc = 0.357 \pm 0.145$, $N=12$).

3.2.1 Influence of Δ dB on female encounter rate

In a natural habitat background noise and abiotic influences affects a receiver’s ability to distinguish sound sources according to perceived sound level differences. This was simulated by increasing the level of Δ dB in three different ‘65 dB aggregations’ (shown in figure 4). In those aggregations in which males exhibit a significant correlation between source levels and the percentage of garnered broadcast area (Fig. 4 A and C), increasing Δ dB interestingly increased the chances for loud males to attract a higher proportion of females (Fig. 5). Such an increase was absent in aggregation B in which male spacing prevented a correlation between sender source level and the percentage of accrued broadcast area.

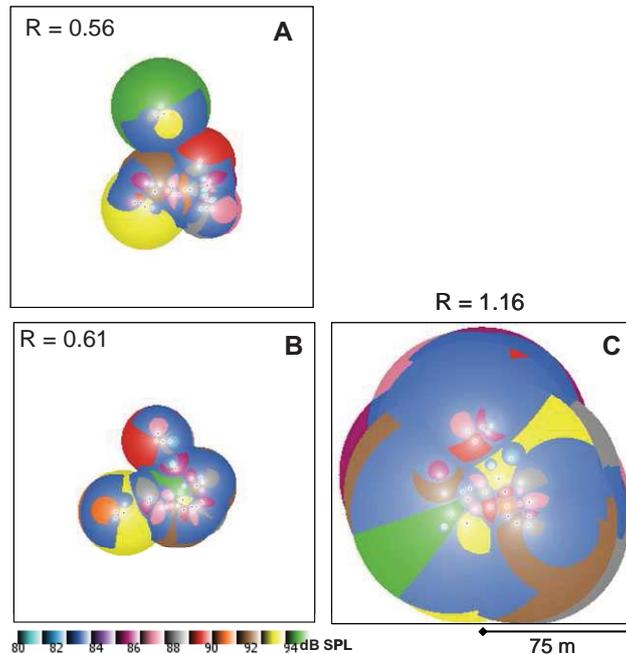


Figure 4. Three aggregations in which senders either broadcast their signals on ground (left graphs) or from elevated signalling positions (right graph). In all aggregations the same 30 senders were spaced in a way that the nearest neighbour was perceived by 65 ± 4 dB SPL. Pearson cc of the source levels of senders and garnered broadcast area: A: $r = 0.76$; B: $r = 0.65$; C: $r = 0.76$. The average nearest neighbour distance in left aggregations is about 6.5 m and in the right aggregation 10.5 m. Δ dB = 2; Sender density: 0.0026 N/m^2

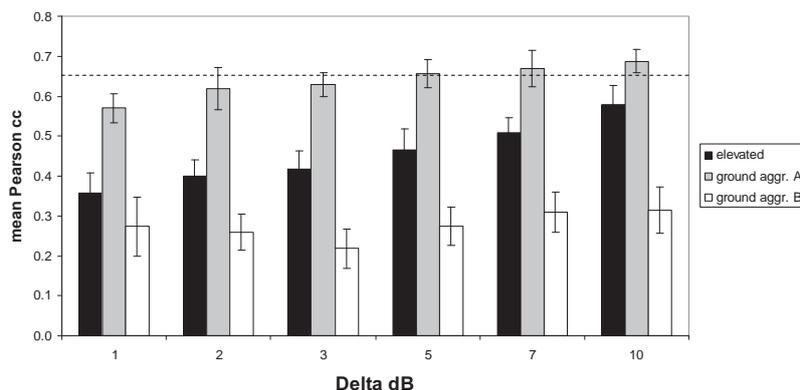


Figure 5. Influence of Δ dB on the correlation of sender source level and female encounter rate. The Pearson correlation coefficients between the source levels of senders and the percentage of attracted females was calculated in three different ‘65 dB aggregations’. Sender assemblages are shown in Fig. 4. Bars represent the mean Pearson cc \pm SD obtained in 10 simulation runs each simulating 1000 female phonotactic runs.

3.2.2 Investigation of turn angle errors

The influence of turn angle errors in phonotactic runs and their impact on female encounter rate was investigated in three different ‘65 dB aggregations’ consisting of the same 30 senders (see Fig. 4). In these aggregations the degree of turn angle errors (*turn_angle_error*) had no significant influence on the correlation of sender level and the percentage of attracted females (Fig. 6).

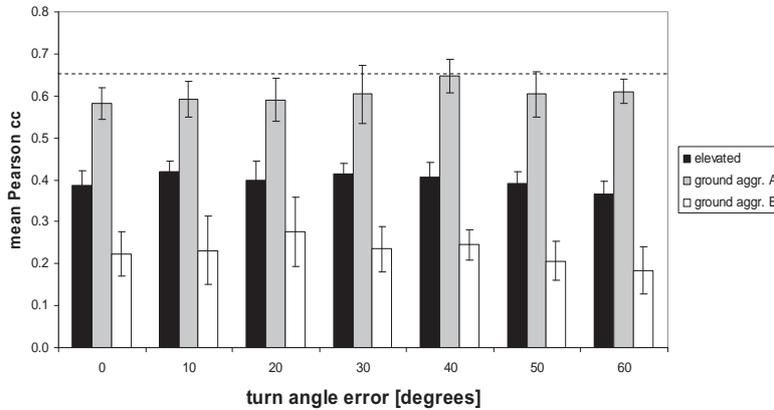


Figure 6. Simulations of different degrees of turn angle errors during phonotaxis. The influence of turn angle error (*turn_angle_error*) on the correlation of sender level and the percentage of attracted females. Signal broadcast was simulated either for sender located on ground or on elevated positions suffering from less excessive attenuation. See figure 4 for male assemblages. Bars represent the mean \pm SD Pearson cc obtained from 10 simulation runs each simulating 1000 female phonotactic runs.

3.2.3 Influence of noise on female encounter rate

Finally the magnitude of signal amplitude fluctuations of the perceived sound level was investigated in three different aggregations consisting of the same 30 senders (Fig. 4). Local signal amplitude fluctuations only marginally affected the correlation between female encounter rates and the source level of senders (Fig. 7). A tendency towards a decrease of such a correlation at higher signal amplitude fluctuations was observed in that aggregation in which the source levels of senders located on the ground showed a correlated with the percentage of garnered area (Fig. 7 grey bars).

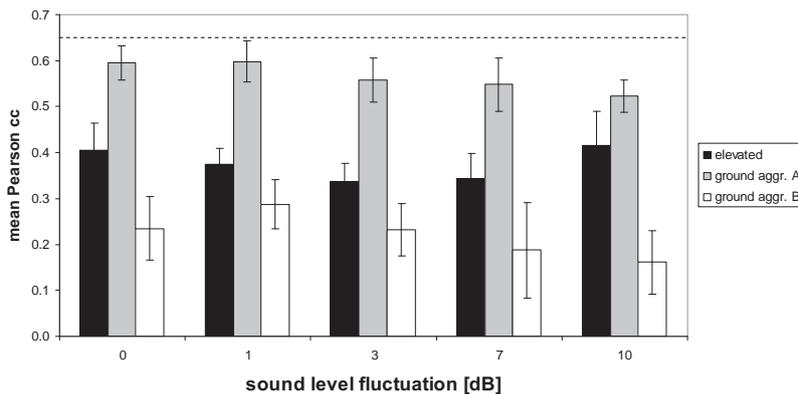


Figure 7. Influence of fluctuations of the perceived sound level on sender attractiveness. ‘65 dB aggregations’ (shown in figure 4) were investigated for a correlation of the source level and the percentage of mate encounters determined in simulations in which the perceived sound level fluctuates. The standard deviation of perceived sound level fluctuations are given on the abscissa. Bars represent the mean \pm SD Pearson cc obtained in 10 simulation runs each simulating 1000 female phonotactic runs.

4 Discussion

Sound intensity constitutes an important call parameter that is associated with calling energetic, [35], and only males of good quality are able to produce calls of high signal amplitude for a longer period of time.

Therefore, signal intensity is thought to constitute an important trait of a sender that is likely associated with his quality and females may assess the source level of senders directly by sequential sampling of males in an aggregation and comparing their sound levels with an internal standard. Another more likely way of selecting louder signallers in an aggregation may constitute a passive attraction of females to a sound source that is perceived louder than others. This however strongly depends on the distance between a receiver and a sender. Calling in dense aggregations increases inter-male competition for limited signal broadcast area and females selecting a male in such an acoustic lek may select a male of good quality as a result of a larger broadcast area of louder males.

Considering the results of the current simulation study, a random spacing of males in an aggregation can be costly for loud males, which often exhibit only a small broadcast area as a result of inter-male competition for broadcast area. Therefore, males do better in keeping a high distance to neighbours, a behaviour which is known to mitigate the competition for broadcast area of two competitors (see [16]). It is therefore no surprise that males in various bushcricket species e.g. *Tettigonia viridissima* and *Metrioptera roeselii* as well as *Platycleis albopunctata*, [2, 7, 22] space themselves in a regular fashion by keeping a distance of 3 – 6 m to nearest neighbours. The simulation results of the current study suggests that especially in aggregations exhibiting a higher male density, sender positioning can heavily affect the accrued broadcast area of individual signallers. Spacing that emerges from ESS optimisation procedure reveals that males spacing themselves in a more regular fashion, better transform signal intensity into broadcast area, even when aggregation density is very high. The arrangement of males in ‘optimised aggregations’ preserved a large broadcast area of loud males and prevents softer singing males from a dramatic reduction of their broadcast area as a consequence of signalling too close to a loud male.

Loud males in optimised spacing scenarios were often found near the border of the habitation area. This spacing makes sense, since the competition for available broadcast area is less strong for senders located near the border of an aggregation. If females would be attracted from outside an aggregation, ‘border males’ would strongly benefit from being located at the border of an aggregation especially when female choosiness is low. In nature border positions are more vulnerable against predators in comparison to central positions, but locations close to the center of an aggregation are accompanied by a higher competition for limited resources, [28], and that holds true for signal broadcast area as a male resource as well. In the insect species *Tettigonia viridissima* females were found to choose the first singing male located near their release points, a fact that reduced male attractiveness in the middle of artificially clumped aggregations, [3]. This could be the explanation why males of this species space out quite regularly in nature $R = 1.2 - 2.1$, [2].

Considering ‘65 dB aggregations’ consisting of senders signalling on ground, it seems that softer signalling males take some portion of the broadcast area belonging to loud males. The exact spacing of softer singing males is important, because a position too close to a loud male almost reduces their own broadcast area. Using the sound level of the nearest neighbour as a distance cue, males may establish a kind of cooperation among softer signalling males by reducing the broadcast area of louder males. Moreover, staying in a certain distance to loud males increases the likelihood of intercepting females that are originally attracted by the louder sender from a greater distance. Females approaching a louder male may come close to a softer singing male, a situation which increases the chances of this male to be chosen. Frogs were found to select the softer singing male despite the presence of a loud competitor calling from at a greater distance [30]. This behaviour reduces search costs for females and may also reduce the vulnerability against visually orienting predators.

Male spacing is often strongly influenced by habitat structure often providing a source of food or enabling sender to broadcast from elevated positions. The influence of habitat structure on male spacing can be excluded for *M. marki* males living in a habitat that offers males a quite homogeneously distribution of bushes that constitute preferred singing locations, [39]. In this species regular inter-male distances are established by means of strategic male spacing exploiting the perceived sound level of the nearest neighbour as a distance cue. Males of this species are preferably located at positions where the signal of nearest neighbour are in the range of 65 ± 4 dB SPL. Simulation of such spacing in the current study using a realistic male density resulted in nearest neighbour distances and a regularity of inter-male spacing similar to what was found in real aggregations of *M. marki*. This however strongly depends on signal transmission properties, which need to suffer from less excessive attenuation. This makes sense since real *M. marki* males preferably signal at positions 1-2 m above ground, [39].

Signals broadcast from elevated positions suffer from less excessive attenuation and in consequence dramatically increases the zone of ambiguity observable in an aggregation (blue area in Fig. 4C). Because of this, distinguishing males by means of perceived differences in loudness becomes a quite difficult task for females in ‘65 dB aggregations’. Although louder males accrued a larger broadcast area in ‘*M. marki* aggregations’, they not necessarily attracted a higher percentage of females. When females were attracted from outside the aggregation the selected male may not belong to one of the loudest males, unless these are surrounding an aggregation (often found in ‘optimised aggregations’). This result strongly suggests that despite the regularity of sender spacing which is found in *M. marki* populations, louder than average signalling males may not attract a higher percentage of females that are passively attracted to the louder sound of competing sound sources. This

suggests that other signal parameters apart from signal amplitude of *M. marki* males, e.g. chorus attendance, may be exploited by females in order to select males of better quality. This is quite surprising considering the fact that larger *M. marki* males are louder, [39].

Interestingly, louder males in a *M. marki* population may profit from a high minimal perceived sound level difference that is necessary for a proper discrimination of the louder of perceived signals (Fig. 5). In habitats exhibiting a high background noise level as a consequence of the simultaneous activity of heterospecific signallers, or due to abiotic noise, females may need to perceive a signal at much higher level in order to be able to discriminate this signal from background and in order to locate a certain signaller. It is therefore no surprise that frogs were less successful in choosing males of high quality according to call parameters in a situation with a high background noise level. This effect of chorus noise on call detection has been studied in several species of hylid frogs, [19, 53]. A result of the current simulation study suggests that in such a situation louder signalling males may attract a higher percentage of females given a ‘65 dB spacing’.

M. marki signals are broadband but exhibit a high spectral density around 10 kHz, [39]. Amplitude fluctuations are 10 to 20 dB larger for sound of 10-50 kHz carrier frequency compared to low frequency sound, [14]. Such amplitude fluctuations are thought to exert detrimental effects on receiver performance relying on intensity cues. Surprisingly, the magnitude of amplitude fluctuations as well as the degree of turn angle errors did not affect the correlation coefficient between source levels and the percentage of attracted females in ‘65 dB aggregations’ (Fig. 6 and 7). Since females in zones of ambiguity performed a pseudorandom walk in the current simulation study, influences arising from amplitude fluctuations and turn angle errors may not be as strong.

5 Conclusions and future outlook

The current simulation study suggests that the accrued broadcast area of acoustically communicating insects in aggregations is significantly positively correlated with the number of attracted females, whereby phonotaxis is based on a passive attraction to the louder of competing sound sources. A random spacing of signallers results in accrued broadcast areas that are not related to the source levels of individual signallers. Interestingly, signallers located on the ground exhibiting a more natural spacing, which is based on the perceived loudness of the nearest neighbour (‘65 dB spacing’), were also unable to transform signal levels into accrued broadcast area. This situation changed as soon as signallers broadcast their signals from elevated positions leading to a positive correlation of source levels and the accrued broadcast areas. Nevertheless, this correlation was not reflected in the number of attracted females, a result which is a consequence of an enlargement of that zone in which signals exhibit similar loudness. This result suggests that other signal parameters apart from signal amplitude of *M. marki* males may be exploited by females in order to select males of better quality.

Interestingly, a positive correlation of source levels and female encounter rates was increased at higher minimally required sound level differences that receivers need in order to head towards the source of a louder signal. This result suggests that louder males may profit from a situation in which a receiver needs to perceive signals at high intensity in order to locate the source of a sound signal. Such a situation is easy imaginable in a chorus situation with many heterospecific signallers contributing to a high background noise level.

In future studies, field measurements of the signal intensity of signallers in combination with their inter-male spacing may provide the basis for a more realistic simulation of the broadcast areas of senders. Whether or not a large broadcast area may lead to a higher female encounter rate, can be derived from experiments investigating female mate sampling behaviour and from studies investigating the abundance of females. Because male spacing may be strongly influenced by mate sampling tactics, [3, 2], both aspects, sender spacing and female sampling tactics, together with ecological influences (e.g. predators) need to be known for a thorough interpretation of the spacing of real signallers belonging to aggregations.

6 References

- [1] Allen, G.R.: *The calling behaviour and spatial distribution of male bushcrickets Sciarasaga quadrata and their relationship to parasitism by acoustically orienting tachinid flies*. Ecological Entomology 20 (1995), 303 - 310.
- [2] Arak, A. and Eiriksson, T.: *Choice of singing sites by male bushcrickets (Tettigonia viridissima) in relation to signal propagation*. Behavioral Ecology and Sociobiology, 30 (1992), 365 - 372.
- [3] Arak, A., Eiriksson, T. and Radesäter, T.: *The adaptive significance of acoustic spacing in male bushcrickets Tettigonia viridissima: a perturbation experiment*. Behavioral Ecology and Sociobiology, 26, (1990), 1 - 7.
- [4] Bailey, W. J.: *Acoustic cues for female choice in bushcrickets (Tettigoniidae)*. In Kalmring, K., and Elsner, N. (eds.), Acoustic and Vibrational Communication in Insects, Verlag Paul Parey. Berlin, 1985, 101 - 110.

- [5] Bailey, W. J., and Thiele, D. R.: *Male spacing behaviour in the Tettigoniidae: An experimental approach*. In Gwynne, D. T., and Morris, G. K. (eds.), *Orthopteran Mating Systems*, Westview Press, Boulder, CO, 1983, 163 - 184.
- [6] Belwood, J.J. & Morris, G.K.: *Bat predation and Its influence on calling behavior in neotropical katydids*. *Science*, 238, (1987), 64 - 67.
- [7] Berggren, A.: *The effect of conspecifics on individual male movement in Roesel's bushcricket, Metrioptera roeseli*. *Ecological Entomology* 30, (2005), 480 - 483.
- [8] Cade, W.: *Alternative male strategies: Genetic differences in crickets*. *Science*, 212, (1981), 563 - 564.
- [9] Cade, W. H.: *Field cricket spacing and the phonotaxis of crickets and parasitoid flies to clumped and isolated cricket songs*. *Zeitschrift für Tierpsychologie*, 55, (1981), 365 - 375.
- [10] Clark, P. and Evans, F.: *Distance to nearest neighbor as a measure of spatial relationships in populations*. *Ecology* 35, (1954), 445 - 453.
- [11] Doolan, J. M.: *Male spacing and the influence of female courtship behaviour in the bladder cicada, Cystosoma saundersii* Westwood. *Behavior Ecology and Sociobiology*, 9, (1981), 269-276.
- [12] Farris, H., Forrest, T. & Hoy, R.: *The effects of calling song spacing and intensity on the attraction of flying crickets (Orthoptera: Gryllidae: Nemobiinae)*. *Journal of Insect Behavior*, 10, (1997), 639 - 653.
- [13] Forrest, T. G.: *Calling song and mate choice in mole crickets*. In Gwynne, D. T., and Morris, G. K. (eds.), *Orthopteran Mating Systems*, Westview Press, Boulder, CO, 1983, 185 – 204.
- [14] Forrest, T. G.: *From sender to receiver: Propagation and environmental effects on acoustic signals*. *American Zoology*, 34, (1994), 644-654.
- [15] Forrest, T.G. and Green D.M.: *Sexual selection and female choice in mole crickets (Scapteriscus: Gryllootalpidae): Modelling the effects of intensity and male spacing*. *Bioacoustics*, 3, (1991), 93 – 109.
- [16] Forrest, T.G. & Raspet, R.: *Models of female choice in acoustic communication*. *Behavioral Ecology* 5, (1994), 293 - 303.
- [17] Gerhardt, H.C.: *Evolutionary and neurobiological implications of selective phonotaxis in the green treefrog, Hyla cinerea*. *Animal Behaviour*, 35, (1987), 1479 - 1489.
- [18] Gerhardt, H.C. & Huber, F.: *Acoustic Communication in insects and anurans. Common Problems and Diverse Solutions*. Chicago and London: The University of Chicago Press. 2002.
- [19] Gerhardt, H.C. and Klump, G.M.: *Masking of acoustic signals by the chorus background noise in the green treefrog: a limitation on mate choice*. *Animal Behaviour*, 36, (1988), 1247 – 1249.
- [20] Klump, G. M. and Gerhardt, H.C.: *Sound localization in the barking treefrog*. *Naturwissenschaften*, 76, (1989), 35 - 37.
- [21] Larsen, O. N., Kleindienst, K.-U. and Michelsen, A.: *Biophysical aspects of sound reception. In cricket behaviour and neurobiology* (ed. F. Huber, T. E. Moore and W. Loher), Ithaca, London: Cornell University Press. 1989, 364 – 390.
- [22] Latimer, W.: *Acoustic competition in bush crickets*. *Ecological Entomology* 6, (1981), 35 - 45.
- [23] Lehmann, G.U.C. & Heller, K.G.: *Bushcricket song structure and predation by the acoustically orienting parasitoid fly Therobia leonidei (Diptera: Tachinidae: Ormiini)*. *Behavioral Ecology and Sociobiology*, 43, (1998), 239 - 245.
- [24] Marten, K. & Marler, P.: *Sound transmission and its significance for animal vocalization*. *Behavioral Ecology and Sociobiology*, 2, (1977), 271 - 290.
- [25] Mhatre, N. & Balakrishnan, R.: *Phonotactic walking paths of field crickets in closed-loop conditions and their simulation using a stochastic model*. *Journal of Experimental Biology*, 210, (2007), 3661- 3676.
- [26] Michelsen, A., Popov, A.V. & Lewis, B.: *Physics of directional hearing in the cricket Gryllus bimaculatus*. *Journal of Comparative Physiology A*, 175, (1994), 153 - 164.
- [27] Montealegre, J.C.R. and Gonzalez, R.: *Determinants of male spacing behaviour in Panacanthus pallicornis (Orthoptera: Tettigoniidae)*. *Ethology*, 113, (2007), 1158 - 1172.
- [28] Morrell, L. and Romey, W.: *Optimal individual positions within animal groups*. *Behavioral Ecology*, 19, (2008), 909 - 919.
- [29] Murphy, C.G. and Floyd, S.B.: *The effect of call amplitude on male spacing in choruses of barking treefrogs, Hyla gratiosa*. *Animal Behaviour*, 69, (2005), 419 - 426.
- [30] Murphy, C.G. and Gerhardt, H.C.: *Mate sampling by female barking treefrogs (Hyla gratiosa)*. *Behav Ecol* 13, (2002), 472 - 480.
- [31] Nityananda, V. & Balakrishnan, R.: *Leaders and followers in katydid aggregations in the field: call intensity, spacing and consistency*. *Animal Behaviour*, 76, (2008), 723 - 735.
- [32] Nityananda, V. Stradner, J., Balakrishnan R. and Römer, H.: *Selective attention in a synchronising bushcricket: physiology, behaviour and ecology*. *Journal of Comparative Physiology A*, 193, (2007), 983 - 991.

- [33] Paul, R.C. & Walker, T.J.: *Arboreal singing in a burrowing cricket, Anurogryllus arboreus*. Journal of Comparative Physiology A, 132, (1979), 217 - 223.
- [34] Pollack, G.S.: *Selective Attention in an insect auditory neuron*. Journal of Neuroscience 8, (1988), 2635 - 2639.
- [35] Prestwich, K.N.: *The energetics of acoustic signaling in anurans and insects*. American Zoology, 34, (1994), 625 - 643.
- [36] Regen, J.: *Über die Anlockung des Weibchens von Gryllus campestris durch telefonische Übertragung der Stridulation des Männchens*. Pflügers Archive 155, (1913), 193 - 200.
- [37] Rheinlaender, J. and Römer, H.: *Acoustic cues for sound localisation and spacing in orthopteran insects*. In The Tettigoniidae: Biology, Systematics and Evolution (ed. W. J. Bailey and D. C. F. Rentz), Bathurst: Crawford House Press. 1990, 248 - 264.
- [38] Robertson, J. G. M.: *Acoustic spacing by breeding males of Uperoleia rugosa (Anura: Leptodactylidae)*. Z. Tierpsychol. 64, (1984), 283 - 297.
- [39] Römer, H. and Bailey, W.J.: *Insect hearing in the field II. Male spacing behaviour and correlated acoustical cues in the bushcricket Mygalopsis marki*. Journal of Comparative Physiology A, 159, (1986), 627 - 638.
- [40] Römer, H. & Krusch, M.: *A gain-control mechanism for processing of aggregation sounds in the afferent auditory pathway of the bushcricket Tettigonia viridissima (Orthoptera; Tettigoniidae)*. J Comp Physiol A, 186, (2000), 181 - 191.
- [41] Römer, H. & Lewald, J.: *High-frequency sound transmission in natural habitats: Implications for the evolution of insect acoustic communication*. Behavioral Ecology and Sociobiology, 157, (1992), 631 - 642.
- [42] Schatral, A., Latimer, W., and Broughton, B.: *Spatial dispersion and agonistic contacts of male bush crickets in the biotope*. Zeitschrift für Tierpsychologie, 65, (1984), 201 - 214.
- [43] Schildberger, K.: *The auditory pathway of crickets: Adaptations for intraspecific acoustic communication*. Fortschritte der Zoologie, 39, (1994), 209 - 225.
- [44] Stabel, J., Wendler, G. & Scharstein, H.: *Cricket phonotaxis: localization depends on recognition of the calling song pattern*. Journal of Comparative Physiology A, 165, (1989), 165 - 177.
- [45] Stradner, J. and Römer, H.: *Reliable coding of small, behaviourally relevant interaural intensity differences in a pair of interneurons of an insect*. Biology Letters, 4, (2008), 711 - 714.
- [46] Thiele, D. and Bailey, W.J.: *The function of sound in male spacing behaviour in bush-crickets (Tettigoniidae, Orthoptera)*. Australian Ecology, (1980), 5, 275 - 286.
- [47] Wagner, W. E.: *Convergent song preferences between female field crickets and acoustically orienting parasitoid flies*. Behavioral Ecology, 7, (1996), 279 - 285.
- [48] Walker, T.J.: *Mating Modes and Female Choice in Short-Tailed Crickets (Anurogryllus arboreus)*. In: Orthopteran Mating Systems. Sexual Competition in a Diverse Group of Insects. (Ed. by D.T.Gwynne & C.E.Morris), Colorado: Westview Press. 1983, 240 - 267.
- [49] Walker, T. J. and Forrest, T. G.: *Mole cricket phonotaxis: Effects of intensity of synthetic calling song (Orthoptera: Gryllotalpidae: Scapteriscus acletus)*. Florida Entomology 72, (1989), 655 - 659.
- [50] Wells, K.D.: *The social behaviour of anuran amphibians*. Animal Behaviour, 25, (1977), 666 - 693.
- [51] Wells, K.D. and Schwartz, J.J.: *The effect of vegetation on the propagation of calls in the Neotropical frog Centrolenella fleischmanni*. Herpetologica, 38, (1982), 449 - 455.
- [52] Wilczynski, W., and Brenowitz, E. A.: *Acoustic cues mediate inter-male spacing in a neotropical frog*. Anim. Behav. 36, (1988), 1054 - 1063.
- [53] Wollerman, L.: *Acoustic interference limits call detection in a neotropical frog Hyla ebraccata*, Animal Behaviour, 57, (1999), 529 - 536.
- [54] Zahavi, A.: *Mate selection - a selection for a handicap*. Journal of Theoretical Biology, 53, (1975), 205 - 214.