Male calling and spacing in natural chorus of *Platygryllus* sp. Implications for masking interference and mate choice.

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A dissertation submitted for the partial fulfilment of
BS-MS dual degree in science.

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Certificate of Examination

This is to certify that the dissertation titled "Male calling and spacing in natural chorus of *Platygryllus* sp. and its Implications for masking interference and mate choice." submitted by Mr. Shivaprasad G Patil (Reg. No. MS10047) for the partial fulfilment of BS-MS dual degree programme of the Institute, has been examined by the thesis committee duly appointed by the Institute. The committee finds the work done by the candidate satisfactory and recommends that the report be accepted.

Dr. N.G. Prasad   Dr. Kuljeet Sandhu   Dr. Manjari Jain
(Supervisor)

Dated: April 24, 2015

Declaration

The work presented in this dissertation has been carried out by me under the guidance of Dr. Manjari Jain at the Indian Institute of Science Education and Research Mohali. This work has not been submitted in part or in full for a degree, a diploma, or a fellowship to any other university or institute. Whenever contributions of others are involved, every effort is made to indicate this clearly, with due acknowledgement of collaborative research and discussions. This thesis is a bonafide record of original work done by me and all sources listed within have been detailed in the bibliography.

Shivaprasad G Patil

(Candidate)

Dated: April 24, 2015

In my capacity as the supervisor of the candidate's project work, I certify that the above statements by the candidate are true to the best of my knowledge.

Dr. Manjari Jain

(Supervisor)

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Notations

- LDMC – Long Distance Mating Call
- CC – Courtship Call
- SS – Spherical Spreading
- TA – Total Attenuation
- EA – Excess Attenuation
- SPL – Sound Pressure Level
- m – Meters
- s – Seconds

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Chapter 1, Introduction to crickets

Chapter 1

1.1 Introduction to crickets

Crickets belong to family Gryllidae (also known as “true crickets"), they are insects somewhat related to grasshoppers. They have somewhat flattened bodies and long antennae. There are about 2400 species of crickets all over the world (Parsons 2001). They tend to be nocturnal and are often confused with grasshoppers because they have a similar body structure including jumping hind legs. Crickets are harmless to humans. Crickets are omnivorous scavengers who feed on organic materials, including decaying plant material, fungi, and some seedling plants. They are cold blooded and solitary in habit. They have incomplete life cycle.

1.2 Morphology of crickets

Crickets are medium to large sized insects. They have chewing mouth parts and their hind legs are stronger than the other two as they are modified for jumping. They have six legs, long antennae and prominent cerci at the end of their abdomen as you can see in Figure 1. The two forewings are stiff and leathery and the two long membranous hind wings are used in flying. Most of the crickets are brown but some are black and tree crickets are green. Males and females have ears on their foreleg which are smooth round or oval structures. Females have a thin tube at the end of their abdomen that they use to lay eggs which is called ovipositor. They are often confused with grasshoppers; crickets have long antennae, their ears are located on their forelegs, they produce calls by rubbing forewings together whereas in case of grasshoppers they have short antennae, their ears are located on abdomen and they produce calls by rubbing their hind legs to edge of forewings.
(B David and T Ananthakrishnan 2004)

1.3 Habitat and Ecology

Crickets are found all over the world in a wide variety of environments (lawns, caves, forests, under rocks, burrows etc). The occcurence of these insects in such wide range of habitats reflects their broad tolerance to the environmental factors. Crickets are usually found on the soil, hiding under dead plants or on live plants. They occur where there is plant material to eat and they are most diverse and abundant in humid areas with lots of plants.

1.4 Taxonomic position

Kingdom: Animalia
Phyllum: Arthropoda
Class: Insecta
Order: Orthroptera
Suborder: Ensifera
Superfamily: Grylloidea
Family: Gryllidae (Laicharting, 1781)

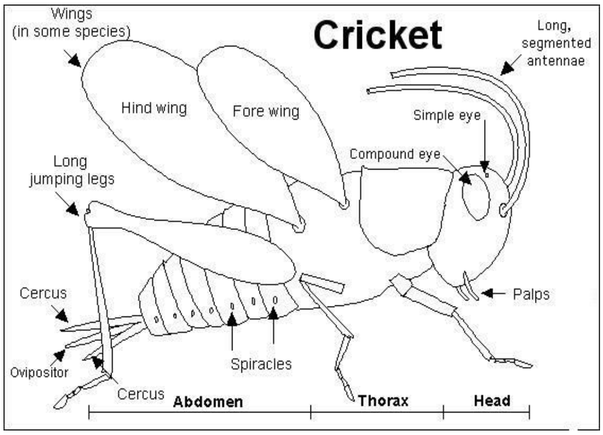


Figure 1: Morphology of a cricket, the one above being a female as there is ovipositor. (Alexander 1962)

1.5 Developmental Cycle

Crickets are hemi-metabolous insects that undergo incomplete metamorphosis (Figure 2), the young ones hatch from the eggs and they look like adults, the only difference being that they don't have wings. At this stage they are called nymphs. These nymphs undergo molts as they grow to become adults. Adults have wings and fully developed reproductive structures. The female's ovipositor begins to show even before it is an adult and increases in length with each successive molt.

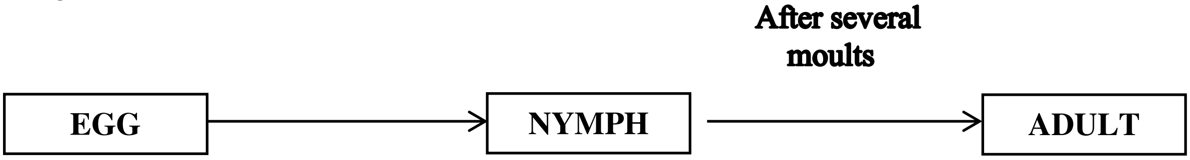


Figure 2: Life cycle of cricket depicting the stages in the life of a cricket.

1.6 Acoustic communication in crickets

Animals use different forms of communication sound, light, chemicals, touch, electric impulses etc. Communication using sound has an advantage as sound can travel over long distances. Insects like crickets, grasshoppers, cicadas produce and receive sound for intra-specific communication. Male crickets produce species-specific calls which are perceived by the females and they perform phonotaxis towards a conspecific male. It depends on the situation what kind of call does the male produce. These calls contain spectral and temporal features that the females recognize and uses to make a mate choice decision. The sound emitted by crickets is known as chirping, the scientific name is stridulation. Only the male crickets chirp. The sound emitted by stridulatory organ, a large vein running along the bottom of each wing covered with teeth much like comb. The chirping sound is created by running top of one wing along the teeth at bottom of other wing as shown in Figure 3. As this is done crickets hold their wings open so that wing membranes can act as acoustic sails.

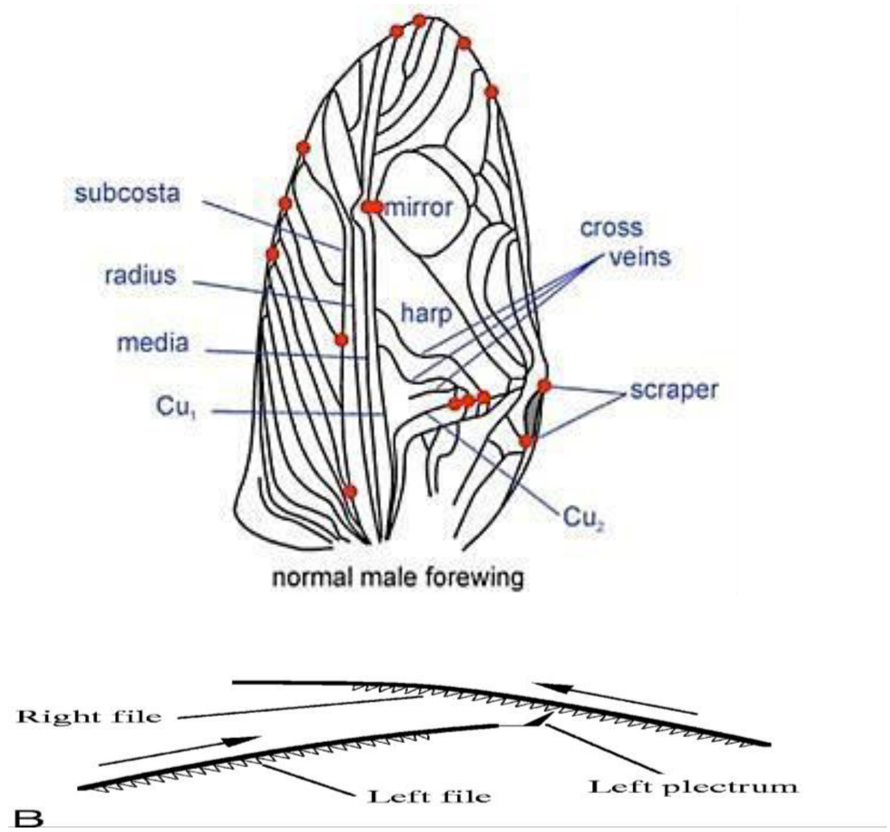


Figure 3: Structure of a male cricket forewing. (Cade 1992 and Jain 2010)

Communication by sound offers several advantages, for example,

- Sound is not limited by environmental barriers.
- It is effective over long distances.
- It is highly variable (wide variety of signals can be created).

While several animals communicate using sound, acoustic communication has a few limitations and disadvantages,

- Sound signals may reveal the location of sender to potential predator.
- It is less effective in noisy environments.
- Sound signals are metabolically expensive to produce.
- Sound signals attenuate—intensity falls rapidly with distance from source. (Acoustic communication, Barry Truax 2000)

Crickets produce four types of calls depending upon the behavioural contexts:

- Long Distance Mating Call -- This call attracts females over long distance and repels other males, and is fairly loud.
- Courtship Call-- Used when a female cricket is in close proximity to male cricket, and is a very quiet call. After this call has been made the male and female pair mate.
- Aggressive Call-- Triggered by chemoreceptors on the antennae that detect the near presence of another male cricket. This may be followed by fight among male crickets.
- Copulatory Call-- Produced for a brief period after a successful mating. (Drill 1993)

1.7 Impact of crickets on Ecosystem

Positive: Crickets breakdown plant material and renew the soil minerals. They are also an important source of food for other animals. They consume large quantities of cellulose rich plant materials and produce fecal pellets that are easily decomposed by bacteria and fungi. Field crickets also consume the seeds of many weed species thus reducing the potential of these rapidly growing, invasive plants to dominate both natural and human generated lawns ecosystems.

Negative: Crickets may injure seedlings and large numbers can be destructive to agricultural crops. Male songs can be quite loud. Crickets can cause damage to clothing, furniture and rubber materials when they invade houses in large numbers.
(B David and T Ananthakrishnan 2004)

Chapter 2

Acoustic communication in *Platygryllus* sp.

2.1 Introduction:

Both vertebrates and invertebrates use sound as means of communication. Sound can vary in different characteristics such as frequency (high pitch vs. low pitch), amplitude (loudness) and periodicity (the temporal pattern of frequency and amplitude). Using these three variables a wide and complex range of signals (from insects mating call to human speech) can be generated and characterised. The human ear is able to detect sound frequencies only within the range of about 20-20,000 hertz but some insects (as well as other animals like bats and dolphins) can produce and detect ultrasonic signals that are well above this frequency range. On the other hand animals such as elephants and whales can produce sound much below 20Hz and such signals are called infrasonic signals (Bradbury and Vehrencamp 2000).

As mentioned in previous chapter crickets communicate acoustically using species-specific calls. The call features of crickets can be characterised in either ,

1) Temporal domain or

2) Spectral domain.

A combination of these two features is used by female crickets to recognise their species –specific calls.

Temporal features

In true crickets, as the file of one forewing is struck by the plectrum of the other a single pulse of sound known as syllable is produced during wing closure. The opening of wings is silent and corresponds to the gaps between syllables. The calling song may have syllables present singly or in group, known as chirps.

A range of different features can be used to uniquely identify species –specific calls. These include:

1. Chirp duration is measured as the time interval between the onset and offset of a chirp.
2. Chirp period is the interval between the onset of a chirp and that of the following chirp.
3. Syllable duration is measured as the time interval between the onset and offset of a syllable.
4. Syllable period is the interval between the onset of a syllable and that of the following syllable. (Greenfield, Roizen 1993)

Temporal features of a call can be represented using a oscillogram that depicts how energy varies with time as shown in Figure 4.

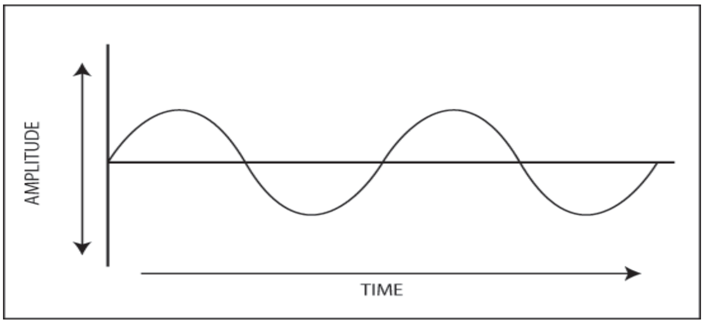


Figure 4: A oscillogram depicting change in amplitude or energy with time.

Spectral features

The file and the plectrum are the primary resonators while the harp is the secondary resonator. As the plectrum strikes each tooth on the file, the harp regions of the tegmina vibrate at a resonant frequency which determines the carrier frequency of the call.

Pure tone sounds result from resonant mechanisms (Bennet-Clark 2003). Field crickets are known to produce pure-tone calls while bush crickets produce broadband calls. That depicts how energy varies with frequency.

Spectral features of a call can be represented using a power spectrum.

Another feature of any sound signal is its sound pressure level, Sound pressure level (SPL) or sound intensity is a logarithmic measure of the effective sound pressure of a sound relative to a reference value. It is measured in decibels (dB) above a standard reference level.

$$SPL = 10 \log \left(\frac{P}{P_o}\right)^2$$

P is sound pressure i.e. force/unit area. (EAG Shaw 1974)

Objective: To study context-dependent calls in a species of field cricket, *Platygryllus* sp.

2.2 Study species -- *Platygryllus* sp.

It is a ground cricket that is usually found in large numbers at places which are moist. These crickets are found on ground and they call from ground. Females are usually found near males. Below are the pictures of male and female *Platygryllus* sp.

Figure5: *Platygryllus* sp. M (on left) and *Platygryllus* sp. F (on right)

(Veins can be seen on wing) (Ovipositor can be seen behind abdomen)

The reason to select *Platygryllus* s for our study:

- They were abundant in number in the field on IISER Mohali campus.
- Were easy to handle and rear in lab.

2.3 Taxonomic position of *Platygryllus* sp.

Kingdom: Animalia

Phyllum: Arthropoda

Class: Insecta

Order: Orthroptera

Suborder: Ensifera

Superfamily: Grylloidea

Family: Gryllidae

Species: Unknown

Genus: *Platygryllus*

2.4 Study site

Study was carried out in IISER Mohali campus, Punjab from August-November 2014. Animals were collected from field and reared in lab to get recordings under low background noise conditions.

Figure 6: Satellite Map showing the locations were study was carried out in IISER Mohali campus (near guest house). Numbers indicate study sites. (Google Maps)

2.5 Materials and Methods

Call recording and Analysis

Animals were collected from IISER Mohali campus and were reared in lab. They were provided with ad-libitum food and water. Calls of individual males were recorded in both field and lab by placing a hand-hold recorder (Sony IC Audio recorder, BCE, Tokyo, Japan) at ½ a meter distance from a calling male. Analysis of calls was done using software called Spectra Plus Professional (trial version) version 3.0 (Pioneer Hill Software, Poulsbo, WA, U.S.A.). SPL measurements were also taken at ½ m away from the animal using sound pressure level meter (Bruel and Kjaer, microphone type 4155). Ad-libitum observations of calling males was also carried out to examine the context in which the calls were produced.

2.3 Results

Recordings from males were made under two different conditions as described below:

Long Distance Mating Call: As the name suggests, this call is produced when the female is far away from the male. It is loud call which is made to attract females.

Males were released in an arena and they were given enough time to get acclimatized to the conditions. The time they take to get acclimatized to the conditions in arena varies for every individual (10min – 1hr). Once they get familiar to the arena the males produce a loud call to attract females which was recorded and this call is called Long Distance Call. This call was recorded for 16 males. Among the 16, for 10 individuals recordings were done in lab and for other 6 individuals recordings were done in field. All the recordings done in lab have multiple replicates across several days for each individual. The recordings done in field could not be analysed as the background noise was too high. Lab recordings from 10 individuals were analysed. A total of 40 calls and 200 chirps were analysed using Spectra Plus Professional (trail version).

Chirp duration, Chirp period, Syllable duration, Syllable period, Carrier frequency were calculated and SPL of LDMC was measured.

2.3.1 A. Temporal features of Long Distance Mating Call

Calls consisted of chirps with 12, 13 and some with 14 syllables. Most common chirp was one with 12 syllables. An oscillogram is shown below to depict chirp duration and chirp period (Figure 7) and Table 1 shows us mean chirp duration and chirp period.

Chirp duration (Mean)	Chirp period (Mean)
0.279+/-0.036 sec	0.692+/-0.09 sec

Table 1: Mean chirp duration and chirp period calculated for 10 individuals.

Chirp rate (per 10 sec) is 14.74 +/- 1.35

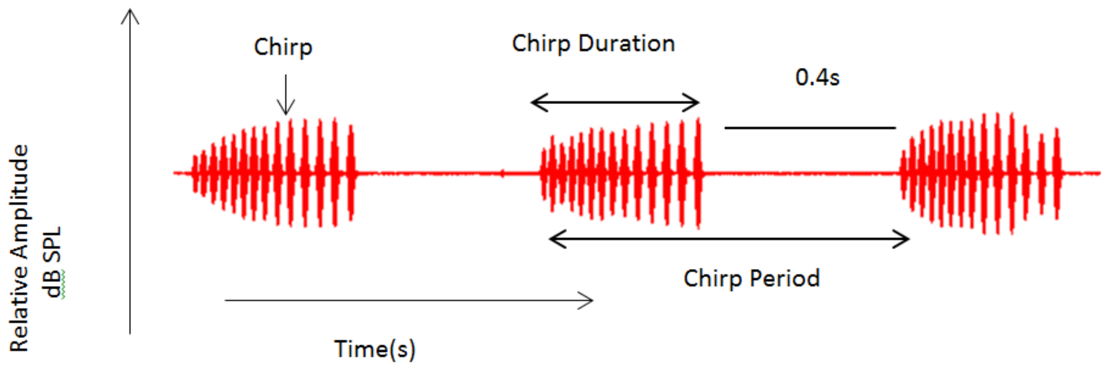


Figure 7: Oscillogram depicting temporal features of long distance call of *Platygryllus* sp.

Energy increases as number of syllables increase. Syllable period increased reaching a maximum at the last period i.e. 13th period which is evident from the Table 2 and Figure8.

Syllable.no.	Syllable duration(Mean)sec	St. Deviation	Syllable period(Mean)sec	St. Deviation
1	0.008	0.002	0.016	0.002
2	0.009	0.002	0.017	0.002
3	0.008	0.001	0.016	0.001
4	0.009	0.002	0.017	0.002
5	0.013	0.022	0.017	0.001
6	0.009	0.002	0.018	0.001
7	0.009	0.001	0.018	0.002
8	0.009	0.002	0.020	0.003
9	0.009	0.002	0.023	0.004
10	0.010	0.003	0.027	0.003
11	0.036	0.160	0.028	0.005
12	0.011	0.005	0.030	0.002
13	0.010	0.001	0.03	0.001
14	0.011	0.002		

Table 2: Mean syllable duration and syllable period calculated for 10 individuals.

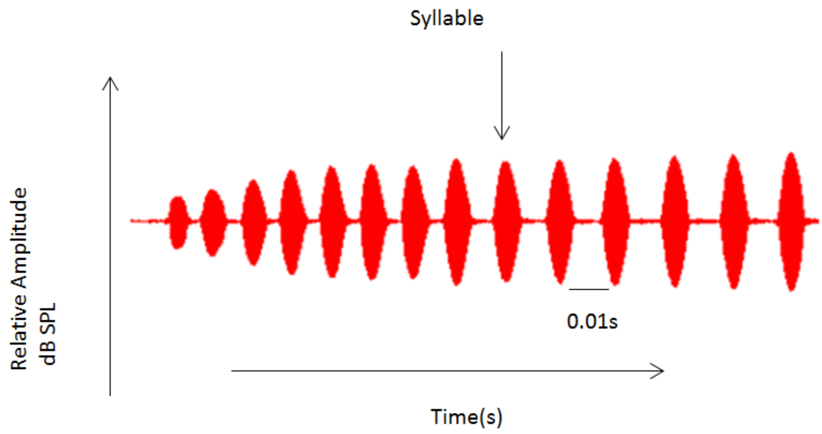


Figure 8: Temporal features of long distance mating call *Platygryllus* sp. showing chirp structure.

SPL measurements were done for 5 individuals at ½ meter distance from the cricket and have been depicted in Table 3.

Male no.	Average SPL	Std. Deviation
M1	64.6 dB	0.185
M2	64.3 dB	0.203
M3	64.1 dB	0.415
M4	64.9 dB	0.385
M6	65.2 dB	0.429

Table 3: Average SPL measurements for five individuals; eight measurements were taken per individual.

2.3.1 B. Spectral features of long distance call

Carrier frequency for LDMC of ten individuals was calculated and Mean Carrier Frequency was 5.28 ± 0.004 kHz as shown in Figure 9.

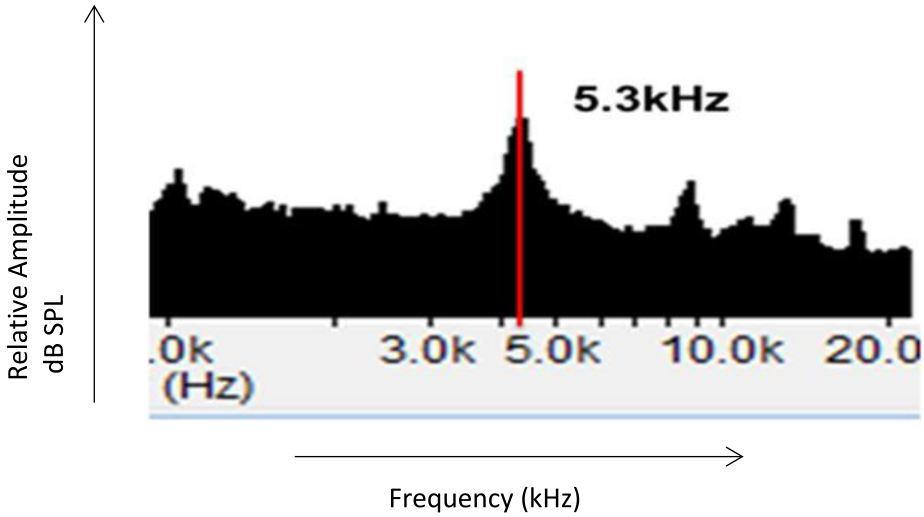


Figure 9: Power spectrum of long distance mating call of *Platygryllus* sp.

2.3.2 Courtship Call

A male and a female were released in an arena and are allowed to acclamatize. After sometime when the male and female are in close proximity to each other they antennate and after that the male produces a short and soft call which is called the courtship call. The name is appropriate because after the production of this call male and the female mate. Mating calls from 4 different mating pairs were recorded and analysed. The courtship calls were composed of 2 types of chirps, one was periodic soft chirp and the other one was loud chirp which was not periodic as you can see in Figure 10.

I could calculate chirp duration and chirp period of loud chirps for four individuals and chirp duration and chirp period of soft chirps for two individuals as shown in the Table 4.

For loud chirps (N=4)

Chirp duration(Mean)	Chirp period(Mean)
0.0607+/-0.0508 sec	0.2541+/-0.2958 sec

Table 4: Mean chirp duration and chirp period calculated for loud chirps of courtship call of *Platygryllus* sp.

I did not calculate the syllable duration and syllable period because these chirp's not periodic. This is evident from the huge standard deviation obtained for chirp period in Table 5.

For soft chirps

Syllable duration and syllable period could not be calculated for soft chirps due the structure of call.

Male no.	Chirp duration	Chirp period
M1	0.038 sec	0.114 sec
M2	0.039 sec	0.122 sec

Table 5: Mean chirp duration and chirp period calculated for soft chirps of courtship call of *Platygryllus* sp.

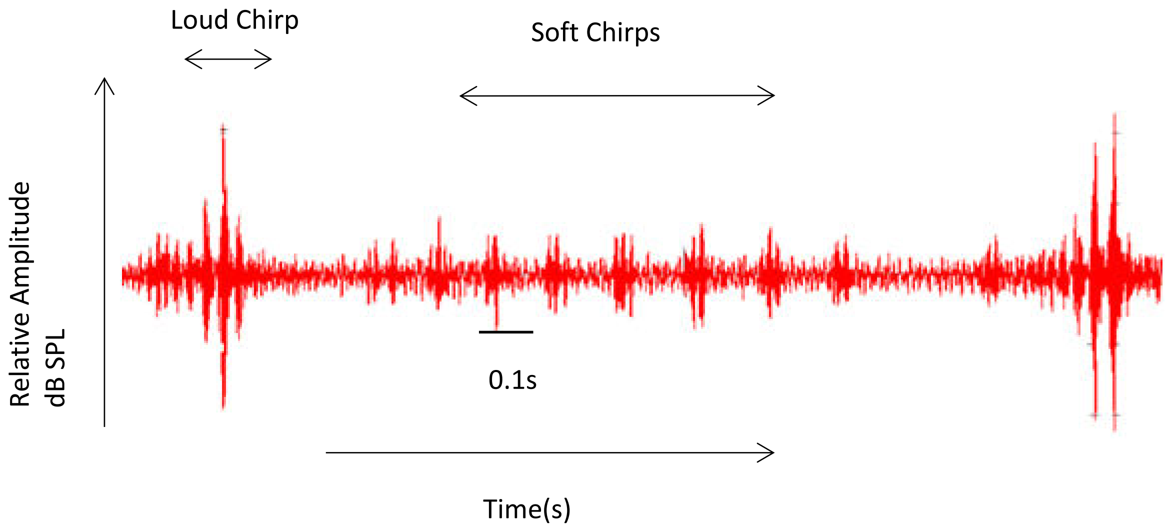


Figure 10: Temporal features of courtship call of *Platygryllus* sp.

2.3.4 Spermatophore Transfer:

During mating, males transfer the sperm in a white sac-like structure called spermatophore which is externally attached to ovipositor of female. After the spermatophore transfer, male guards the female to prevent her from removing the spermatophore prematurely (Hall 2000).

I observed that in *Platygryllus* sp. males transfer spermatophore to female during mating. A detailed structure of a spermatophore is shown in the Figure 11.

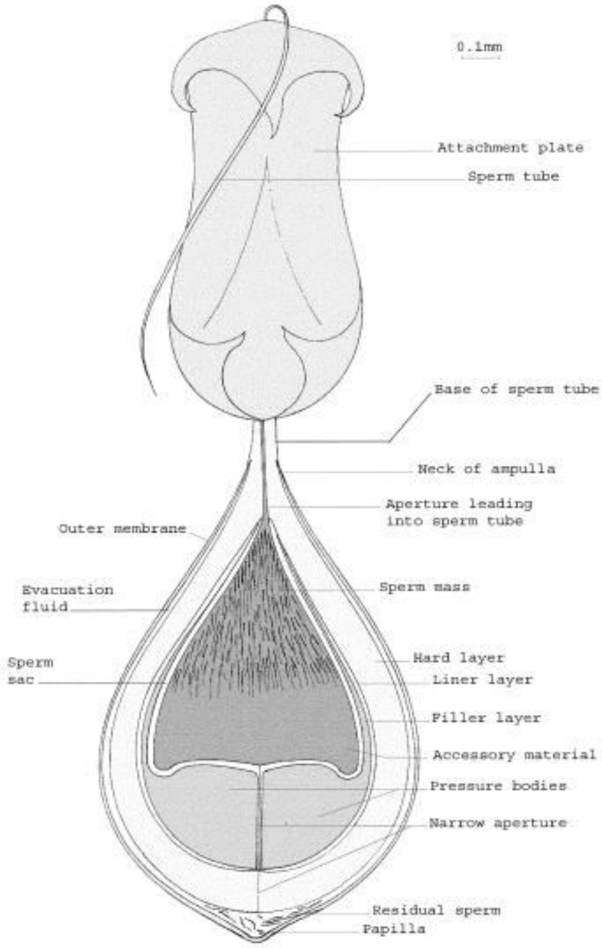


Figure 11: Representation of fully formed spermatophore of *Gryllus bimaculatus* (Hall 2000)

2.3.5 Inter individual variation in temporal features of long distance call of *Platygryllus* sp.

One-way ANOVA was done to see if the mean chirp duration and chirp period among individuals varied and the results can be seen in table 6 and Figure 11.

Inter-individual variation in chirp duration of long distance call of *Platygryllus* sp. (N=10)

ANOVA Table	SS	df	MS
Treatment (between columns)	0.1050	9	0.01167
Residual (within columns)	0.1523	190	0.0008014
Total	0.2573	199	

P value is < 0.0001.

Table 6: Results of one way ANOVA; showing that the means of chirp durations were significantly different.

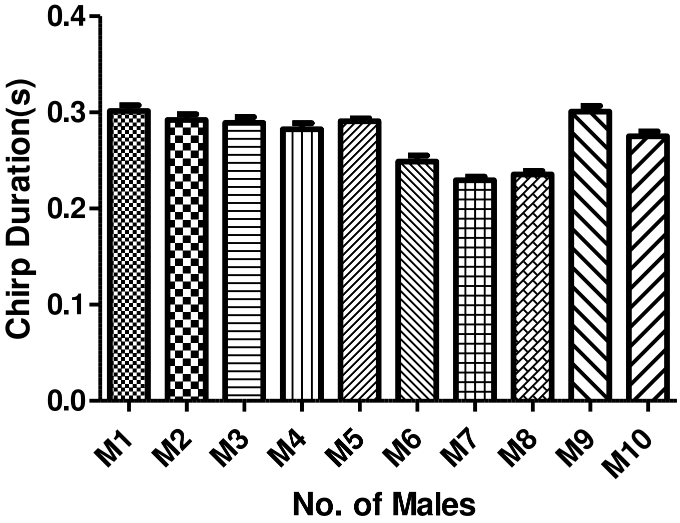


Figure 12: Means of chirp durations of ten individuals with standard deviation.

Inter-individual variation in chirp period of long distance call of *Platygryllus* sp. (N=10)

One way ANOVA was done to look at inter-individual variation in chirp period and results are as shown below in Table 7 and Figure 12.

ANOVA Table	SS	df	MS
Treatment (between columns)	0.9366	9	0.1041
Residual (within columns)	0.6917	190	0.003641
Total	1.628	199	

P value is < 0.0001.

Table 7: Results of one way ANOVA; showing that the means of chirp periods were significantly different.

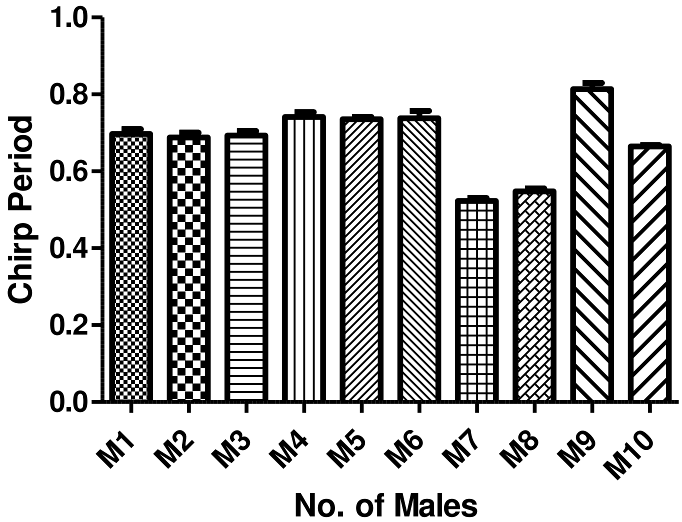


Figure 13: Means of chirp periods of ten individuals with standard deviation.

2.4 Discussion:

Two types of calls were recorded in *Platygryllus* sp.; long distance mating call and courtship call. It was found that different song types are used by *Platygryllus* sp. to create different signals depending upon different behavioural context. Similar results have been found in several other species; *Gryllus* integer (Cade 1992), *Gryllus* bimaculatus (Simmons 1986). In these species a third type of call 'aggressive call' was also recorded which I could not record for our species.

Chirp duration and Chirp period varied significantly among individuals. These dynamic features of song often correlate with attributes of the calling individual such as physical condition or quality (Wagner & Hoback 1999; Ryder & Siva-Jothy 2000) and are used by female crickets in discriminating between males during mate choice (Wagner 1996; Berg & Greenfield 2005). When I did multiple comparisons test I found out that the chirp durations and chirp periods of all males differed from that of male 6,7 and 8 and these three individuals lead to the overall difference when I did a ANOVA.

When the male and female mated, male transferred a white sac-like structure called the spermatophore to the female (Hall 2000). Spermatophore might contain proteins that might be essential for the female to reproduce. The structure of the spermatophore in the house cricket, *Acheta domesticus*, was first described by Khalifa (1949), while much later a more detailed study using both light and electron microscopy was reported by Fullwood (1989) on the field cricket, *Gryllus bimaculatus*. It has been found out that the male transfers spermatophore to females in several species of crickets; *Gryllodes supplicans* (Scott 1983), *Acheta domesticus* (Snell 2000) etc . Males guard the female after mating so that they don’t eat spermatophore and ensure that the sperm transfer is complete. (Scott 1984).

Chapter 3
Habitat acoustics and Sound Transmission

3.1 Introduction:

Sound is a mechanical wave that results from the back and forth vibration of the particles of the medium through which the sound wave is moving. Sound is produced when an object vibrates and disturbs the air molecules to generate compression waves that travel in all directions away from the source. These waves are perceived when they collide with our eardrum and cause a disturbance which is detected by sensory neurons. Sound can travel through solids, liquids and gases and hence, it can be used as a means of communication by animals in terrestrial and aquatic environments. Sound is a variation in pressure. A region of increased pressure on a sound wave is called a compression. A region of decreased pressure on a sound wave is called a rarefaction. Sound waves are longitudinal waves as the motion of particles in the medium will be parallel to the direction in which the energy is being transported. When sound waves move through a medium, they have high and low pressure regions and hence is referred as pressure wave. Any detector of sound will detect these fluctuations in pressure as the sound wave travels through it. (Roger et al 2010)

As sound travels in a medium, with increasing distance from the source, there is loss in SPL which is referred to as transmission loss. Transmission loss is the accumulated decrease in the acoustic energy and can happen due to:

1) Spherical Spreading and
2) Attenuation, which can happen due to absorption or scattering of sound waves by obstacles, viscosity of the medium and thermal losses.

Spherical Spreading

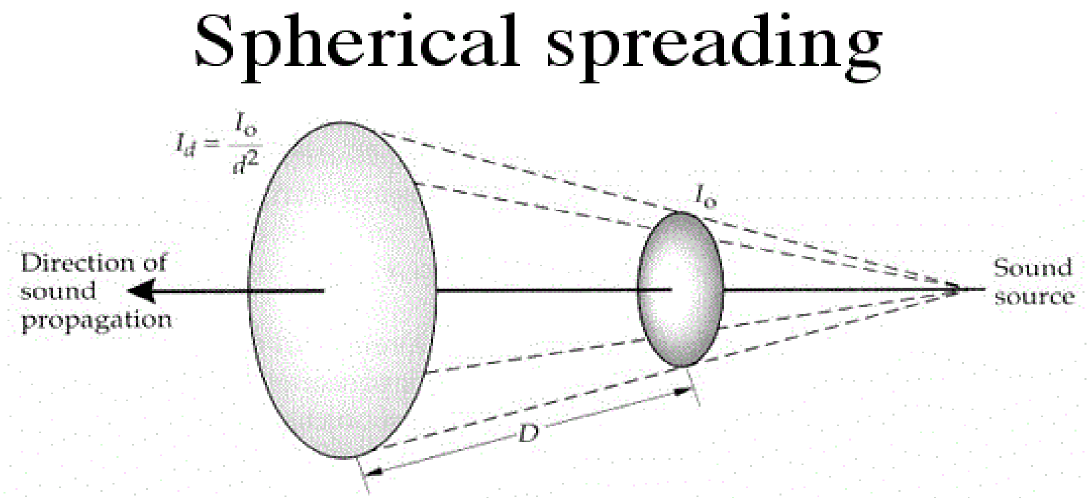
It describes the decrease in intensity of sound when a sound wave propagates away from a source uniformly in all directions. The average amount of sound transmitted per unit time through a unit area in a specific direction is intensity. The amount of energy per unit time is power and therefore intensity is the amount of power transmitted through a unit area in a specific direction.

Consider sound as a spreading sphere that radiates equally in all directions then the power across sphere would be:

$$P=4\pi r^2 I$$

where P is the total power, r is the radius of the sphere and I is the intensity.

Io is the intensity at origin and Id is the intensity at distance d from the origin of



sound source.

Figure 14: Loss in sound intensity follows the inverse square. (Forrest 1992).

As distance increases the radius of sphere increases but the power across surface area, remains constant and as a result of this intensity drops inversely as square of the distance as shown in Figure 14. SPL however decreases with the reciprocal of distance. Transmission loss due to spherical spreading amounts to a 6 dB loss of SPL every doubling of distance.

Excess attenuation (EA)

Attenuation of sound pressure level due to factors other than geometric spreading, (including diffraction, scattering, barriers, weather, turbulence, vegetation and any other effects) is called Excess Attenuation. (Larsen 1993)

Attenuation

The total reduction in SPL due to all possible mechanisms is referred to as Total attenuation. It is the sum of attenuation due to spherical spreading (SS) and the excess attenuation (EA), which amounts to transmission loss due to all other effects.

$$(TA = SS + EA)$$

Ground effect

When source and receiver are both close to ground, the sound wave reflected from ground may interfere destructively with the direct wave as shown in Figure 15. This results in severe attenuation of sound along the ground for sound sources that are close to the ground such as field crickets. It is therefore expected that *Platygryllus* sp., being a ground cricket species will also suffer severe attenuation due to the ground effect thereby limiting its range of transmission.

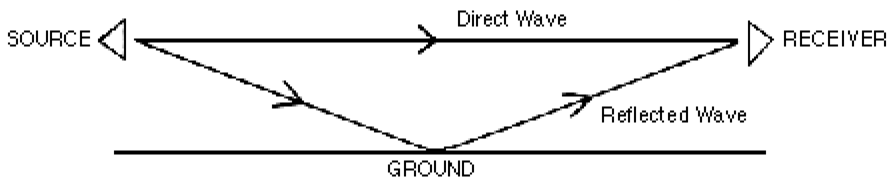


Figure 15: Depicting ground effect that is faced by animals that communicate on ground. (Attenborough 1988)

Objective: To conduct sound transmission experiments to estimate the average distance over which LDMC of *Platygryllus* sp. can be heard by conspecific males and females.

3.2 Materials and Methods:

The sound transmission experiments were carried out in May 2015 due to logistical constraints the experiments needed to be done in the day time for which a suitable time slot, during which ambient temperature is similar to ambient temperature in peak calling, needed to be found. Towards this, prior to transmission experiments day and night time temperatures wrer measured using a pocket weather meter (Kestrel 3000 Pocket weather station). For the night time temperature ambient temperature was measured during peak activity of calling which was found to be around 26 degree Celsius. In the day time hourly temperature reading were made for five days (between 8AM to 7PM). Day-time ambient noise measurements were made using a sound level meter (Bruel and Kjaer type 2231; microphone type 4155) a 20 kHz high-pass and 20 Hz low-pass with 1/3-octave band pass filter centered at 5 kHz. These experiments were carried out in the natural habitat of the species during which LDMC of *Platygryllus* sp. was played using speaker playback setup and this was carried out in five locations. Species average SPL was used for output from a speaker placed on the ground. Call of a male was played using a speaker and it was made sure that the SPL at 0.5 meter was around 64.6dB which is the average SPL of long distance call of males (N=5) as measured in lab conditions.

Call was played from speaker and SPL measurements were taken along the straight line along the speaker for every doubling of distance at 0.5m, 1m, 2m, 4m, 8m and 16m from the speaker and along with it ambient noise at all these distances from speaker was measured. An additional SPL measurement was made at 10m. At every position 3 SPL measurements were taken and averaged to compensate for random fluctuations. The same procedure was repeated at all the locations. Total attenuation was calculated in order to estimate maximum transmission radius of the call. This will give the maximum distance over which the call can be heard by a conspecific male or female. Although EA was also calculated, TA is the biologically meaningful measure of maximum range of detection.

Excess attenuation was calculated for each measurement according to Arak and Erickson (1992).

$$\delta j = \boldsymbol{I}i - \boldsymbol{I}j - 20log(dj)/0.5$$

where δj is excess attenuation at distance j, $\boldsymbol{I}i$ is SPL at distance 0.5m (nearest distance from the speaker where SPL was measured) from the speaker, $\boldsymbol{I}j$ is SPL at distance *j* and the logarithm is to base 10.

3.3 Results:

3.3.1 Temperature Profile

Based on temperature measurements it was found that the time between 10:40AM and 1:00PM was more similar to peak calling time temperatures of 26 degree Celsius therefore this slot was chosen to conduct the transmission experiments.

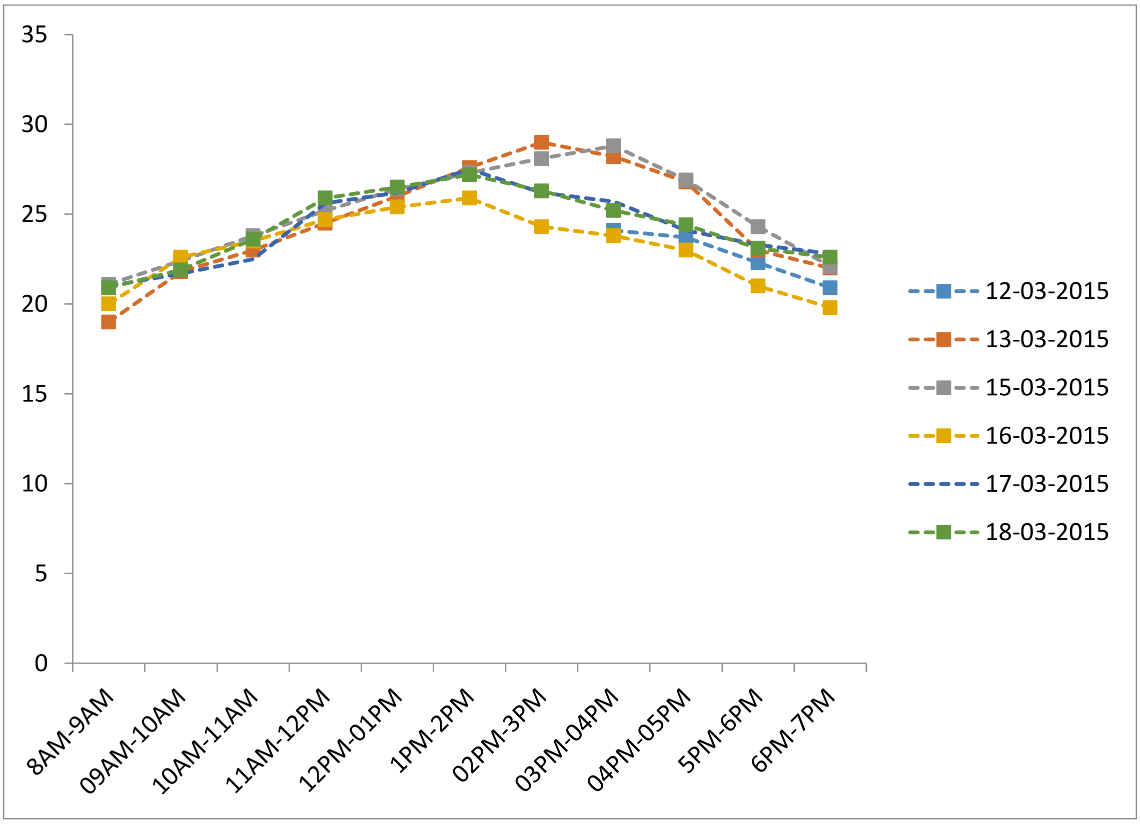


Figure 16: Ground temperature recordings from 8AM to 7PM for six days from 12 to 18th March 2015.

3.3.2 Total Attenuation

SPL measurements of the LDMC at each position for all five locations were averaged and were plotted against distance (meters) as shown in Figure17. Since the ambient noise level was recorded to be 36 dB, using this as the cut-off, the average transmission radius of LDMC of *Platygryllus* sp. was estimated to be 8 meters from source.

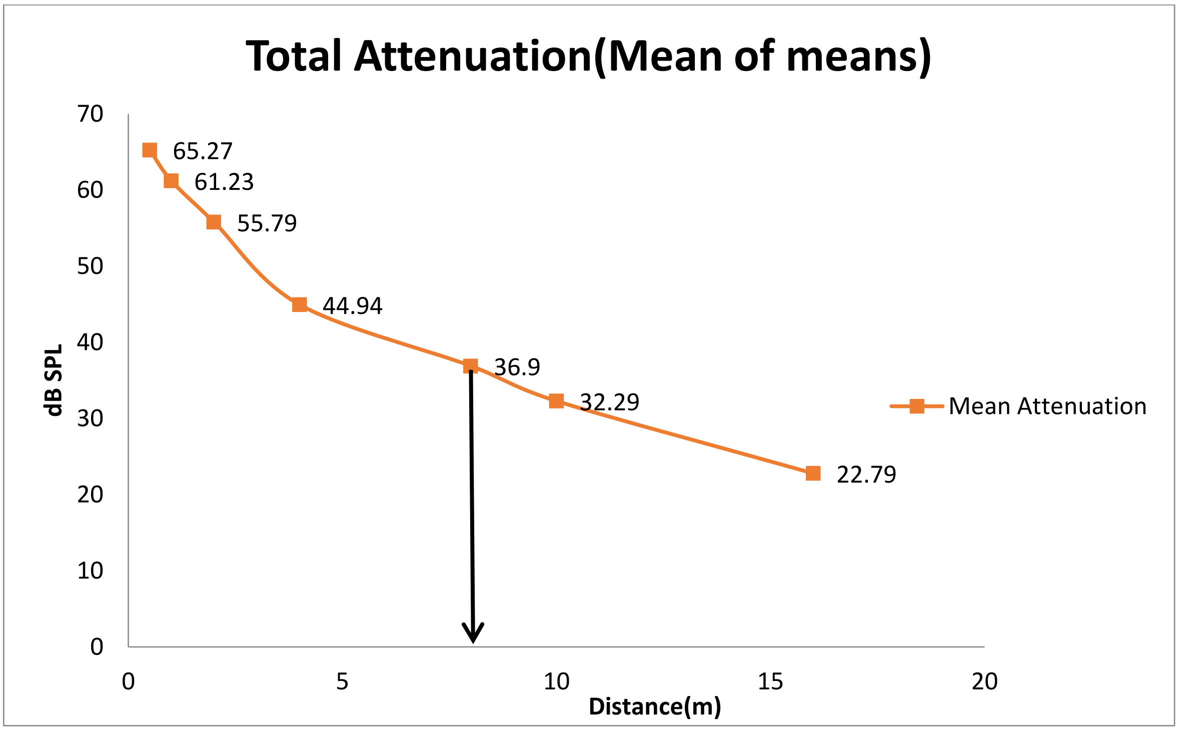


Figure 18: Total Attenuation of LDMC of *Platygryllus* sp. in the natural habitat of the species.

Table 8: Mean SPL measurements at increasing distances from speaker in five different locations.

Sl.no	Distance (meters)	Location 1 Mean SPL (dB)	Location 2 Mean SPL (dB)	Location 3 Mean SPL (dB)	Location 4 Mean SPL (dB)	Location 5 Mean SPL (dB)	Mean of means SPL (dB)
1	0.5	65.7	65.2	66.07	64.5	64.87	65.27
2	1	61.1	61.64	63.44	62.57	57.4	61.23
3	2	53	53.87	61.6	60.77	49.7	55.79
4	4	45.5	44.04	45.5	45.67	43.97	44.94
5	8	37.44	32.54	38.24	36.7	39.57	36.9
6	10	32.34	26.67	36.4	29.1	36.94	32.29
7	16	25.3	20.14	21.8	23.1	23.4	22.79

3.3.3 Excess attenuation

EA was found to vary at different distances from the source and the maximum value was recorded to be 5.4 dB as shown in Figure 19.

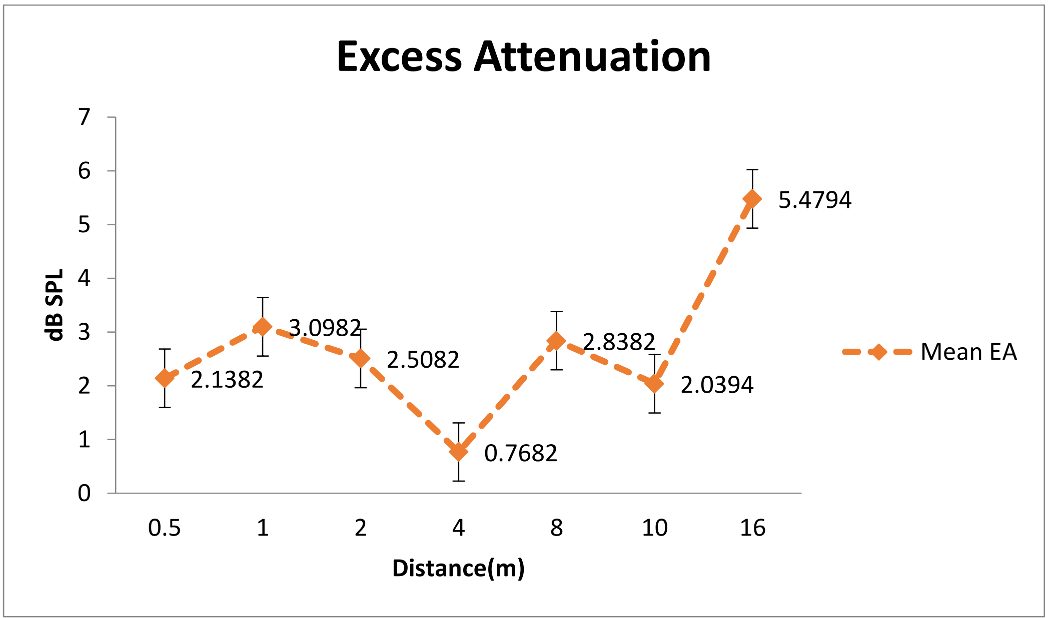


Figure 19: Excess attenuation of call in field of *Platygryllus* sp. with distance.

3.4 Discussion:

The maximum transmission range of LDMC of Platygryllus sp. was found to be 8m at which point the sound attenuates to the ambient noise level of about 36 dB. Previous study by Jain and Balakrishnan (2012) carried out on 12 ensiferan species reports maximum distance of signal detection (as derived from the attenuation profiles) to be more than 10m in several species, even when the SPL at source was comparable to *Platygryllus* sp. That study, however, was carried out in a rain forest and it is likely that the transmission properties of a rain forest habitat is different from that of this habitat. Thus it may be concluded that *Platygryllus* sp. calls suffers severe attenuation along the ground in its natural habitat.

Behavioural threshold is the threshold (SPL) up to which a female can detect the call of its species is unknown for this species. This is why I have taken ambient noise level as a cut-off to estimate maximum transmission distance. Using this cut-off as mentioned above the transmission radius was estimated at 8m. However, it is quite likely that the females have a behavioural threshold which is much above this cut-off. Deb and Balakrishnan (2014) have reported a behavioural threshold of 45 dB in another cricket species (*Oecanthus henrii*). When I used 45 dB as a cut-off then the average transmission distance is reduced to 4m.

The habitat might play an important role in determining the distance over which calls can be detected and received by receivers. Features of the habitat such as foliage density, foliage angle and other vegetation characteristics may alter the attenuation profile of a call. Thus the habitat may itself impose selective pressure on the evolution of signal structure for animals that use acoustic signals for long distance communication (Morton 1975) such as crickets and katydids. Since attenuation profiles determine transmission distance, they can potentially affect probability of masking, signal detection and discrimination, thereby mediating male-male competition and female mate choice decisions.

Chapter 4

Male spacing across chorus and its implications on masking interference.

4.1 Introduction

Aggregation behaviour in animals can be found in almost every animal taxa, from insect to mammals. In group-living animals, aggregation favours interaction and information exchange between individuals. W.D. Hamilton (1971) proposed a theory to explain why individuals prefer to aggregate, where he hypothesized that there is reduction in predation risk if animals group together and all group members benefit from it. He put forward a hypothesis called the 'Selfish Herd Hypothesis' which posits that in order to reduce risk of predation animals reduce nearest neighbour distances thereby reducing their own risk at the expense of the animals around it. This would imply that by aggregation animals are diluting the risk of predation on themselves (Parish and Hamner 1997).

A study was done to test this hypothesis and it was found out that average number of attacks per prey in aggregation is less as compared to that when an individual is in isolation (Lung 2003).

There are two kinds of benefits an individual can get by being member of a group i.e.

1) Passive benefits— Benefits simply accrued by being a member of a group like more food, dilution, reproduction etc.
2) Active benefits— Benefits accrued by individuals as a consequence of the decisions they make like positional effects (which position to be at in a group) within group with respect to food, predation and energetic expenditure (Parish and Hamner 1997)

The disadvantage of being in a group is that there will be competition for food and mates because the same patch will be shared by other individuals and sometimes competition among individuals may lead to aggressive interactions (Young 1997).

Male crickets of many species are usually solitary but it has been found out that in some species males form aggregates. Since crickets communicate acoustically their song may make them conspicuous to eavesdropping , predators and parasites. Aggregation behaviour in crickets may thus serve to reduce risk of predation and parasitism as opposed to situations when predator avoidance and individuals in aggregates might be less conspicuous to parasites they signal individually (Burk 1982; Greenfield 1994). Further, Huber and Gerhardt (2002) proposed that females may get more attracted to males that called from aggregates than those who called in isolation.

Crickets signal acoustically to attract potential mates over long distances. They can do so singly or in aggregates of multiple males, thus forming what is known as choruses. Conspecific females listen to these calls, locate the male and perform phonotaxis to approach the male in order to mate with it (Alexander 1960). However, in a chorus where many males are advertising, which male is the female going to choose? This would depend on whether females exercise mate choice at all. Assuming that females do exercise mate choice, the female may use one of many sampling strategies to sample potential males, some of which require the female to be able to hear multiple males at the same time.

Further, given that multiple males signal concurrently in close proximity to each other, does the call of different males overlap with each other? This may result in what is known as masking interference where similar signals overlap in time and frequency, thereby impeding signal recognition by receivers. It is to be expected that such a scenario will result in males competing with each other for acoustic space and the females being able to hear multiple potential males at the same time. Whether such a scenario exists or not would depend on natural male spacing in the field, relative female positions and the transmission distance of the calls of the males.

In this study I examined whether males of *Platygryllus sp.* exists in aggregations i.e. chorus. I investigated natural male-spacing behaviour and using transmission radius (as calculated in Chapter 2) estimated the probability that the acoustic space of males overlap and the chance that a female in that chorus will be able to hear more than one male at a time. If such be the case, the female can potentially hear multiple males at the same time and reduce effort and risk of visiting individual males before making mate-choice decision. To summarise, signalling in chorus can affect both males and females (Alexander 1975 and Gibson 1983):

Male perspective

1) Males have to compete with other males for mates, food and other resources.
2) Signalling in chorus can attract more females than if a male calls individually.
3) Might reduce predation pressure.

Female perspective

1) Females can sample large number of males and then choose a potential mate.
2) Might pose a problem for sound localization mechanism.

Objectives:

1) To check whether males signal in choruses
2) To examine inter-male distances and check if it varies across choruses
3) To estimate acoustic space overlap between males in chorus
4) To study implications of acoustic space overlap of males on female mate sampling strategy.

4.2 Materials and methods:

Male spacing in natural chorus: Field work for this study was conducted during the peak calling season of the species between 28/08/14 to 25/09/14 during v6:30 PM to 9:30 PM which is the peak time for activity of *Platygryllus* sp. Five locations in IISER Mohali campus where *Platygryllus* sp. individuals were found were chosen (as shown in Figure

6, Chapter 1). Calling males were located psychoacoustically and their positions were marked with a flag. In two choruses females positions were also marked. The next day inter-male distances between each marked male were measured using measuring tape. The furthest pair was no more than 30 m apart. This was done in all five locations.

Reconstruction of chorus: For the purpose of this analysis I defined a 'chorus' as an aggregation of males where any two males were no more than 30 m apart. This demarcation was a result of natural distribution of males in the field. Using the inter-male distances, I reconstructed the choruses using a program written in Python to get co-ordinates of individual males from inter-male distances in order to graphically represent the aggregation of calling males. I considered the first male to be at that point (0,0) and the second one is then mapped to (0,d), where d is the distance between male 1 and 2. and I then calculated the location of the third male using the distance formula:

$$\sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2}$$

Then using the three points the program maps the rest of the males. This program does not need all the inter-male distances to get to the co-ordinates. (Code attached in Appendix A).

Calculation of Acoustic space overlap: Using the estimate of transmission range, male positions and their calling SPL I computed the active spaces (area over which the call of a male can be heard by a conspecific) of males in five choruses. Since the SPL of the call attenuates to 36dB at 8m (results from Chapter 3), radius of the circle of active space was taken to be 8m around the position of male in 2D space. A custom-written Matlab program was used to construct an active space and the code can be seen in Appendix A. The same process was used to compute active space using 4 m as the transmission radius as derived from an assumed behavioural threshold of 45 dB.

4.3 Results:

4.3.1 Male spacing in natural choruses

I found out that males of *Platygryllus* sp. call in choruses where the inter-male distance can be less than 1 m in some cases, whereas it could be more than 30 m in other cases (example, Chorus 1 Table 14).

To examine variation in inter-male distance across choruses, at first normality tests were done to see if the distribution of data is normal and I found out that the data does not follow a normal distribution and the details are given in Table 9.

Shapiro-Wilk normality test	
W	0.8778
P value	< 0.0001
Passed normality test (alpha=0.05)?	No
P value summary	***

Table 9: Normality tests done on the data collected for inter-male distances across five choruses.

All these tests show that the data does not follow a normal distribution. So to check for inter-male distance variation across choruses I did Kruskal-Wallis test and to compare inter-chorus inter-male distance. I also Dunn's Multiple comparison test and the details are shown in Table 10 and Figure 20.

Kruskal-Wallis test	
P value	< 0.0001
Exact or approximate P value?	Gaussian Approximation
P value summary	***
Do the medians vary signif. (P < 0.05)	Yes
Number of groups	5
Kruskal-Wallis statistic	31.65

Dunn's Multiple Comparison Test	Difference in rank sum	Significant? P < 0.05?	Summary
ch1 vs ch2	-15.05	No	ns
ch1 vs ch3	-26.43	Yes	*
ch1 vs ch4	-38.48	Yes	***
ch2 vs ch3	-11.38	No	ns
ch2 vs ch4	-23.43	Yes	*
ch2 vs ch5	-9.525	No	ns
ch3 vs ch4	-12.05	No	ns
ch3 vs ch5	1.850	No	ns
ch4 vs ch5	13.90	No	ns

Table 10: Statistics of Kruskal-Wallis and Dunn's Multiple Comparison test.

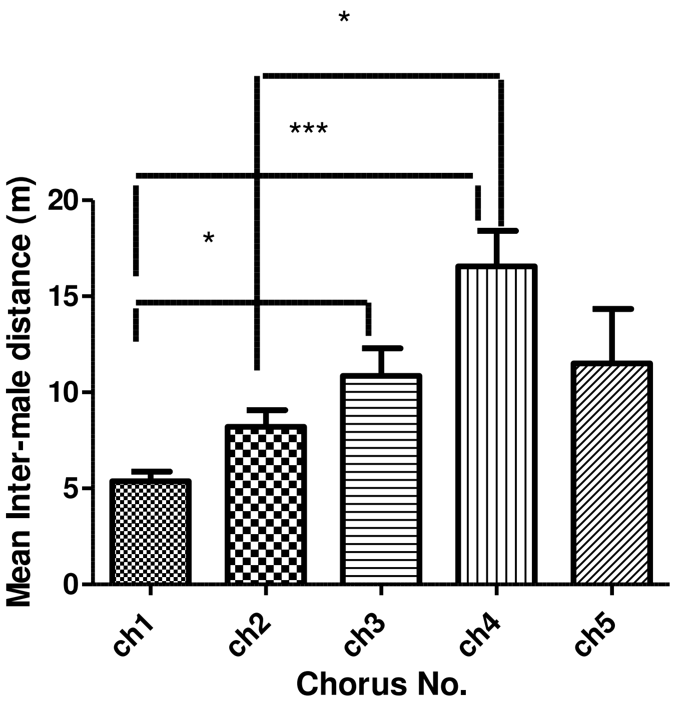


Figure 20: Mean inter-male distances vary across chorus.

It is clearly evident that the inter-male distances vary from chorus to chorus and this might depend on the location of the chorus and some factors like water content, amount of food etc. The mean inter-male distances across chorus along with standard deviation and standard error are shown in Table 11.

	Chorus 1	Chorus 2	Chorus 3	Chorus 4	Chorus 5
Mean	5.378	8.204	10.86	16.56	11.52
Std. Deviation	2.565	3.867	4.506	8.315	6.924
Std. Error	0.5031	0.8647	1.425	1.859	2.827

Table 11: Mean Inter-male distance across chorus.

4.3.2 Variation of inter-female distances in chorus one and two.

Females were marked only in chorus one and two because the location where other three choruses were mapped had thick grass and hence I was unable to localise and mark the females. Normality tests were done to if the distribution of data is normal and I found out that the data does not follow a normal distribution (Table 12).

Shapiro-Wilk normality test	
W	0.9529
P value	0.0005
Passed normality test (alpha=0.05)?	No
P value summary	***

Table 12: Normality tests done on the data collected for inter-female distances from chorus one and two.

All these tests show that the data does not follow a normal distribution. So to check for inter-female distance variation across choruses I did Mann Whitney test and the results are shown in Table 13 and Figure 21. Inter-female distances of chorus 1 do not vary significantly from that of chorus 2. (Table 13).

Mann Whitney test	
P value	0.4185
Exact or approximate P value?	Gaussian Approximation
P value summary	ns
Are medians significantly different? (P < 0.05)	No
One- or two-tailed P value?	Two-tailed
Sum of ranks in column A,B	6008 , 662
Mann-Whitney U	443.0

Table 13: Statistics of Mann Whitney test.

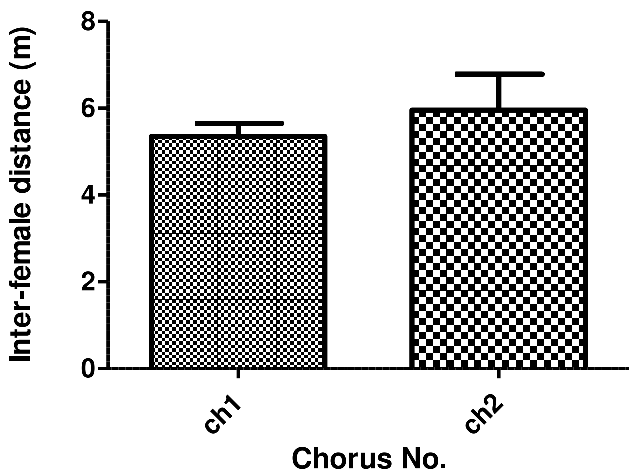


Figure 21: Mean inter-female distances from chorus one and two.

4.3.3 Reconstruction of Choruses.

Inter-male distances from all five choruses were taken and all five choruses were reconstructed. As an example, inter-male distances and its reconstructed co-ordinates of chorus one is shown below in table 14 and Figure 22. For plots of other choruses refer to appendix.

Inter-male distances	1	2	3	4	5	6	7	8	9
1	0								
2	7.8	0							
3	3.8	5.3	0						
4	3.12	5	0.74	0					
5	3.35	10.7	7	6.54	0				
6	4.5	8.85	6.78	6.46	3.64	0			
7	5.75	7.96	3.68	4.1	7.68	5.8	0		
8	4.38	6.18	1.67	2.22	7.23	6.06	2.2	0	
9	3.3	11.1	6.5	5.9	0.64	3	7.17	6.68	0

Table 14: Inter-male distances among males in chorus one which had nine males.

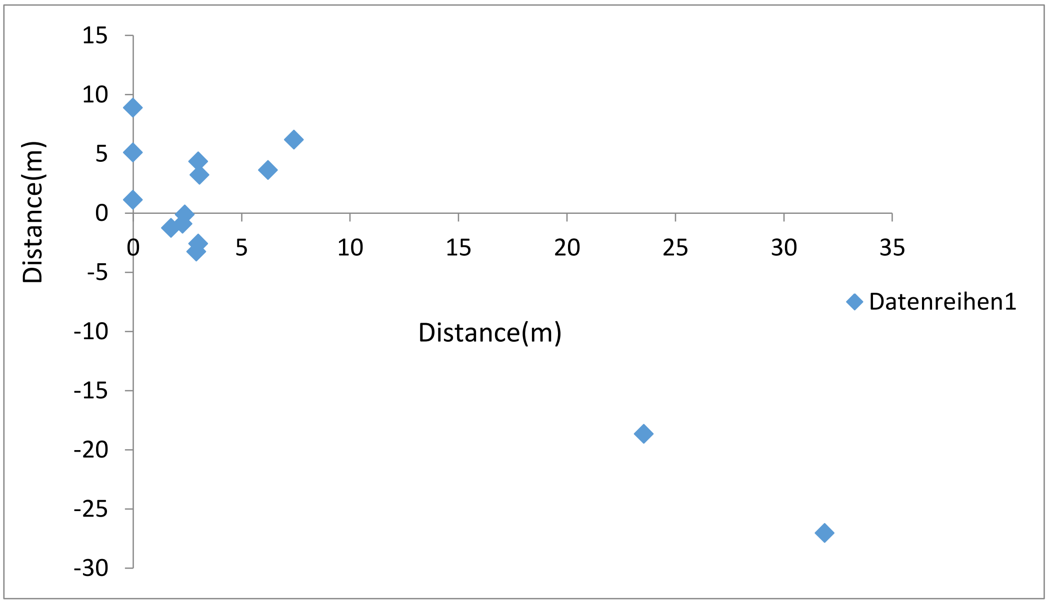
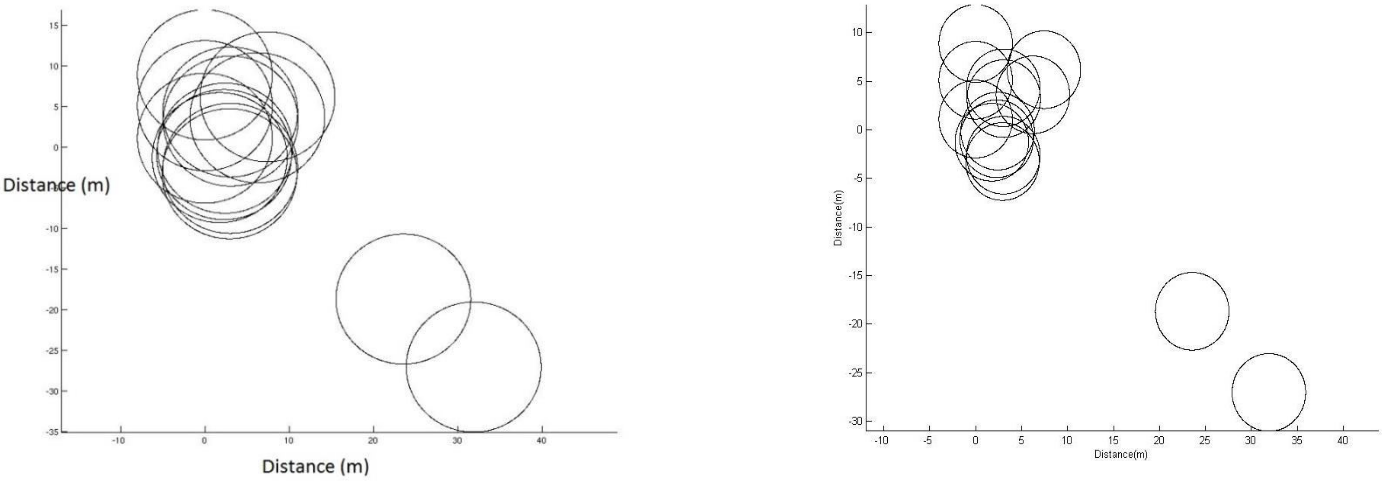


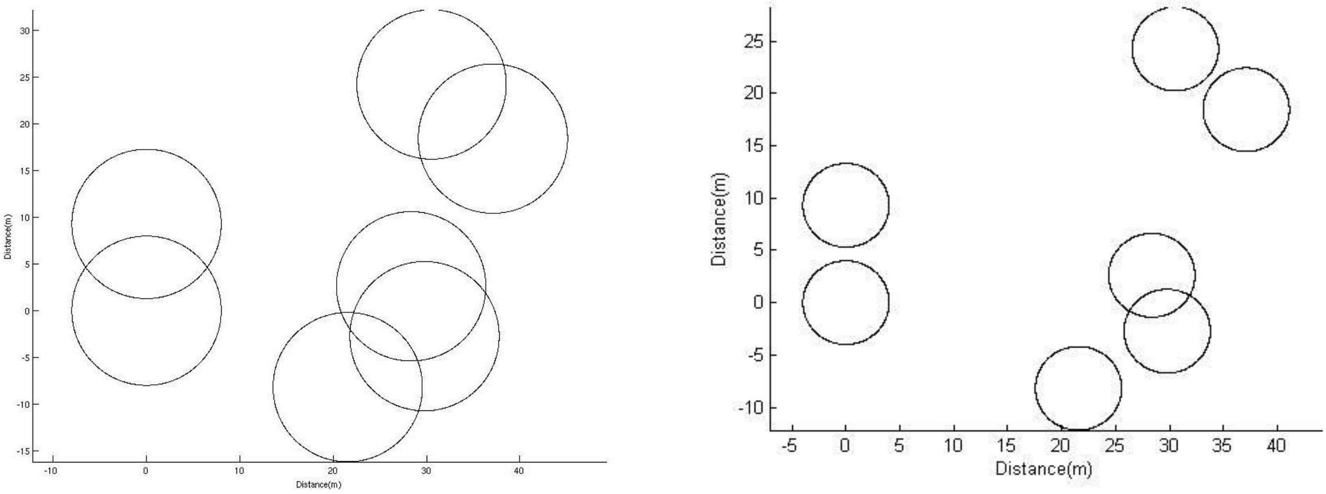
Figure 22: Co-ordinates of chorus one re-constructed using the program.

4.3.4 Spatio-acoustic organisation of calling males in chorus.

There is high amount of overlap between acoustic spaces of calling males which suggests that female can hear multiple males at the same time when the transmission range is 8m and the overlap of acoustic space decreases when I considered the transmission range to be 4m.



Chorus 1



Chorus 4

Figure 23: Acoustic spaces of males in chorus one and four considering the maximum transmission distance to be 8m (on left hand side) and 4m (right hand side).

In sitautions where the transmission radius was taken to be 4 m, the acoustic overlap between males seems to have decreased as compared to those which have a transmission distance of 8 m. Even when I consider that the call can only travel up to 4 m there still is overlap in acoustic spaces of males in chorus one and two but the overlap is less in acoustic spaces of males in chorus three, four and five (Appendix B).

4.4 Discussion:

Calling males of *Platygryllus* sp. showed an aggregated distribution in space similar to that seen in other field crickets (Campbell & Shipp 1979; Cade 1981; Campbell 1990) and bushcrickets (Weidemann et al. 1990; Arak & Eiriksson 1992). It has been hypothesized that forming aggregates attracts more females (Gerhardt & Huber 2002) although it increases competition for females and acoustic space amongst males. The aggregates or choruses were such that the acoustic spaces of males overlapped to a large extent. Similar results have been found in some bushcricket species such as *Mygalopsis* marki, *Decticus* verrucivorus and *Tettigonia* viridissima (Romer & Bailey 1986; Weidemann et al. 1990).

4.4.1 Male spacing in natural choruses of Platygryllus sp.: implication for males

In this study, since multiple males are calling at the same time in a chorus their calls would overlap in time and space resulting in masking interference with other signalling males (Romer & Krusch 2000). It is to be expected that males in dense choruses (chorus one) are likely to suffer severe masking interference than those who call from sparser choruses. To escape masking, males can adopt various strategies including increasing the SPL of their call or increasing nearest neighbour distance. Another strategy to reduce masking would be to phase shift their calls to avoid temporal overlap of signals resulting in asynchrony (Cody and Brown 1969, Romer 1998). Chorus one and two are relatively dense as compared to the other three as they were mapped when the activity of *Platygryllus* sp. was at peak. The latter choruses were mapped later in the season and hence they are sparse. In sparse choruses males would face less competition. On the other hand, females would have less choice and may adopt sequential sampling to find potential mates but if the males use this strategy the predation risk is going to be higher. This suggests that the strategies might change from season to season.

4.4.2 Male spacing in natural choruses of Platygryllus sp.: implication for females

As the acoustic spaces of overlapped to a large extent it is likely that the female could hear multiple males at a time (if we assume that females are distributed randomly in a chorus). If such is the case, then the female has to make a decision to mate with one male. Many sampling strategies have been put forward (Real 1990; Luttbeg 1996) and these strategies compare the traits of males and make a decision to choose a potential mate. It is assumed that the females by mating with males that have the preferred trait receive direct or indirect benefit because the assumption is that males with preferred traits are of higher quality. There are four strategies; *(1) the best-of-N strategy, (2) the simultaneous sampling strategy, (3) the fixed threshold strategy and (4) the sliding threshold strategy*.

- *Best of N strategy* is where female is going to sample N males and choose the male with highest quality (Janetos 1980). It has been proposed that best of N strategy will be chosen in a system if the cost for sampling males is low (Reynolds & Gross 1990; Gibson & Bachman 1992). This can be found in species that form leks, where male are found in large numbers and female can quickly sample them (Trail & Adams 1989; Fiske & Kalas 1995; Rintamäki et al. 1995).
- *Simultaneous sampling strategy* is where a female gathers information about potential mates at the same time and makes a decision before approaching the males (Wittenberger1983).
- *Fixed threshold strategy* is where a female samples until she finds a male whose quality exceeds a particular threshold value.
- *Sliding threshold strategy* is similar to fixed threshold strategy except in this case the threshold value keeps on changing according to the information gathered (Reid & Stamps 1997).

Although ddifferent strategies can be adopted for mate sampling, the choice of the strategy will need to be weighed against the costs incurred by the female such as time and energy costs of sampling and predation risk (Jennions& Petrie 1997).

The strategy female chooses may also depend on the social conditions, as shown in a study on G. lineaticeps where the females may use sequential sampling strategy when male densities are low and when the male densities are higher they use fixed threshold strategy (Beckers 2011).

In this study, females in chorus one and two have a higher chance to hear multiple males at a given time, allowing simultaneous mate sampling strategy in order to find potential mates as the best choice. This strategy would require less energy expenditure and risk of predation is likely to be less. If there is larger density of males then the female can choose the best one but it might have a problem to locate the position of male. Whether females in *Platygryllus* sp. exercise mate sampling at all, and if so, which strategy they use, whether the strategy changes from chorus to chorus and through the season needs to be investigated in the future. To do so, it will be critical to carry out field observations and lab-based manipulative experiments.

Chapter 5

Conclusions

- There are two types of context dependent calls in *Platygryllus* sp. One is the long distance mating call which is a loud call to attract mates over long distances and the other one is courtship call which is a soft call produced when male and female are in close proximity to each other. Production of this call is usually followed by mating.
- The average SPL of long distance mating call is 64.62(±) 0.4 dB (N=5).
- Temporal features (chirp duration and chirp period) of LDMC of *Platygryllus* sp. varied significantly between individuals (N=10).
- Sound Transmission experiments revealed that the maximum transmission range of a LDMC of *Platygryllus* sp. is 8m, assuming a hearing threshold of 36 dB.
- If we consider a behavioural threshold of 45dB, the transmission range is reduced to 4m.
- Male *Platygyrllus* sp. called in aggregations where the nearest neighbours could be less than 1m apart while other pairs spaced more than 30 m from each other.
- The inter-male distances varied across choruses.
- In our study on crickets (*Platygryllus* sp.) where the males use their calls to attract females, I showed that the acoustic spaces of males overlap considerably.
- And as a consequence of this a female is likely to hear multiple males at a time. The results suggest that simultaneous sampling might be the best strategy that the females can adopt for mate sampling in order to make mate-choice decisions.
- Chorus one and two had much higher overlap in acoustic spaces of males as compared to the other three choruses.
- Chorus one and two were dense choruses while three, four and five were sparser. If we consider that the transmission range is 4m (derived from a assumed behavioural hearing threshold of 45 dB) then the overlap of acoustic spaces of males decreases.

- In this situation the female might choose sequential sampling to make mate choice decision.
- The reason for chorus three, four and five being sparse is that they were mapped in a latter season when the activity was not at peak. In these chorus males will have less competition and on the other hand female will have less choice.
- This indicates that male spacing behaviour and consequently competition for acoustic space in males and the sampling strategies that the females may adopt will vary not only from chorus to chorus but also from season to season.

Future Directions

- I calculated the attenuation profile of the signal but I did not look at signal to noise ratio or signal distortion. Given that the habitat alters the signals in multiple ways it is important to examine all features of signal degradation before determining the active spaces of males.
- I looked at male spacing and assumed that females are distributed randomly in a chorus but if we want to calculate actual masking probability or examine probability of mate sampling, we need to have the inter-male-female distances relative to males. With this we can calculate the probability that at a given point how many males a female can hear.
- We do not know the behavioural threshold for *Platygryllus* sp. and I assumed that the female can detect the call of a male until it goes below ambient noise. It might not be the case in reality the female might not detect calls that are as soft as 36 dB. To determine actual hearing thresholds either electrophysical measurements or behavioural experiments need to be carried out on females with varying SPL of the call.
- Since I found out that there was a huge overlap in acoustic spaces of males, they could alter the features of their call and one could test what kind of altered feature the female prefers.
- It will also be interesting to examine whether the females in this species exhibit mate choice and if so, what sampling strategies they exhibit.

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Appendices:

Appendix A:

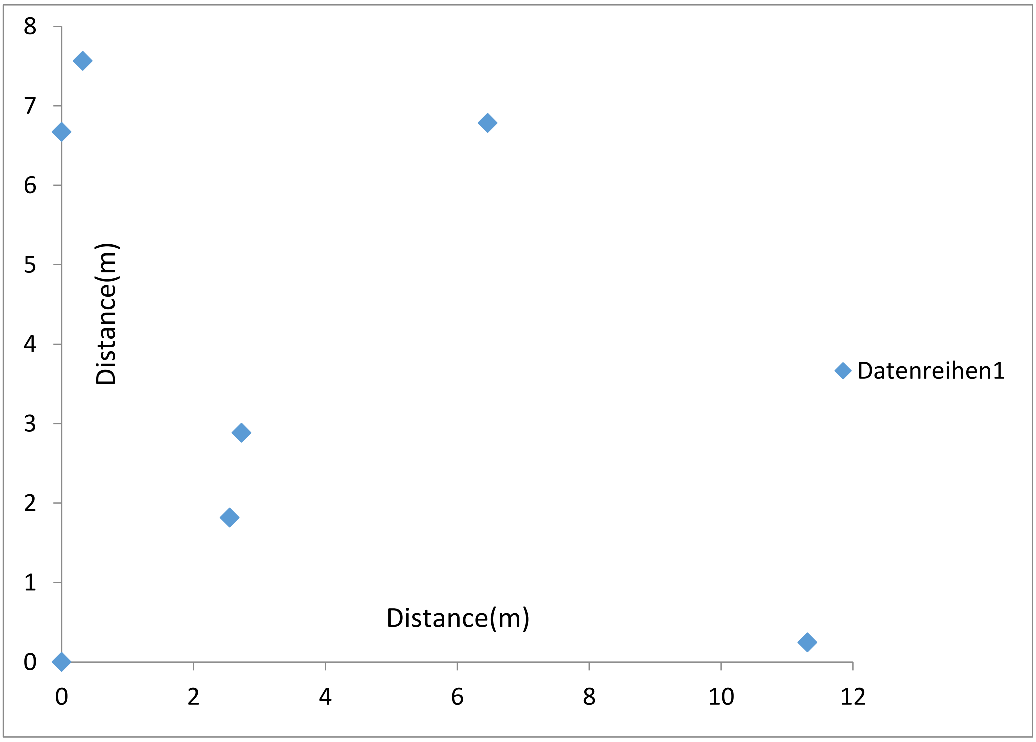
Code to get co-ordinates from inter-male distances.

```
#p=1
#d1=1
 #d2=2**0.5 #d=[2**0.5,1,1]
d=[] F = open("dis.txt", "r")
for i in F: a=i.split('\t') a=map(float,a)
d+=[a] #print d F.close()
#exit()
def get_cord(a,d):
b=a[1][1] y=(((d[0]**2-d[1]**2)/b)+b)/2.0
c=a[-1]
x=abs(d[-1]**2-(y-c[1])**2)**0.5+c[0]
return [x,y]
p=float(d[0][0])
a=[[0,0],[0,p],[1,1]]
d1=d[1][0] d2=d[1][1]
a[2][1]=(((d1**2-d2**2)/a[1][1])+a[1][1])/2.0
a[2][0]=(d1**2-a[2][1]**2)**0.5
 k=open("pts.dat",'w')
for i in a:
print>>k, i[0],i[1]
t=len(a)-1 while t<len(d):
d1=d[t]
#print d1
#exit()
pt=get_cord(a,d1)
print>>k, pt[0],pt[1]
t=t+1
 def dis(a,b):
return ((a[0]-b[0])**2+(a[1]+b[1])**2)**0.5
```

Inter-male distances and its reconstructed co-ordinates of chorus two, three, four and five are shown below.

Chorus 2 which had 7 males.

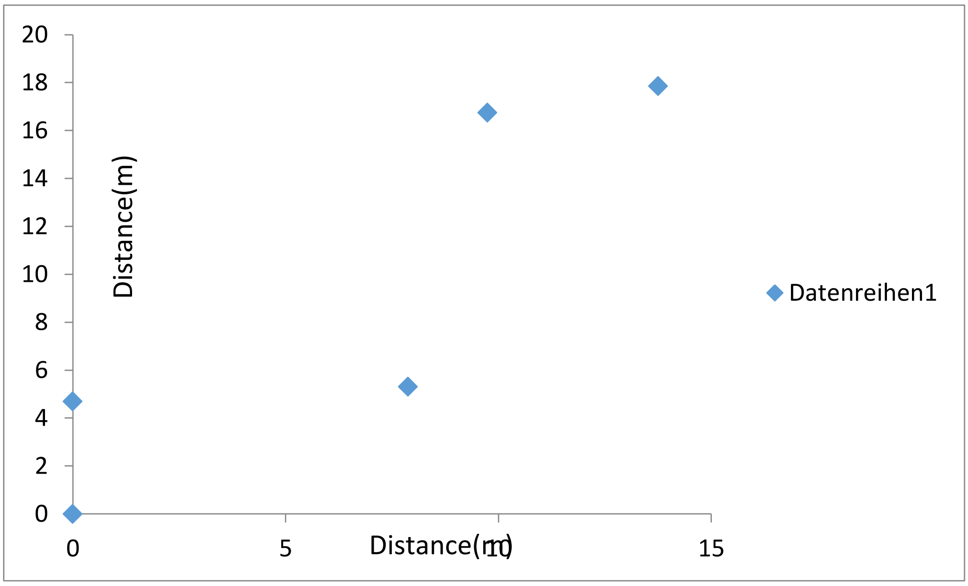
Inter-male distances	1	2	3	4	5	6	7
1	0						
2	6.67	0					
3	7.57	0.95	0				
4	2.63	5.21	6.16	0			
5	11.27	9	6.19	10.57	0		
6	10.17	10.46	5.26	12.77	2.86	0	
7	10.14	12	13.2	15.2	5.8	5.32	0



Chorus 2 re-constructed using the program.

Chorus 3 which had 5 males.

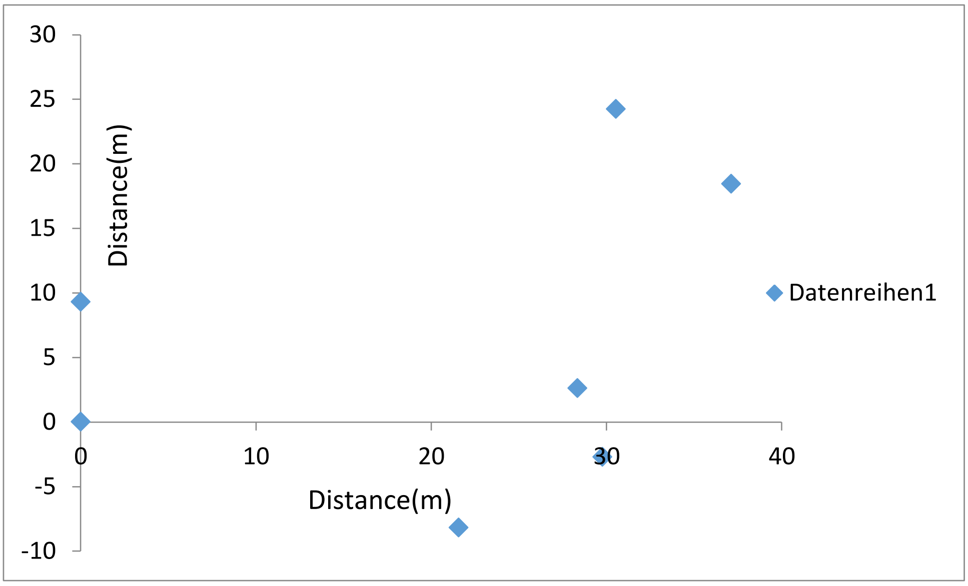
Inter-male distances	1	2	3	4	5
1	0				
2	4.7	0			
3	9.5	7.9	0		
4	17.79	13.07	11.07	0	
5	16.75	12.05	11.59	4.18	0



Chorus 3 re-constructed using the program.

Chorus 4 which had 7 males.

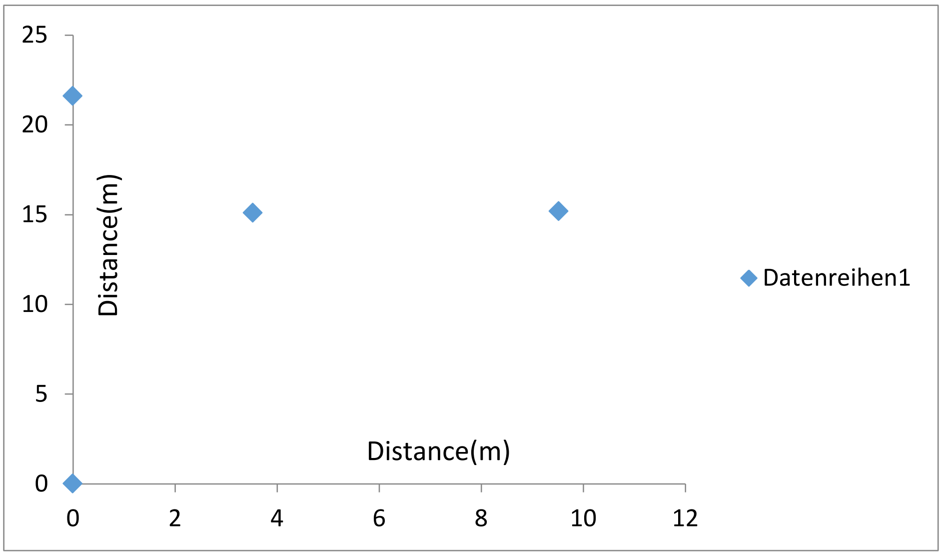
Inter-male distances	1	2	3	4	5	6	7
1	0						
2	9.3	0					
3	23.06	27.76	0				
4	13.4	17.8	9.87	0			
5	17.6	7.3	30.84	23.5	0		
6	22.6	12.1	33.65	17.7	4.7	0	
7	10.3	12	12.76	5.4	19.5	24.05	0



Chorus 4 re-constructed using the program.

Chorus 5 which had 4 males.

Inter-male distances	1	2	3	4
1	0			
2	21.6	0		
3	15.5	7.4	0	
4	15	6	3.6	0



Chorus 5 re-constructed using the program.

Code to construct acoustic spaces of males in chorus.

```
function [ h ] = circles(x,y,r,varargin)
%% Check inputs:
% x = input('Type x coordinate of center');
% y = input('Type y coordinate of center');
% r = input('Type radius of circle');
```

```
assert(isnumeric(x),'Input x must be numeric.')
assert(isnumeric(y),'Input y must be numeric.')
assert(isnumeric(r),'Input r must be numeric.')

if ~isscalar(x) && ~isscalar(y)
    assert(numel(x)==numel(y),'If neither x nor y is a scalar, their dimensions must
match.')
end
if ~isscalar(x) && ~isscalar(r)
    assert(numel(x)==numel(r),'If neither x nor r is a scalar, their dimensions must match.')
end
if ~isscalar(r) && ~isscalar(y)
    assert(numel(r)==numel(y),'If neither y nor r is a scalar, their dimensions must match.')
end

%% Parse inputs:

% Define number of points per circle:
tmp = strcmpi(varargin,'points')|strcmpi(varargin,'NOP')|strcmpi(varargin,'corners')|...
    strncmpi(varargin,'vert',4);
if any(tmp)
    NOP = varargin{find(tmp)+1};
    tmp(find(tmp)+1)=1;
    varargin = varargin(~tmp);
else
    NOP = 1000; % 1000 points on periphery by default
end

% Define rotation
tmp = strncmpi(varargin,'rot',3);
if any(tmp)
    rotation = varargin{find(tmp)+1};
    assert(isnumeric(rotation)==1,'Rotation must be numeric.')
    rotation = rotation*pi/180; % converts to radians
```

```
    tmp(find(tmp)+1)=1;
    varargin = varargin(~tmp);
else
    rotation = 0; % no rotation by default.
end

% Be forgiving if the user enters "color" instead of "facecolor"
tmp = strcmpi(varargin,'color');
if any(tmp)
    varargin{tmp} = 'facecolor';
end

%% Begin operations:

% Make inputs column vectors:
x = x(:);
y = y(:);
r = r(:);
rotation = rotation(:);

% Determine how many circles to plot:
numcircles = max([length(x) length(y) length(r) length(rotation)]);

% Create redundant arrays to make the plotting loop easy:
if length(x)<numcircles
    x(1:numcircles) = x;
end

if length(y)<numcircles
    y(1:numcircles) = y;
end

if length(r)<numcircles
    r(1:numcircles) = r;
```

```
end

if length(rotation)<numcircles
    rotation(1:numcircles) = rotation;
end

% Define an independent variable for drawing circle(s):
t = 2*pi/NOP*(1:NOP);

% Query original hold state:
holdState = ishold;
hold on;

% Preallocate object handle:
h = NaN(size(x));

% Plot circles singly:
for n = 1:numcircles
    h(n) = fill(x(n)+r(n).*cos(t+rotation(n)), y(n)+r(n).*sin(t+rotation(n)),'',varargin{:});
end

% Return to original hold state:
if ~holdState
    hold off
end

% Delete object handles if not requested by user:
if nargout==0
    clear h
end

end
```

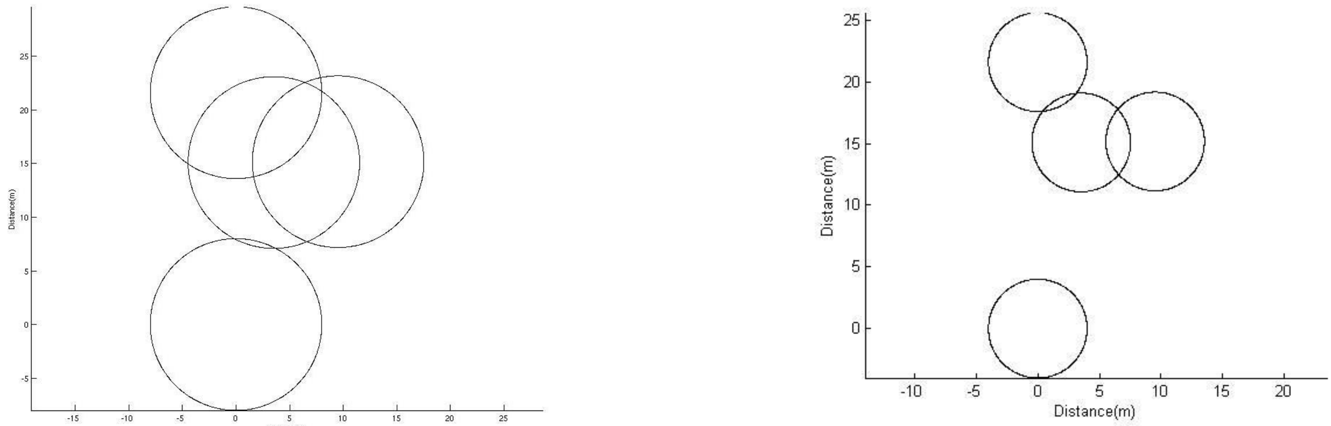
The code mentioned above was taken from Matlab tutorial and we have to write a simple code that uses the code mentioned above to construct active spaces of calling males.

```
function make_circle
% x = input('Type x coordinate of center: ');
% y = input('Type y coordinate of center: ');
% r = input('Type radius of circle: ');
l=load('/home/srlab/Desktop/pytho.dat');
x=l(:,1);
y=l(:,2);
r=8;
circles(x, y, r, 'facecolor','none');
axis equal;
end
```

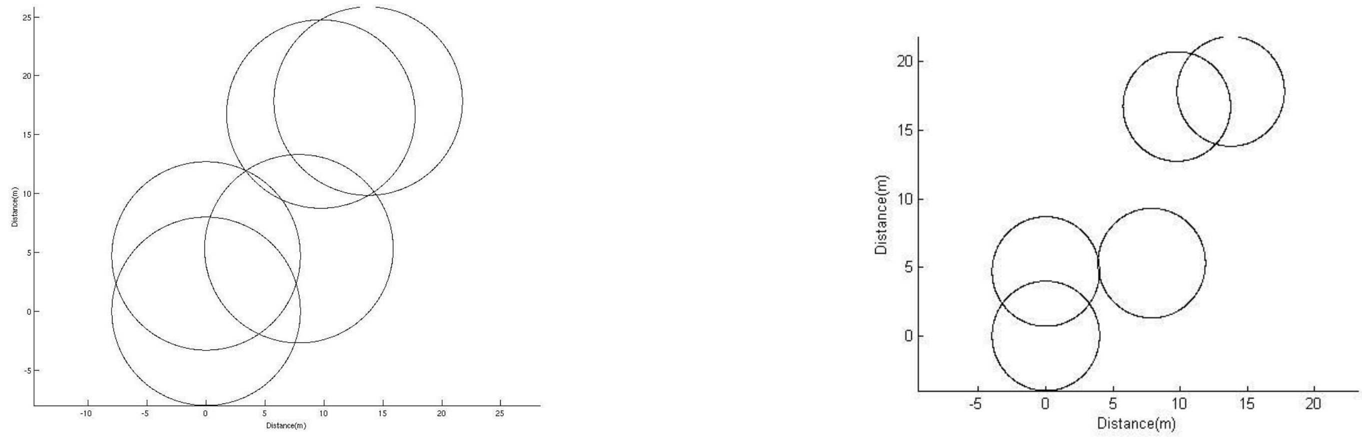
Using these two codes active spaces were constructed for calling males in all five choruses.

Appendix B:

Acoustic spaces of males in chorus two, three and five considering the maximum transmission distance to be 8m (on left hand side) and 4m (right hand side).



Chorus 5



Chorus 3

Chorus 2

****