Acoustic Signals as Means of Premating Isolation in Field Crickets of Genus *Teleogryllus*

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Certificate of Examination

This is to certify that the dissertation titled **"Acoustic signals as means of pre-mating isolation in field crickets of genus *Teleogryllus*"** submitted by **Ms. Samridhi Panwar** (Reg. No. MS12049) for the partial fulfilment of BS-MS dual degree program 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   Prof. Somdatta Sinha   Dr. Manjari Jain

(Thesis Supervisor)

Dated: 21st April, 2017

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.

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Date: April 21st, 2017

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
(Thesis Supervisor)

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Abstract

Species delimitation is the process of identifying biological diversity at species level and defining their boundaries. It is also helpful in discovering new species. There are different methods for delimiting species boundaries such as morphological traits, DNA-barcoding, phylogenetic methods and reproductive isolation. One type of reproductive isolation is behavioural isolation which restricts mating between two different species due to difference in their mating behaviour. Acoustics can be used as a means to delimit species boundaries in field crickets. In crickets male produces different call types to attract females and this call is species specific i.e. females respond only to the calls of their conspecific males. In male crickets there is a sound producing apparatus known as file (row of teeth or pegs) present on the forewing which helps in sound production by the process known as Stridulation. Peg number, size and file length can be different in different species which can be the reason for difference in calls of different species.

Chapter 1. Basic Concepts

1.1 Classification of Organisms

The basic unit of classification of organisms is Species and it was first coined by Charles Darwin.

Species is a term "arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms."

(Darwin 1859)

Classification of organisms is very important as it helps in the identification of organisms and serves as the universal language between scientists throughout the world (Swain et al., 1988). This is crucial to scientific research as the classification of an organism into different groups and categories allows us to understand the biological interrelationship between them and their evolution. With increasing rate of extinction, it has become essential to classify all the existing organisms.

The earliest tool that was used in the classification of organisms is Classical taxonomy in which organisms were categorized first into larger, then more specific groups. The relationship between things and their ranking in this system was a combination of both morphology, the form and structure of organisms, and phylogeny, evolutionary history. Under classical taxonomy, two morphologically dissimilar organisms were considered two different individual species (Taylor, 2009). Classical taxonomy is extremely beneficial for species recognition with key morphological traits and for the management of biological specimens in museums (Hillis, 1987). However, classical taxonomy has remained insufficient in delineating species in many ways (Jorger et al., 2013). In case of cryptic species, Classical taxonomy fails to delineate species and two or more different species are classified under one species name since they all are morphologically indistinguishable (Tahseen, 2014). For example, Arthropods are group of organisms which contain many cryptic species (Pfenninger et al., 2009). The recognition and description of cryptic species and speciation in this group has serious implications for human health, pest management and studies of coevolution and species interactions (Bickford, 2006). Another example of cryptic species is Fungi which are very diverse but very least well- studied organisms. Commercially important as pests, decomposers, fermenters and pathogens, we might also be missing out on many 'Valuable' aspects of their biodiversity.

To overcome the above mentioned problem of species delineation based on morphological traits, it has become essential to employ other tools apart from morphological traits to delimit species boundaries. Researchers have come up with various other methods to delimit species boundaries such as methods based on phylogeny and gene-flow statistics (Sei M, 2007), using whole genome sequences (Varghese, 2015), DNA barcoding (Kekkonen, 2015).

1.2 Biological Species Concept

Ernst Mayr in 1942 formulated the Biological Species Concept and stated species as "Populations or group of Populations that can actually or potentially interbreed that is they can breed together but they are reproductively isolated from other groups" (Mayr, 1963). The Biological Species Concept emphasizes that a species is an interbreeding population of individuals sharing common descent and that members of that community share a niche constituting an ecological entity in nature. Many criticisms and problems are also associated with this concept. It applies only to sexually reproducing species and cannot be used with exclusively asexual organisms such as prokaryotes, amoeba and protists. Distinguishing between species on the basis of reproductive separation is problematic because it can be difficult to determine how much reproductive separation is needed to distinguish between species. It cannot be applied to many relevant biological specimens like fossils. Biological Species Concept fails to explain reproductive isolation when there is a hybridization between different population groups (Taylor, 2009). Yet, it remains the most widely used concept by the scientists in delineating species (Schwentner et al., 2011).

1.3 Speciation

The evolutionary formation of new biological species, usually by the division of single reproductively isolated species into two or more genetically distant species (Wolf, 2010). There are three stages of speciation, first isolation of populations and isolating barriers. Second, divergence in traits of separated populations and third reproductive isolation of populations on their secondary contact. The main mechanism driving speciation is reproductive isolation.

1.4 Reproductive Isolation

It is the key term used in the Biological Species Concept. Reproductive isolating barriers are mechanism that disrupt gene flow. Reproductive isolation occurs when members of one population are unable to breed with members of other population (Raychoudhury, 2015). There are different types of isolating barriers:

1.4.1 Premating isolating mechanisms: This mechanism is the first line of isolation where one species is not able to mate with the other species (Taylor, 2009).

Common premating isolation mechanisms:

a) Geographical isolation: It occurs when populations cannot mate due to physical barriers such as mountains, rivers, etc.
b) Ecological isolation: It occurs when species cannot mate because they occupy different habitats.
c) Temporal isolation: The species cannot mate because they mate or breed in different times of the day, year or season regardless of occupying the same geographical region or habitat.
d) Behavioral isolation: It occurs when species cannot mate because they have different courtship and mating rituals. This kind of isolation is the first line of isolating mechanism and occurs due to certain different specific behaviour between species (for example species-specific vocalization and chemical signals). This is one of the most important mechanism for speciation (Raychoudhury, 2015).

e) Mechanical or physical incompatibility: This kind of isolation occurs due to incompatibility in reproductive structures of different species due to which they cannot mate.

1.4.2 Prezygotic isolating barrier:

This type of isolation is also known as 'Gametic isolation' i.e. inspite of transfer of gametes fertilization cannot take place due to species-specific chemical signals and zygote is not formed.

1.4.3 Postzygotic isolating barriers:

In this type of isolation successful transfer of gametes and fertilization takes place. The two species can mate together successfully and form 'hybrid offspring' which are often sterile and non-viable. Most of them die in the premature stage as it is difficult for them to survive in the niche. Even if they survive they cannot mate or reproduce and their population will disappear from the next generation (Taylor, 2009).

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Chapter 2. Introduction to Field Crickets

Crickets are small nocturnal insects which belong to the family Gryllidae and order Orthoptera. Young crickets are known as nymphs and undergoes molting (shedding of skin) to become adults. They are distributed throughout the world and are found from top canopy of the tree, to the level of bushes, grasses, ground, and bottom of the caves and deep burrows. They mainly rely on the green plants, fruits, seeds and other organic remains for food source (Alexander, 1962).

Crickets are characterized by long antennas, two pairs of legs for walking and two hind legs for jumping. Ears are present on the first pair of legs and are called tympanum (Otte, 2007). Female cricket contains ovipositor which is used for laying eggs and is often used as a physical character to identify females. Males of the most cricket species produce species-specific calls to attract females for mating purpose (Bennet-Clark, 2003). Females in return recognize these species-specific calls by identifying certain features of these calls and perform positive phonotaxis to reach towards the calling male (Meckenhauser et al., 2013).

Table 2.1. Taxonomic classification of Teleogryllus mitratus

Kingdom	Animalia
Phylum	Arthropoda
Class	Insecta
Order	Orthoptera
Suborder	Ensifera
Superfamily	Grylloidea
Family	Gryllidae
Subfamily	Gryllinae
Genus	*Teleogryllus*
Species	*T.mitratus*

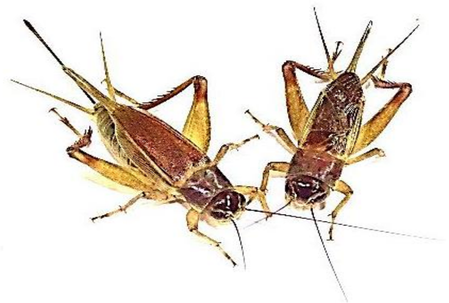

Fig 2.1
Teleogryllus sp. Female (left) and male (right)
Female (left) and male (right)

Field crickets vary in size between 15-25 millimetres depending on the species and can be of different colours such as black, brown, etc. Females are identified by the presence of an ovipositor, a spike-like appendage which is about 0.75 inches long, on the hind end of the abdomen between two cerci. Females bury their fertilized eggs with the help of this ovipositor. Length of ovipositor varies in different species and can be used to identify females of different species. Unlike females, males do not have ovipositor.

Males are able to produce sound or chirps and are identified through sound. The acoustical properties of their calling song provide an indication of past and present health. Females evaluate each song and move towards the one they prefer.

2.2 Sound Production Mechanism in crickets

Forewings of male crickets are modified and bear sound-producing structures. The forewings are raised during sound production. They produce sound by rubbing their raised forewings together and this process is known as ‘Stridulation’. The forewings include a row of teeth on the underside of one wing that is scrapped against by the edge of the other forewing. The hardened edge of the other forewing is called the plectrum. As the plectrum engages the row of teeth (called the file) it produces a burst of sound called a ‘pulse’ which is then amplified by other structures on the forewing, the harp and the mirror. Hence, every wing closure corresponds to a pulse and the opening of the wings is silent. The resulting sound is typically highly stereotypic and species-specific which is then used by the females to recognize and locate their conspecific males.

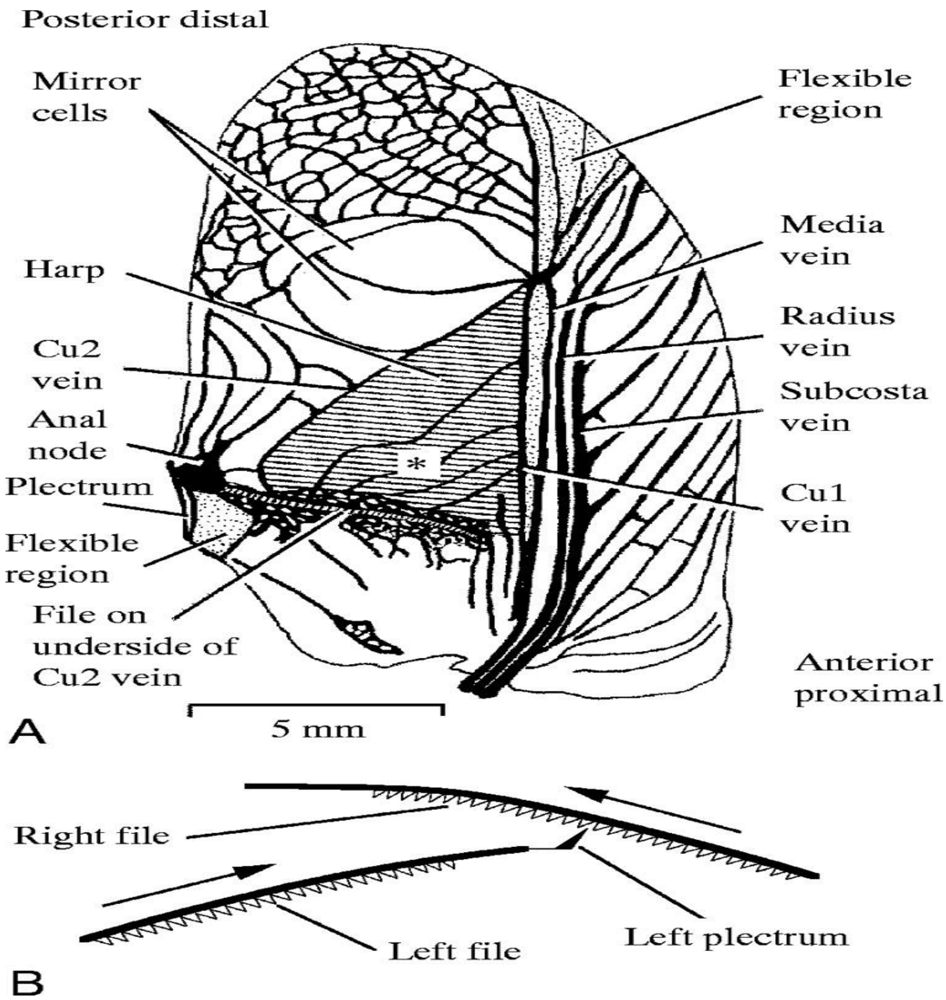

Fig 2.2 Wing structure of Male cricket (Bennet-Clark et al., 2002).

2.3 Spectral and Temporal features of a cricket call

Syllable is the basic unit of call.

● Chirp period: It is the measurement of the time interval between the onsets of a chirp to the onset of the following next chirp.

● Chirp duration: It is the measurement of total time interval of a single chirp. It measures the time interval of the onset from the first syllable to the offset of the last syllable of same chirp.

● Syllable period: It is the measurement of time interval between the onsets of the syllable to the onset of the following syllable.

Syllable duration: It is the measurement of time duration of a single syllable i.e. measurement of the time interval between onset and offset of a syllable.

● Number of syllables per chirp: It is the measurement of total number of syllables produced in a single chirp.

● Peak frequency: It is the frequency at which maximum energy is concentrated.

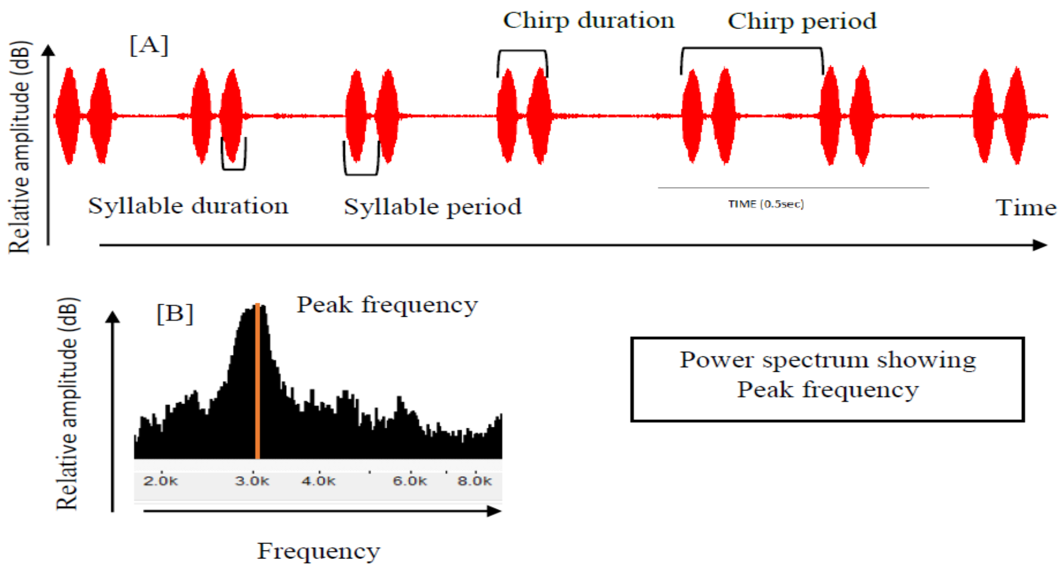

Fig 2.3 Spectral and temporal features of a call

2.4 Different call types

Crickets can produce different call types in context of different behaviours.

1. The calling song or long-distance mating call: Loud chirping sound produced by the male cricket to attract females.
2. The courting song or courtship call: This is a very soft chirping call and is produced by the male in response to antennation by the female or whenever the female is in proximity.
3. The aggressive call: This is similar to long-distance mating call with very loud, fast and sharp chirping signal which is produced when the male sense the presence of another male nearby.
4. The post-copulatory call: This is irregular chirping produced by the males after successful mating.

I wanted to study species delimitation using acoustics behaviour in field crickets.

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Chapter 3. Behavioural Isolation in Crickets

3.1 Study system and Objectives for the thesis

3.1.1 Study System: *Teleogryllus mitratus*

Crickets of *Teleogryllus mitratus* are dark brown in colour and have two narrow yellow bands along the internal margins of eyes (Chopard, 1961). Males are smaller than females and they usually call from burrows. The separation of first 4 veins of lateral field from the rest is of greater degree (Townsend, 1980).

3.1.2 Sampling sites: IISER Mohali and Kasaragod, Kerala

The population of crickets sampled from IISER Mohali campus was found to be of *T.mitratus* and the population sampled from Kasaragod, Kerala was found to be morphologically similar to population found in IISER Mohali. There were two different types of calls recorded for individuals of Kerala population:

1) Call type I: Similar to call produced by individuals of population found in IISER Mohali campus
2) Call type II: Different from call produced by individuals of population found in IISER Mohali campus.

Since the individuals of two populations were morphologically identical but some males of Kerala population produced different call compared to *T.mitratus* found at IISER Mohali campus, I wanted to check the following in my thesis:

1) To check whether the males of the two call types (Call type1- same as *T.mitratus* of IISER Mohali and Call type2- different from *T. mitratus*) belong to same or different species using behavioural isolation paradigm.
2) To find whether there are structural differences in the sound-producing apparatus (forewing) of these two call types producing individuals.

3.2 Objective 1:

To find out whether the males of the two call types (Call type I and call type II) belong to same or different species using behavioral isolation paradigm

Crickets are known for their species-specific calls. Males produce calls and the females respond only to their conspecific call (call produced by the male of their species) and perform phonotaxis (B.Hedwig, 2005). In crickets temporal and spectral features of a call have certain pattern and serve as cues for recognising species (Pollack GS, 1979) and these patterns are species-specific.

Using this information, I hypothesised that since males of Kerala population produce two different types of calls (Call type I and call type II), they should belong to different species. To test this hypothesis I performed playback experiments.

3.3 Experimental Methodology:

All phonotaxis experiments were conducted in an arena made of thick thermocol pieces joined together and the base of arena was covered with soil to create natural environment for the experiment. Two speakers were placed 2m apart from each other and female was released at a point equidistant (2m) from both the speakers. Video recordings of the trials was done using Sony cybershot camera and it covered the whole experimental arena. Red light was used throughout the experiment to create natural conditions for the crickets.

All the experiments were conducted between 6:30-10:00 pm (since crickets are nocturnal and most active during this time). No-choice playback experimental paradigm was used i.e. only one speaker was active at a time. Playback calls to the female were played from only one speaker at a time (at one end of arena) and the other speaker was kept silent. So the speakers were active alternatively and this was done to ensure that there is no visual and side bias due to speakers.

For playback experiments 3 different types of male call recordings were used:

a. *Teleogryllus mitratus* (Call type I ; conspecific call IISER Mohali ; positive control)

b. *Teleogryllus sp.* (Call type II ; test call ; Kerala)

c. *Acanthogryllus asiaticus* (Heterogeneric call ; Negative control)

Some highly motivated females can show response and phonotaxis towards any random call type i.e. they are not specific only to their call type so negative control was used to identify such females and remove them.

Fig 3.1: Experimental setup for Playback experiments

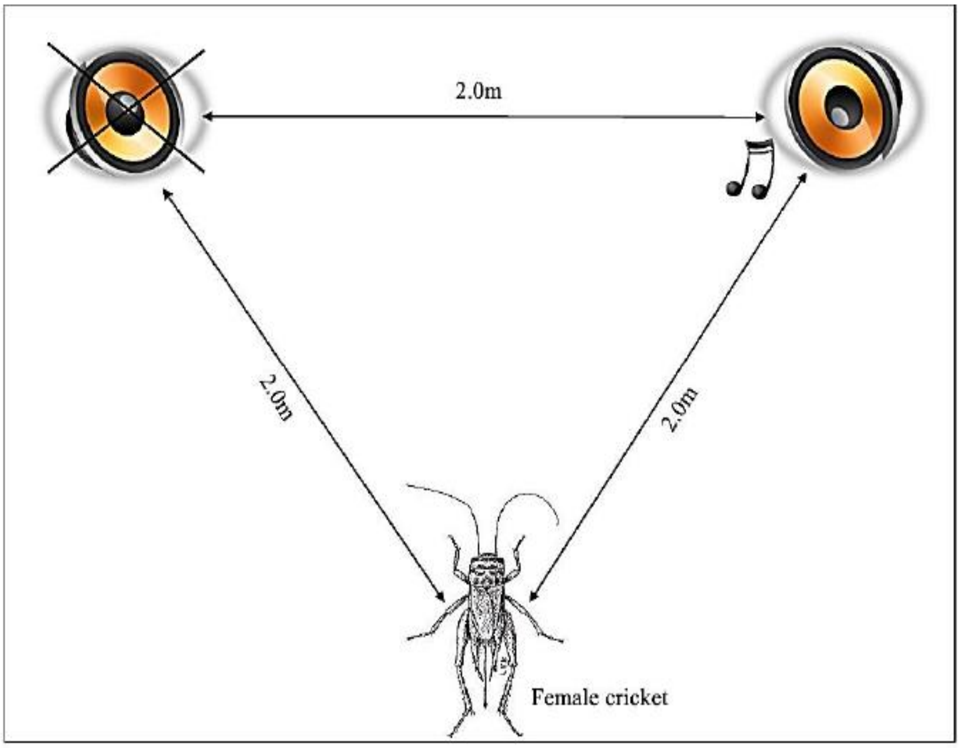

Fig 3.2: Schematic representation of the experimental setup for No-choice experiments (Only one speaker active at a time)

3.4 Experimental Protocol

1. Call was placed from only one speaker at a time using Audacity software.
2. Average sound pressure level (SPL) used for each call was 67dB and it was measured using SPL meter kept at 0.5m from the speaker.
3. Time given to each female to acclimatize to the arena was 5 minutes.
4. Each female was observed for 10 minutes after release in the arena making total experimental time per female per song to 15 minutes.
5. The start of the phonotactic approach was considered as soon as the female started moving from the release point.
6. The end of phonotactic response was considered as soon as the female reached the semicircle drawn around the centre of the speaker.
7. Each female was subjected to three different trials across different nights and the order of presentation of calls was randomised.
8. To control for side bias, active speaker position was swapped from left to right after every trial.

9. To control for any chemical cues, soil was shuffled after each trial.

10.Total of 19 females were used for the experiment out of which 7 died before all the three trials were completed on them making effective N=12

11. Each female was given a minimum break of 24 hours before she was used again for the trial.

• Positive phonotaxis was considered when the female reached the active speaker within 15 minutes time.

• No phonotaxis was considered if the female did not go to the active speaker or it went to the silent speaker.

• Negative response was considered if the female went to the active speaker with wrong call or it roamed around freely in the arena.

3.5 Results

All the 12 females of *T.mitratus* (IISER Mohali campus) responded to call type I but did not respond to neither call type II (Kerala call) nor heterogeneric call (*Acanthogryllus asiaticus*) suggesting that males of Call type II belong to different species other than *mitratus*.

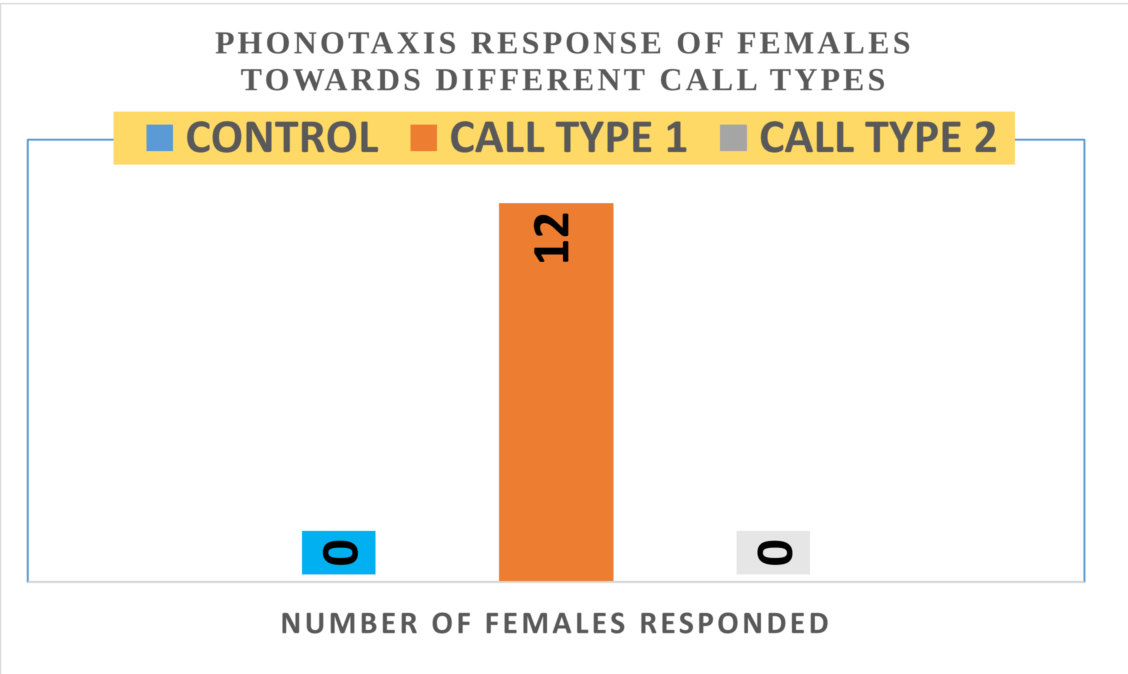

Fig3.3: Graphical representation of female response to different call types

3.6 Discussion

The isolating behaviour experiment using acoustics with IISER Mohali females strongly suggests that individuals of Call type II belongs to different species. *Teleogryllus mitratus* females responded strongly only to its conspecific (Call type I) male calls during the playback experiments. Females showed no response (or rejection) when exposed to the call type II indicating that call type II males are likely to be a different species than *T.mitratus*. No female approached the calls of heterogeneric species. These experiments reaffirm that in crickets acoustic signals serve as a means of premating isolation and are important in delimiting species boundaries.

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Chapter 4. Analysis of Sound Producing Apparatus

4.1 Objective 2

To determine any structural differences in the sound producing apparatus (forewing) of these two call types to discriminate the species.

Introduction

Insects produce sound by different mechanisms and the dominant mode of Orthopteran sound production is through Stridulation. Crickets rub a scraper (plectrum) on the upper side of one wing against a file (elytron) with stridulatory teeth (also known as pegs) on the lower side of the other wing. The files and scrapers are usually well developed on both wings in crickets, but males typically use the scraper on the left wing to excite the teeth on the file of the right wing (Acoustic communications in insects and anurans: Common problems and diverse solutions- HC Gerhardt, 2002).

In stridulating insects the number, spacing and acoustic properties of the file and stridulatory teeth contribute to the fine-scale patterns of amplitude modulation at any given tooth-impact rate. Even the minimal variation in any sound producing structure in insects can lead to production of different types of sound in closely related species. For example, in two closely related species of Cicada *M.cassini* and *M.septendecim* produce signals with different carrier frequency and different bandwidths (Young and Josephson, 1983; Bennet-Clark and Young, 1992).

My aim was to study the sound producing apparatus of different species of Crickets and to check whether there is any difference between number of sound producing structures such as pegs (which constitute th number of pegs in anterior, middle and posterior region and total number of pegs on the wing.

Samples from different populations of *Teleogryllus sp.* were analysed and number of pegs were counted.

1. Dudhwa National Park (DNP): a) Chandan Chowki (*T.mitratus*) b) Bansinagar (*T.occipitalis)*
2. IISER Mohali (*T.mitratus)*
3. Kadari (*T.mitratus)*
4. Kasaragod (*T.mitratus)*
5. Kasaragod (n.sp.)

4.2 Experimental Methodology:

1. Dried forewing (right) samples were used for counting the number of pegs.
2. L shaped file (row of pegs) was divided into three sections from left to right (left-Posterior part, middle part and right-Anterior part) to make counting easy.
3. Leica M series stereo microscope was used for calculating the number of pegs.
4. Leica software was used to take images of each forewing file and for doing measurements.
5. Total file length from posterior end to anterior end was also measured for each wing.

e whole file on cricket forewing) in different species. I counted number of pegs in anterior, middle and posterior region and total number of pegs on the wing.

Samples from different populations of *Teleogryllus sp.* were analysed and number of pegs were counted.

6. Dudhwa National Park (DNP): a) Chandan Chowki (*T.mitratus*) b) Bansinagar (*T.occipitalis)*
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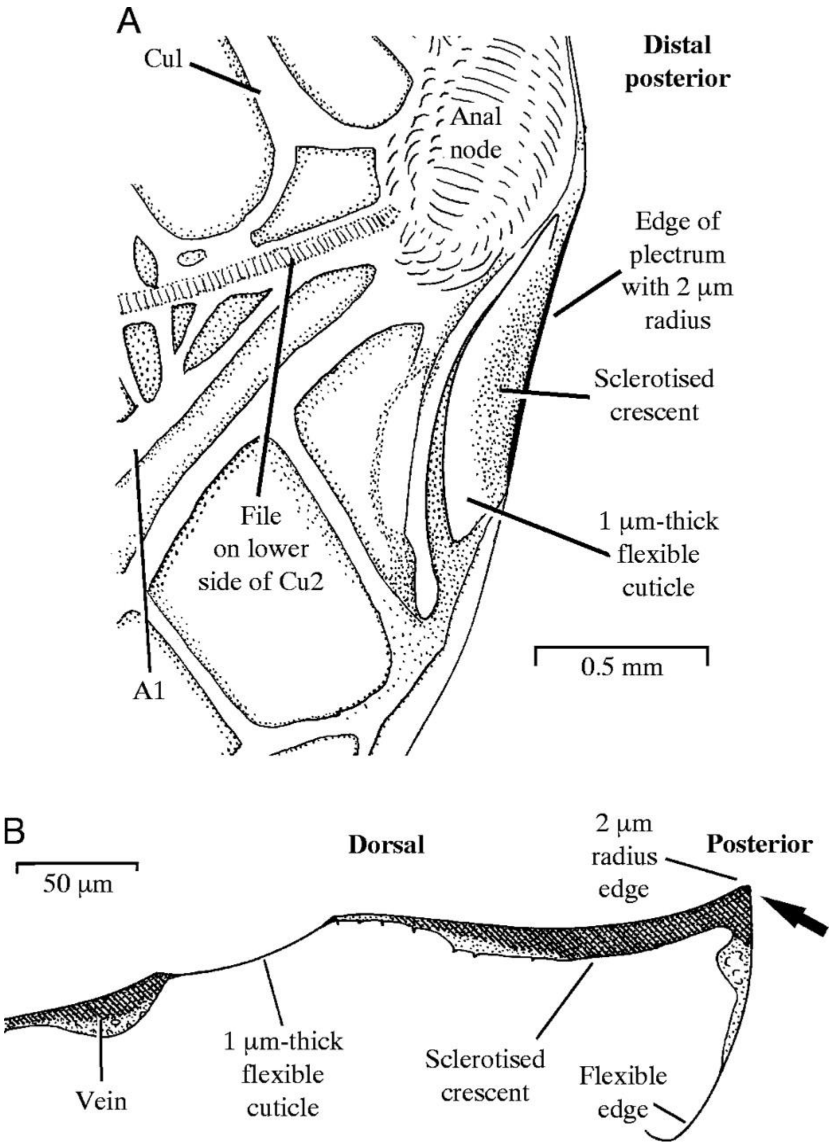

Fig 4.1: schematic representation of file on Cricket wing.

Fig4.2: Pegs as seen under stereo microscope

4.3 Results:

Table 4.1

Location of Sample and sample ID	No of pegs in anterior part	No of pegs in middle part	No of pegs in posterior part	Total no of pegs
MJO_143 (CC)	63	115	28	206
MJO_120 (BN)	70	148	22	240
MJO_791 (Kadari)	71	125	40	241

MJO_769 (Kadari)	69	122	50	241
MJO_140 (CC)	60	106	37	203
MJO_866 (Kasaragod)	65	153	40	258
MJO_213 (IISRM)	62	112	31	205
MJO_256 (IISERM)	67	109	41	220
MJO_257 (IISERM)	50	128	37	215
MJO_792 (Kadari)	55	140	57	248

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