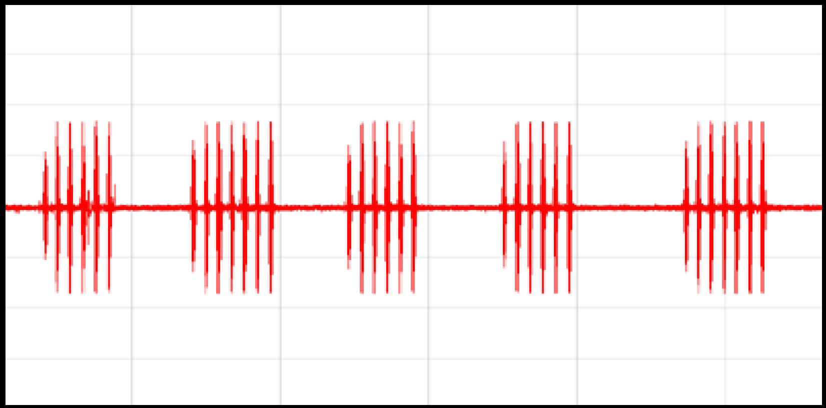
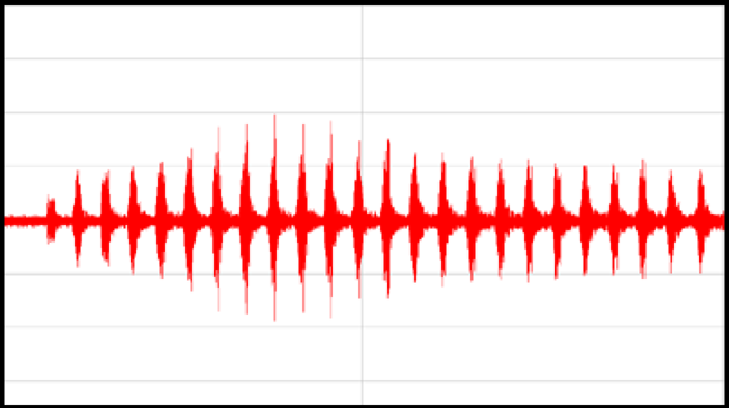
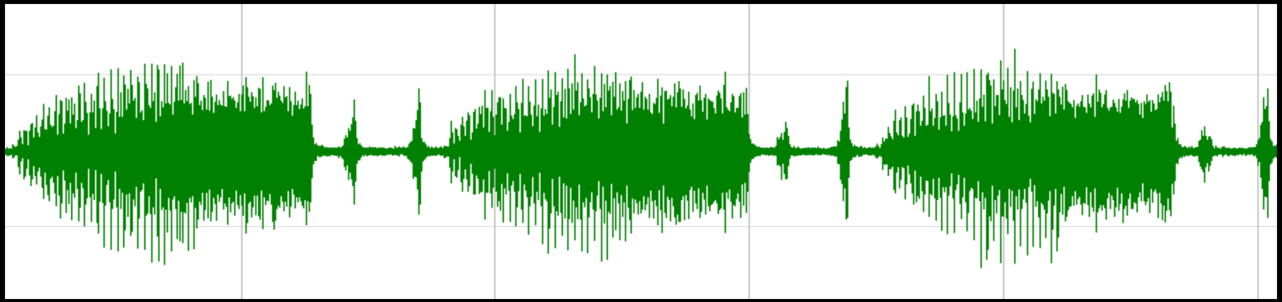
FOREST ACOUSTICS: COMMUNICATION IN THE CACOPHONY

Rohini Balakrishnan
Centre for Ecological Sciences
Indian Institute of Science





The structure, diversity, perception, function, ecology and evolution of acoustic communication signals



CRICKETS AND GRASSHOPPERS

Order

ORTHOPTERA

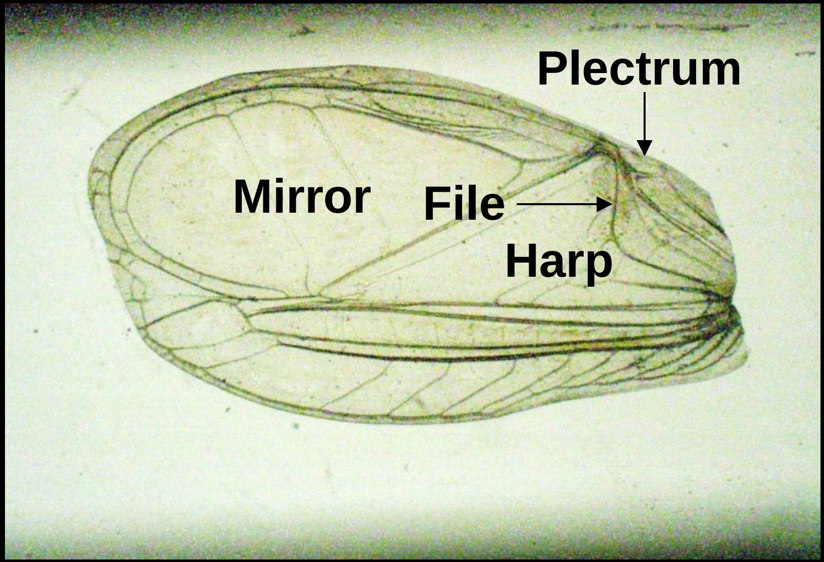
Suborder

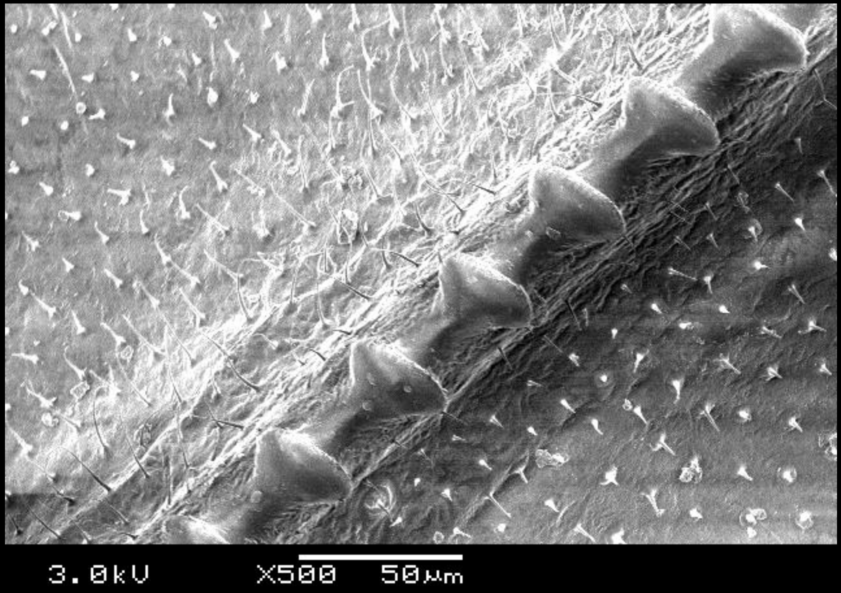
ENSIFERA (Crickets) Wing stridulation Ears on forelegs	CAELIFERA (Grasshoppers) Leg-wing stridulation Ears on abdomen

Superfamily

GRYLLACRIDOIDEA Femoro-abdominal Stridulation	GRYLLOIDEA (True crickets)	TETTIGONIOIDEA (Katydids)

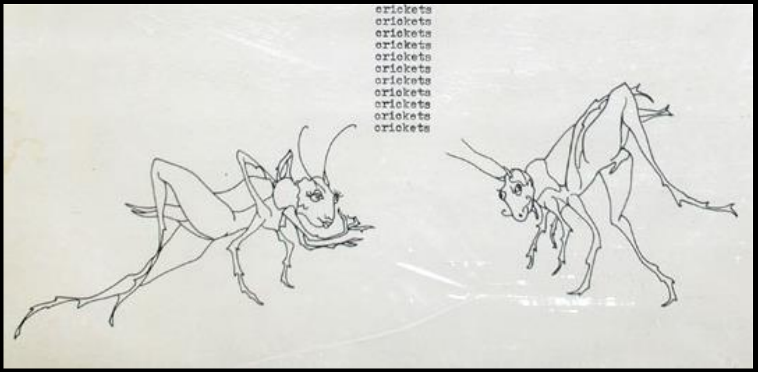
SOUND PRODUCTION

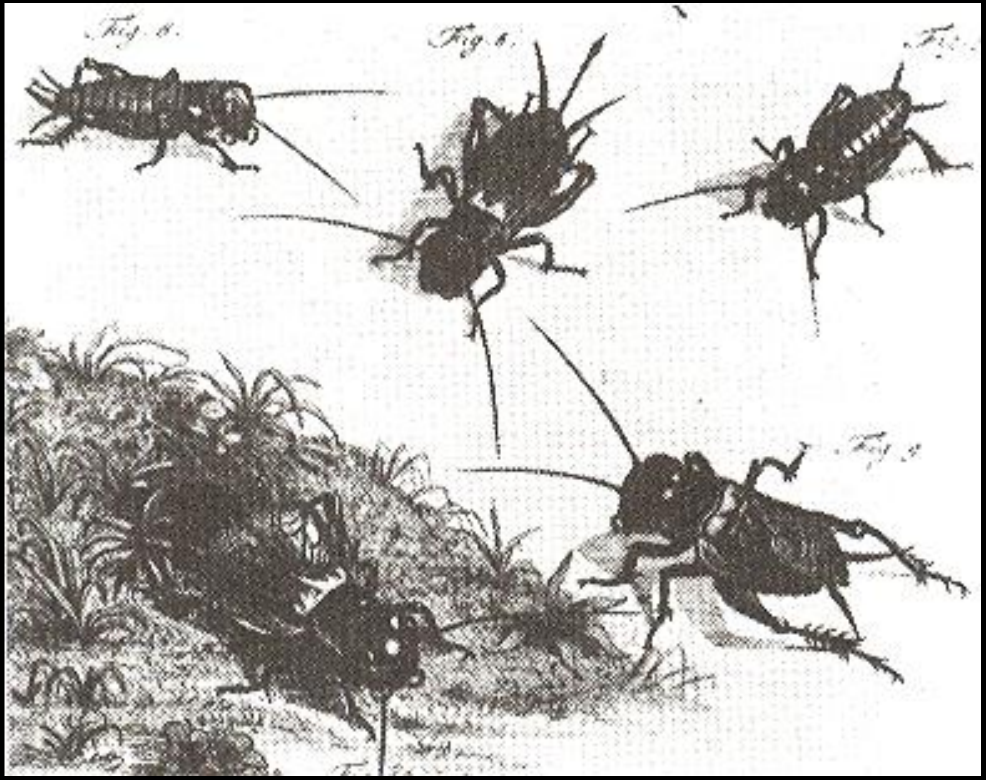




SOUND RECEPTION

MALE CRICKETS SING TO ATTRACT FEMALES

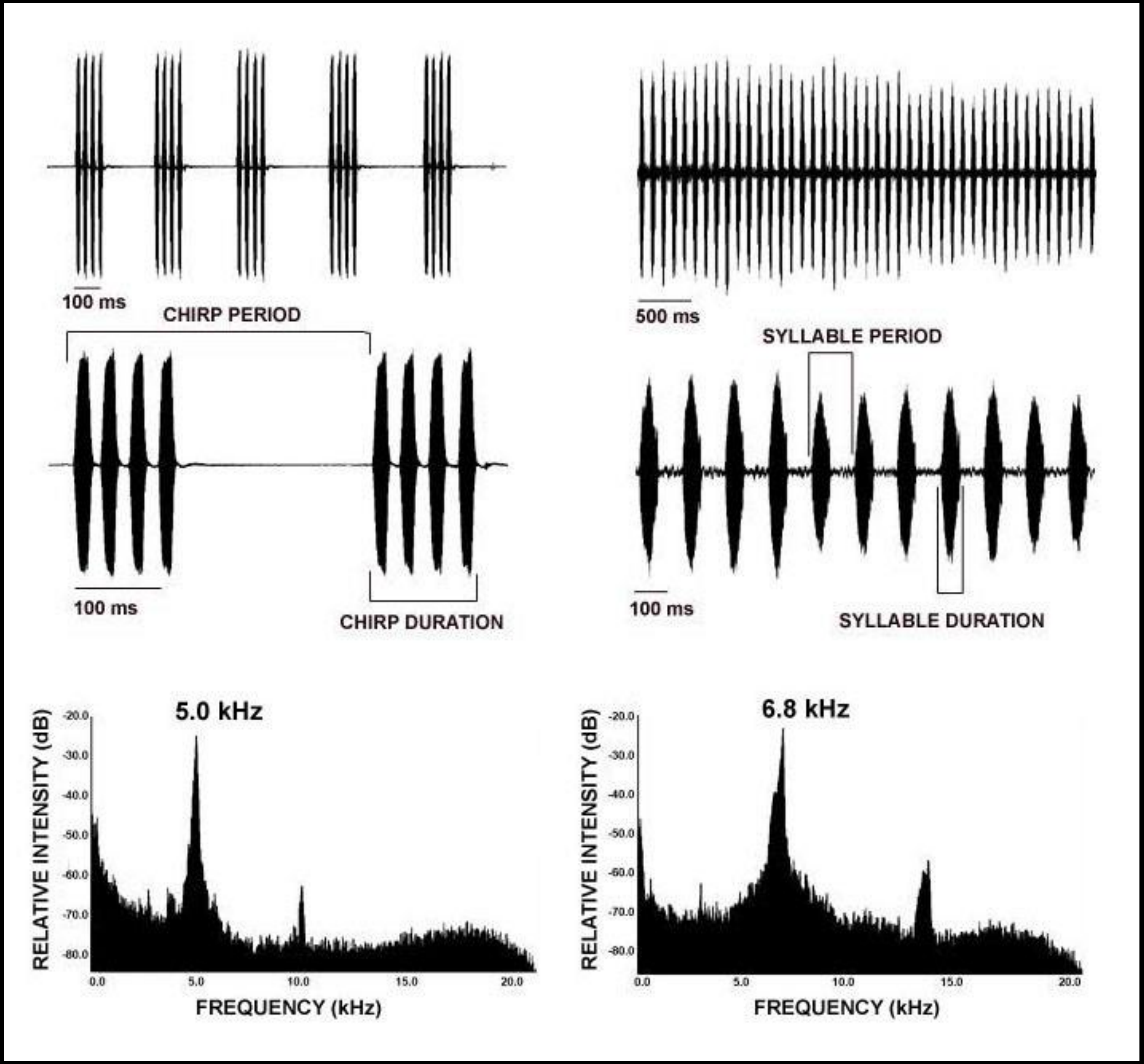




Roesel von Rosenhof, 1705-1759
(In: Weber & Thorson, 1989)

ACOUSTIC CUES ARE SUFFICIENT TO ATTRACT FEMALES

SPECIES-SPECIFIC SONGS

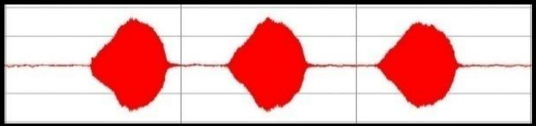


Gryllus bimaculatus *Itaropsis sp.*

COMMUNICATION

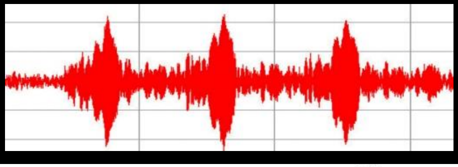
Sender

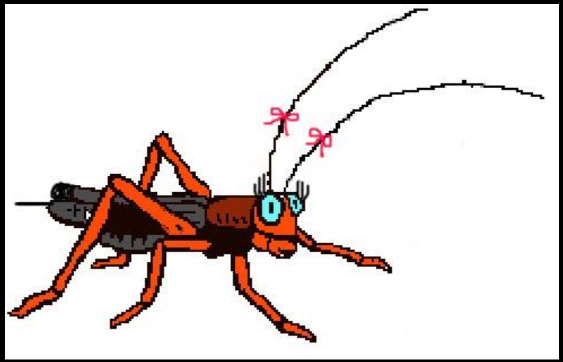
Signal



Medium

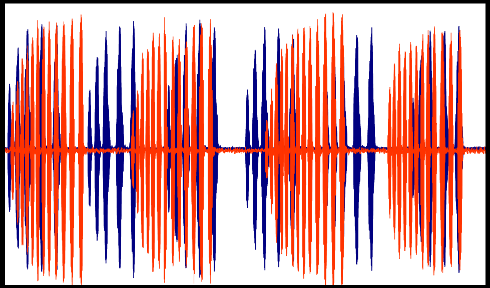
Distortion





Receiver

Competing callers



Masking

THE DUSK CHORUS: CACOPHONY







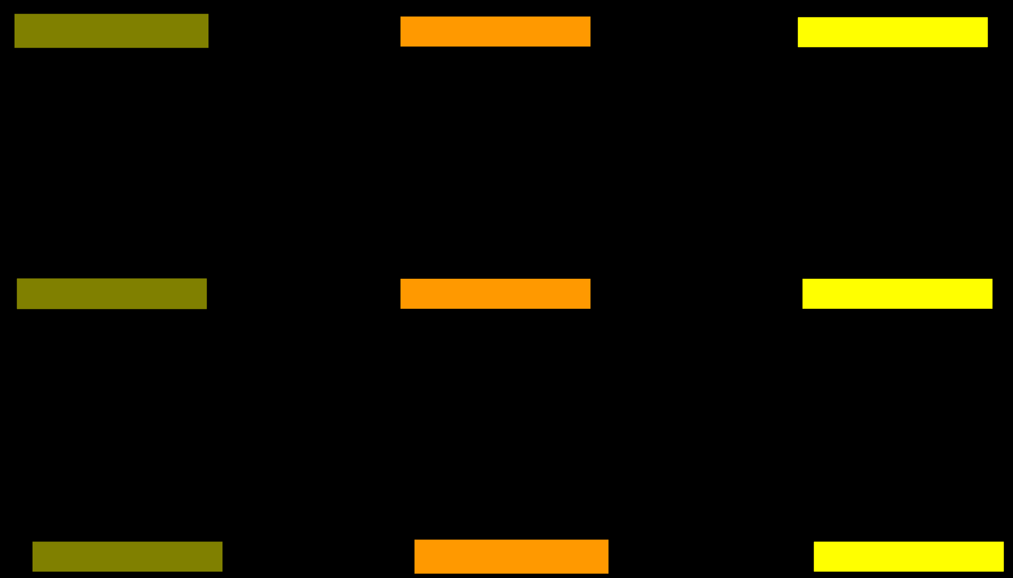


SOLUTIONS TO ACOUSTIC INTERFERENCE

SENDER STRATEGIES

The call structures and spatio-temporal signalling patterns of species in acoustic communities may result from the need to minimise acoustic interference

TEMPORAL PARTITIONING



Seasonal (months)

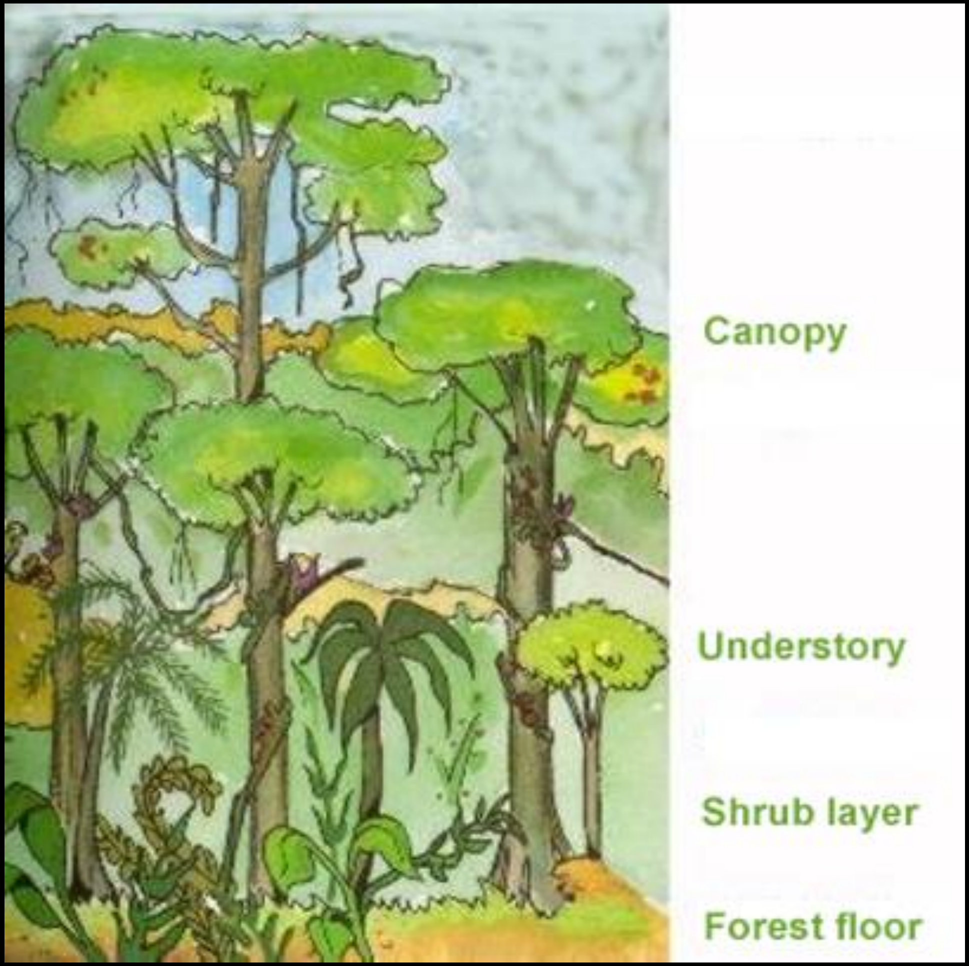
Circadian

(hours)

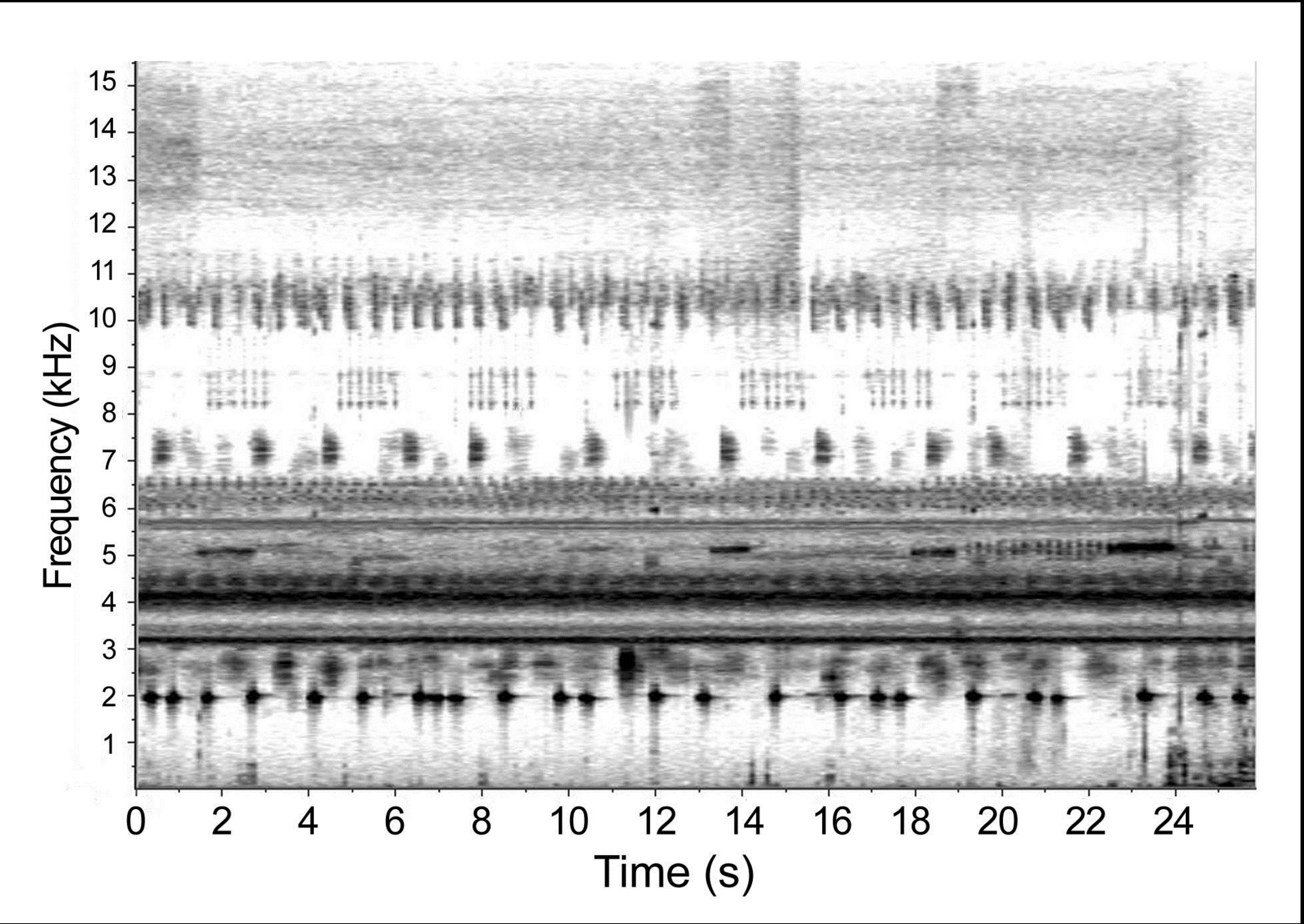
Fine temporal (seconds)

Species 1 2 3

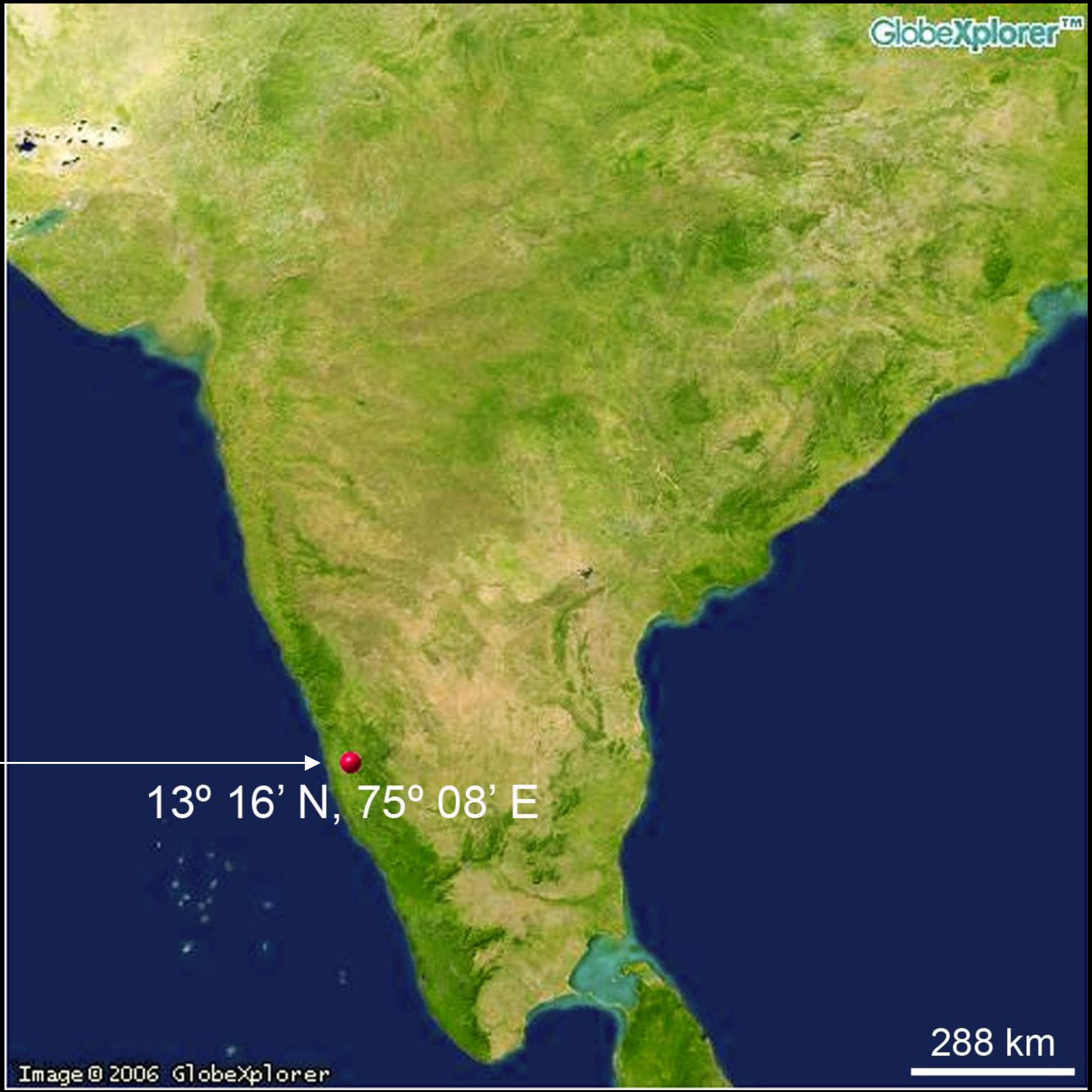
SPATIAL PARTITIONING



PARTITIONING IN ACOUSTIC SPACE



KUDREMUKH NATIONAL PARK



KUDREMUKH NATIONAL PARK

Twenty species of crickets were found and calls analysed

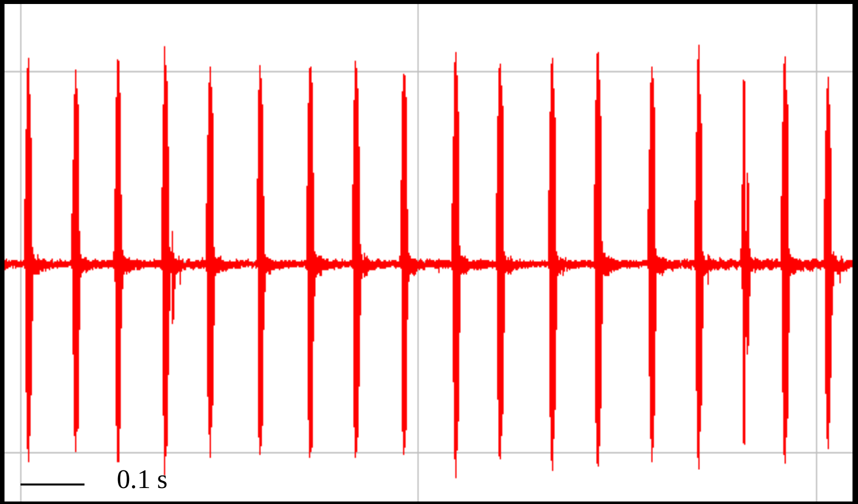
Ensifera
(Crickets)

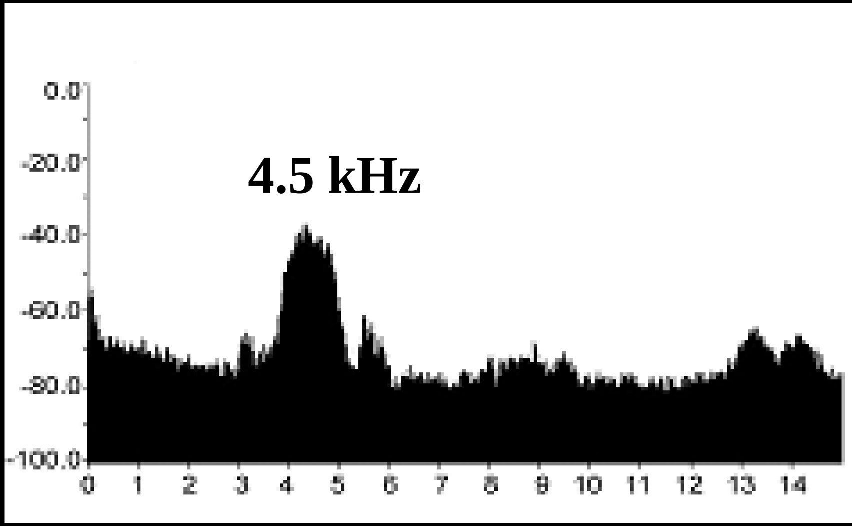
Grylloidea
(True crickets)
10 genera , 10 species

Tettigonioidea
(Katydids)
7 genera, 9 species

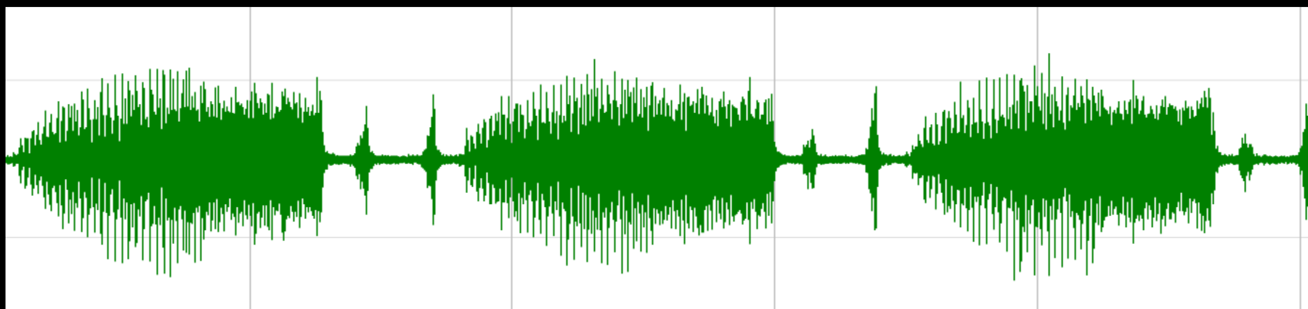
Gryllacridoidea
(Raspy Crickets)
1 genus, 1 species

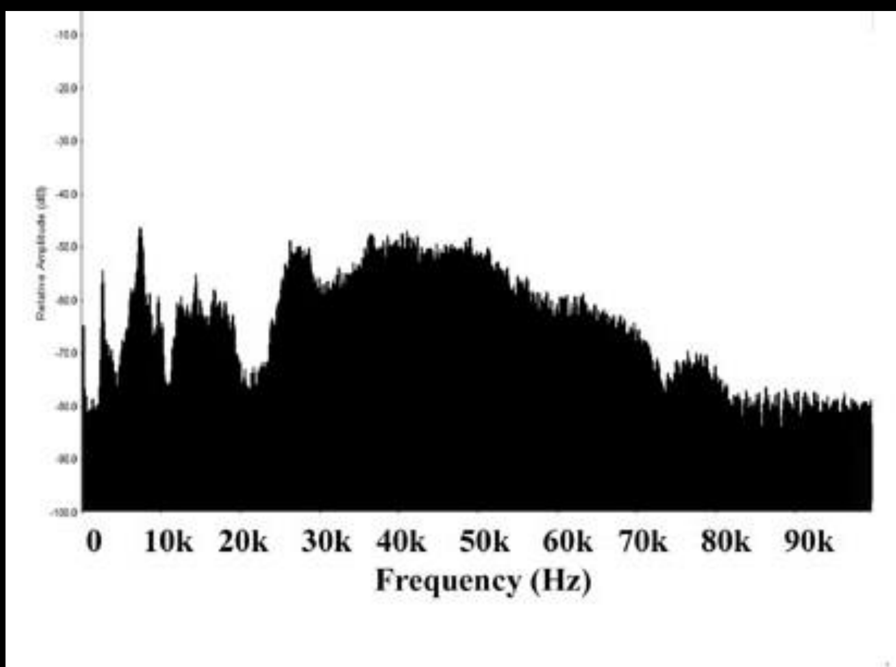
Landreva sp. (Log cricket)





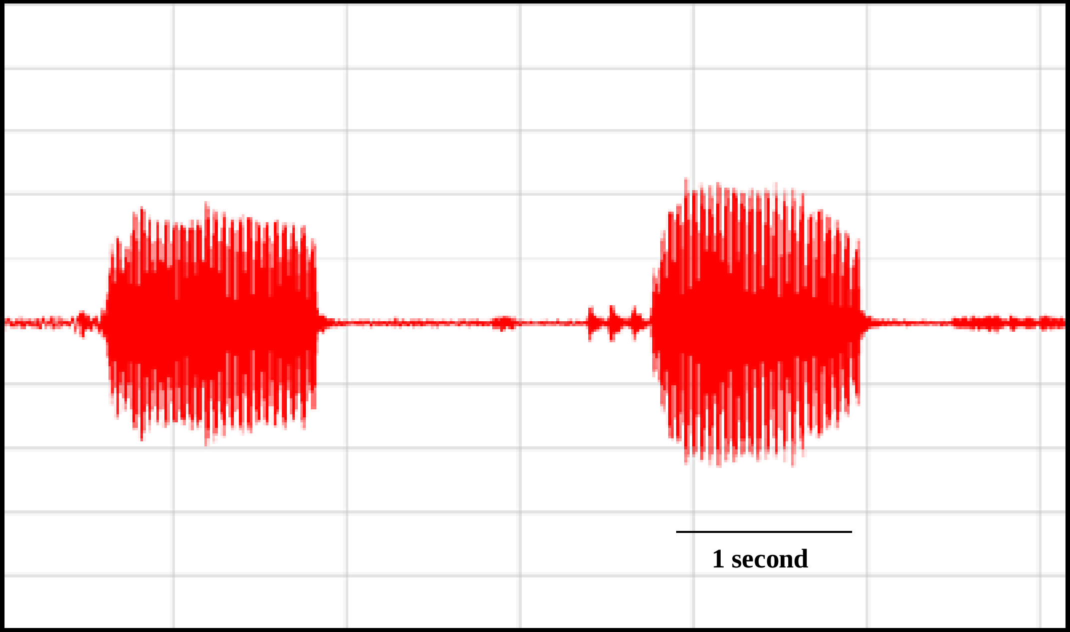
Mecopoda sp. “Two-part” (Mecopodinae)

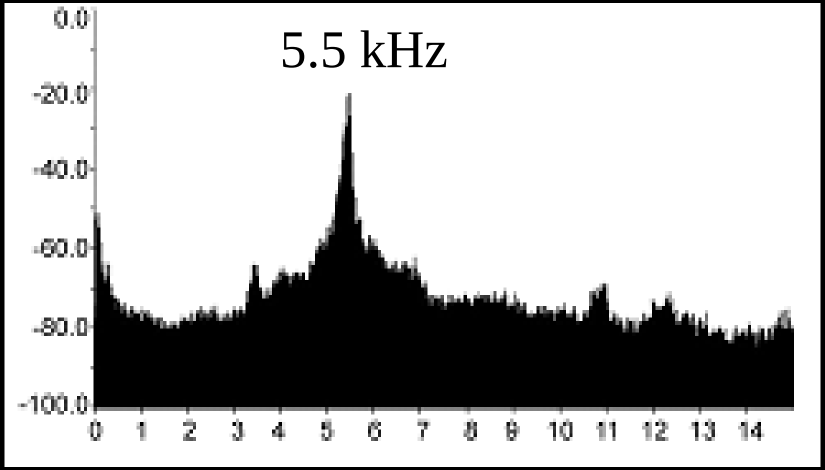




Katydid (Ground)

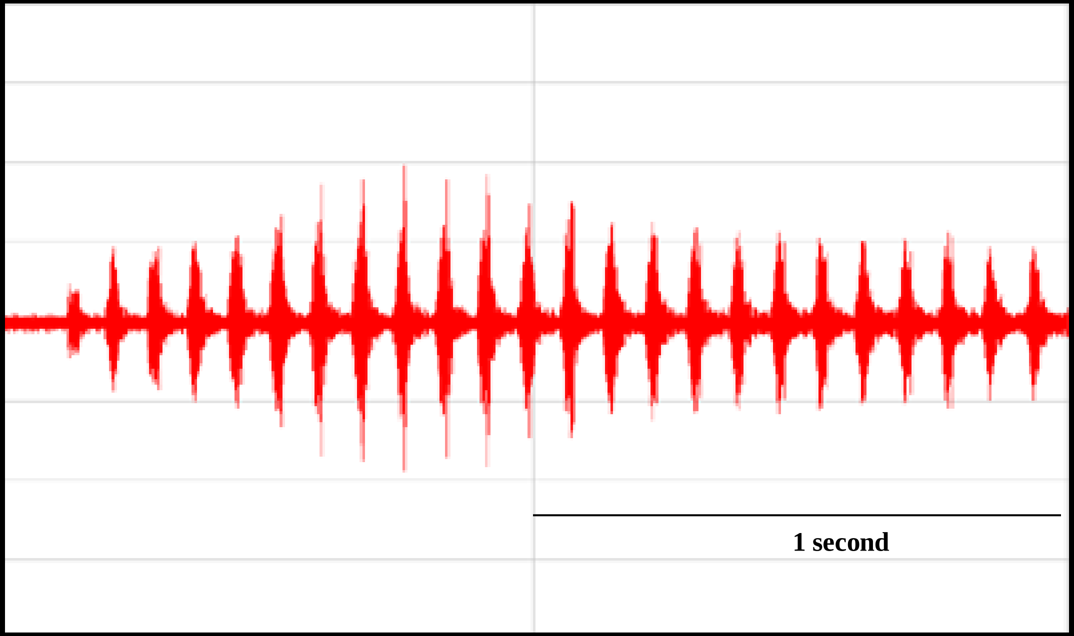
“Whiner” (Podoscirtinae)

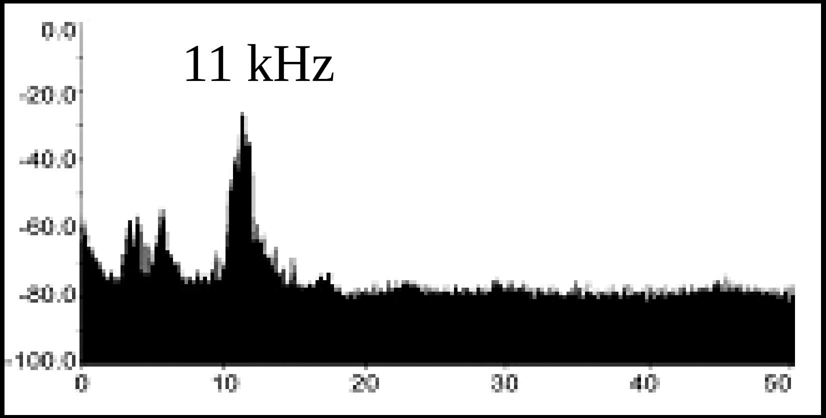




True cricket
(Understorey)

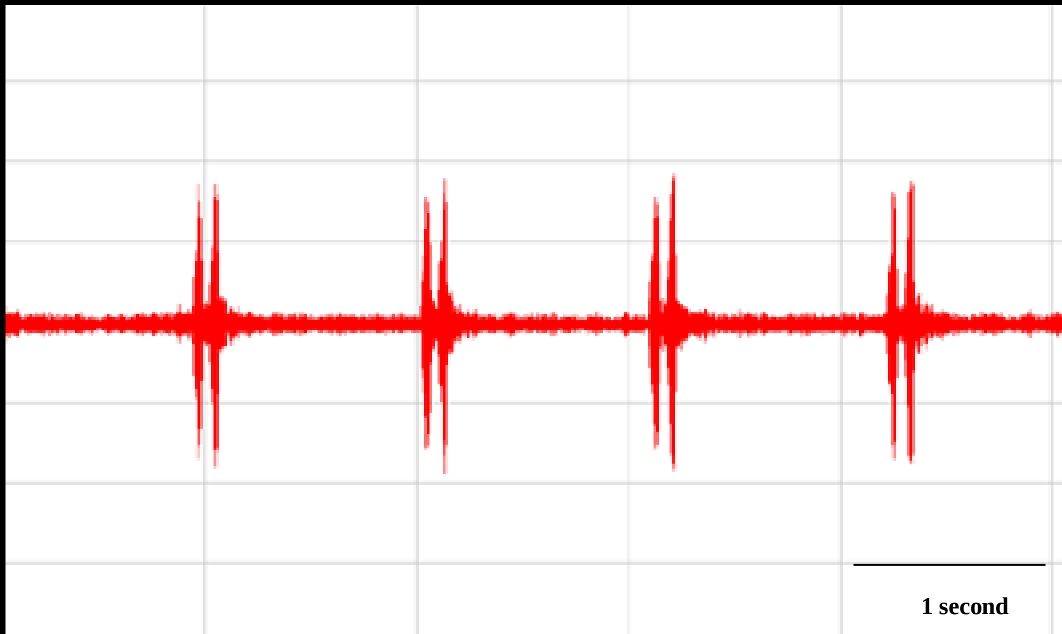
Brochopeplus sp. (Pseudophyllinae)



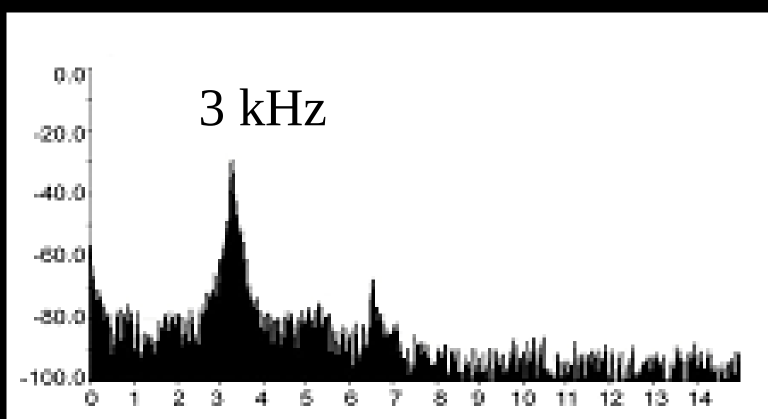


False leaf katydid
(Understorey)

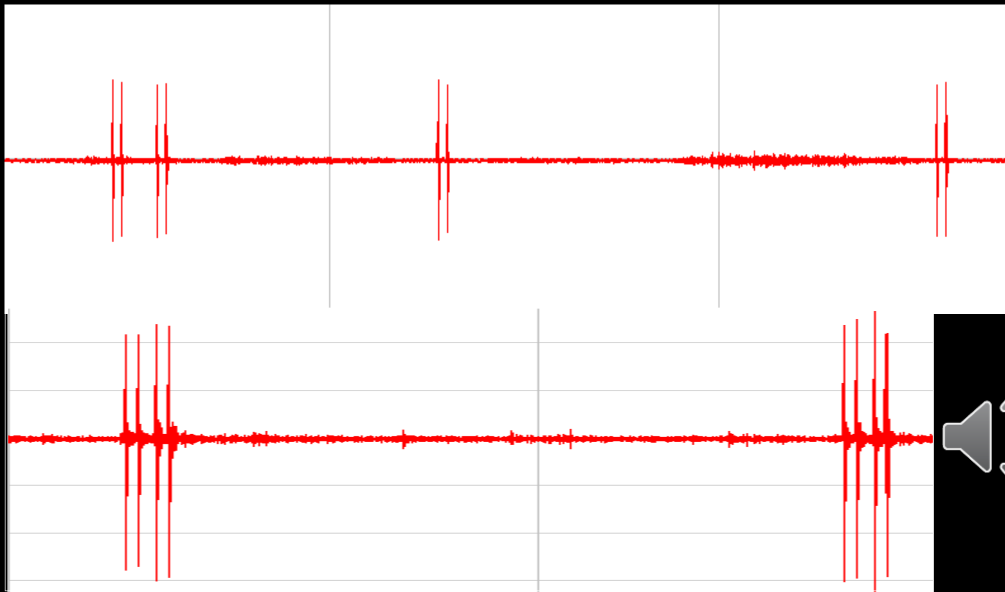
“Whistler” *Onomarchus uninotatus* (Pseudophyllinae)

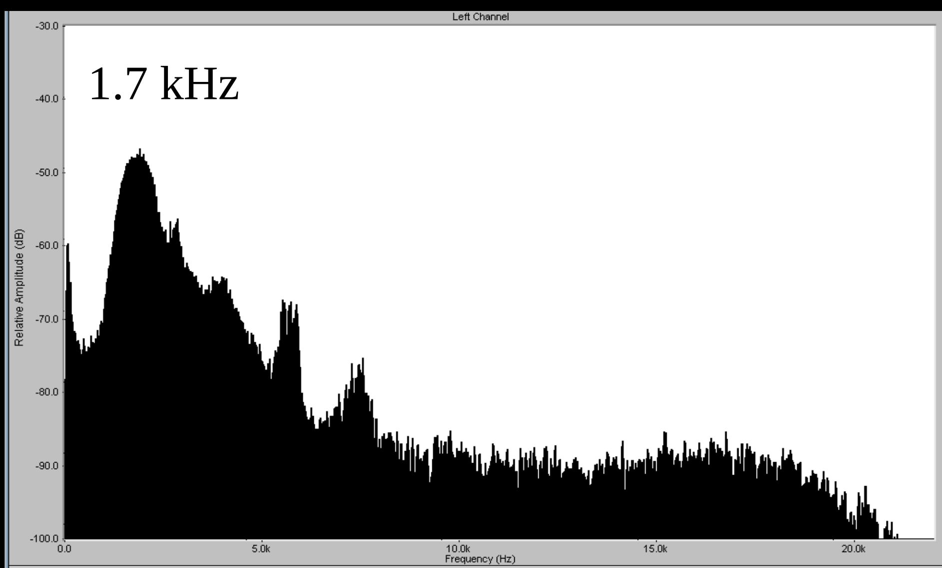


False leaf katydid
(Canopy)



Gryllacropsis sp. (Gryllacridoidea)





Tree weta
(Canopy)

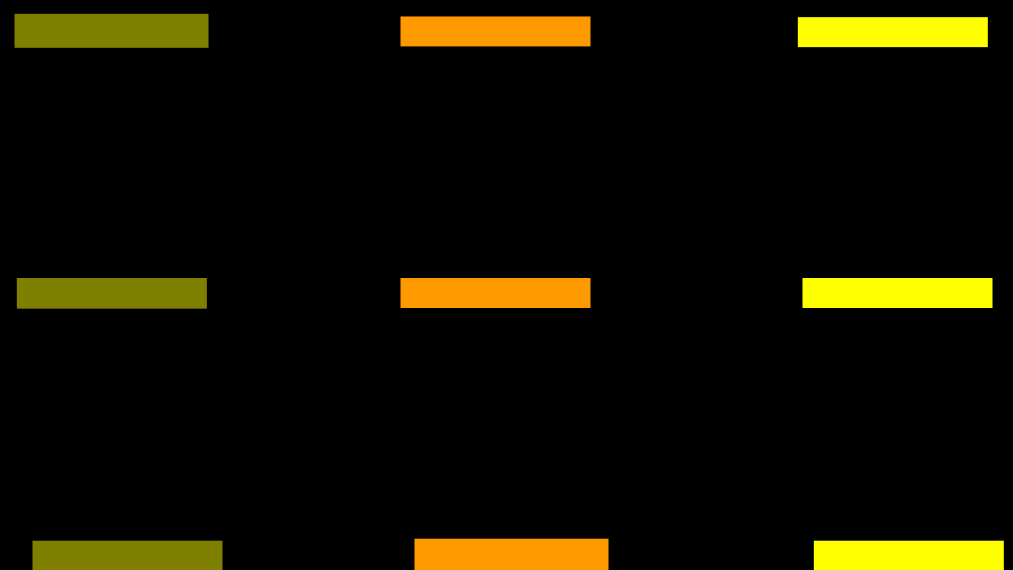
TEMPORAL PARTITIONING

Seasonal (months)

Circadian

(hours)

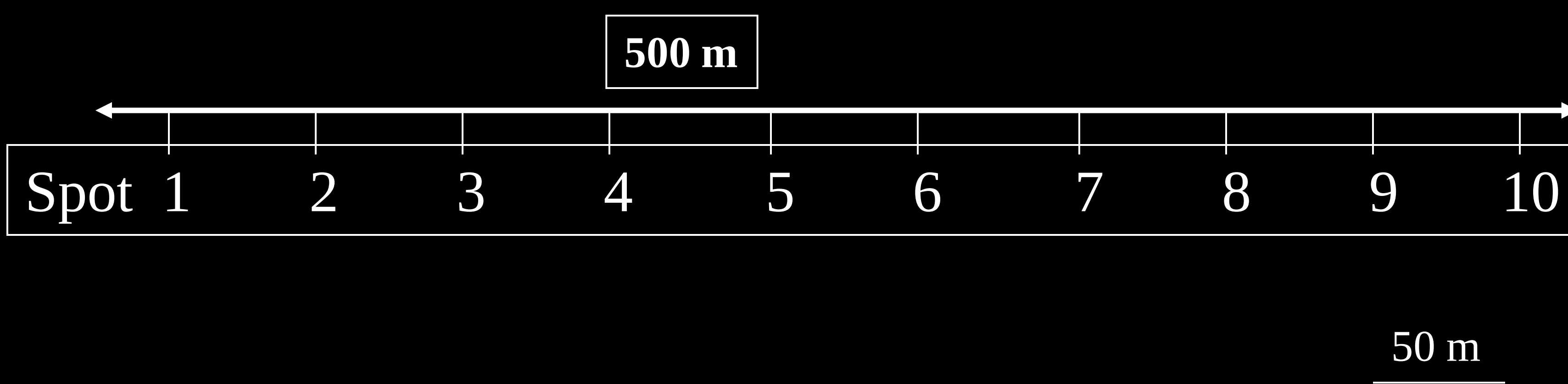
Fine temporal (seconds)



Species 1 2 3

DIEL CALLING PATTERNS ACOUSTIC SPOT SAMPLING

- **Two transects of 500 m length were laid at each site.**
- **In the 500 m transect, 10 spots were marked that were 50 m apart from each other.**

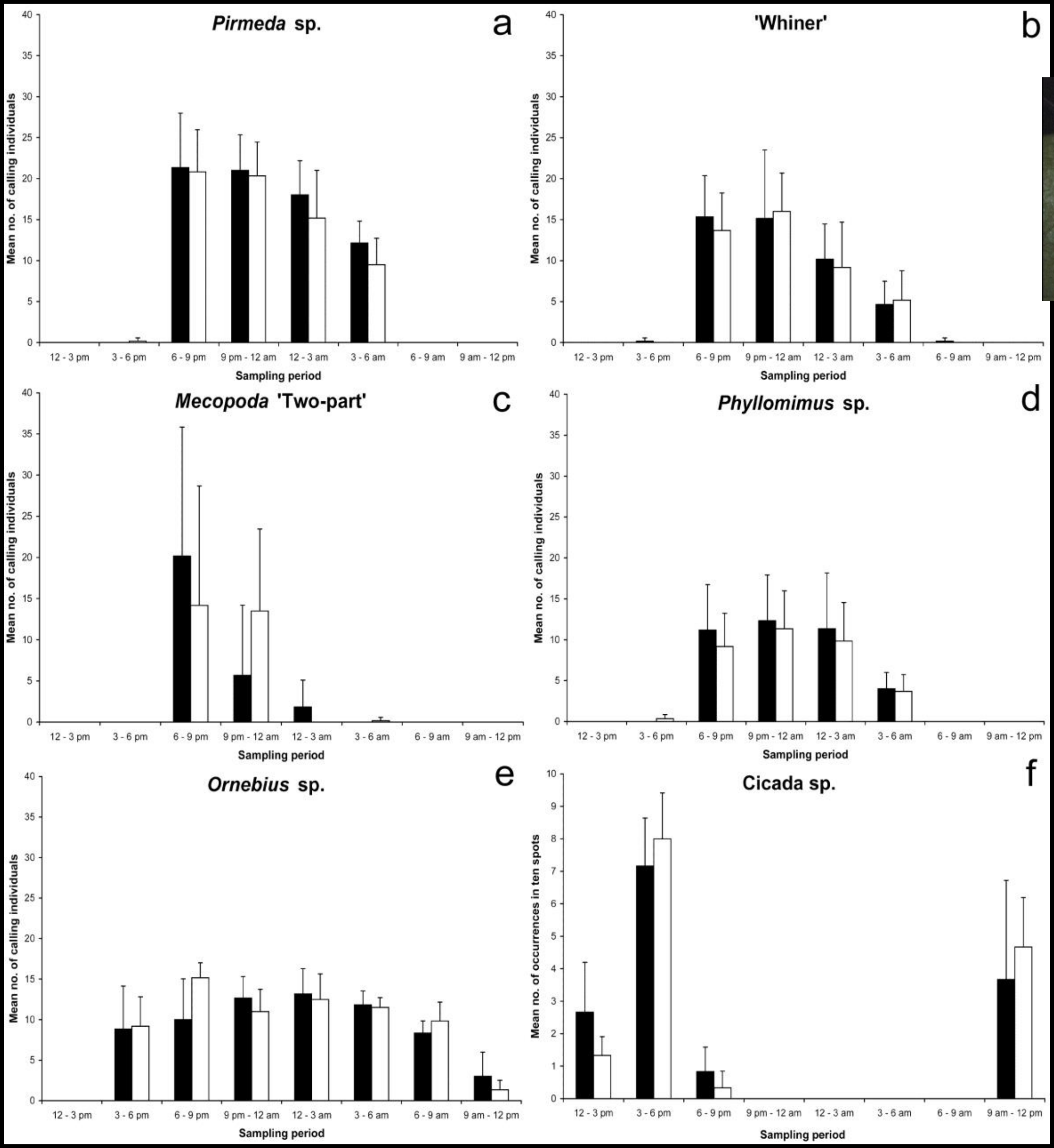


Transects sampled in 3-hour periods around the clock

The number of call types and calling individuals noted in a 5 minute period at each spot

Ambient noise recordings made using a recorder

CALLING PATTERNS OF INDIVIDUAL SPECIES



(Diwakar & Balakrishnan, 2007)

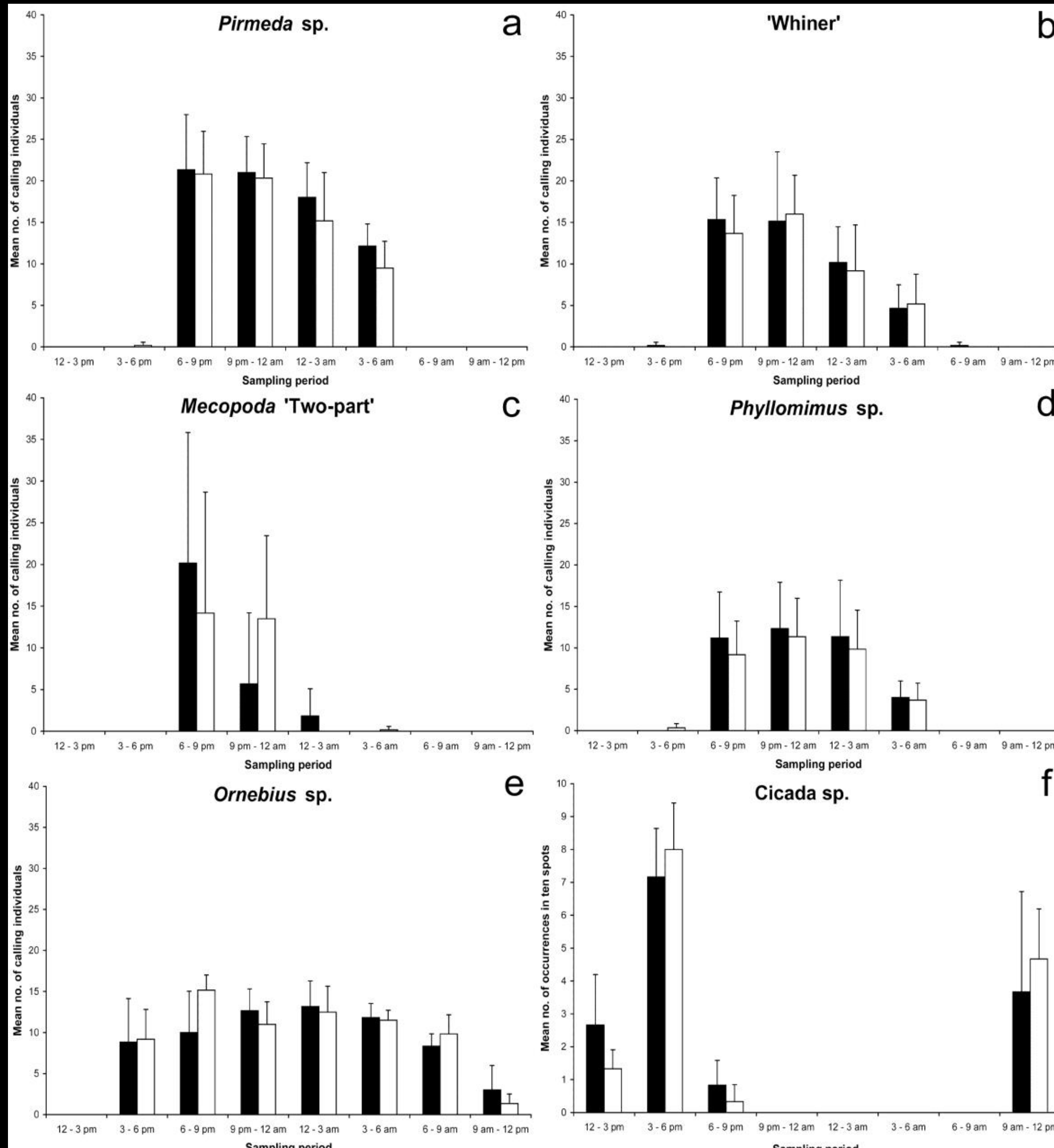
DIEL PATTERNING: SUMMARY

Dusk chorus starts abruptly and dies off slowly after midnight

No dawn chorus of crickets

No temporal partitioning of calling between cricket species on a diel scale

CALLING PATTERNS OF INDIVIDUAL SPECIES



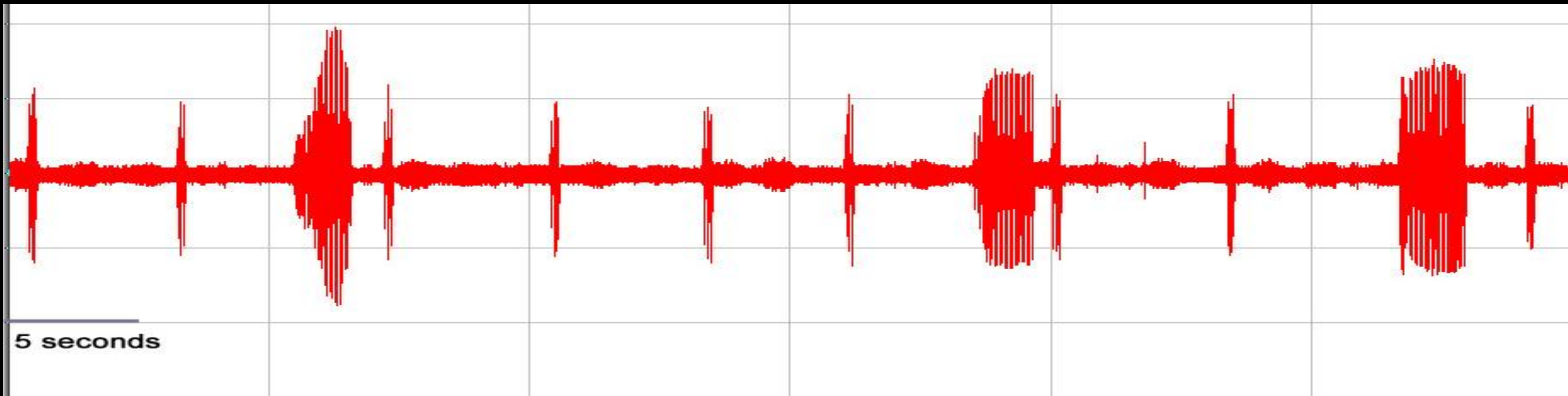
(Diwakar & Balakrishnan, 2007)

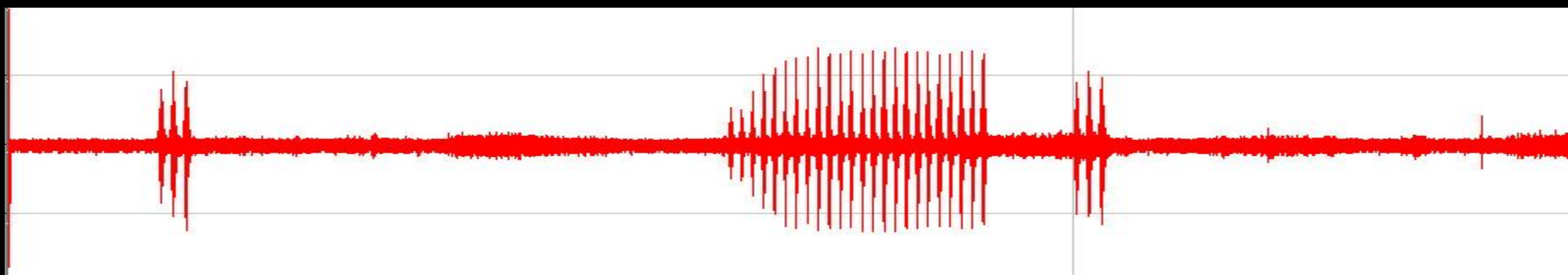
MATRIX OF TEMPORAL MASKING PROBABILITY

code	Sc	La	Ph	Wh	Xa	Or	Mic	Pi	Phy	15k	El	On	Gry	Me2	MeT	MeH
Sc		0.17	0.42	0.67	0	1	0.75	0.92	0.92	0.25	0.25	0.17	0	0.25	0.25	0
La	0.03		0.31	0.83	0.16	0.55	0.55	0.84	0.75	0.27	0.41	0.27	0.06	0.64	0.08	0.05
Ph	0.07	0.26		0.76	0.09	0.72	0.79	0.86	0.83	0.04	0.13	0.09	0.05	0.42	0.07	0.03
Wh	0.04	0.29	0.31		0.15	0.71	0.66	0.84	0.80	0.18	0.24	0.23	0.09	0.49	0.06	0.04
Xa	0	0.26	0.18	0.74		0.68	0.63	0.79	0.71	0.16	0.13	0.08	0	0.34	0.05	0
Or	0.07	0.20	0.32	0.76	0.15		0.72	0.79	0.74	0.15	0.19	0.19	0.05	0.38	0.07	0.04
Mic	0.06	0.22	0.38	0.78	0.15	0.79		0.80	0.73	0.15	0.20	0.18	0.06	0.36	0.05	0.04
Pi	0.06	0.28	0.33	0.79	0.15	0.69	0.64		0.76	0.15	0.22	0.23	0.08	0.48	0.06	0.05
Phy	0.06	0.27	0.35	0.82	0.15	0.71	0.64	0.82		0.17	0.20	0.23	0.07	0.56	0.07	0.05
15k	0.08	0.43	0.08	0.83	0.15	0.65	0.60	0.75	0.75		0.45	0.30	0.10	0.53	0.05	0.03
El	0.06	0.52	0.20	0.90	0.10	0.66	0.62	0.88	0.72	0.36		0.22	0.06	0.50	0.10	0
On	0.04	0.32	0.13	0.81	0.06	0.62	0.53	0.87	0.79	0.23	0.21		0.15	0.66	0	0.06
Gry	0	0.22	0.22	0.94	0	0.50	0.56	0.83	0.72	0.22	0.17	0.44		0.67	0.06	0.06
Me2	0.03	0.36	0.28	0.79	0.11	0.58	0.49	0.83	0.89	0.18	0.22	0.31	0.11		0.04	0.06
MeT	0.23	0.38	0.38	0.92	0.15	0.92	0.62	0.92	1	0.15	0.38	0	0.08	0.31		0.08
MeH	0	0.27	0.18	0.73	0	0.64	0.64	0.82	0.82	0.09	0	0.27	0.09	0.64	0.09	

Five minute time windows

FINE TEMPORAL PARTITIONING



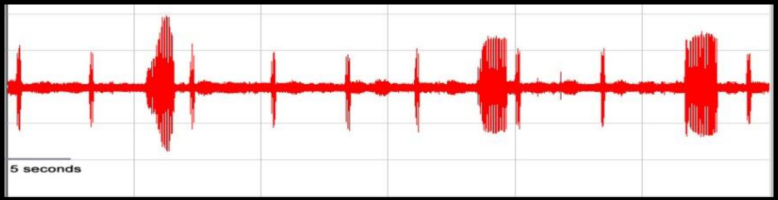


MATRIX OF FINE TEMPORAL MASKING PROBABILITY

code	Sc	La	Ph	Wh	Xa	Or	Mic	Pi	Phy	15k	El	On	Gry	Me2	MeT	MeH
Sc		0.08	0.59	0.08	0.69	0.06	0.07	0.05	0.28	0.00	0.04	0.12	0.06	0.73	1.00	0.87
La	0.35		0.55	0.10	0.69	0.06	0.07	0.06	0.27	0.00	0.04	0.11	0.05	0.74	1.00	0.87
Ph	0.36	0.08		0.14	0.67	0.05	0.07	0.05	0.25	0.00	0.03	0.11	0.05	0.73	1.00	0.90
Wh	0.36	0.08	0.69		0.66	0.07	0.09	0.08	0.19	0.00	0.08	0.11	0.06	0.78	1.00	0.92
Xa	0.34	0.08	0.56	0.10		0.06	0.08	0.05	0.27	0.00	0.04	0.10	0.05	0.73	1.00	0.88
Or	0.34	0.07	0.48	0.10	0.68		0.03	0.07	0.27	0.00	0.03	0.11	0.06	0.73	1.00	0.85
Mic	0.30	0.08	0.60	0.12	0.69	0.02		0.03	0.09	0.00	0.02	0.11	0.05	0.74	1.00	0.88
Pi	0.38	0.09	0.49	0.07	0.66	0.07	0.05		0.32	0.01	0.15	0.04	0.06	0.79	1.00	0.81
Phy	0.31	0.08	0.64	0.11	0.69	0.06	0.33	0.04		0.01	0.02	0.11	0.05	0.73	1.00	0.88
15k	0.38	0.08	0.59	0.07	0.72	0.06	0.07	0.12	0.18		0.03	0.08	0.05	0.73	1.00	0.88
El	0.37	0.07	0.55	0.10	0.64	0.06	0.04	0.09	0.10	0.00		0.16	0.07	0.68	1.00	0.76
On	0.31	0.08	0.59	0.10	0.70	0.06	0.08	0.16	0.24	0.01	0.04		0.07	0.74	1.00	0.87
Gry	0.24	0.07	0.53	0.07	0.69	0.06	0.07	0.09	0.26	0.01	0.06	0.10		0.69	1.00	0.86
Me2	0.35	0.08	0.58	0.10	0.68	0.06	0.08	0.05	0.26	0.00	0.05	0.11	0.05		1.00	0.88
MeT	0.34	0.08	0.57	0.10	0.68	0.06	0.07	0.06	0.26	0.00	0.04	0.11	0.05	0.74		0.88
MeH	0.34	0.08	0.58	0.11	0.68	0.06	0.08	0.06	0.27	0.00	0.04	0.11	0.05	0.74	1.00	

TEMPORAL OVERLAP

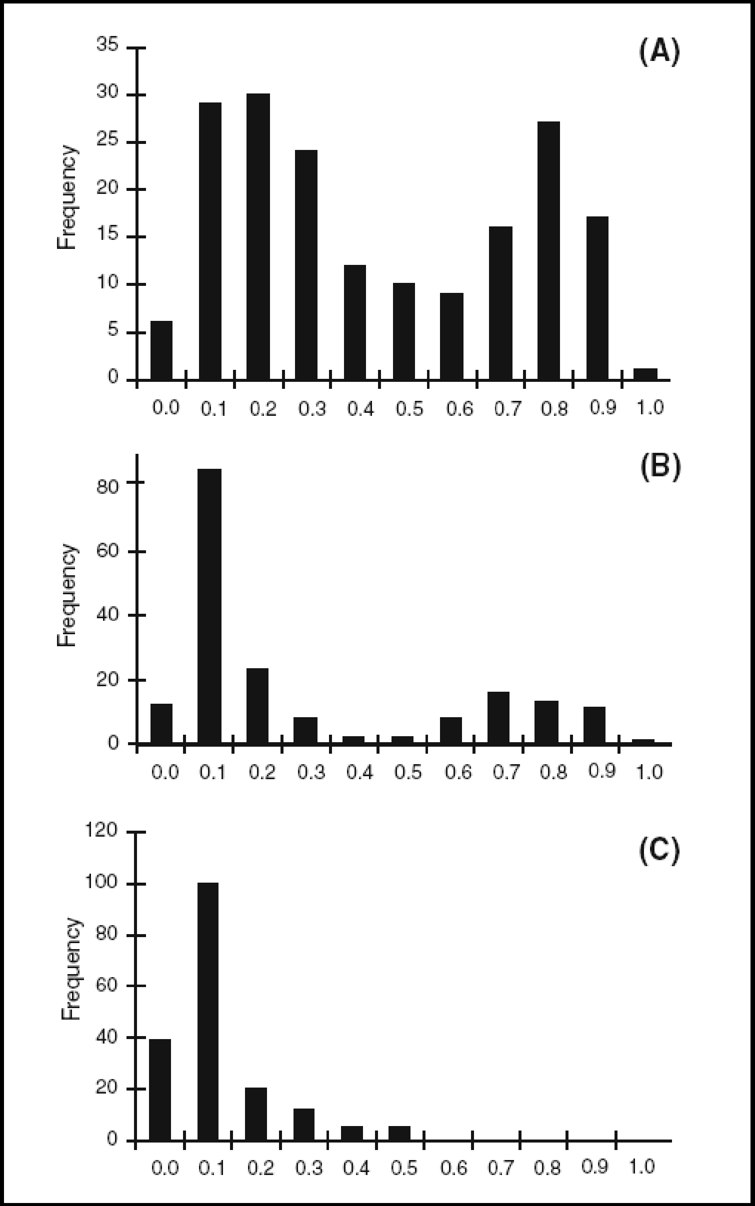
Probability of calling together in 5 min windows
(Gross Temporal Overlap)



Temporal pattern   Seconds

(Fine Temporal Overlap)

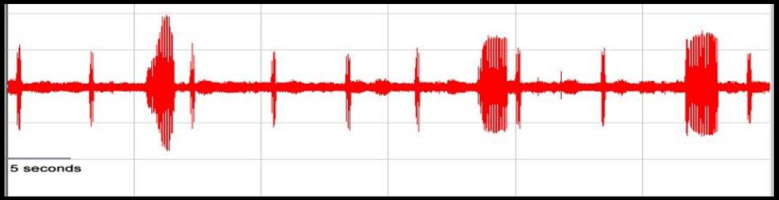
Product of GTO and FTO
(Effective Temporal Overlap)
Median ETO = 0.04



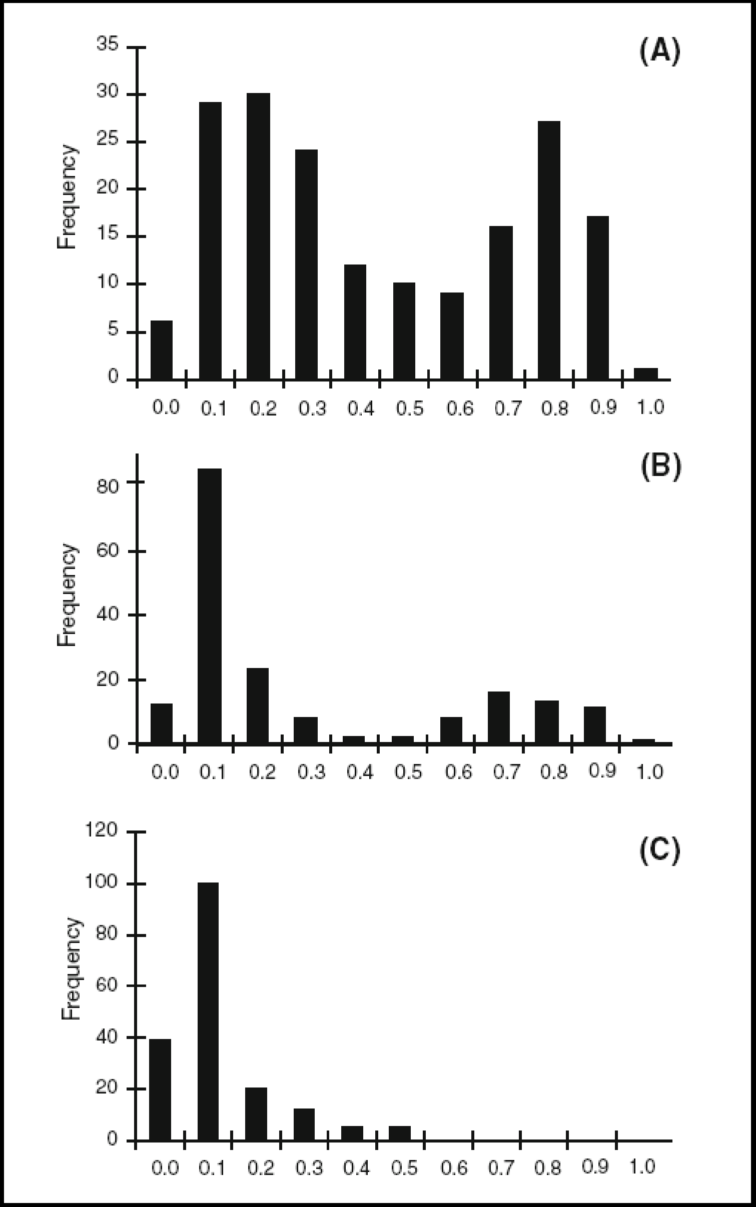
(Jain et al., 2014)

TEMPORAL ACOUSTIC INTERFERENCE

A significant negative correlation between GTO and FTO:

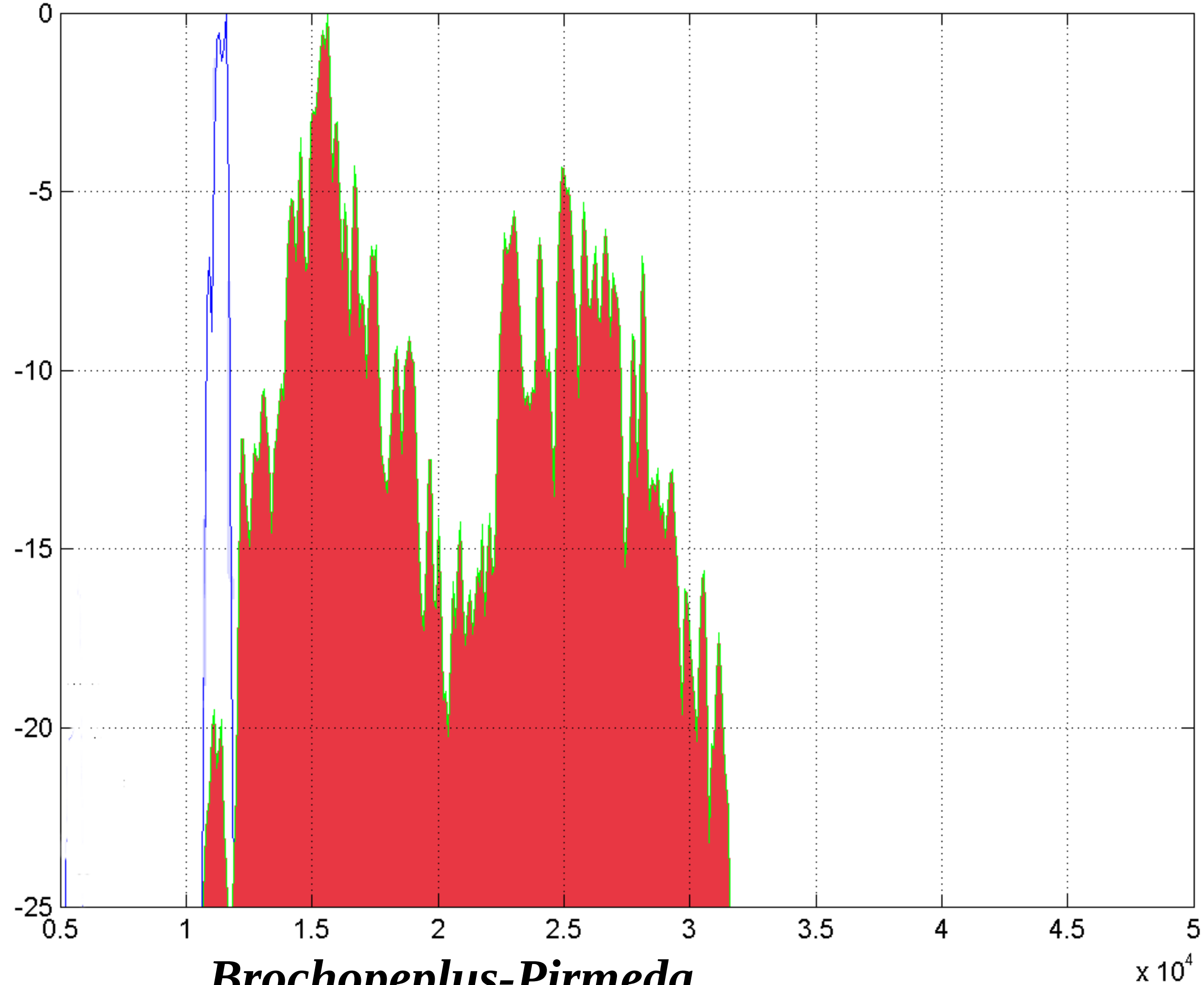


Species pairs that experience high temporal overlap may avoid calling together



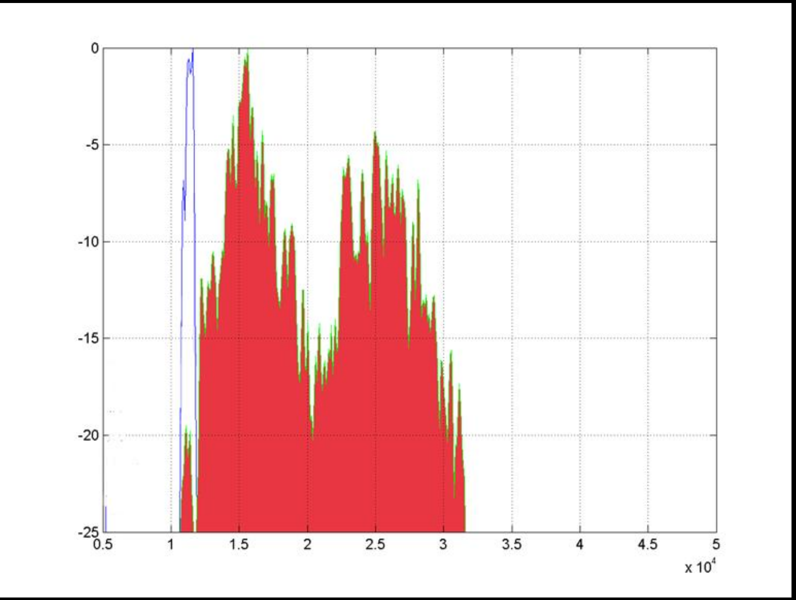
(Jain et al., 2014)

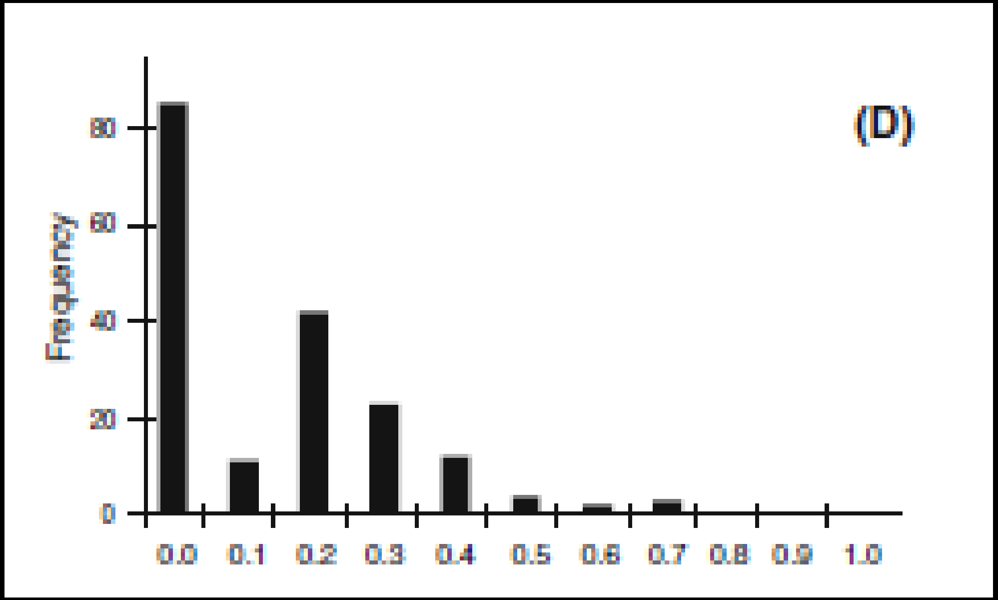
SPECTRAL OVERLAP

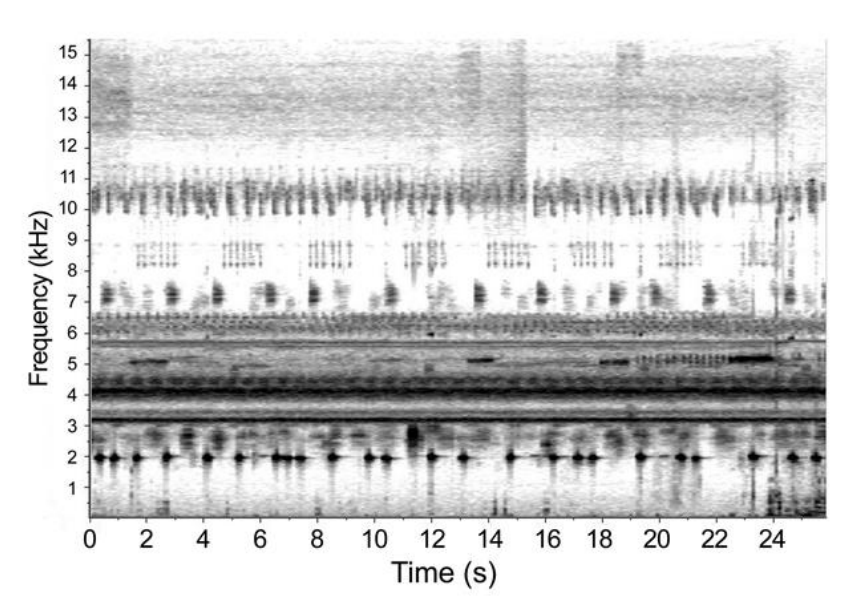


Brochopeplus-Pirmeda

SPECTRAL OVERLAP

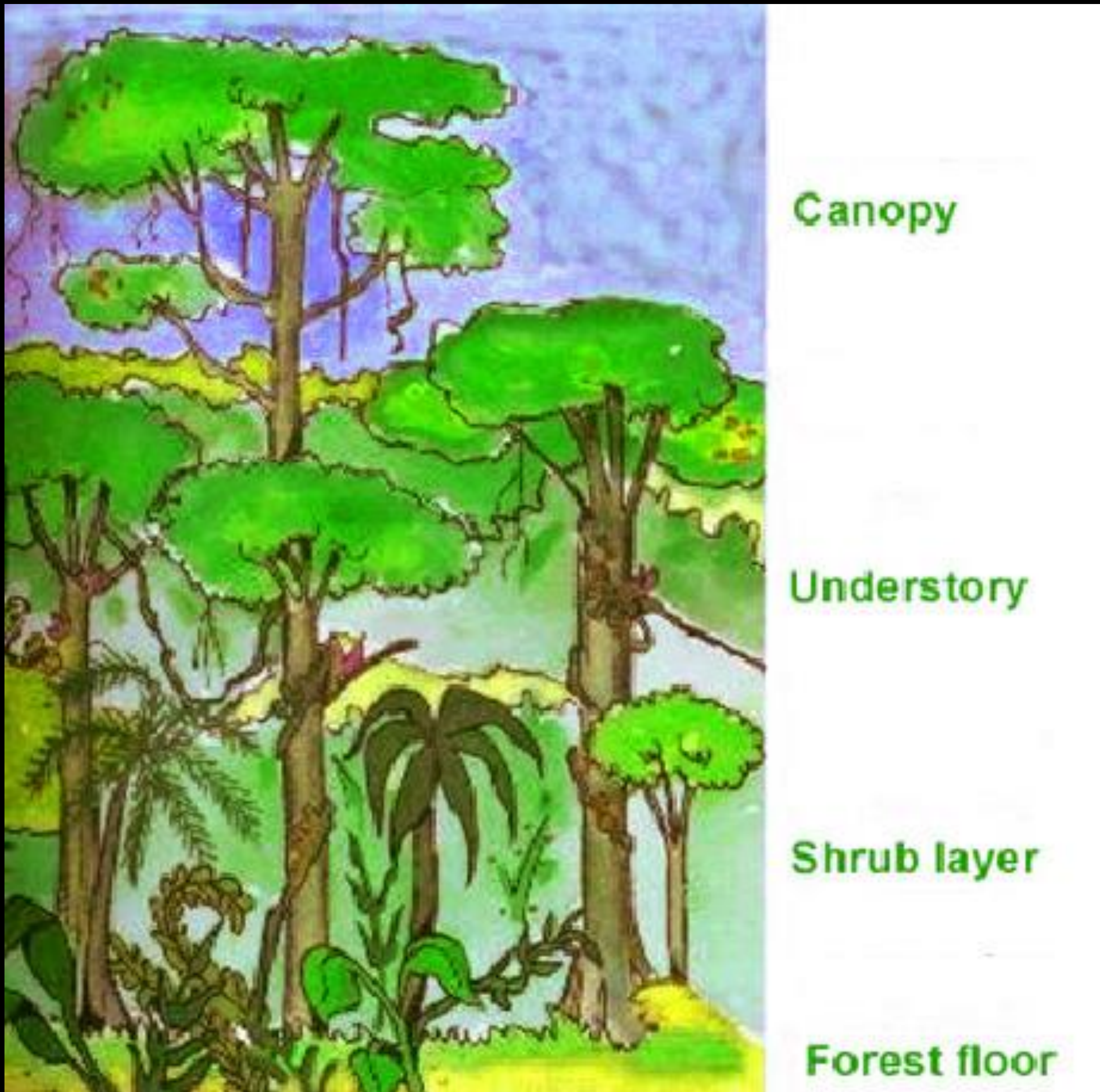






(Jain et al. Evol. Ecol. 2014)

HABITAT ACOUSTICS AND VERTICAL STRATIFICATION



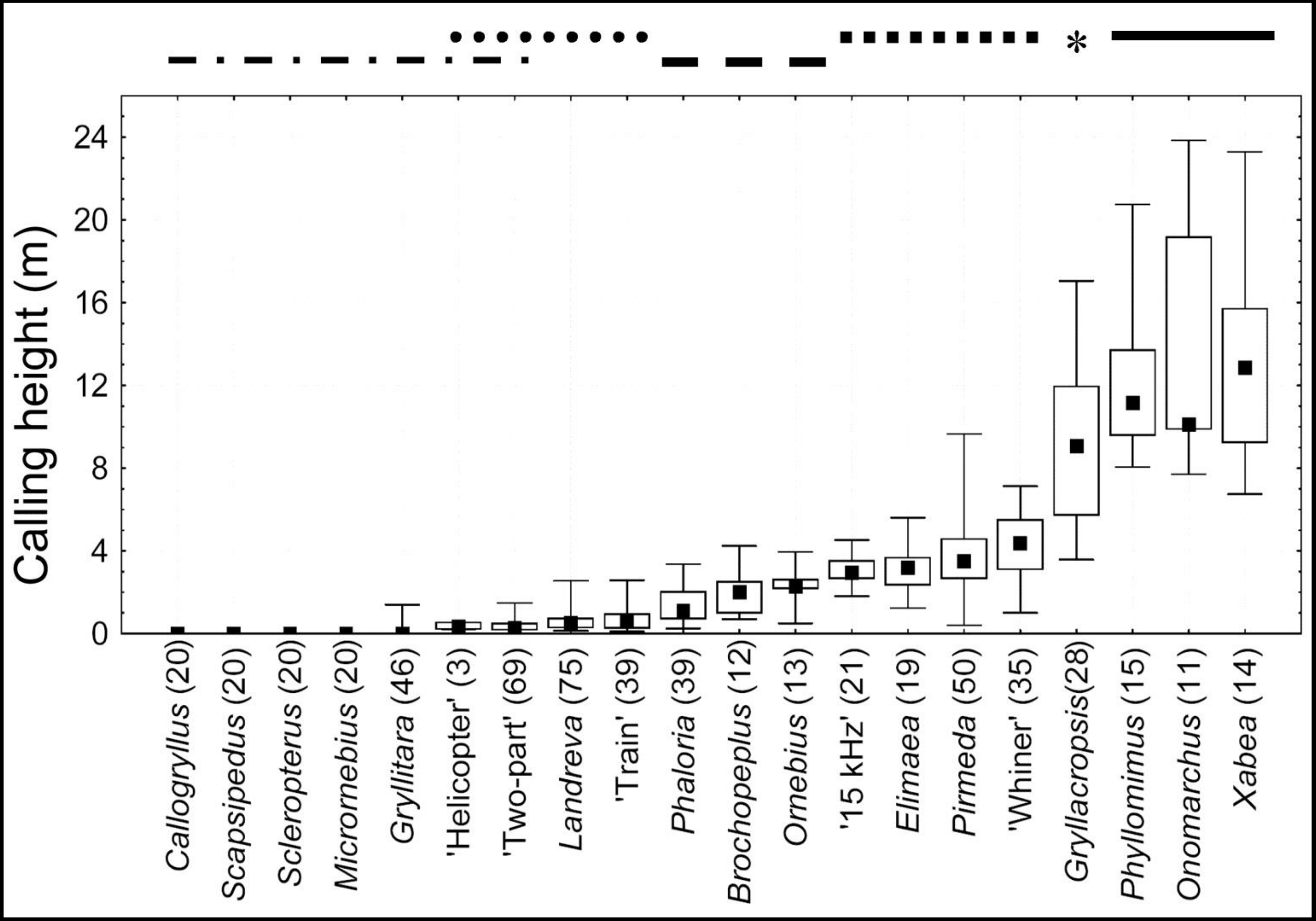
3.2 kHz

11 kHz

Broad-
band

4.86 kHz

VERTICAL STRATIFICATION



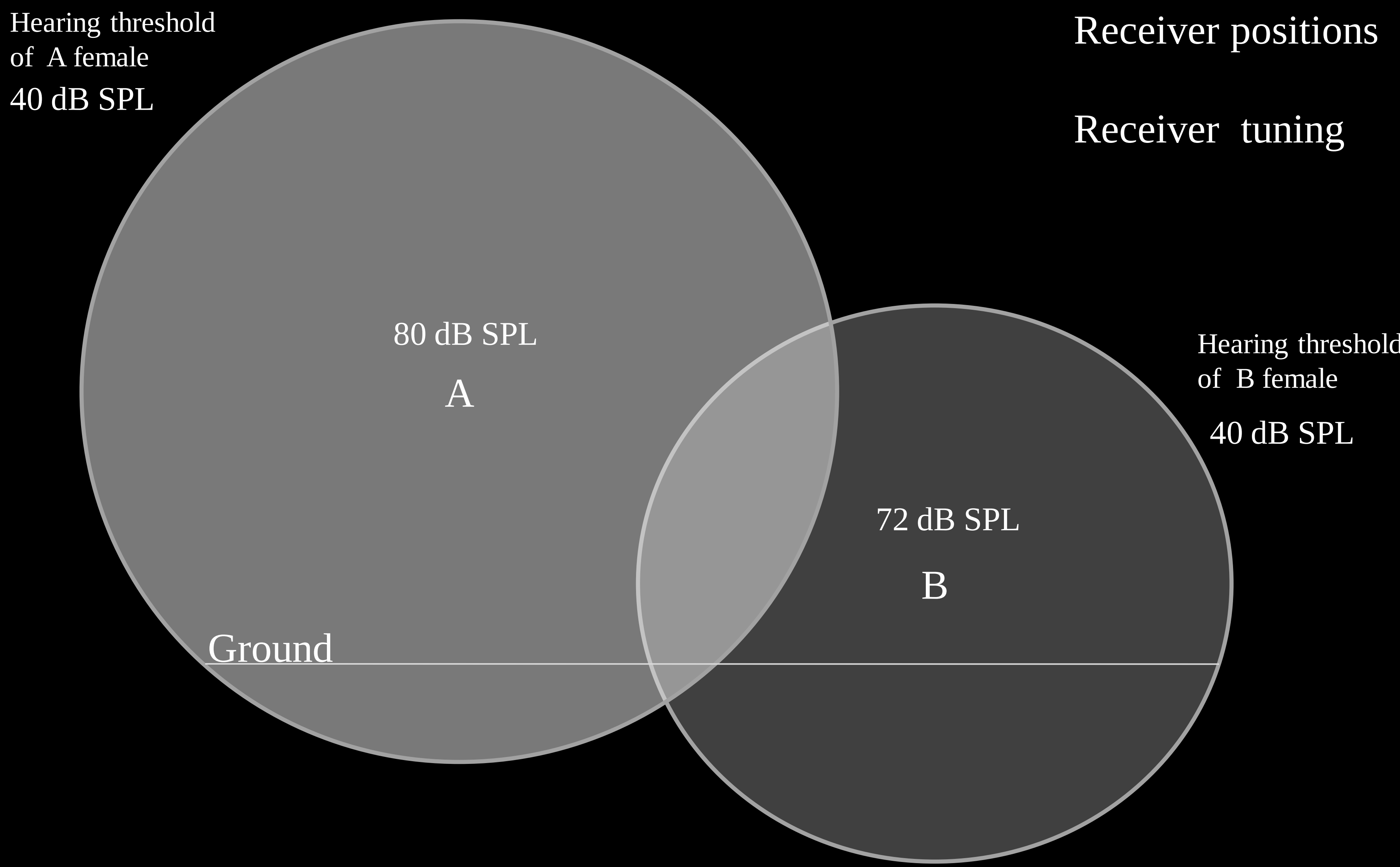
(Diwakar & Balakrishnan, 2007)

PAIRWISE SPATIAL MASKING

Spherical spreading

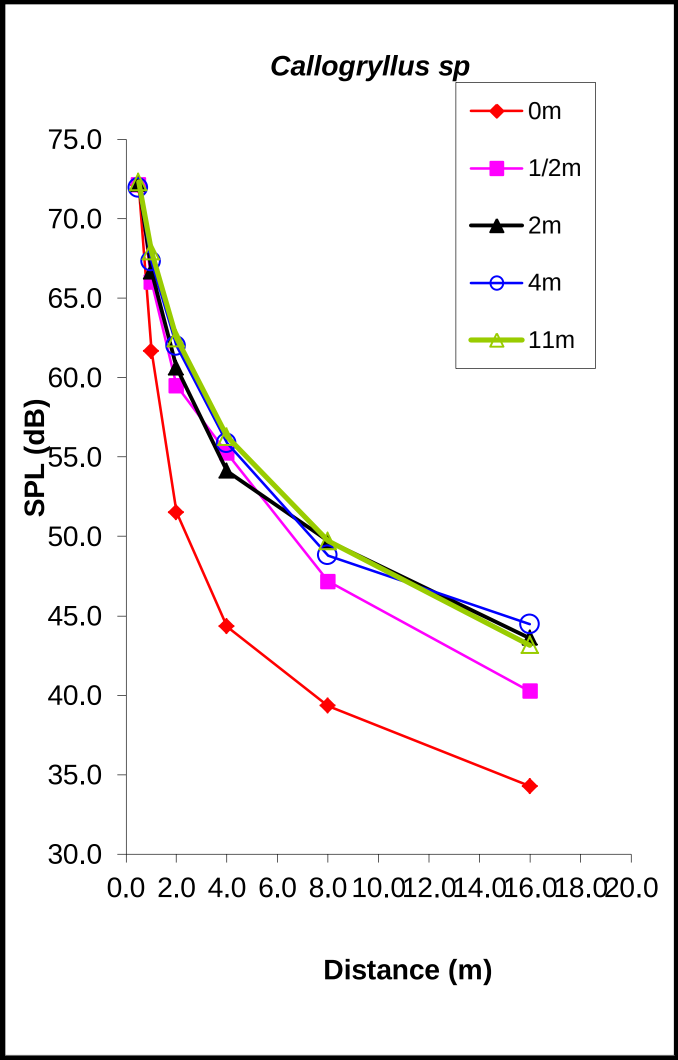
Receiver positions

Receiver tuning

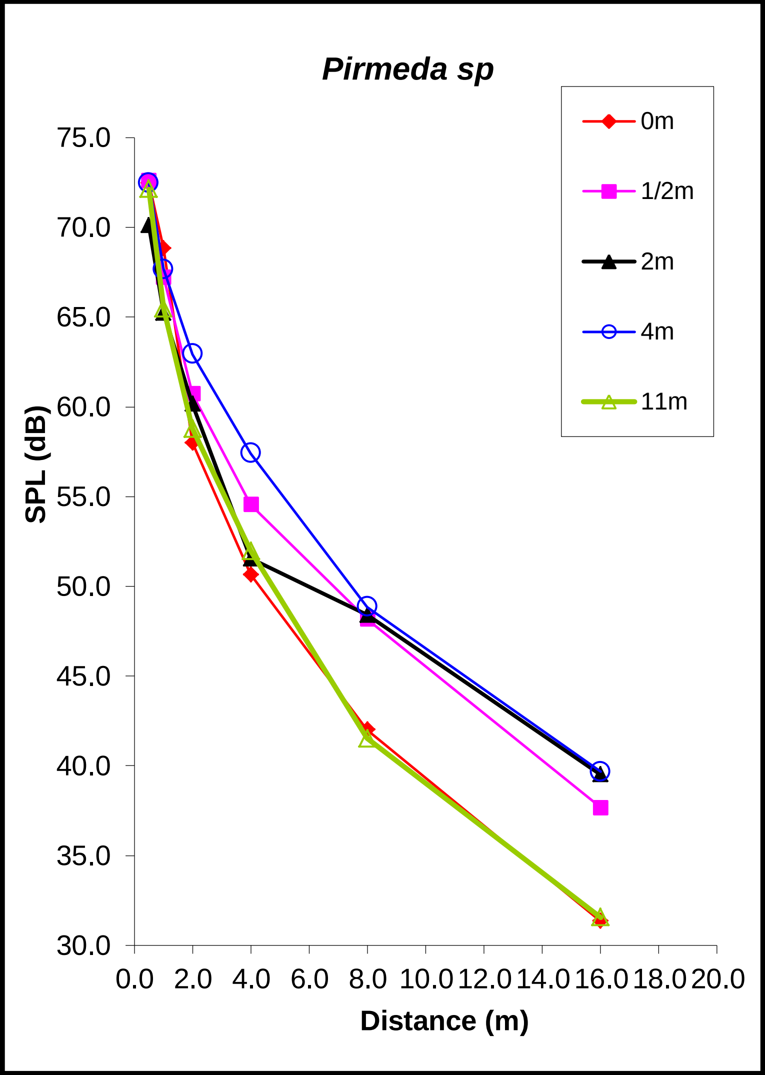


TRANSMISSION EXPERIMENTS

ATTENUATION



Ground dwelling field cricket

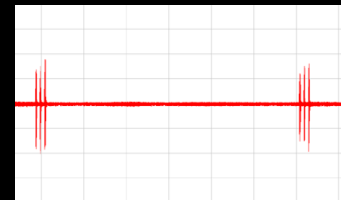
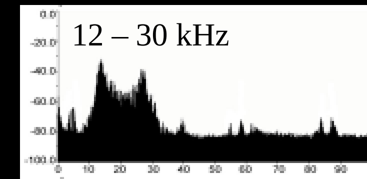


Understorey false leaf katydid

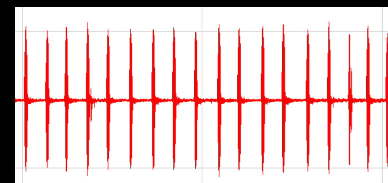
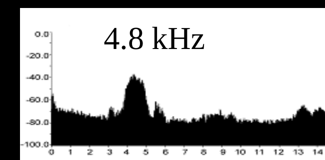
(Jain & Balakrishnan, 2012)

SPATIAL MASKING

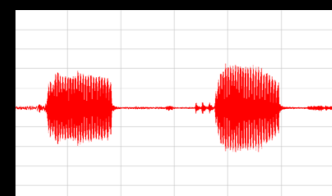
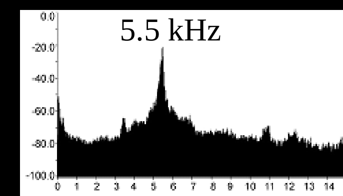
Pirmeda rosetta

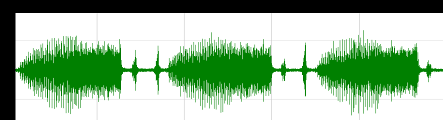
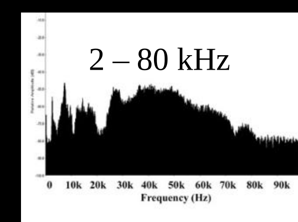
Landreva sp.

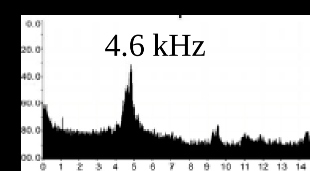
‘Whiner’

Mecopoda ‘Two-Part’

Phaloria sp.

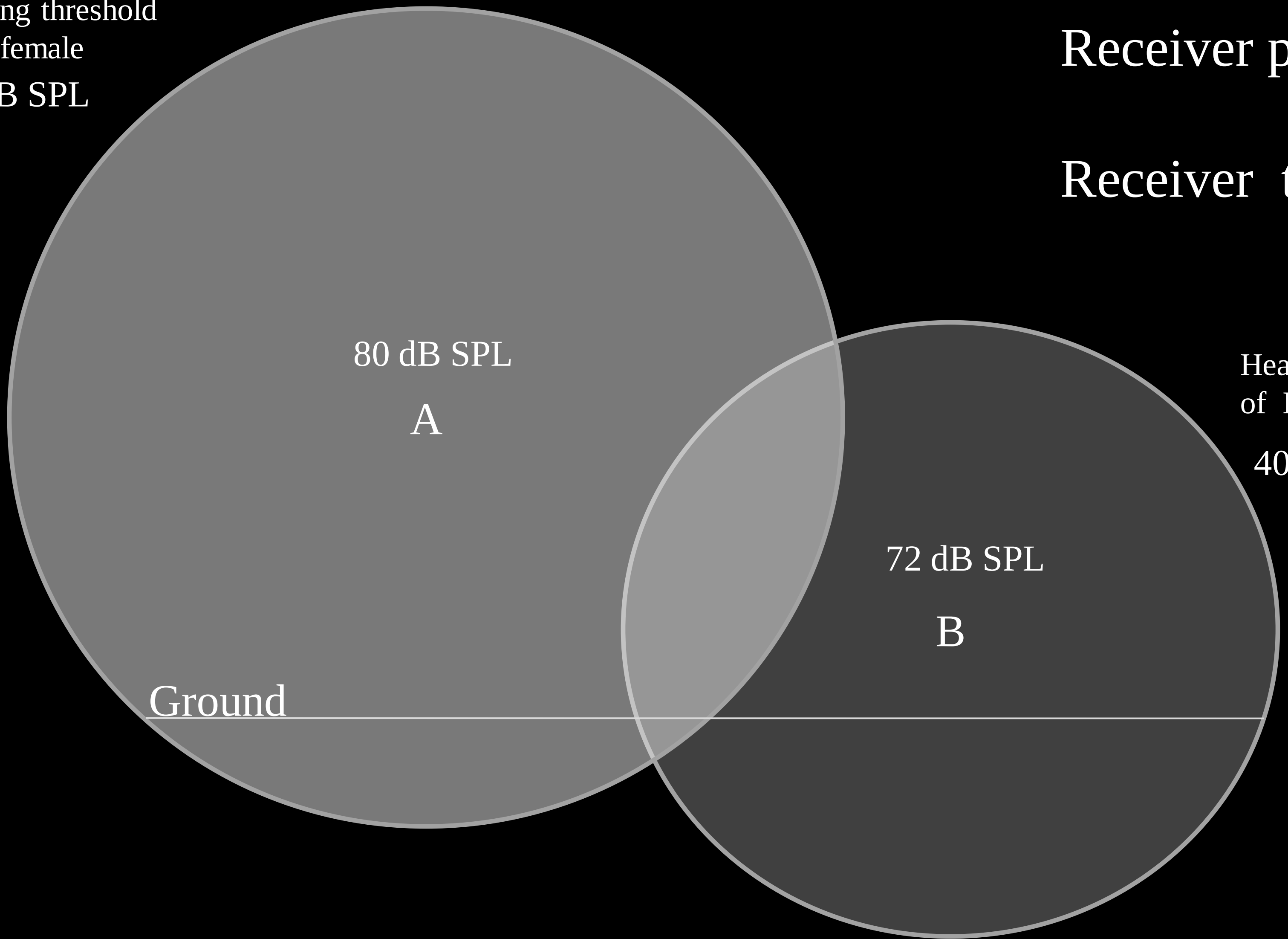



PAIRWISE SPATIAL MASKING

Spherical spreading

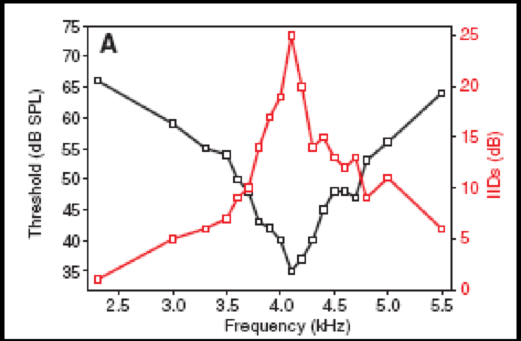
Receiver positions

Receiver tuning



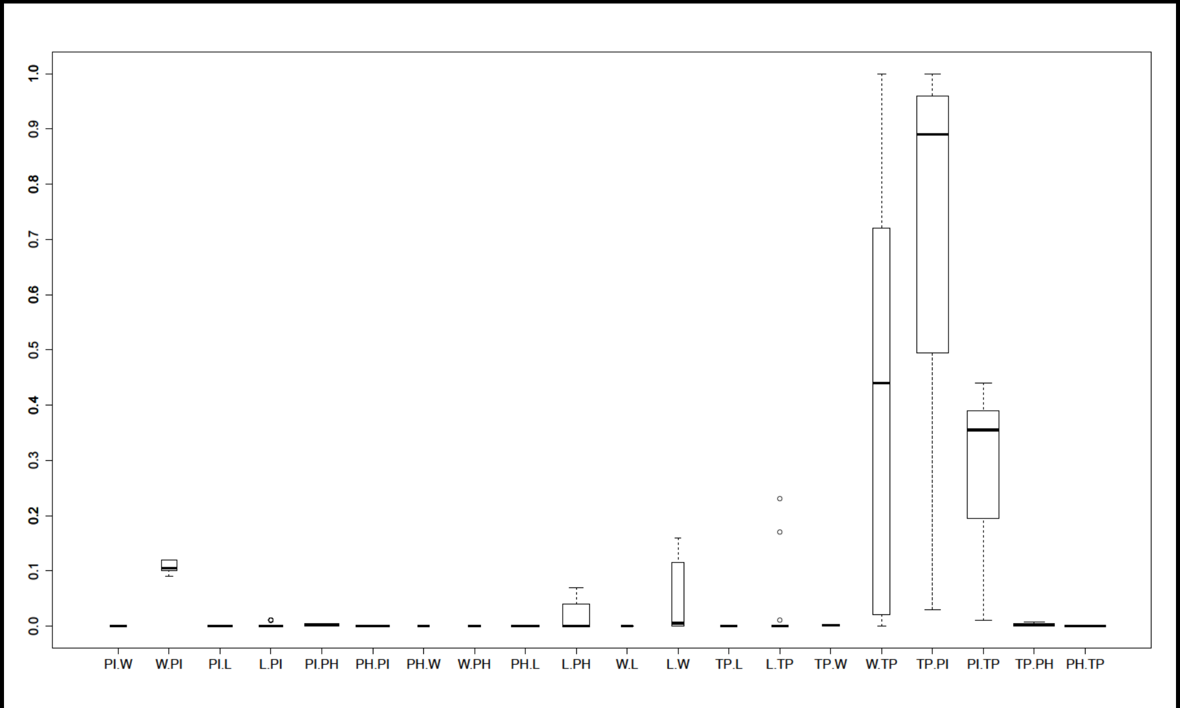
SPATIAL MASKING

Tuned receivers



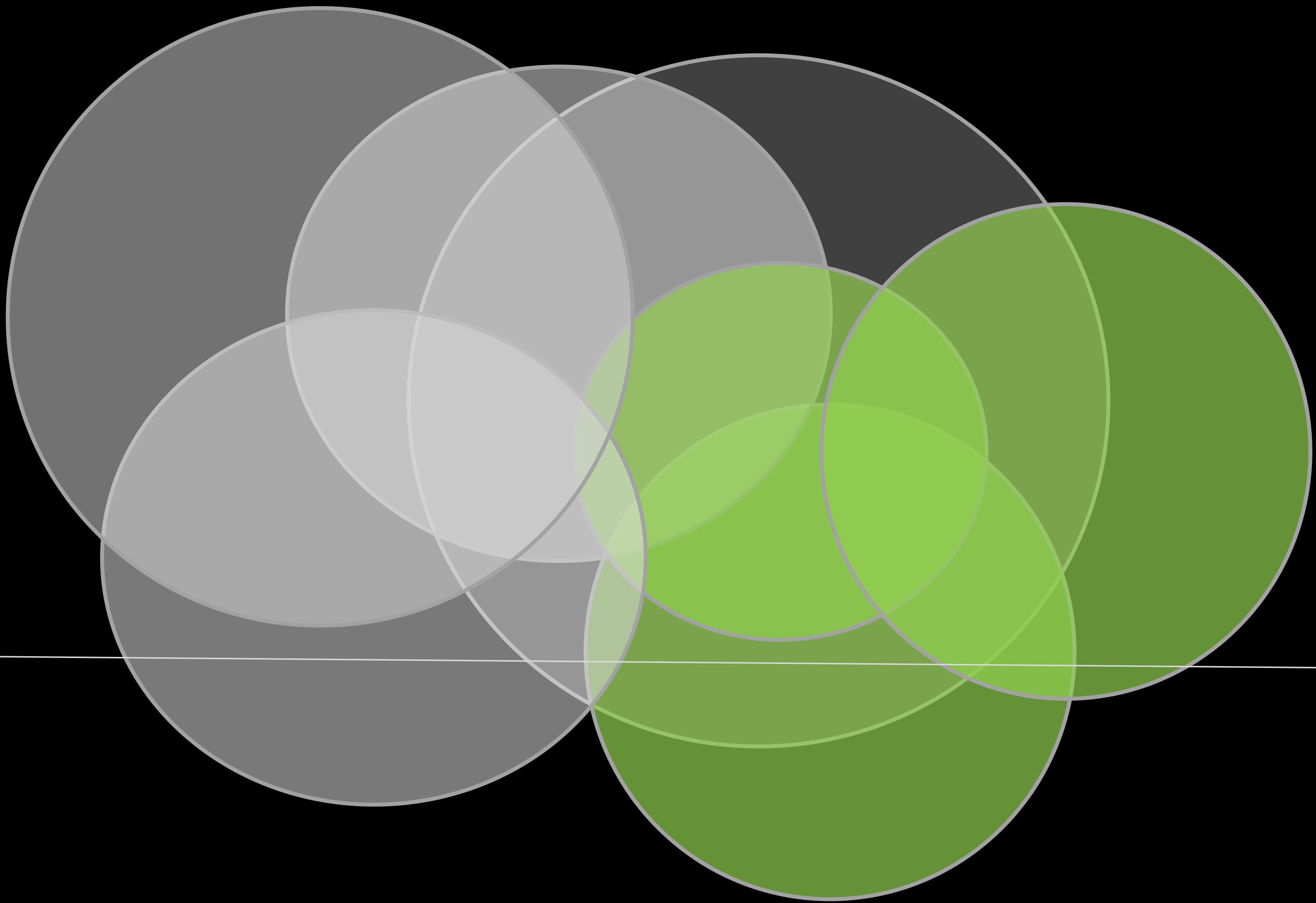
(Schmidt et al. 2011)

Spatial Masking Probability

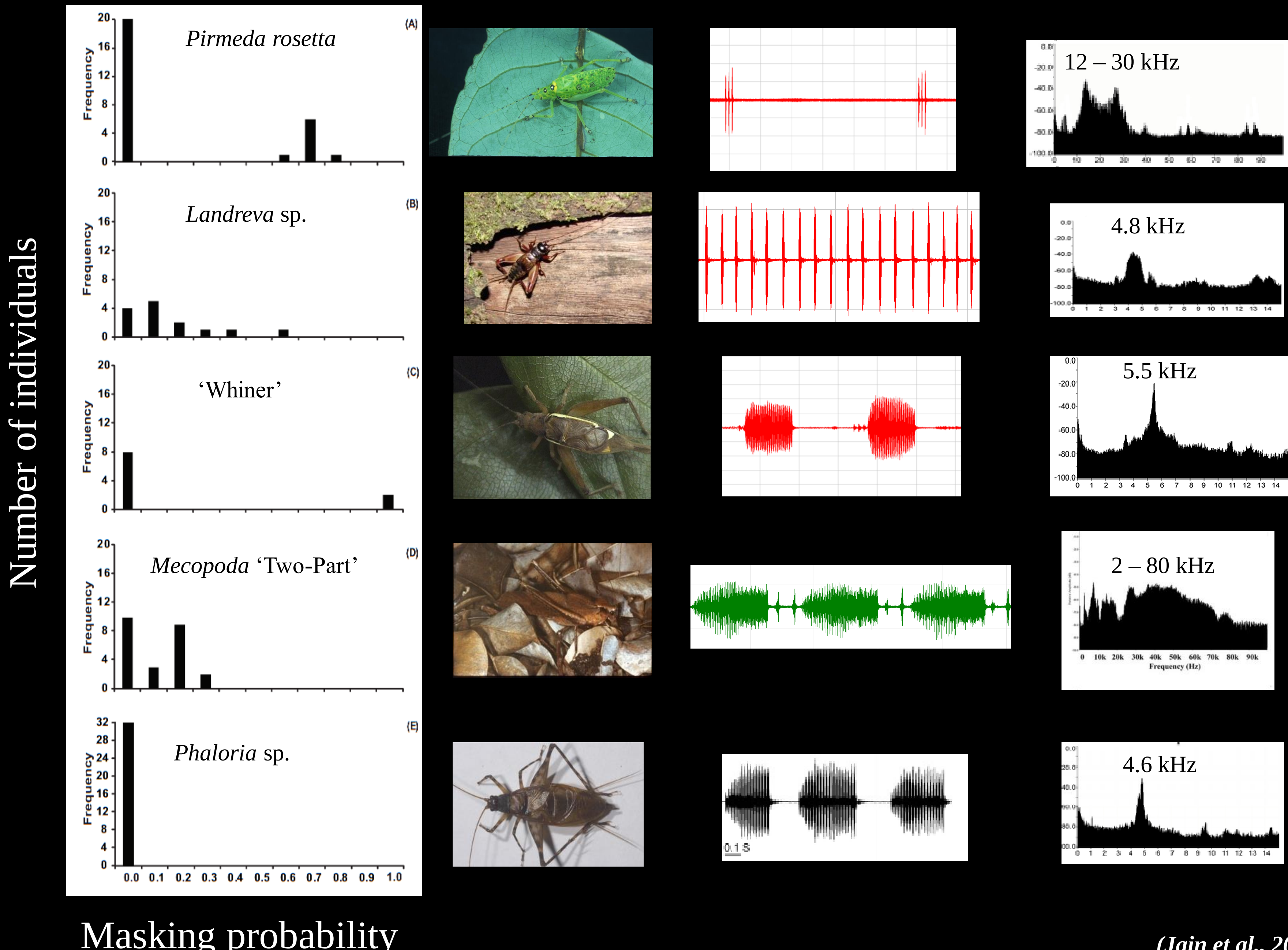


(Jain et al. 2014)

NATURAL CHORUSES



SPATIOTEMPORAL MASKING IN NATURAL CHORUSES



(Jain et al., 2014)

CACOPHONY OR SOUNDS OF SILENCE?

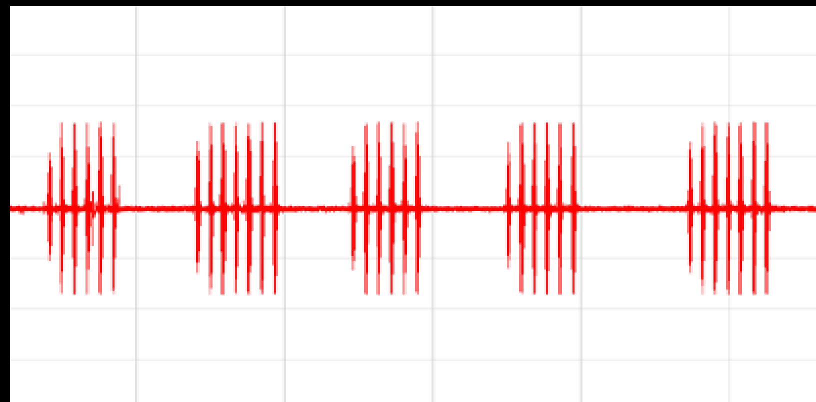
When all axes of separation are taken into account,

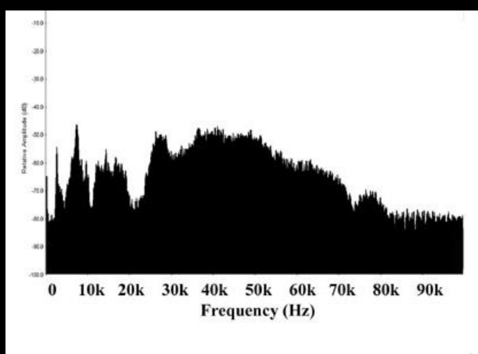
Median Masking Probabilities are close to zero!

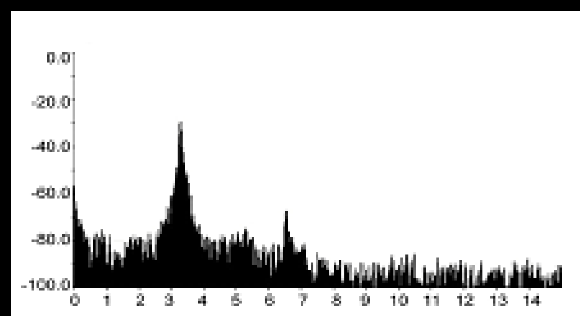
(Jain et al. 2014)

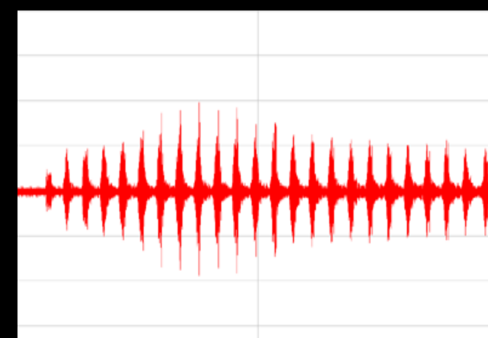
THE ACOUSTIC COMMUNITY: CHANCE OR NECESSITY?

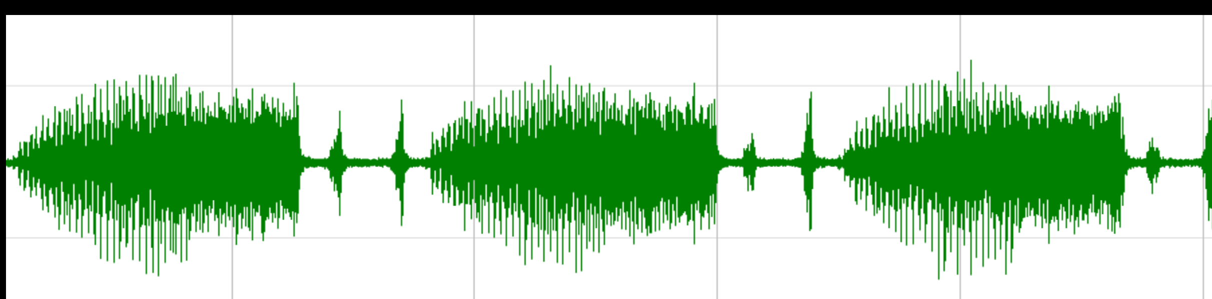
OPTIMALITY IN THE COMMUNICATION NETWORK?

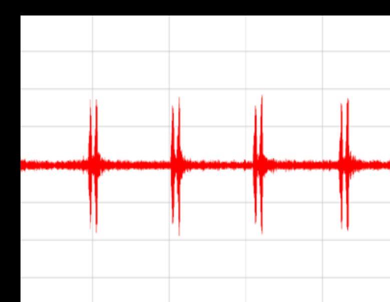








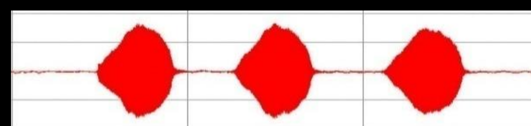




COMMUNICATION

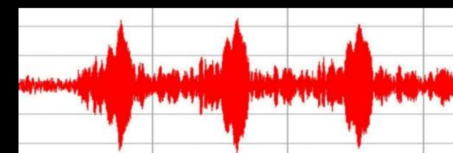
Sender

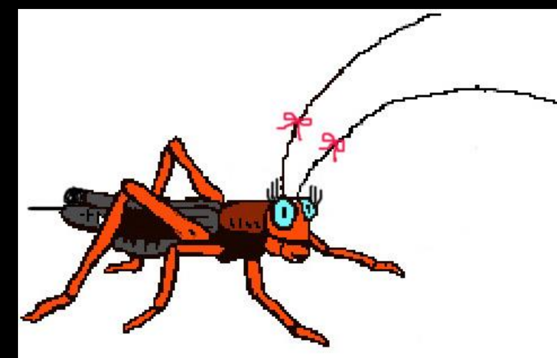
Signal



Medium

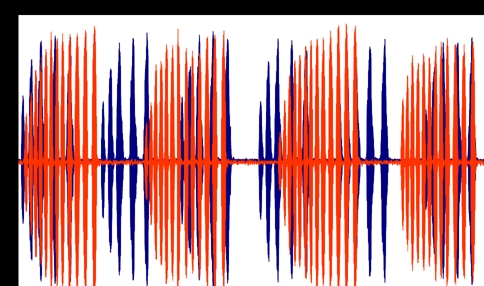
Distortion





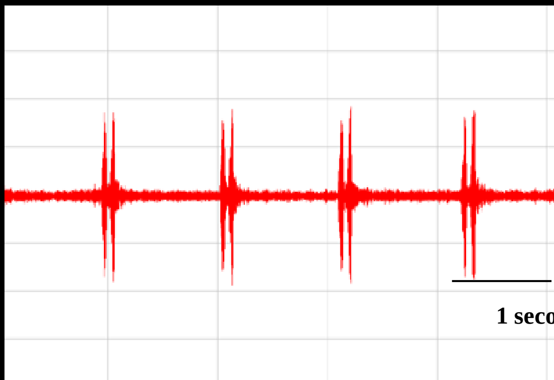
Receiver

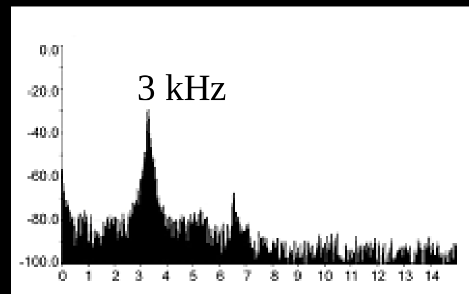
Competing callers

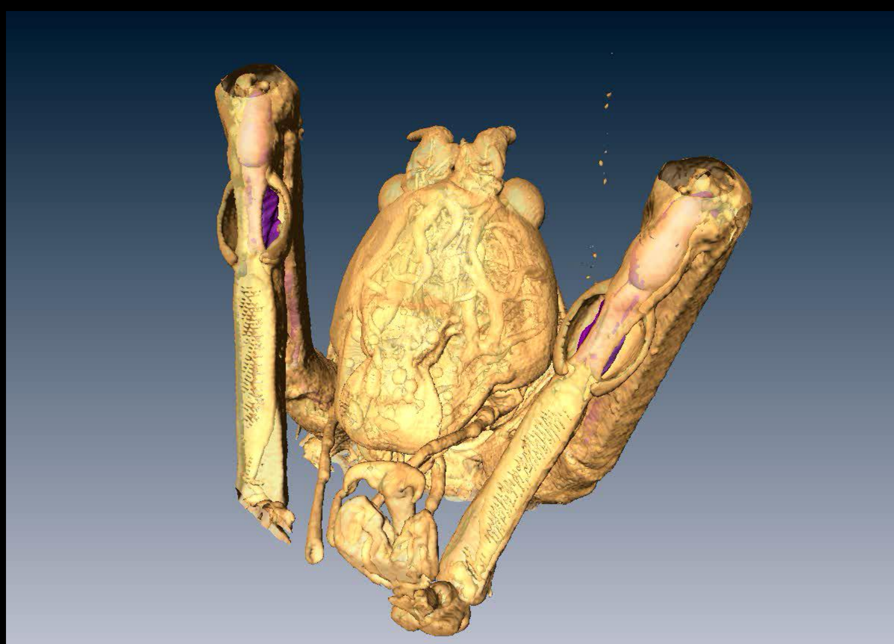


Masking

RECEIVER AUDITORY TUNING



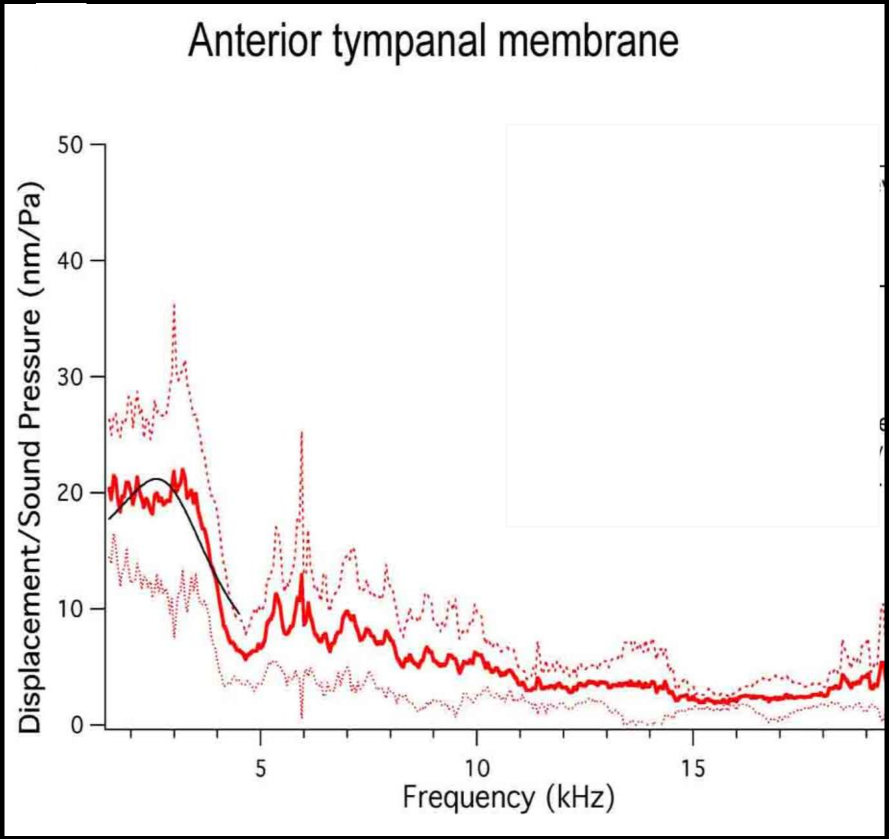


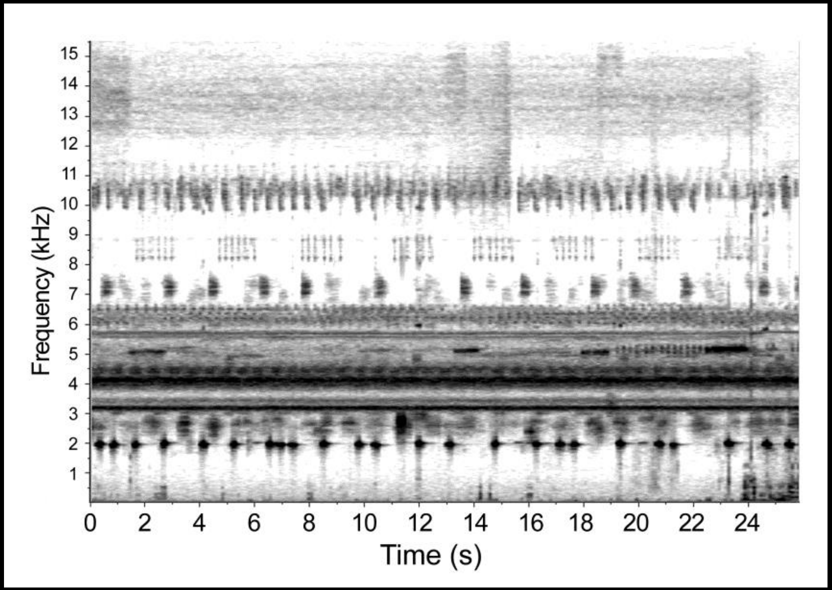


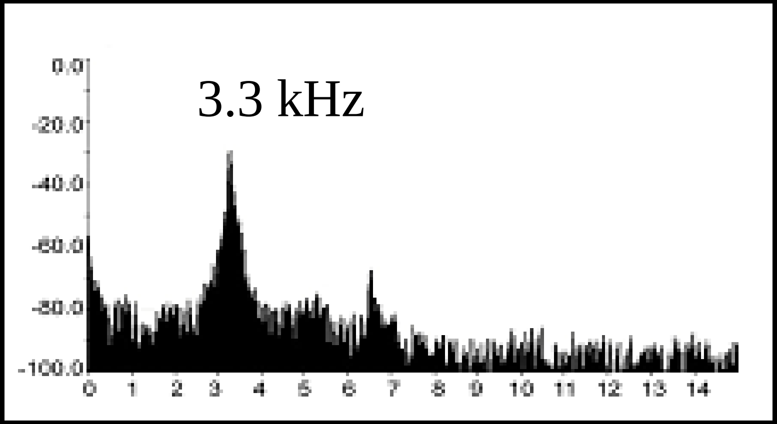
"Whistler" (*Onomarchus*)

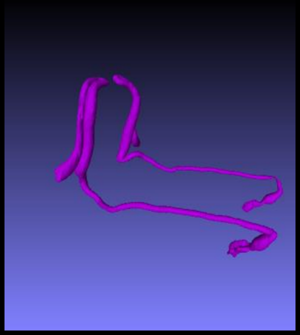
(Rajaraman et al., 2013)

THE EARDRUM: A MECHANICAL LOW PASS FILTER!









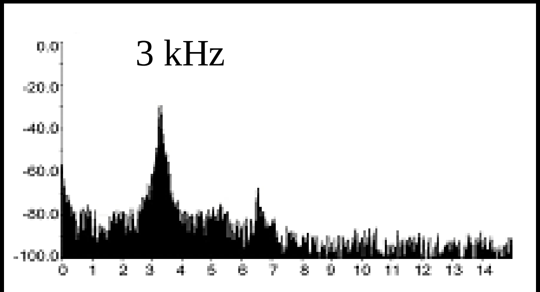
(Rajaraman et al., 2013)

SIGNAL EVOLUTION

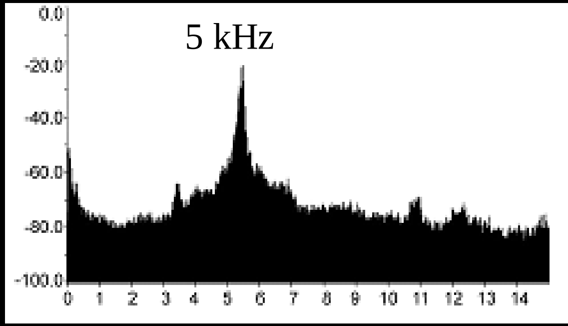
Sexual selection

Predation

Phylogenetic constraints

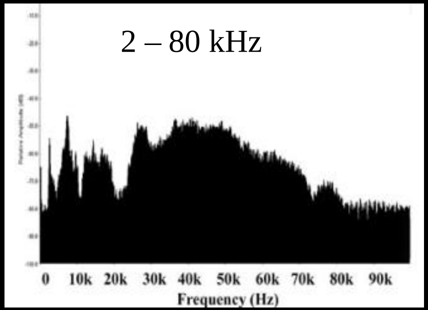


Katydid



True cricket

3 – 9 kHz



Katydid

Habitat acoustics

Masking interference


BATS OF KUDREMUKH

20 SPECIES





Rhinolophus rouxii
Rhinolophus lepidus
Rhinolophus beddomei

Pipistrellus affinis
Pipistrellus ceylonicus
Pipistrellus coromandra
Pipistrellus mimus
Myotis horsfieldii
Harpiocephalus harpia
Tylonycteris pachypus
Hesperotenus tickelli
Scotophilus kuhlii
Murina cyclotis
Megaderma lyra
Megaderma spasma

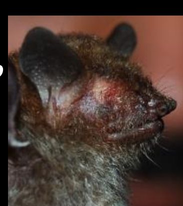






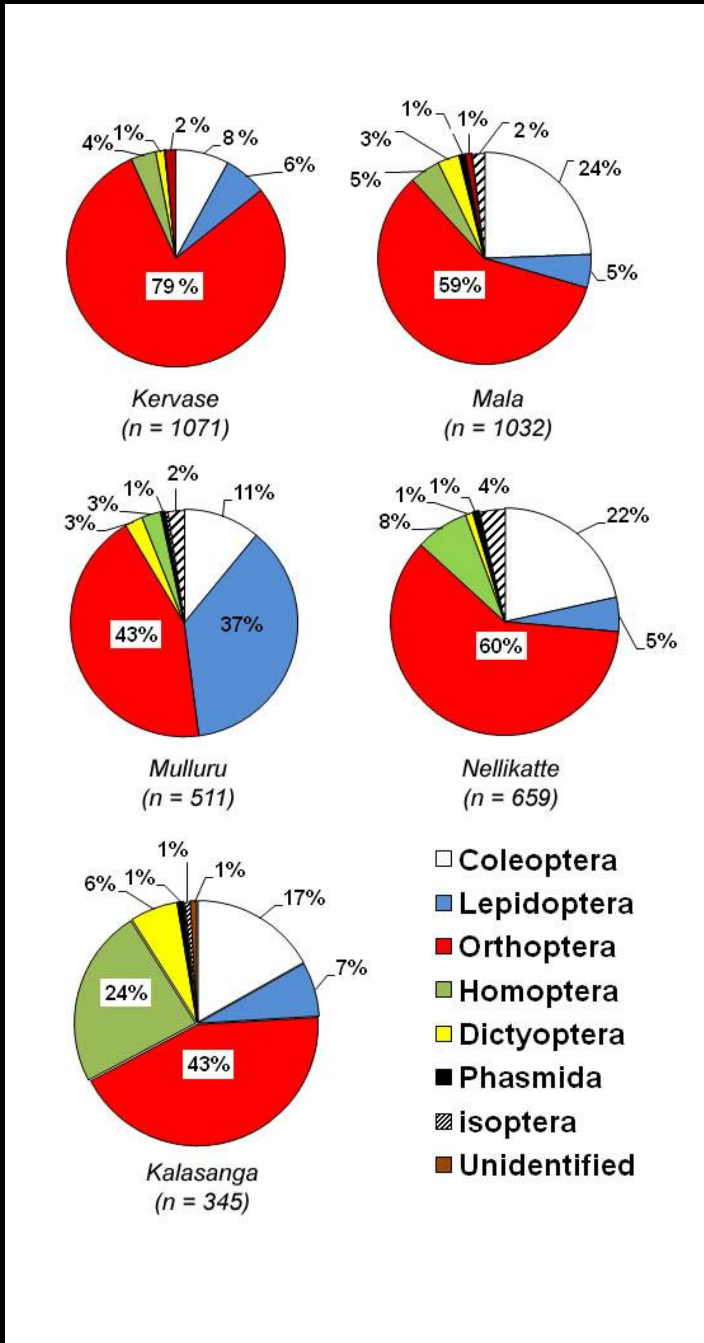



(Raghuram et al., 2014)



Megaderma spasma

Diet composition of *M. spasma* at different roosts



ORTHOPTERA

Tettigoniidae: 98%

Gryllidae: 2%

(Raghuram et al. 2015)

Are male katydids, who call, preyed upon more heavily than females, who are silent?

Katydids

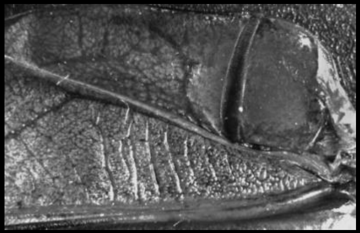
Females : Males

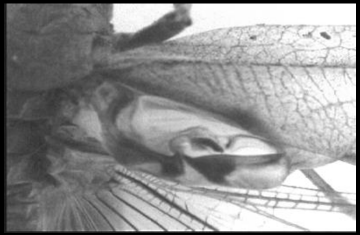
Ovipositors: Forewings with stridulatory apparatus

1.8

Female forewings : Male forewings

1.85



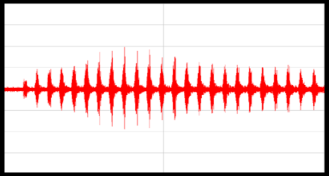


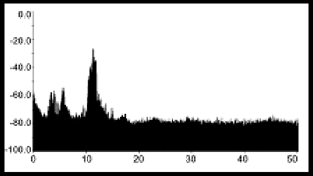
No, female katydids are preyed upon

in significantly higher numbers than males

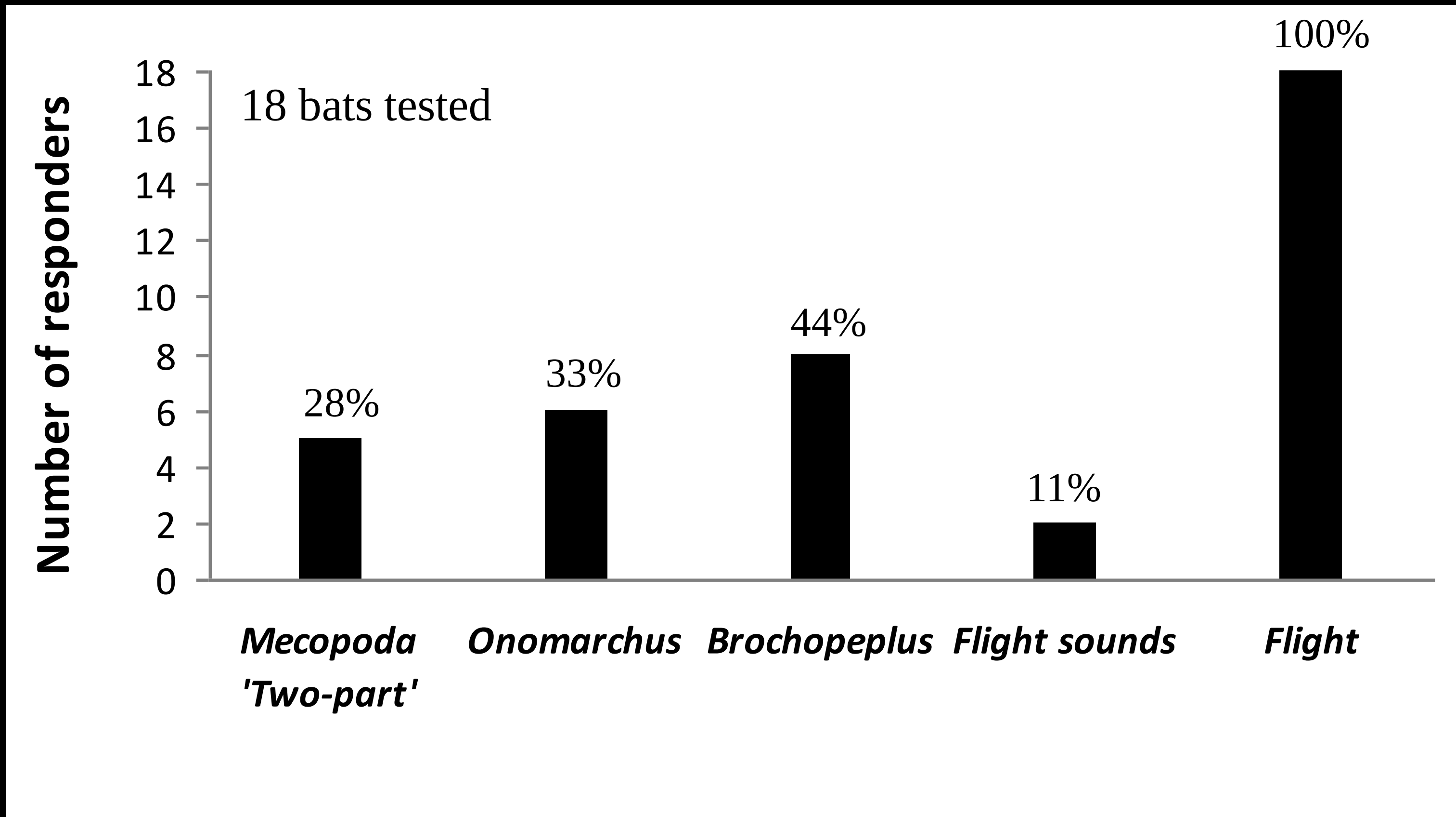
Raghuram et al., Proc. R. Soc. B (2015)

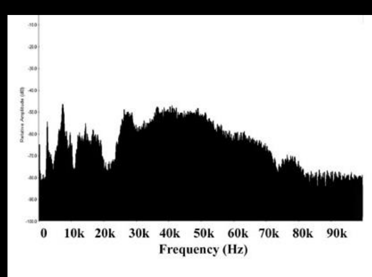
PLAYBACK EXPERIMENT

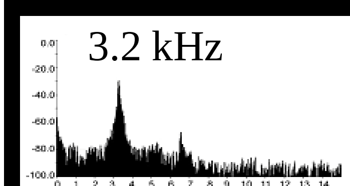


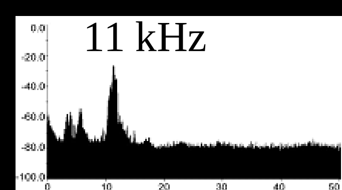


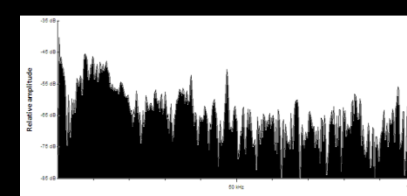
MEGADERMA SPASMA: PLAYBACK EXPERIMENTS IN OUTDOOR FLIGHT TENT









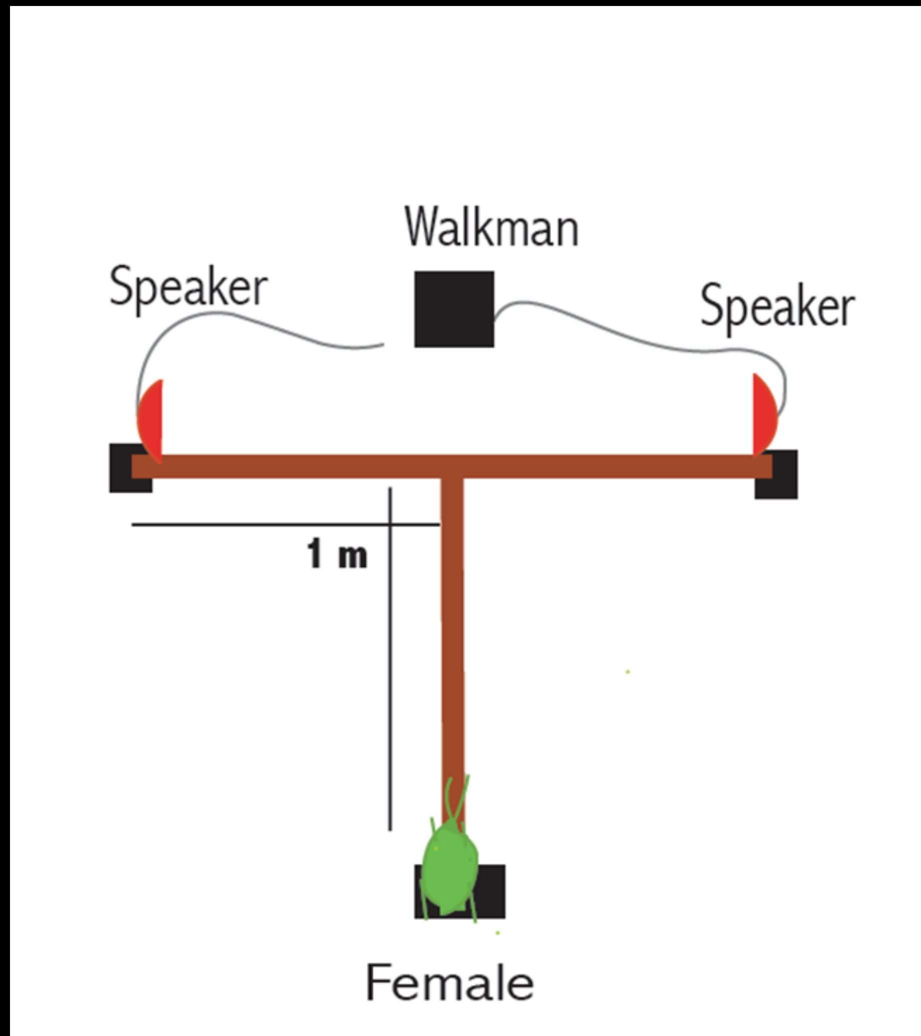


Duty cycle 95% 13% 14%

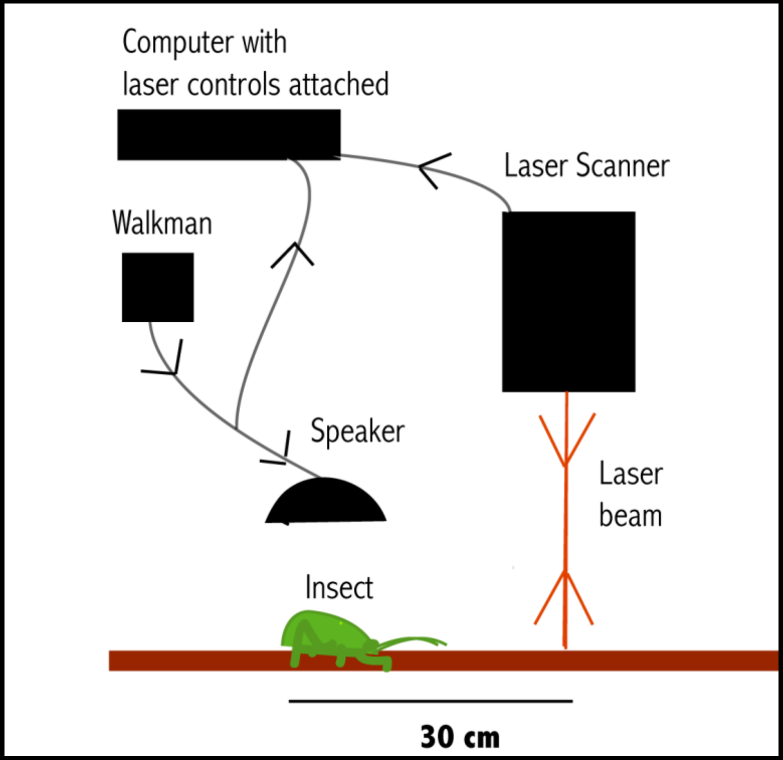
Raghuram et al., Proc. R. Soc. B (2015)

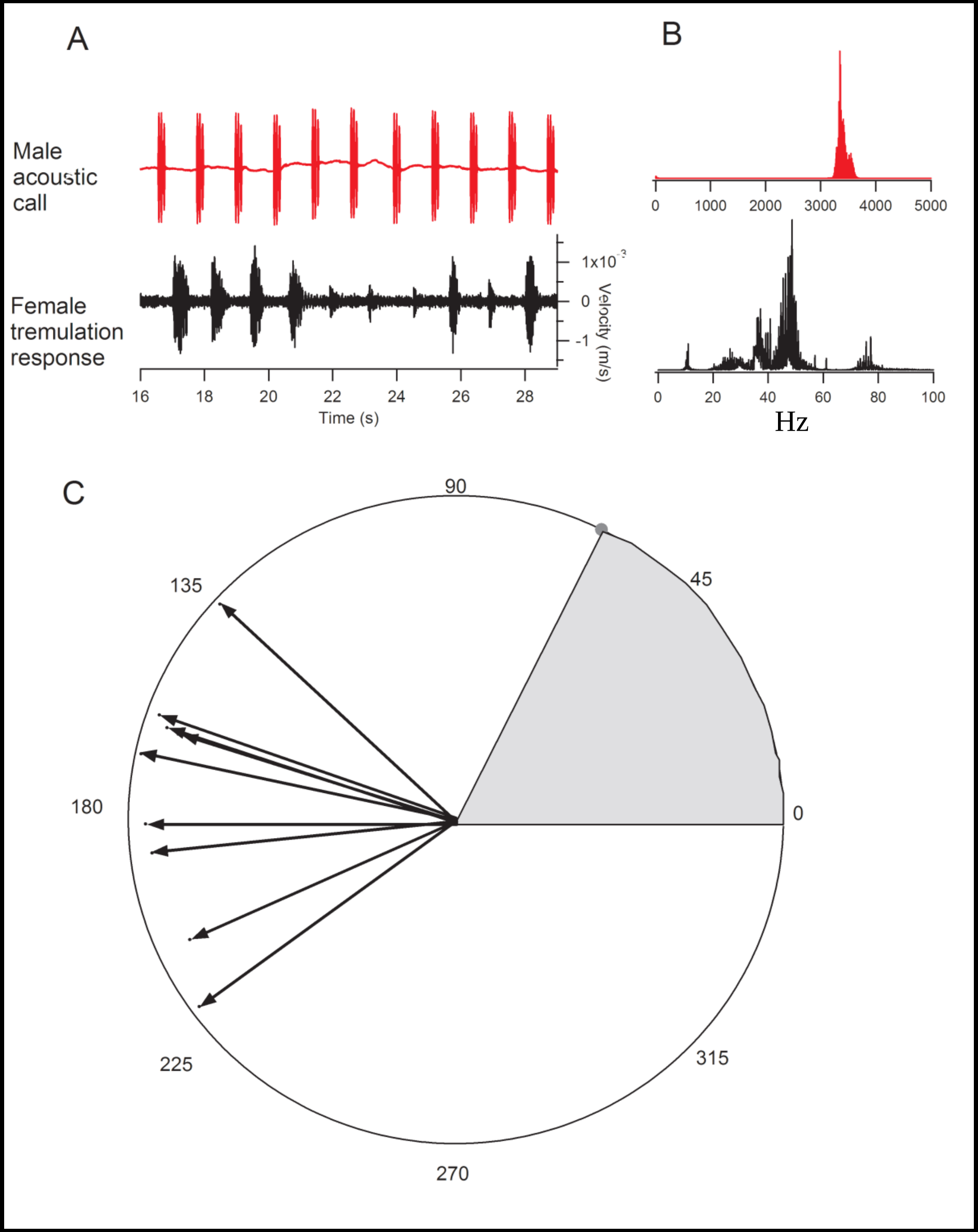
FLYING FEMALES ARE 2-3 TIMES MORE LIKELY TO BE CAPTURED THAN CALLING MALES!

FEMALE MOVEMENT



A NOVEL MULTIMODAL DUET



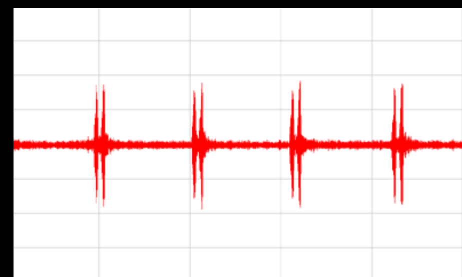


(Rajaraman et al. 2015)

PREDATOR-PREY INTERACTIONS: CRICKETS AND BATS

Onomarchus uninotatus
(False leaf katydid of KNP)

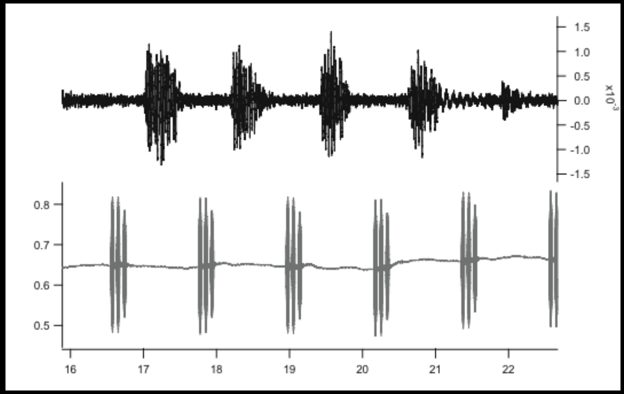
Males call for females



Megaderma spasma

preys upon katydids
especially females

A novel communication system and predator evasion response
Female katydids respond to male acoustic signals with silent vibrational signals rather than risky flight



Female response
(Vibrational signal)

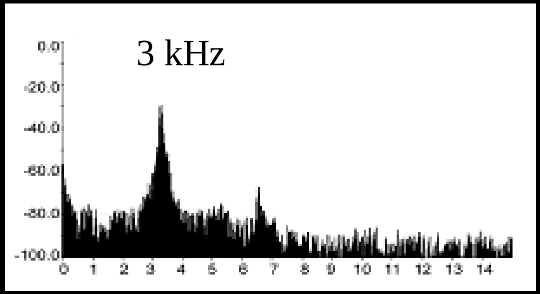
Male call
(Acoustic signal)

SIGNAL EVOLUTION

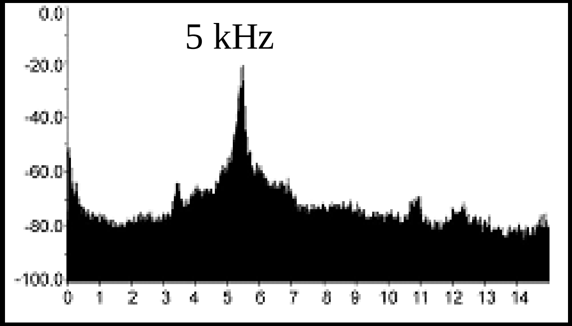
Sexual selection

Predation

Phylogenetic constraints

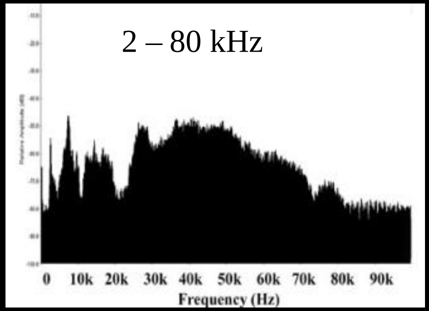


Katydid



True cricket

3 – 9 kHz



Katydid

Habitat acoustics

Masking interference

ACKNOWLEDGMENTS

H. Raghuram

Swati Diwakar

Manjari Jain, Jimmy Bahuleyan

Rittik Deb, Diptarup Nandi

Vamsy Godthi, Rudra Pratap

Sudhakar Gowda

Daniel Robert

Kaveri Rajaraman

Ministry of Environment & Forests, Government of India

Karnataka State Forest Department

THE DUSK CHORUS: SYMPHONY

Community Ecology

Biophysics

Neurobiology

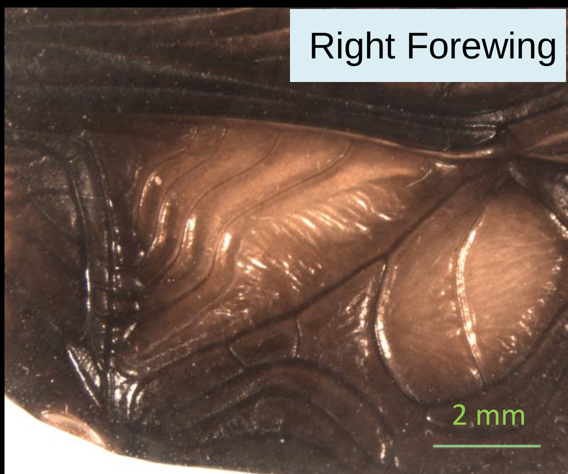
Acoustic Communication

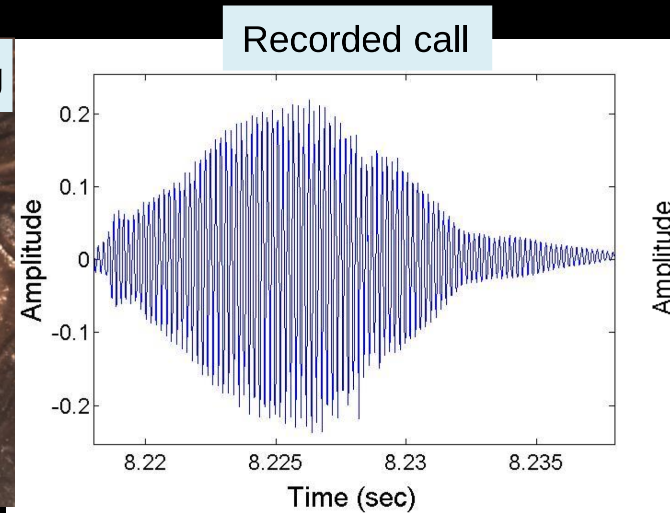
Systematics

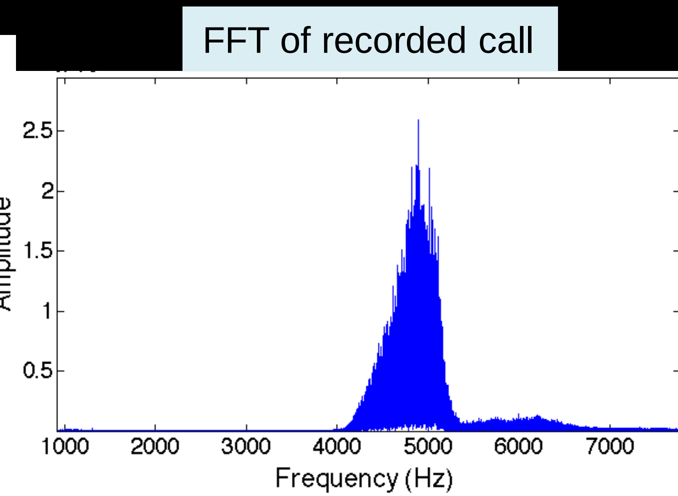
Evolution

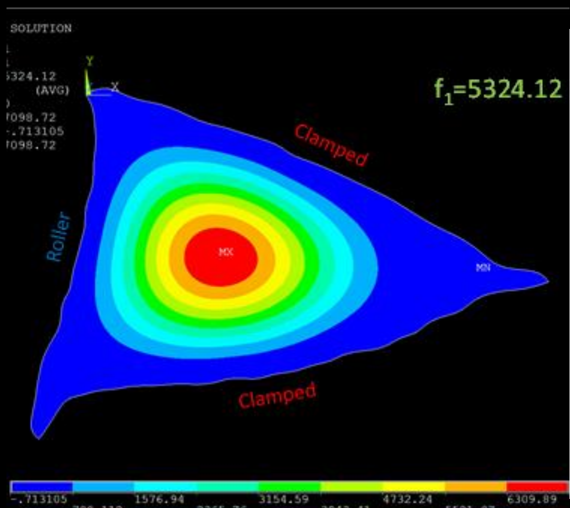
Behavioural Ecology

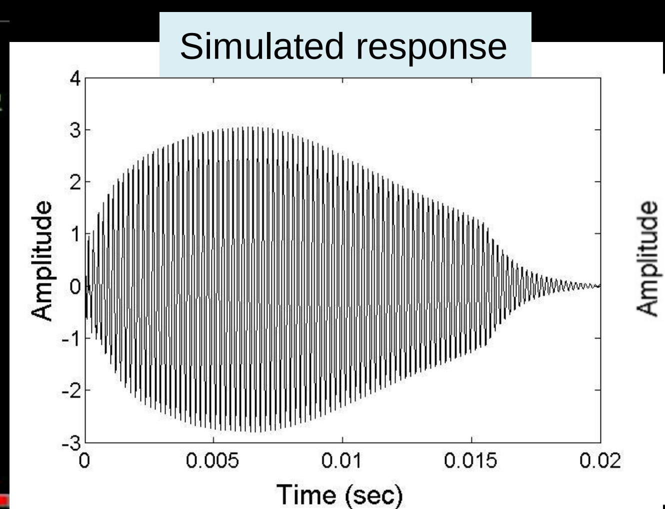
Finite Element Analysis of the Harp

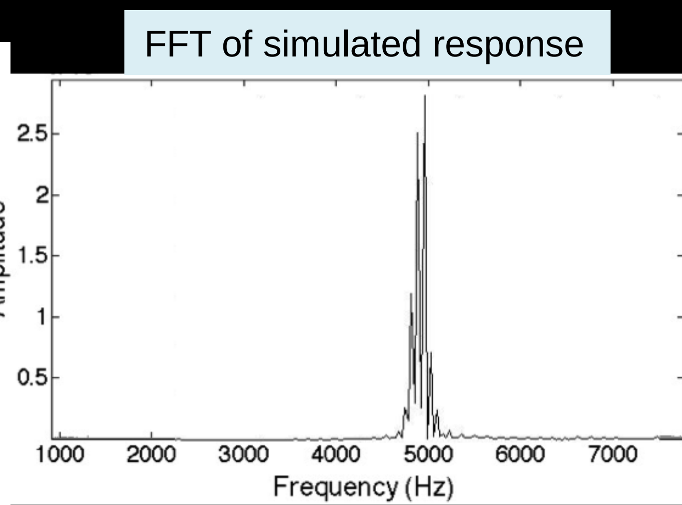












Vamsy Godthi & Rudra Pratap

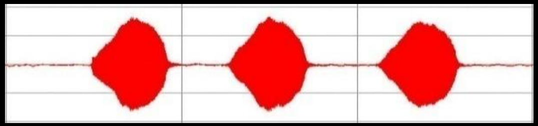
What?
When?
Where?

Who?

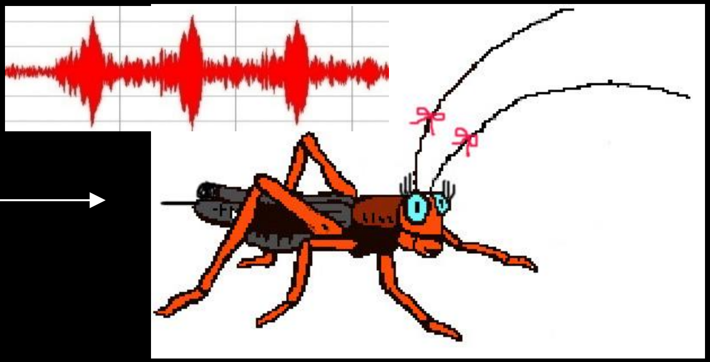
Signal

Predator Who?

Sender



Receiver Where? How?



Medium

What?

Competing callers and calls

Who?
What?
When?
Where?

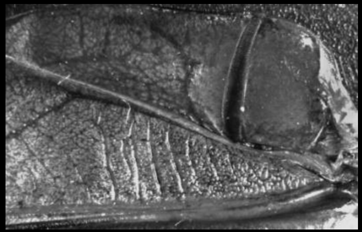
Are male katydids, who call, preyed upon

more heavily than females, who are silent?

Katydids

243 ovipositors = Females (64%)

137 forewings
with stridulatory apparatus = Males (36%)



No, female katydids are preyed upon

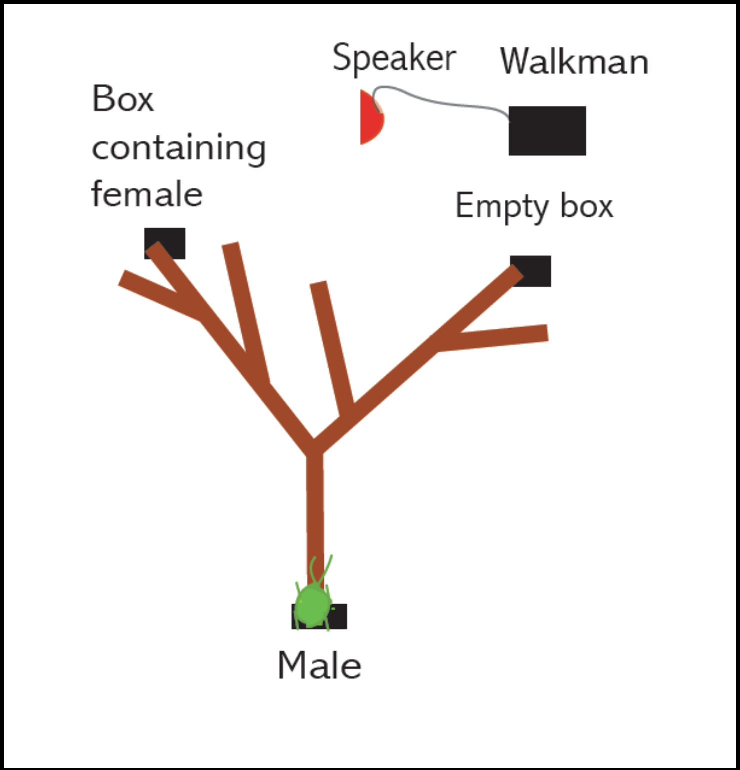
in significantly higher numbers than males

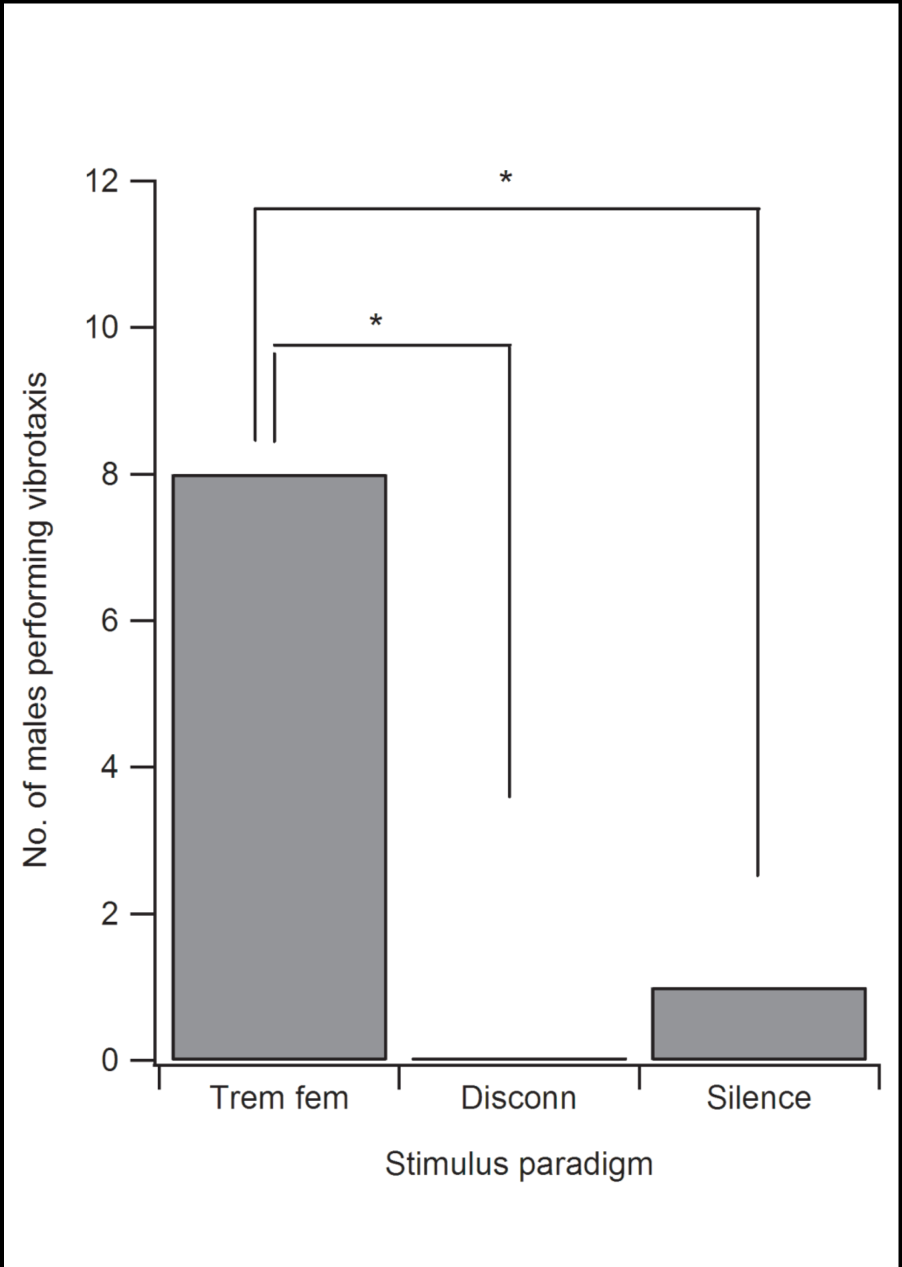
H. Raghuram

MALE VIBROTAXIS

TO

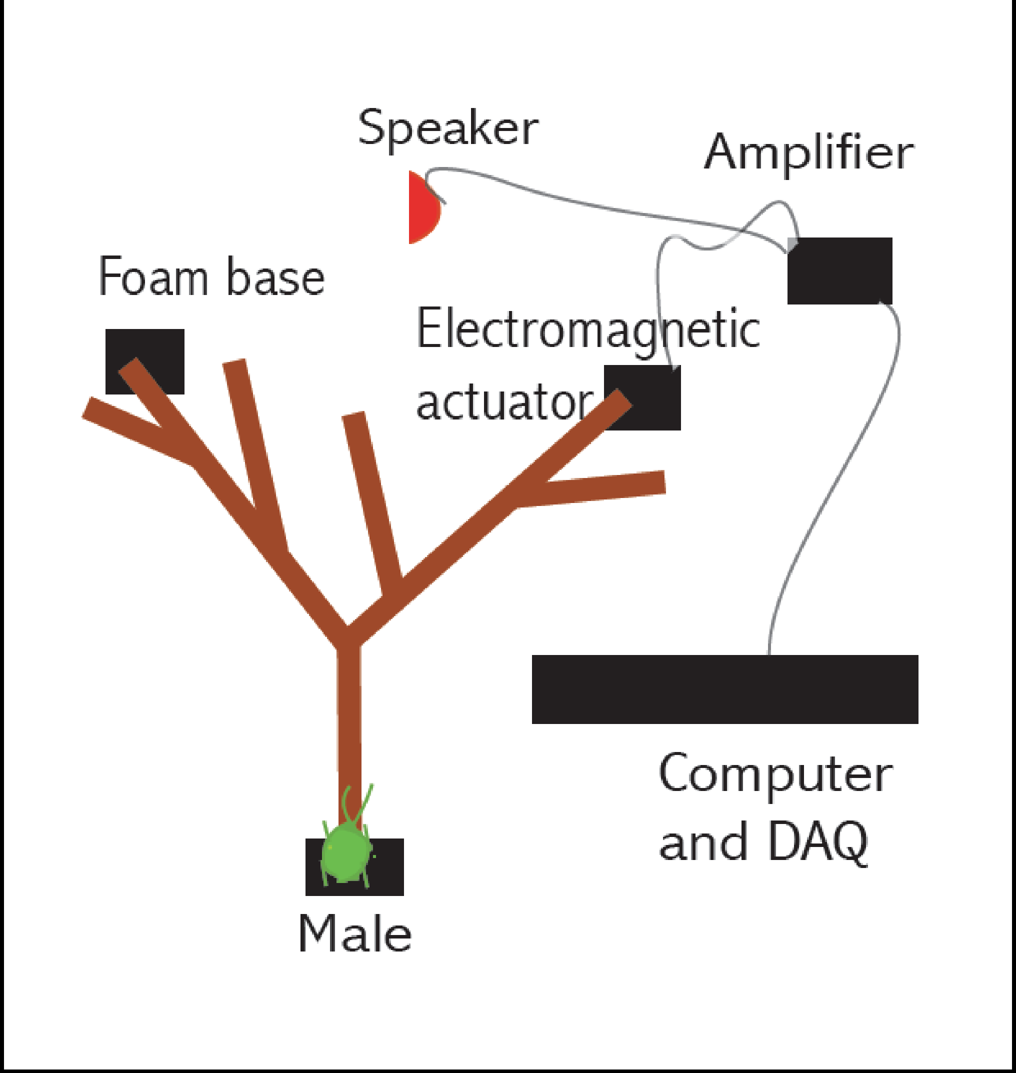
TREMULATING FEMALE

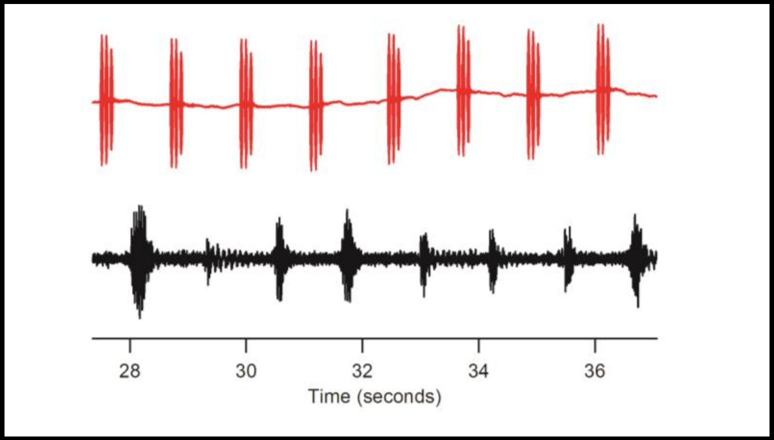




(Rajaraman et al. 2015)

VIBROTAXIS PLAYBACK SET-UP





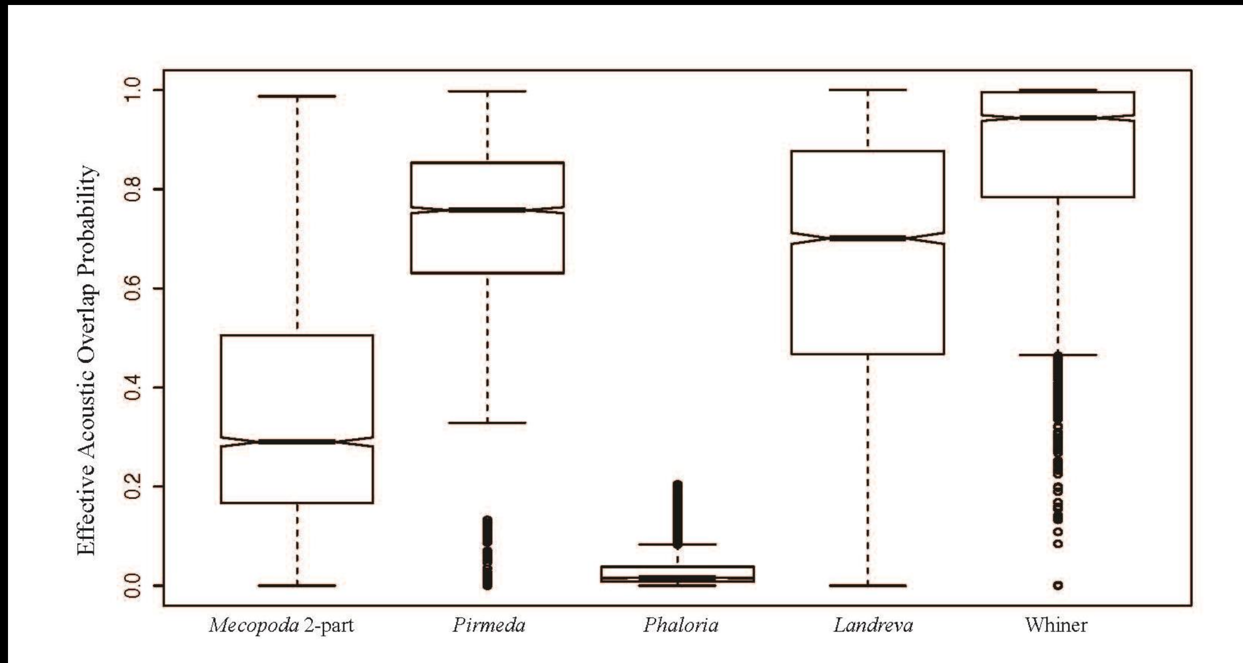
ACOUSTIC BUFFERING

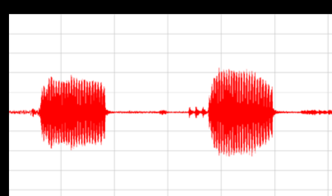
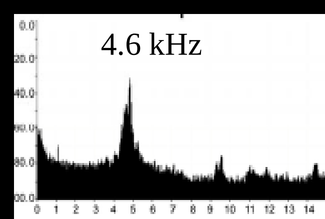


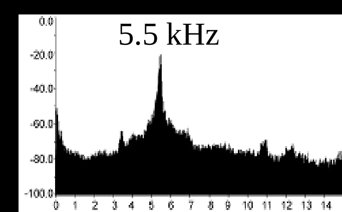


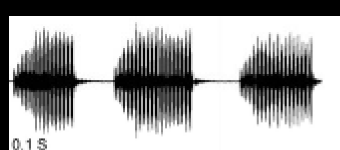
















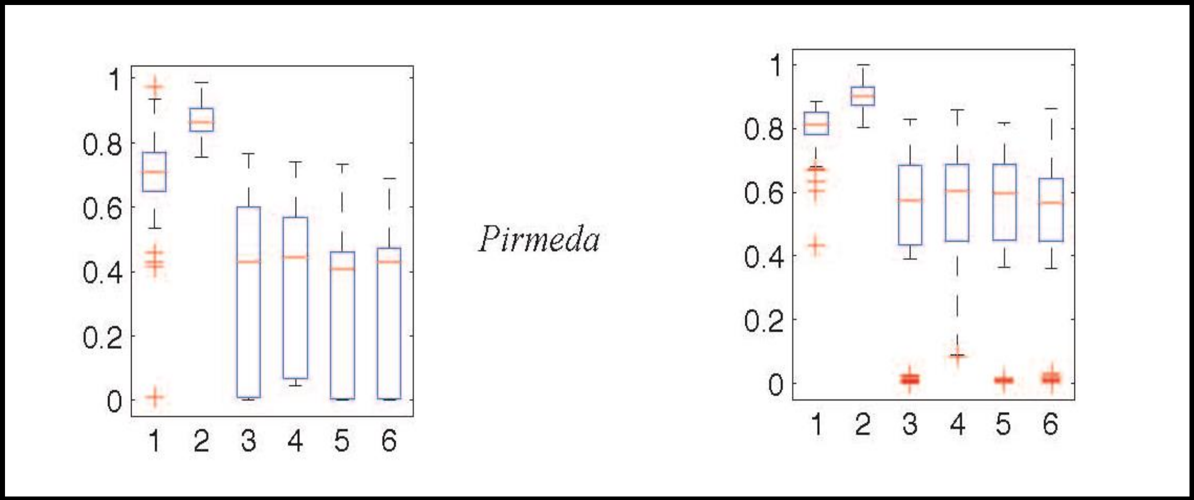
(Balakrishnan et al. 2014)

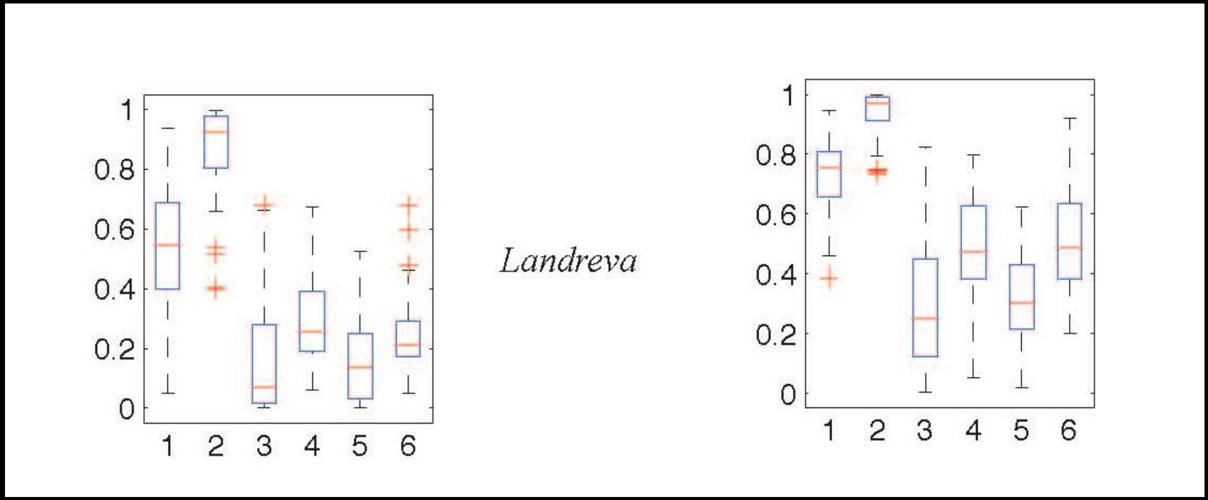
NO SIGNIFICANT NEGATIVE CORRELATIONS IN CALLING ACTIVITY

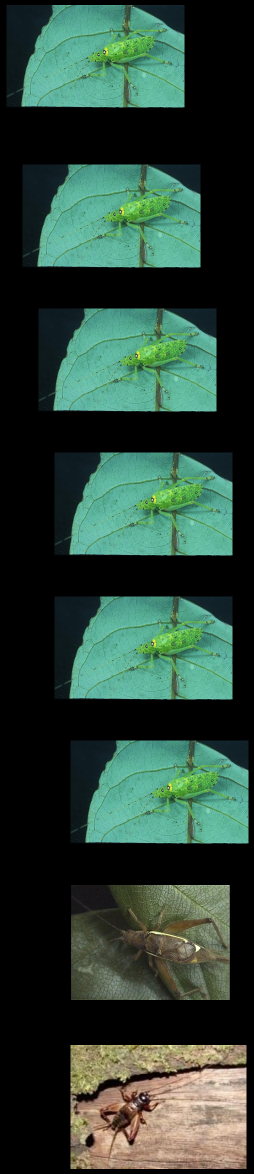
1	0.82	0.92	0.66	0.71	0.67	0.87	0.72	0.9	0.74	0.75	0.89	0.96	0.64	0.68
0.82	1	0.96	0.84	0.69	0.71	0.83	0.876	0.89	0.93	0.67	0.96	0.83	0.64	0.62
0.92	0.96	1	0.86	0.79	0.74	0.83	0.872	0.95	0.9	0.79	0.98	0.9	0.61	0.75
0.66	0.84	0.86	1	0.71	0.55	0.44	0.74	0.74	0.81	0.88	0.82	0.61	0.43	0.79
0.71	0.69	0.79	0.71	1	0.94	0.57	0.91	0.91	0.61	0.58	0.85	0.7	0	0.96
0.67	0.71	0.74	0.55	0.94	1	0.7	0.95	0.91	0.6	0.34	0.85	0.71	0	0.8
0.87	0.83	0.83	0.44	0.57	0.7	1	0.75	0.85	0.73	0.38	0.85	0.91	0.64	0.41
0.72	0.88	0.87	0.74	0.91	0.95	0.75	1	0.95	0.77	0.49	0.94	0.77	0.22	0.79
0.9	0.89	0.95	0.74	0.91	0.91	0.85	0.949	1	0.8	0.63	0.98	0.9	0.38	0.82
0.74	0.93	0.9	0.81	0.61	0.6	0.73	0.773	0.8	1	0.64	0.87	0.66	0.63	0.57
0.75	0.67	0.79	0.88	0.58	0.34	0.38	0.492	0.63	0.64	1	0.69	0.64	0.54	0.73
0.89	0.96	0.98	0.82	0.85	0.85	0.85	0.942	0.98	0.87	0.69	1	0.9	0.5	0.78
0.96	0.83	0.9	0.61	0.7	0.71	0.91	0.767	0.9	0.66	0.64	0.9	1	0.61	0.62
0.64	0.64	0.61	0.43	0	0	0.64	0.218	0.38	0.63	0.54	0.5	0.61	1	0
0.68	0.62	0.75	0.79	0.96	0.8	0.41	0.792	0.82	0.57	0.73	0.78	0.62	0	1
-0.4	-0.3	-0.3	-0	0.01	-0.1	-0.53	-0.19	-0.3	-0	-0.12	-0.3	-0.6	-0.53	0.12

SPECIES DOMINANCE AND MASKING

Masking Probability







Composition

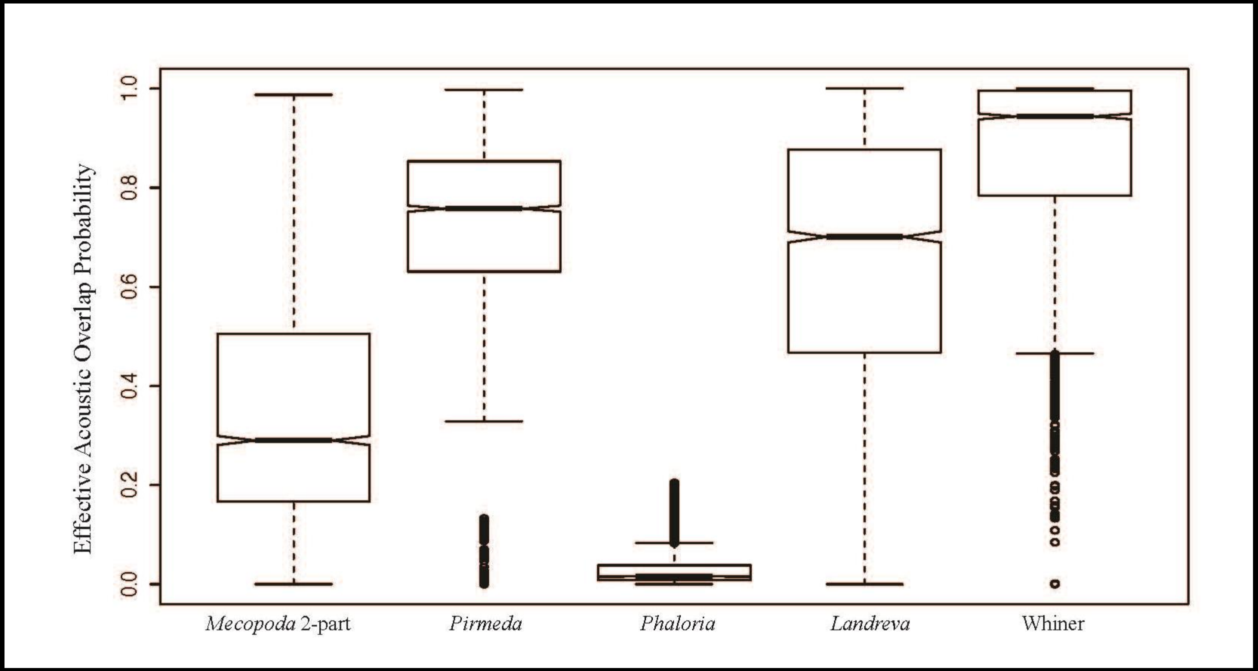
ACOUSTIC BUFFERING







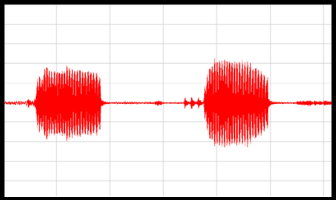


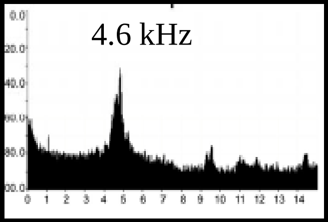



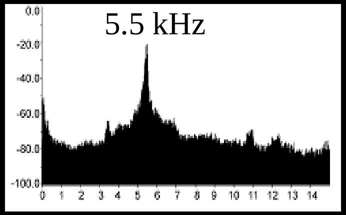






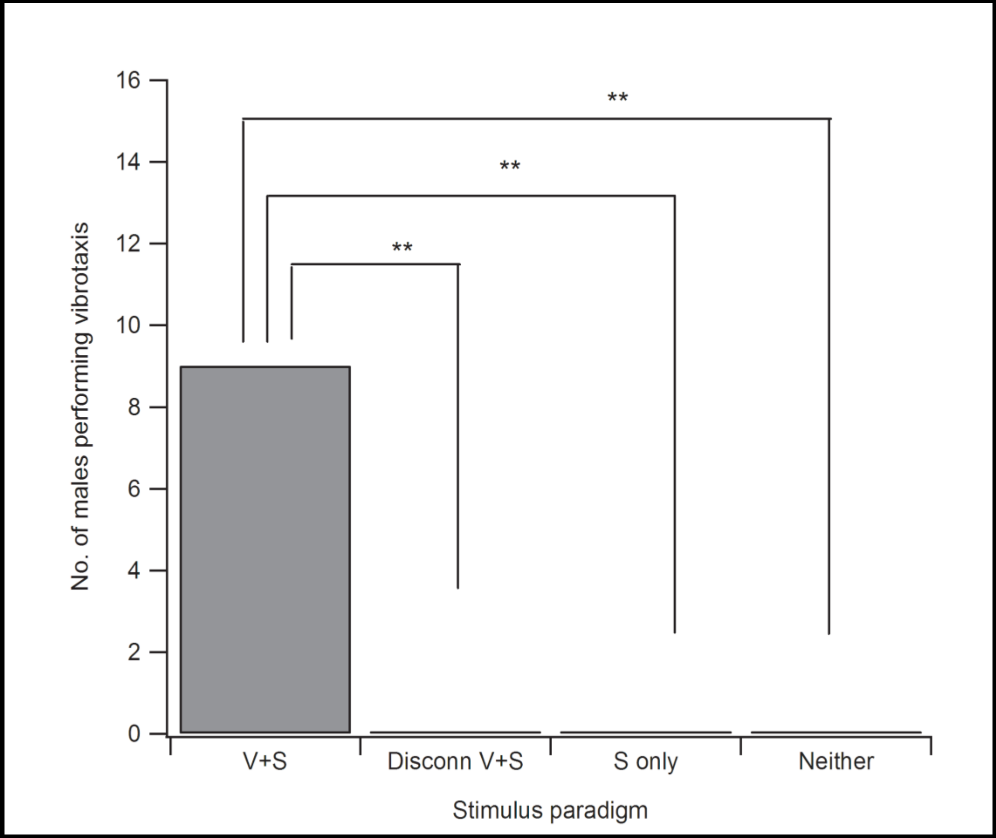



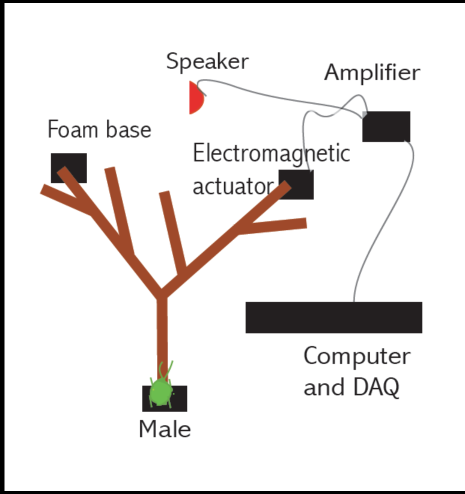




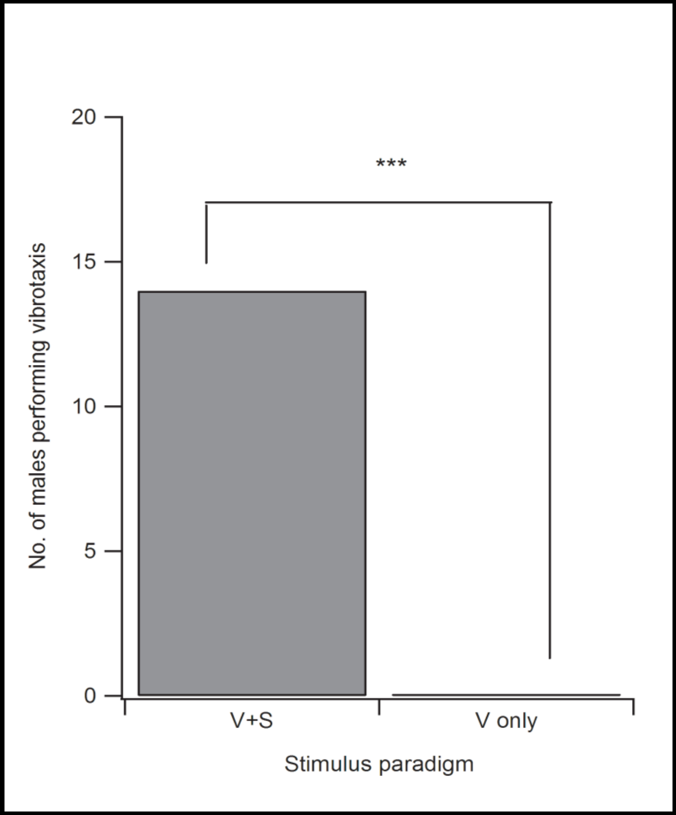

(Balakrishnan et al. 2014)

MALE VIBROTAXIS TO DUET PLAYBACK





SOUND ONLY



VIBRATION ONLY

(Rajaraman et al. 2015)

CONCLUSIONS

A novel multimodal duetting communication system

Female tremulation response has a fixed timing relation with respect to the male acoustic signal

Female tremulation response is specific to conspecific male call

Males approach female tremulation signals but only if

Both acoustic and vibratory components of the duet are present