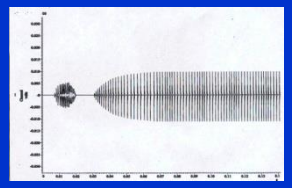


Animal Choruses Emerge from Receiver Psychology (A Tale of Two Synchronies)

Michael D. Greenfield

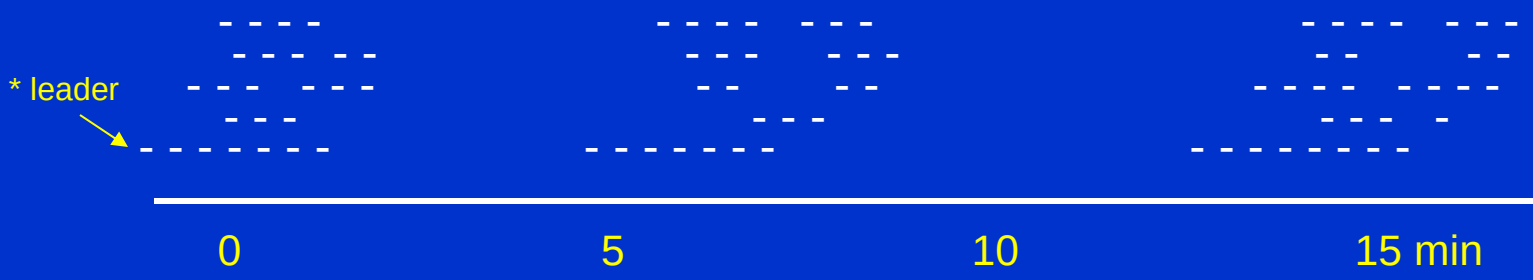
Univ. St. Étienne (ENES), France
Univ. Kansas (Ecol & Evol Biol), USA

Labex CeMEB
Mediterranean Center for
Environment and Biodiversity

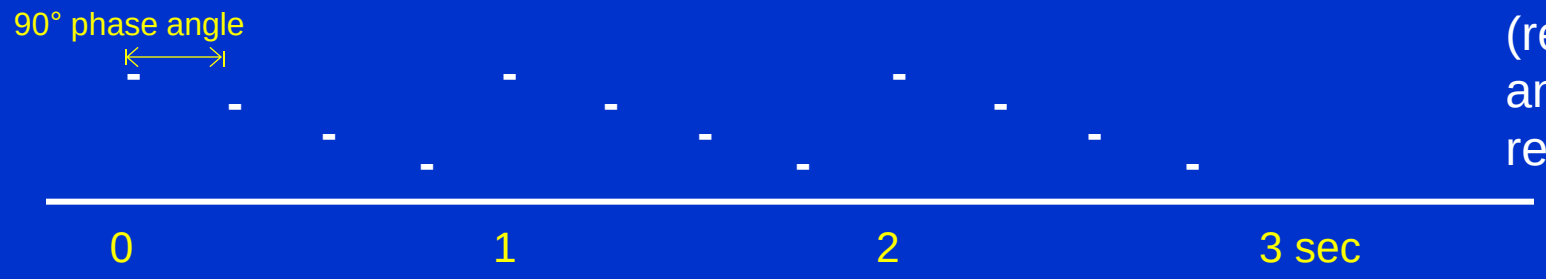
What is an animal chorus ? (It's about time)

Temporal adjustments in broadcasting at three levels of precision :

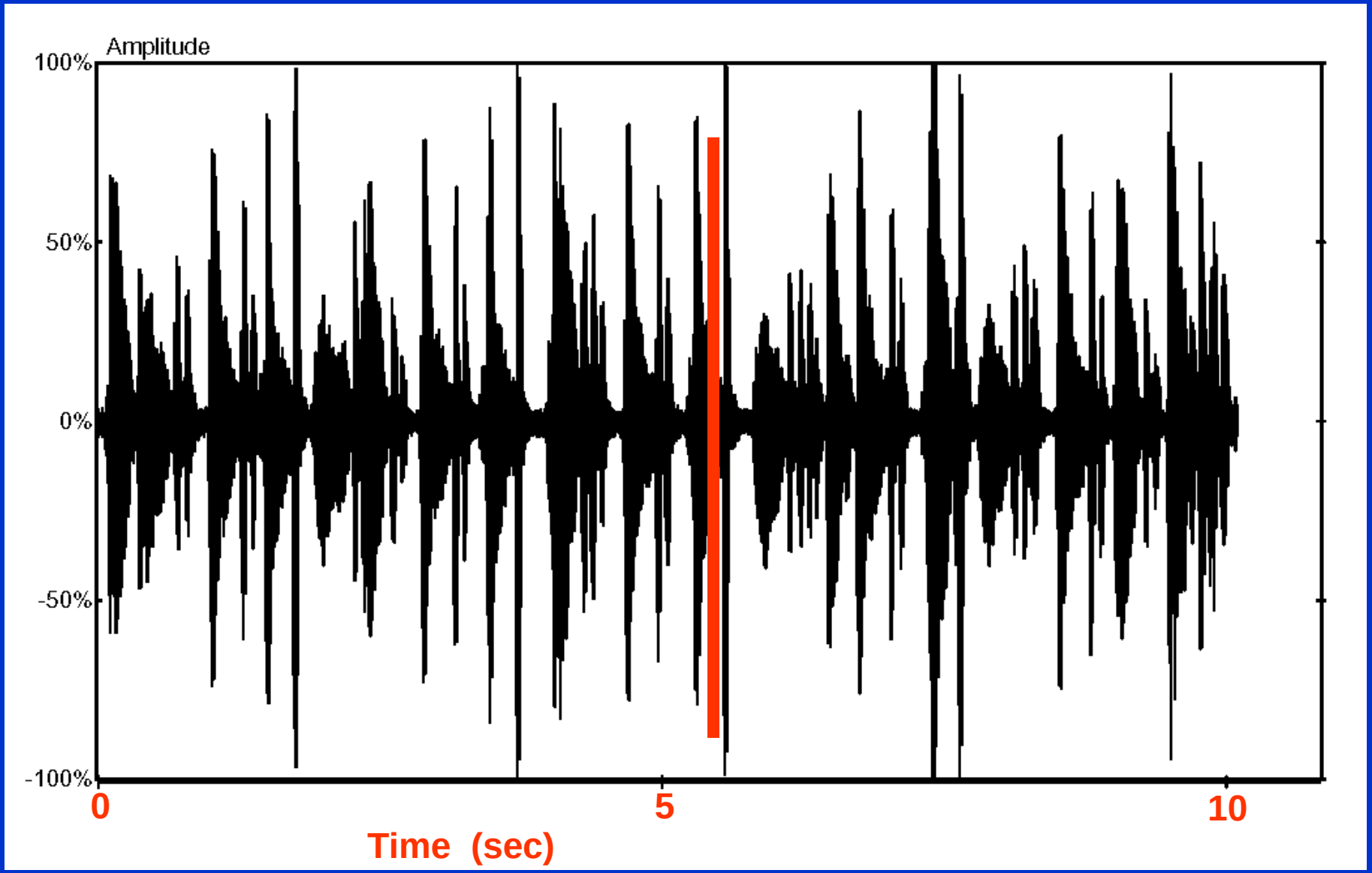
(an evening chorus)



(collective singing bouts)



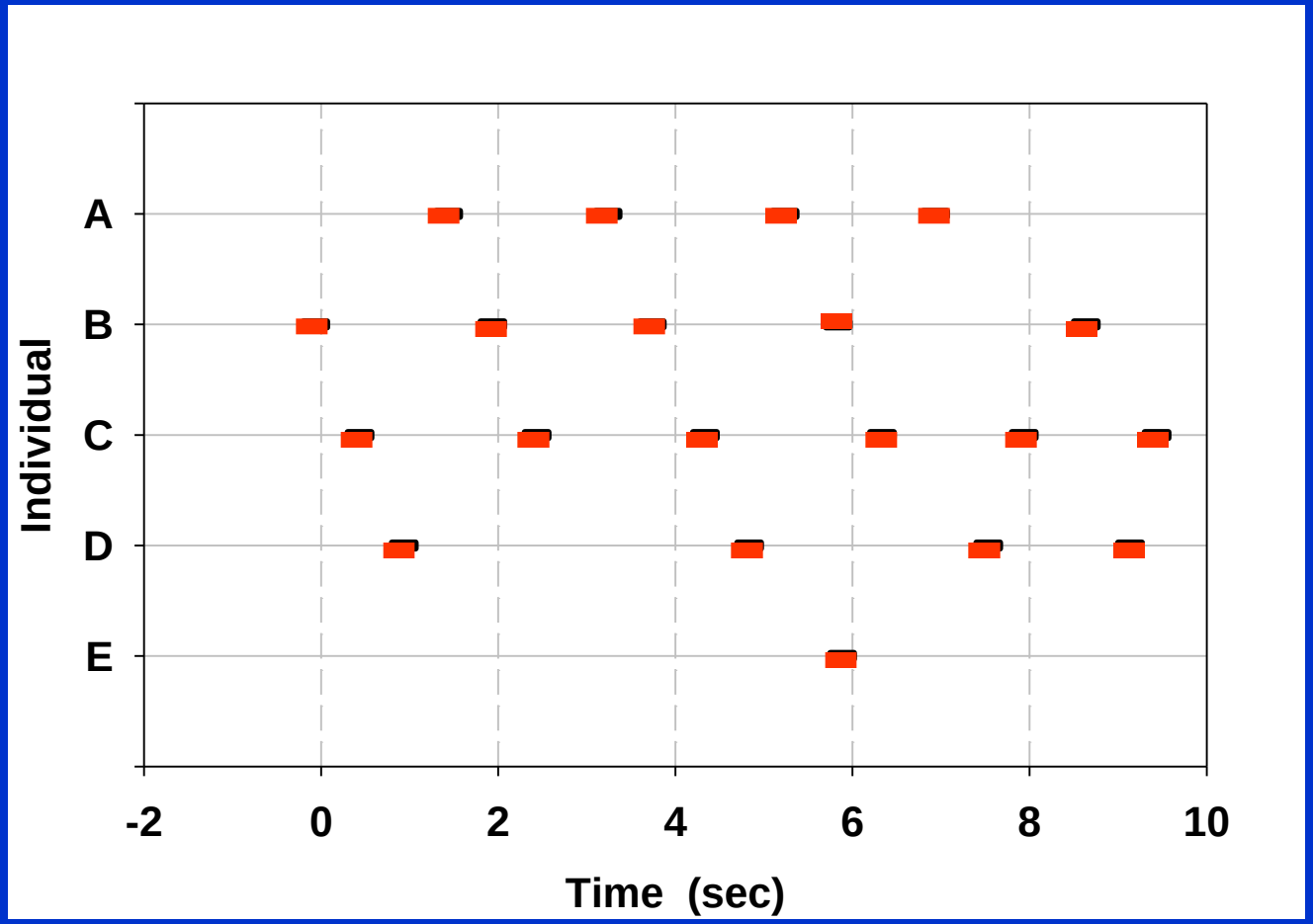
(regular rhythm and precise phase relationships)



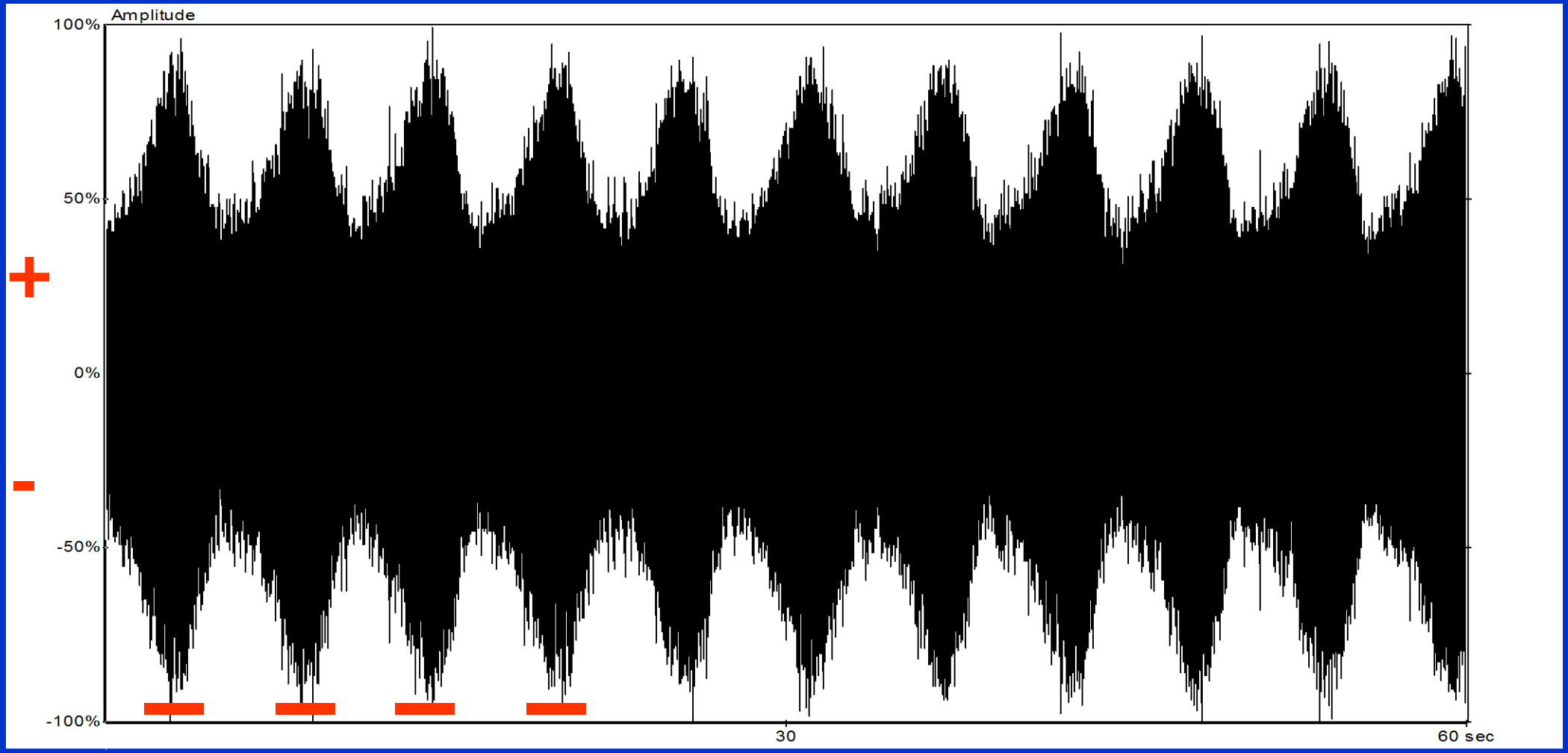
Physalaemus pustulosus (Túngara frog; Anura: Leptodactylidae);

5 Male Chorus

Physalaemus pustulosus (Túngara frog; Anura: Leptodactylidae); 5 Male Chorus



Frogs have rules



***Magicicada cassini* (Cicadidae);**
Periodical Cicada (17-year)
Synchronous Chorus; Brood IV; June 1998; Douglas Co., Kansas

Pteroptyx tener (Lampyridae);

Synchronous fireflies of the Indo-Malayan Region

Kumari Nallabumar 2002

Strogatz & Stewart 1993

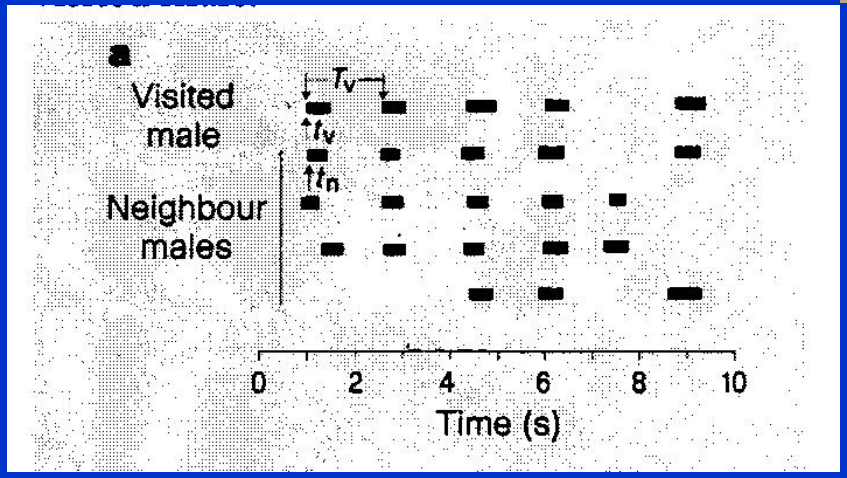
synchronicity - sample shots - 2015

Uca annulipes

(Crustacea: Ocypodidae);

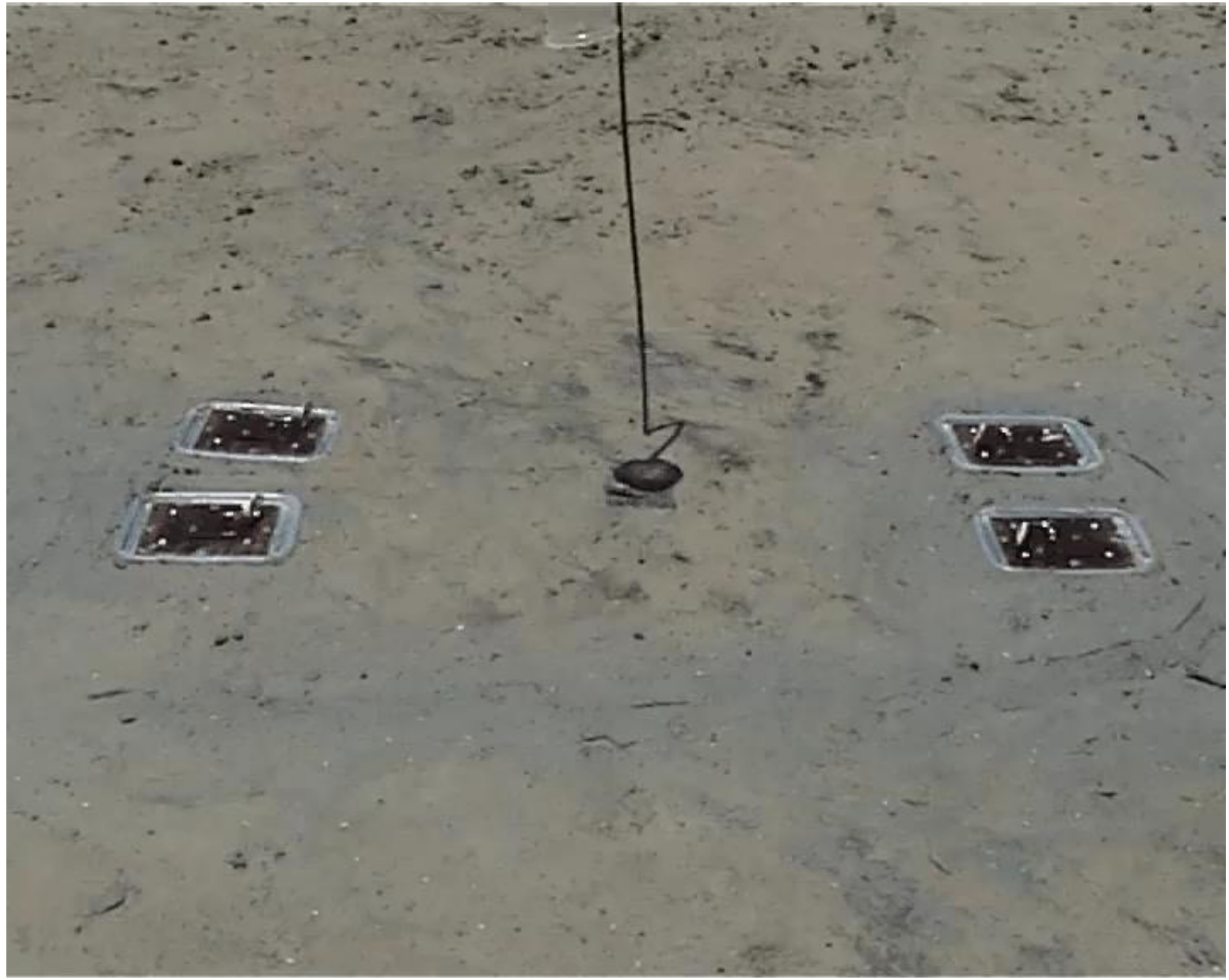
Western Indo-Pacific;

Synchronized waving



Synchronized courtship in fiddler crabs;

Backwell et al. 1998



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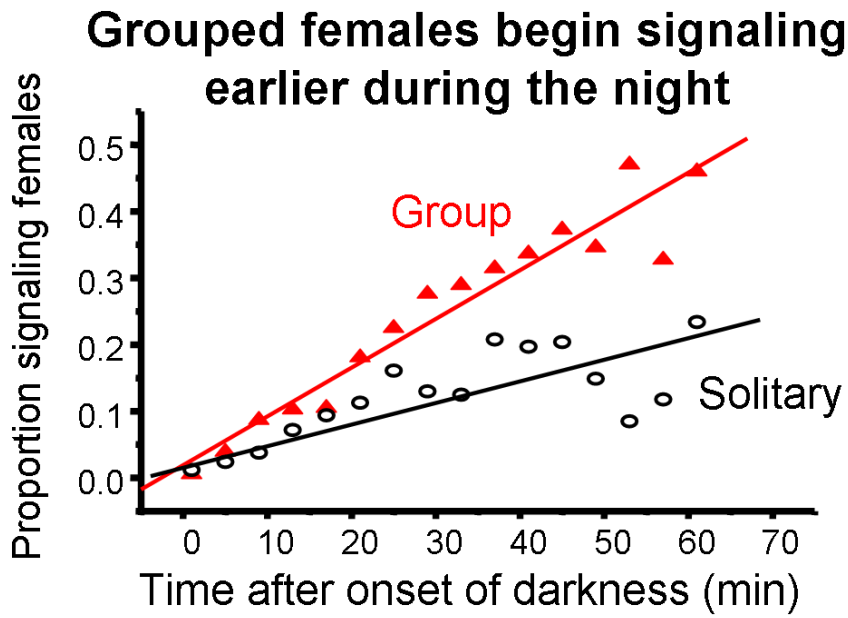
Behavioral Ecology
doi:10.1093/beheco/arl069

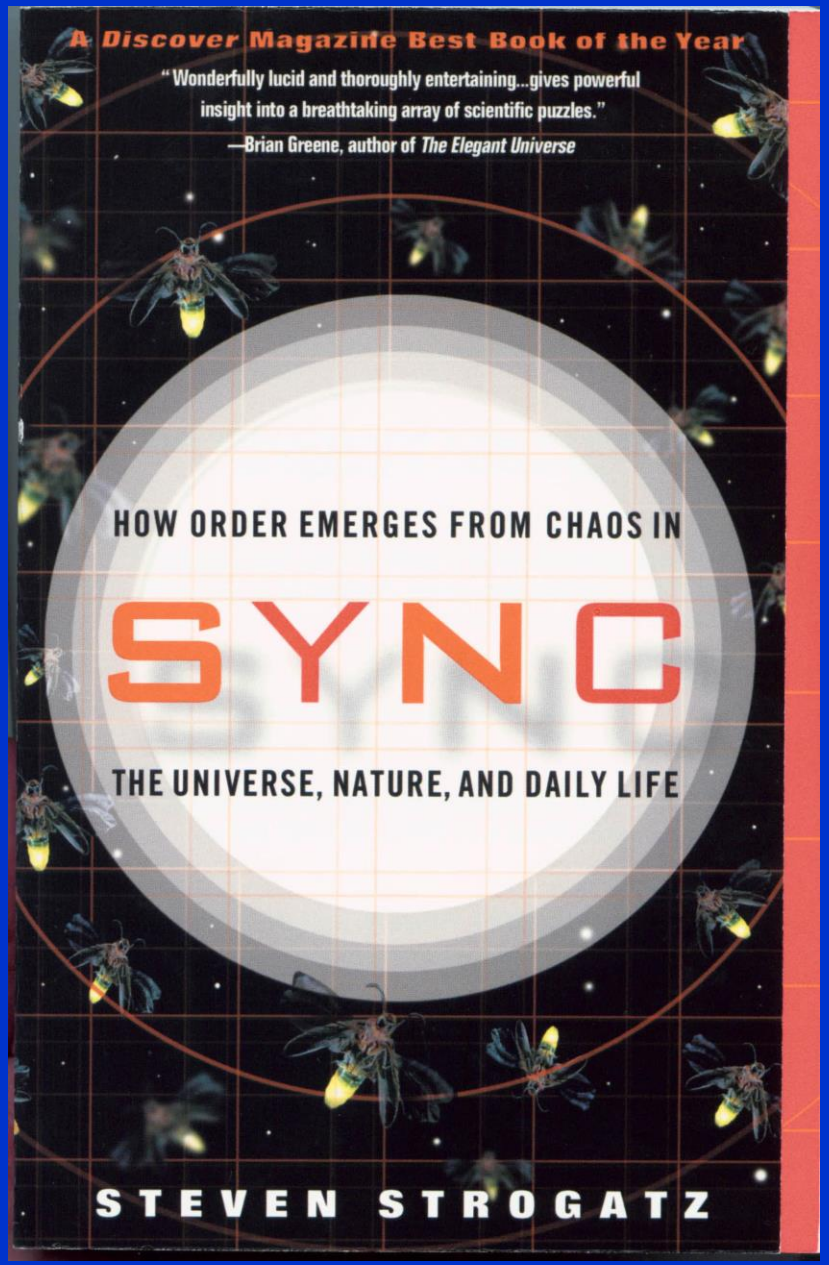
Female pheromonal chorusing in an arctiid moth, *Utetheisa ornatrix*

Hangkyo Lim[a] and Michael D. Greenfield[a,b]
[a]Department of Ecology and Evolutionary Biology, University of Kansas, 1200 Sunnyside Avenue, Lawrence, KS 66045, USA and [b]Institut de Recherche sur la Biologie de l'Insecte, CNRS UMR 6035, Université François Rabelais de Tours, Parc de Grandmont, 37200 Tours, France

We report an unusual case of communal sexual display in the arctiid moth *Utetheisa ornatrix* that we designate "female pheromonal chorusing." As in most moths, female *U. ornatrix* release a long-distance sexual advertisement pheromone during a nightly activity period. We arranged *U. ornatrix* females in 2 types of signaling conditions: grouped and solitary. When the females were grouped with neighboring signaling females (grouped), they initiated pheromone release sooner, continued release with less interruption and over a longer total period, and performed the release with faster abdominal pumping than observed in isolated females (solitary). This differs from the usual form of sexual communication in moths: female (chemical) signalers, male receivers, and a general lack of interaction among females. At mating, male *U. ornatrix* transfer a large spermatophore that may enhance female reproductive success and which represents either mating effort or paternal investment. This action results in an extended postmating male refractory period leading to a female-biased operational sex ratio. We argue that this biased sex ratio generates intrasexual competition among females, to which they respond by elevating signaling effort such that the likelihood of at least matching their neighbors' signals is increased. In the field, *U. ornatrix* are clustered around patches of host plants, and we also explore the possibility that pheromonal chorusing is driven by cooperation among groups of related—or nonrelated—females. *Key words:* Lepidoptera, mating system, operational sex ratio, sexual selection, signal competition. *[Behav Ecol]*

Utetheisa ornatrix **(Lepidoptera : Arctiidae)**




A Discover Magazine Best Book of the Year
"Wonderfully lucid and thoroughly entertaining...gives powerful insight into a breathtaking array of scientific puzzles."
—Brian Greene, author of The Elegant Universe
HOW ORDER EMERGES FROM CHAOS IN
SYNC
THE UNIVERSE, NATURE, AND DAILY LIFE
STEVEN STROGATZ


NIAS
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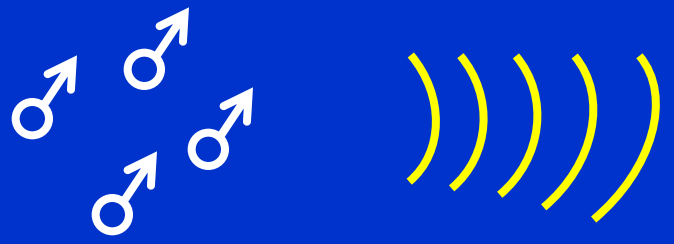
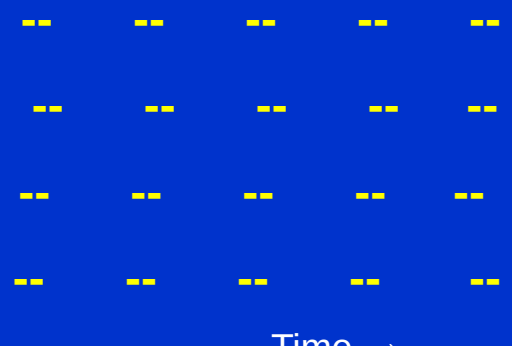
Synchrony and Rhythmic Interaction
From Neurons to Ecology
29 July - 2 August 2019, Leiden, the Netherlands
NIAS
Lorentz center
www.lorentzcenter.nl

Specialized rhythmic chorusing : potential adaptive features

*** Retention of species-specific rhythm or call envelope**





*** Evasion of predators ; detection of predators**

*** Maximization of collective signal intensity of local group**

*** Unmasking of sexually-selected signal characters ;**
ability to detect and evaluate rivals

(Greenfield 2005)

Alternative to the adaptationist paradigm : (the null hypothesis)

Choruses might also arise simply as an ‘emergent property’ of local interactions between singing neighbors. That is, the overall chorus structure per se, even when very complex and seemingly specialized, is neutral in terms of preference by female receivers and the benefits that male signalers might accrue from generating it.

(Greenfield & Schul 2008 ; Greenfield 2015)

How might this work ?

3-step pathway :

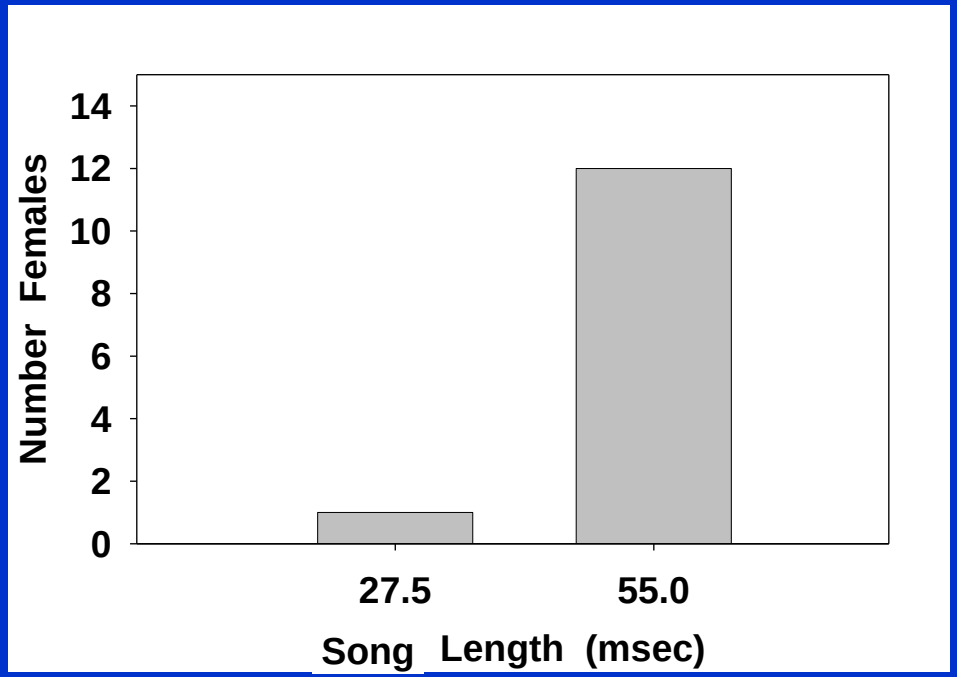
Collective singing patterns in choruses simply emerge from the ‘receiver psychology’ of female perception and preference.

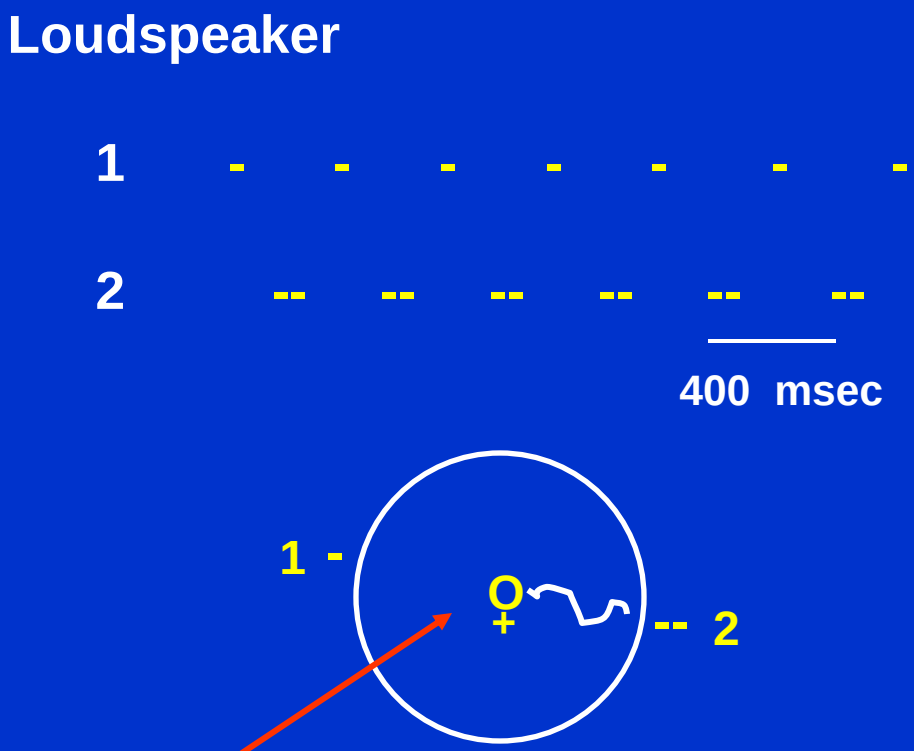
1) Females ignore male calls that follow a neighbor’s by a brief interval.

2) Males adjust call rhythm (phase) upon hearing a stimulus or neighbor.

3) When multiple males use equivalent adjustments an expansive chorus of synchrony and/or alternation may arise.

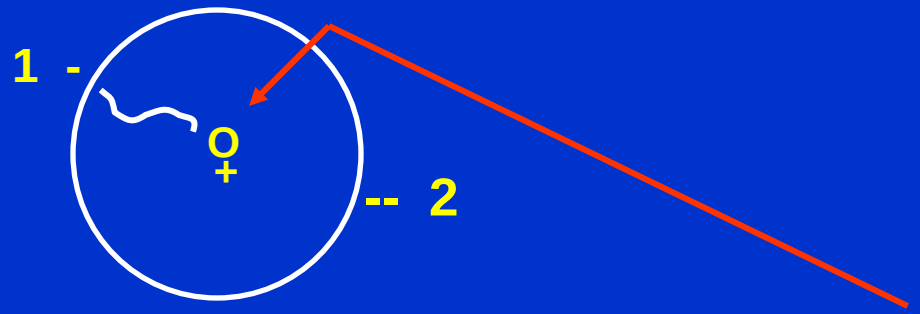
Importantly, the display can be generated in the absence of any selection expressly favoring synchrony or alternation.



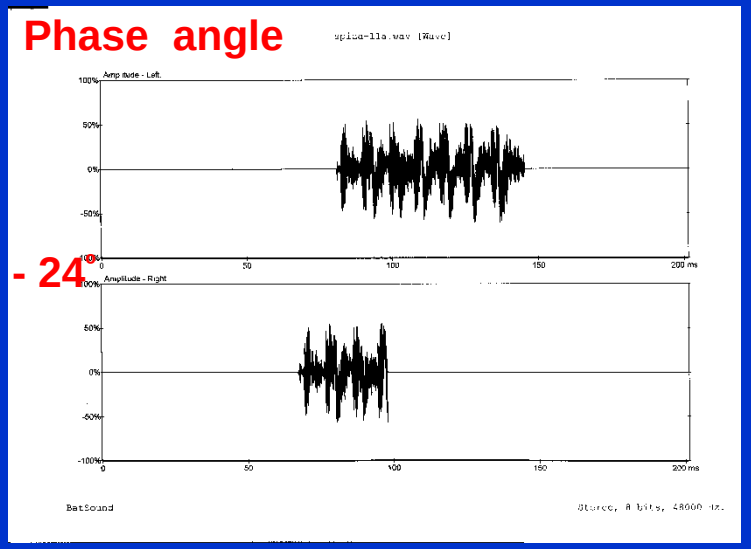


Neoconocephalus spiza (Orthoptera : Tettigoniidae) :

female preference for song length



***Neoconocephalus spiza* : female preference for leading song overrides song length**



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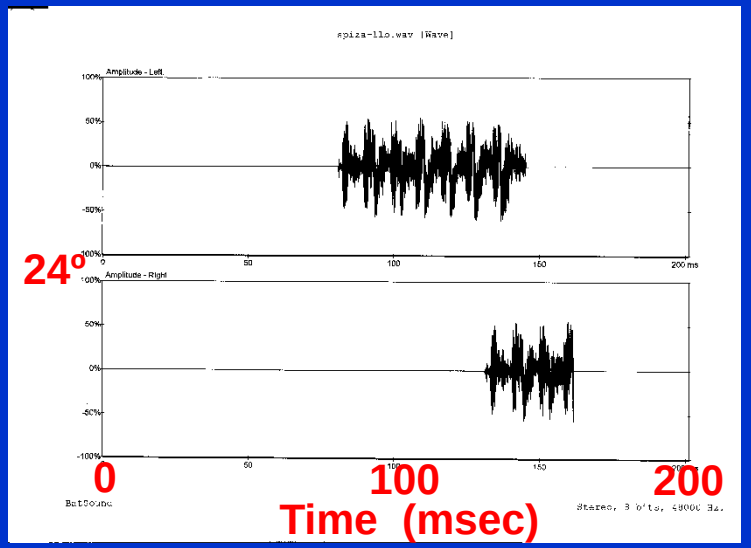
12



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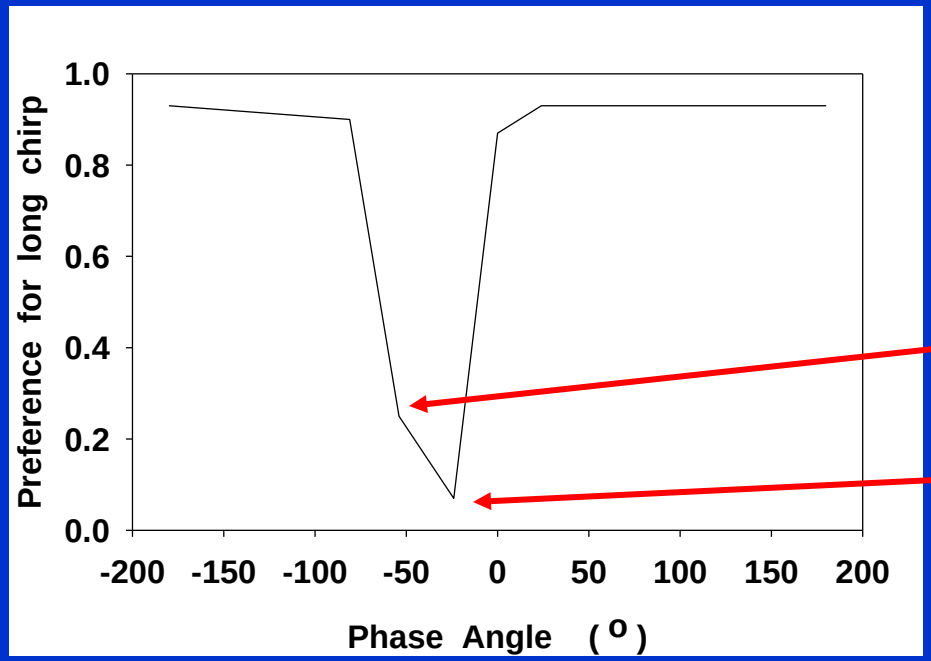
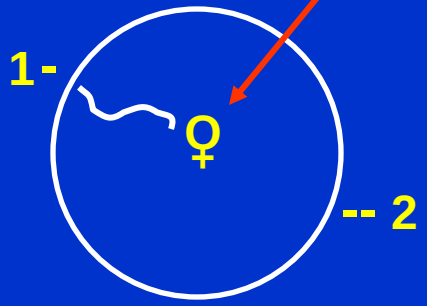
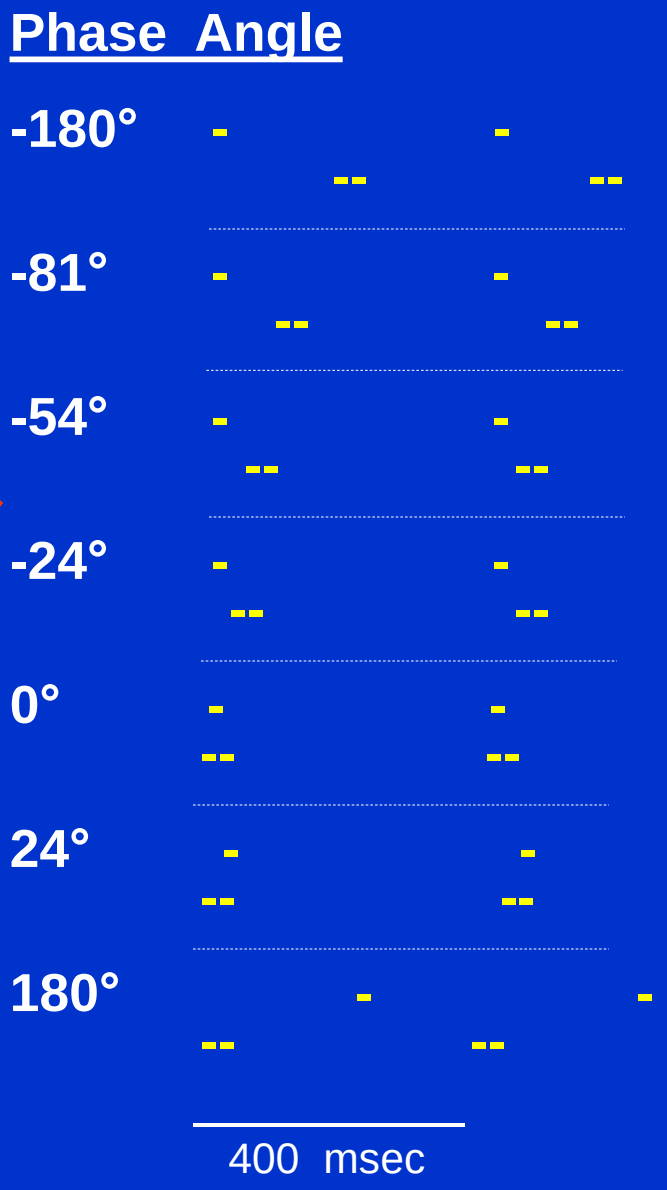


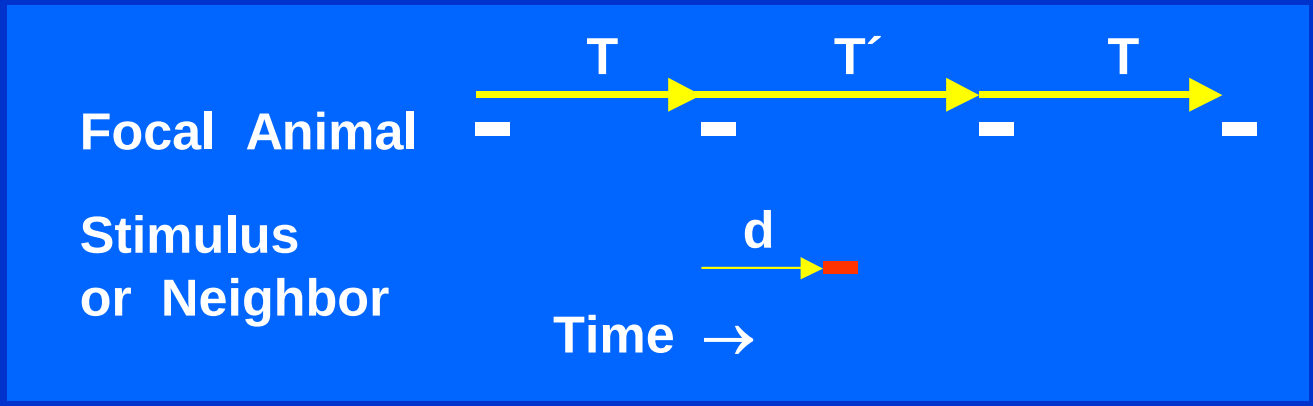
Greenfield & Roizen 1993





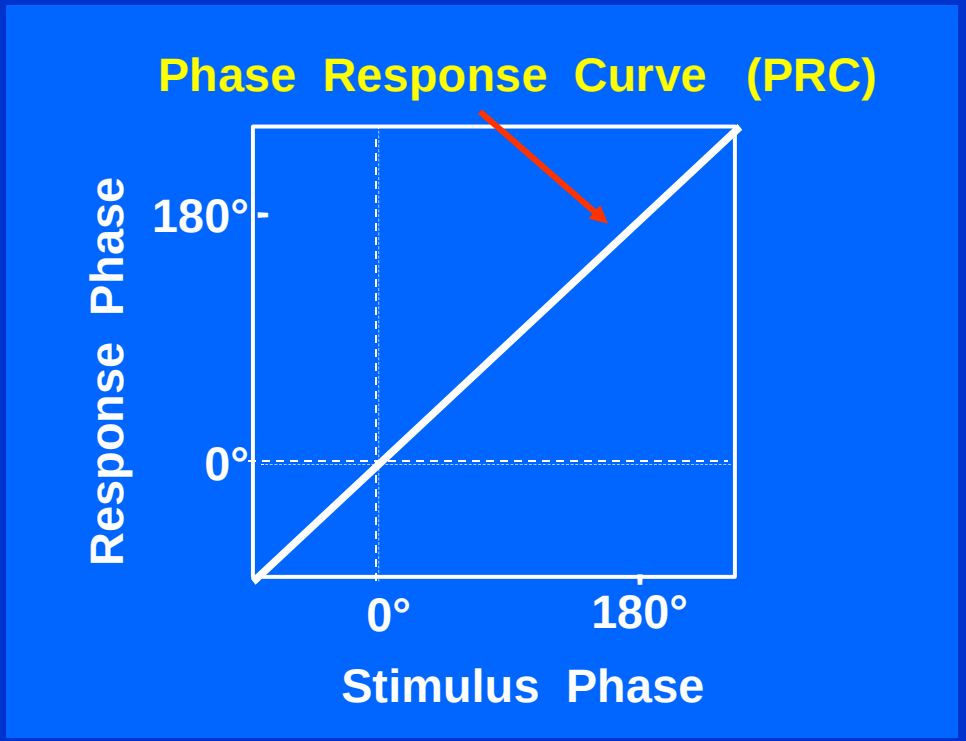
Neoconocephalus spiza **- precedence effect in female phonotaxis**

Inhibitory Resetting :



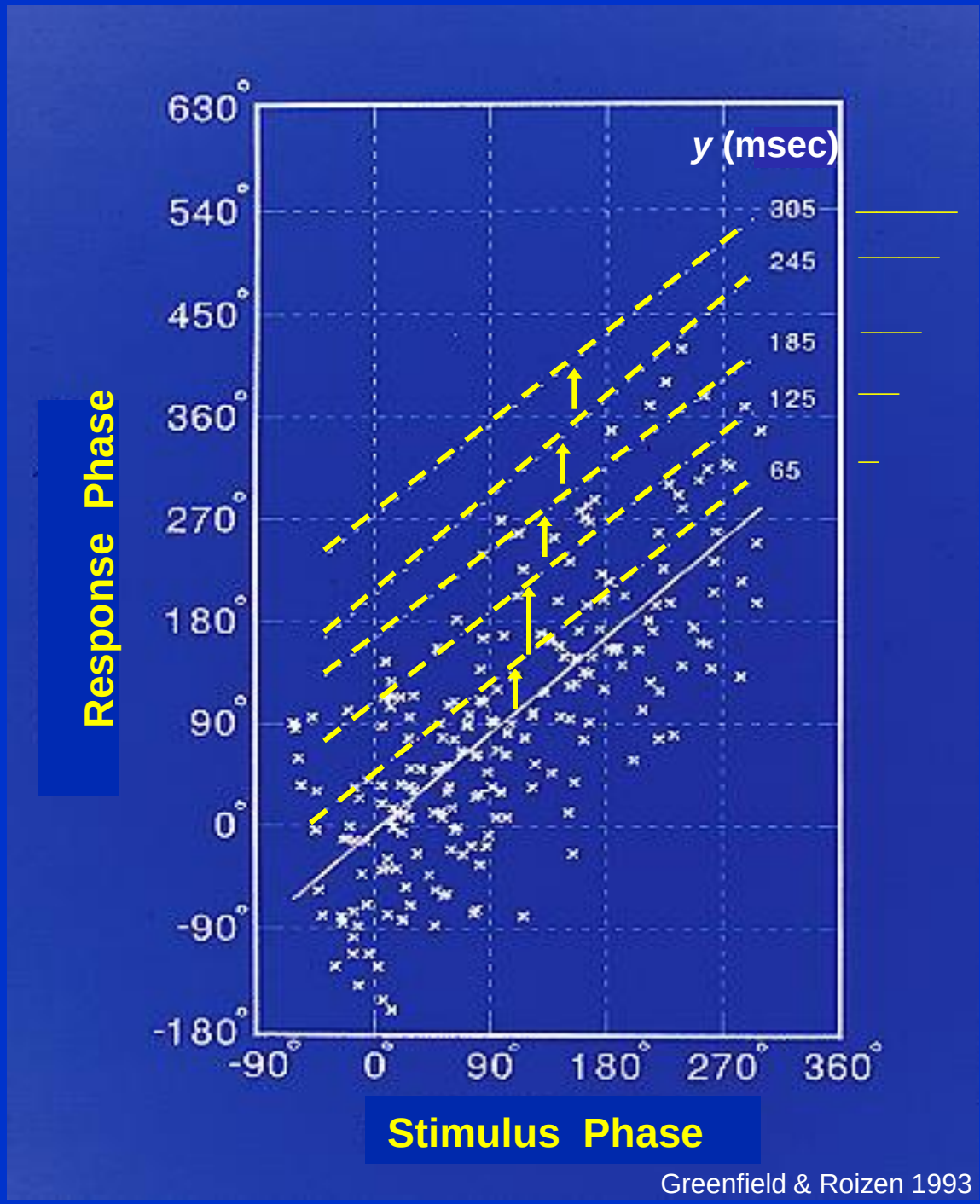
Stimulus Phase = (d / T) • 360°

Response Phase = {(T´ - T) / T } • 360°

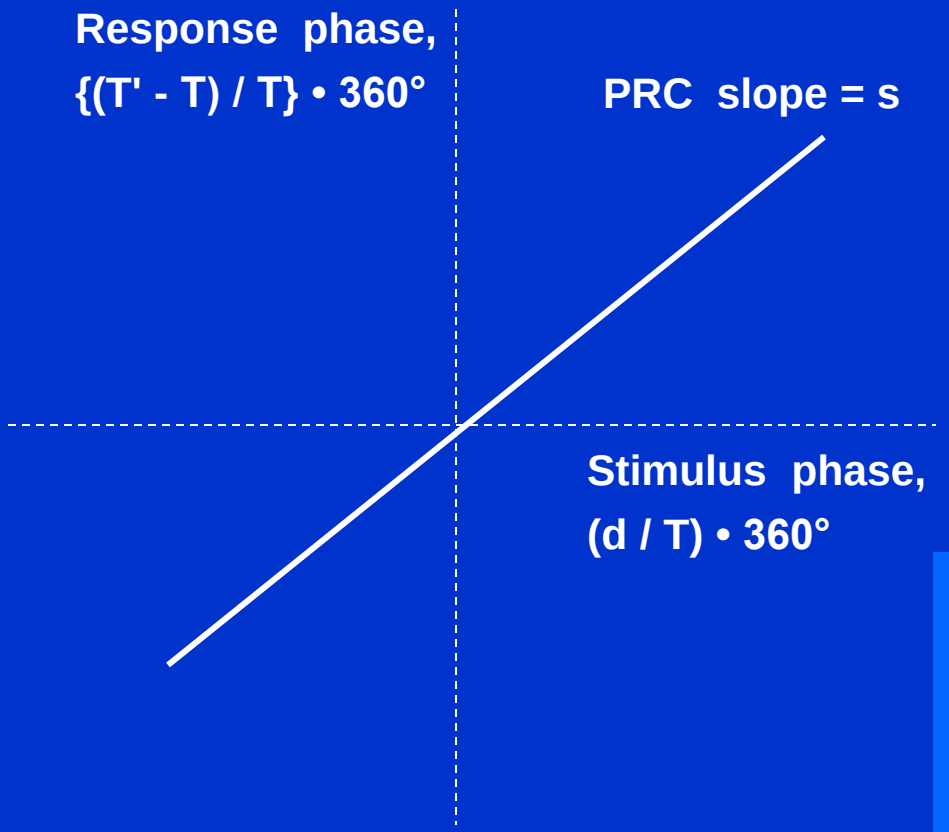


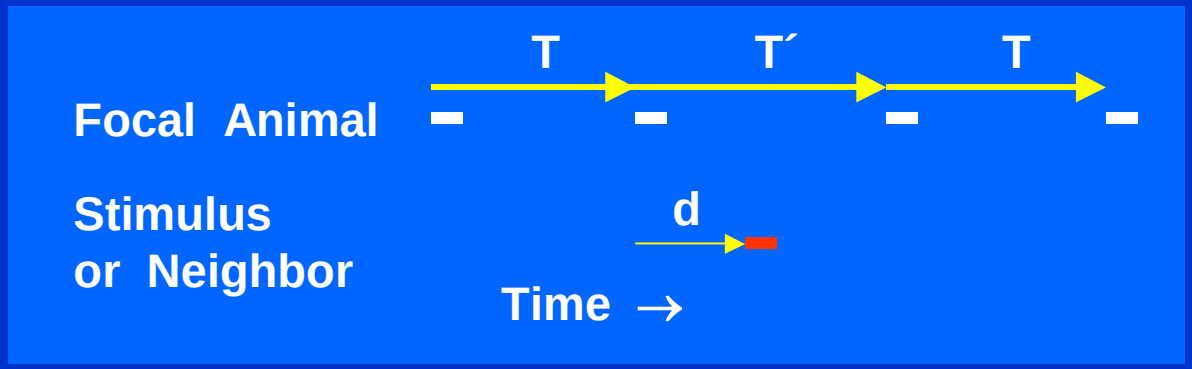
Neoconocephalus spiza (Tettigoniidae) :

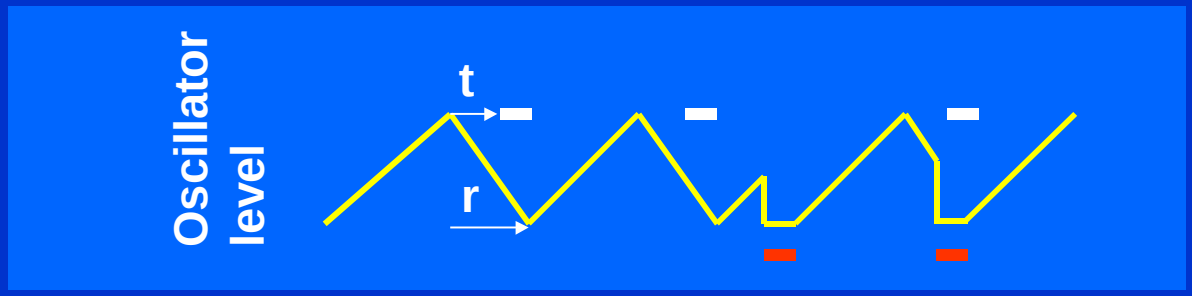
PRC intercepts adjusted by stimulus length



Greenfield & Roizen 1993







Basic model :

$T' = (T + \varepsilon) + (s \bullet d)$, where ε is a stochastic element

Full model :

$T' = (T + \varepsilon) + s\{(d + l / v) - (r - t)\} + (y - x)$

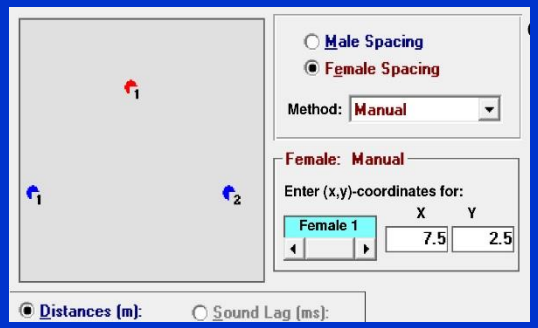
Greenfield, Tourtellot & Snedden 1997

Monte Carlo Simulation

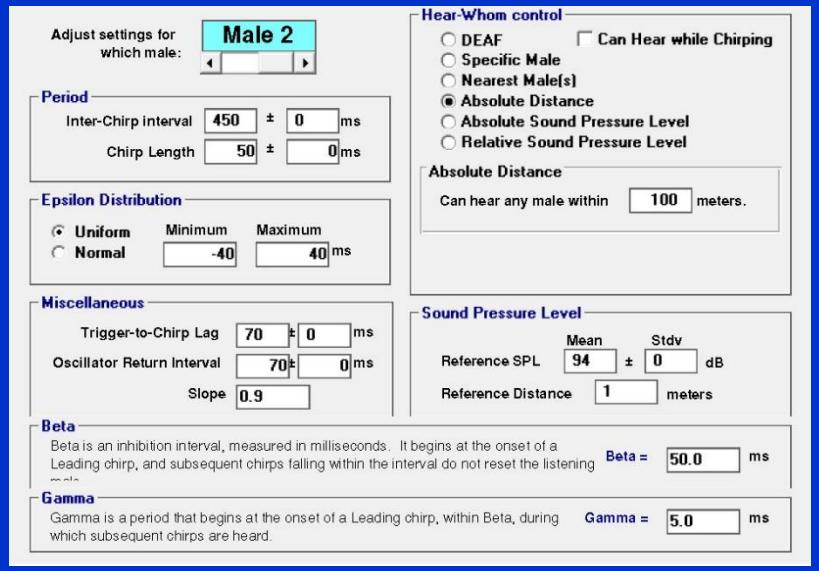
Michael Tourtellot

VisualBASIC® Maestro

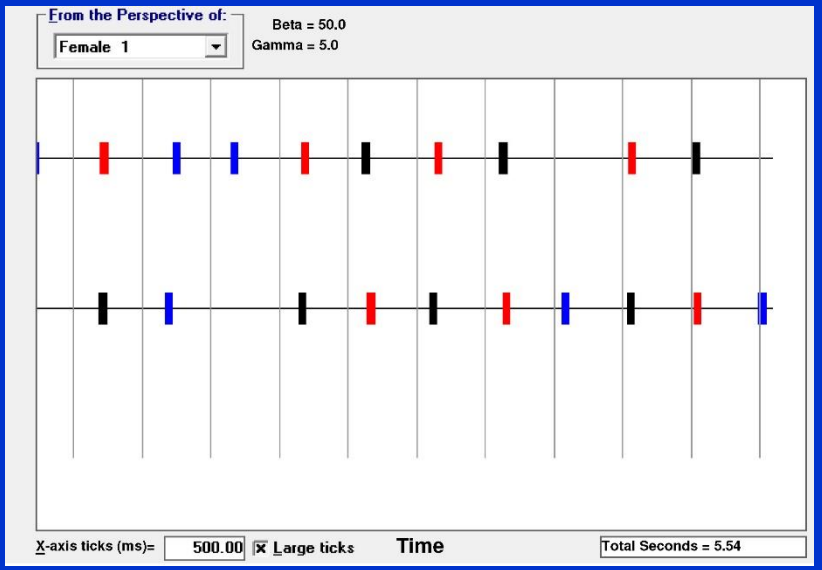
Monte Carlo Simulation



Spacing ; 2 males separated by 5 m ;
1 female

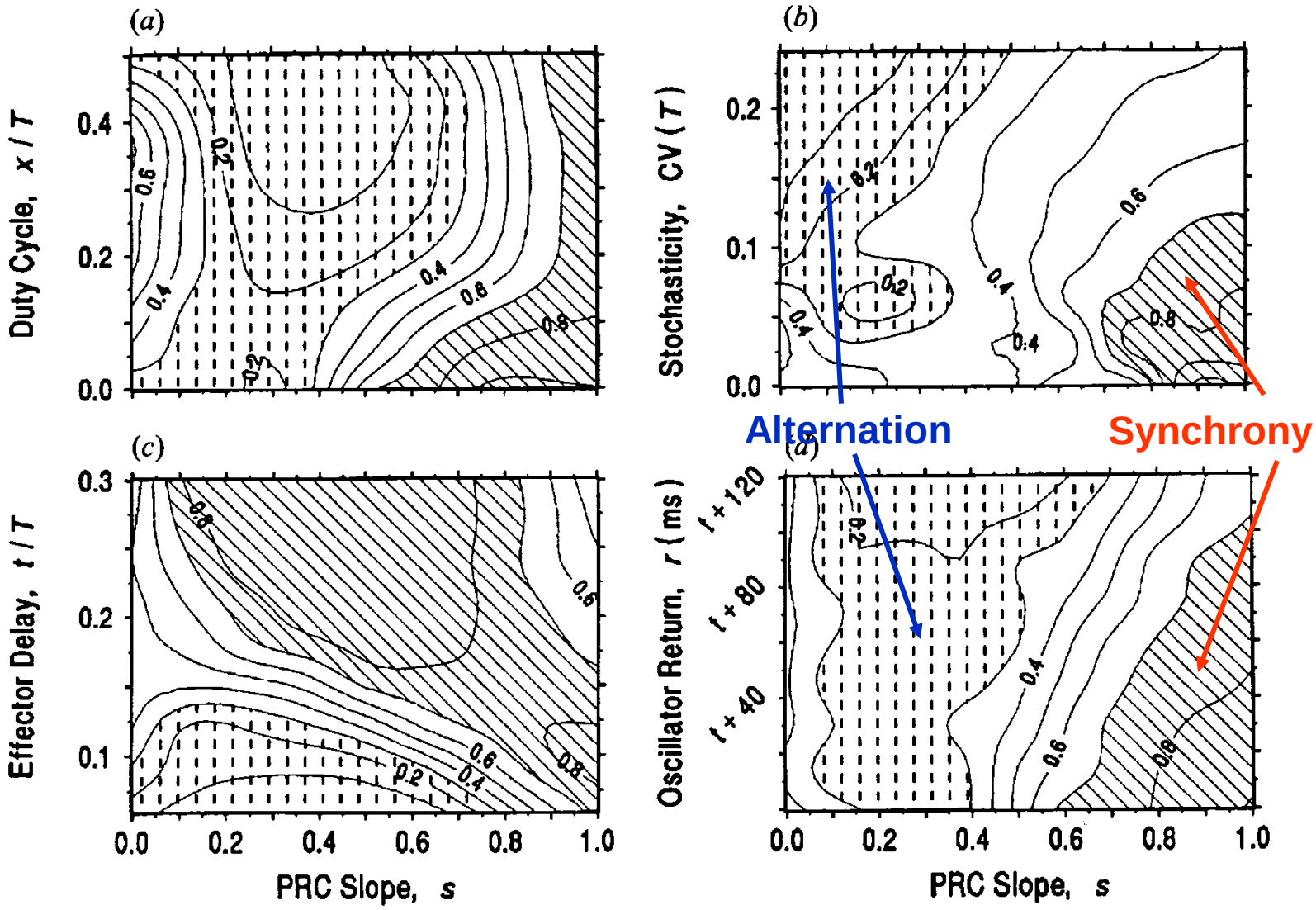


Male song adjustment parameters



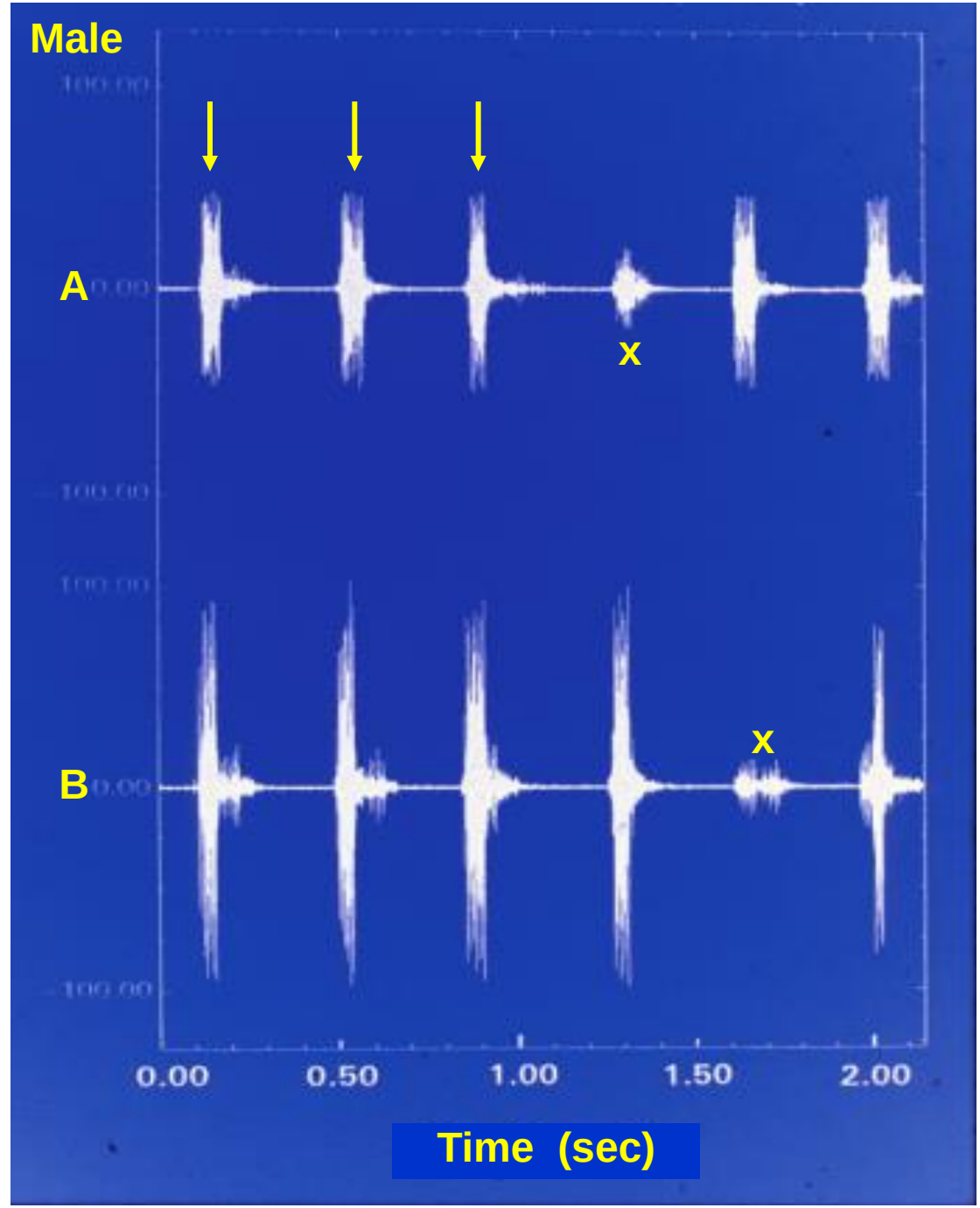
Calls of the 2 males ; mostly synchronized

Monte Carlo Simulation :



Greenfield et al. 1997

Neoconocephalus spiza
(Tettigoniidae: Conocephalinae);
Central America;
(imperfect) synchrony



3-step pathway :

Collective singing patterns in choruses simply emerge from the ‘receiver psychology’ of female perception and preference.

1) Females ignore male calls that follow a neighbor’s by a brief interval.

+

No experimental evidence for coevolution between male and female traits

?

2) Males adjust call rhythm (phase) upon hearing a stimulus or neighbor.

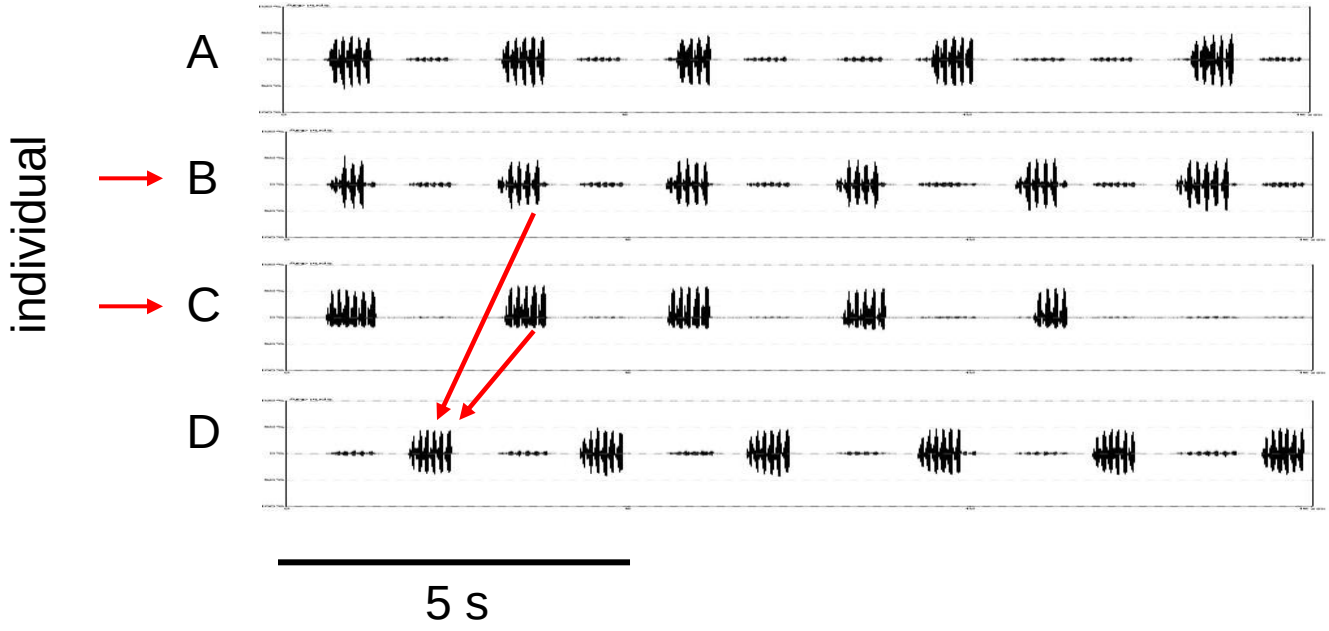
+

3) When multiple males use equivalent adjustments an expansive chorus of synchrony and/or alternation may arise.
Importantly, the display can be generated in the absence of any selection expressly favoring synchrony or alternation.

+

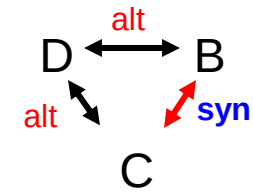
Question 1 :
Did male song adjustment (inhibitory resetting) coevolve with female response to relative call timing (leading vs. following calls) ?

Tettigoniidae ; Bradyporinae



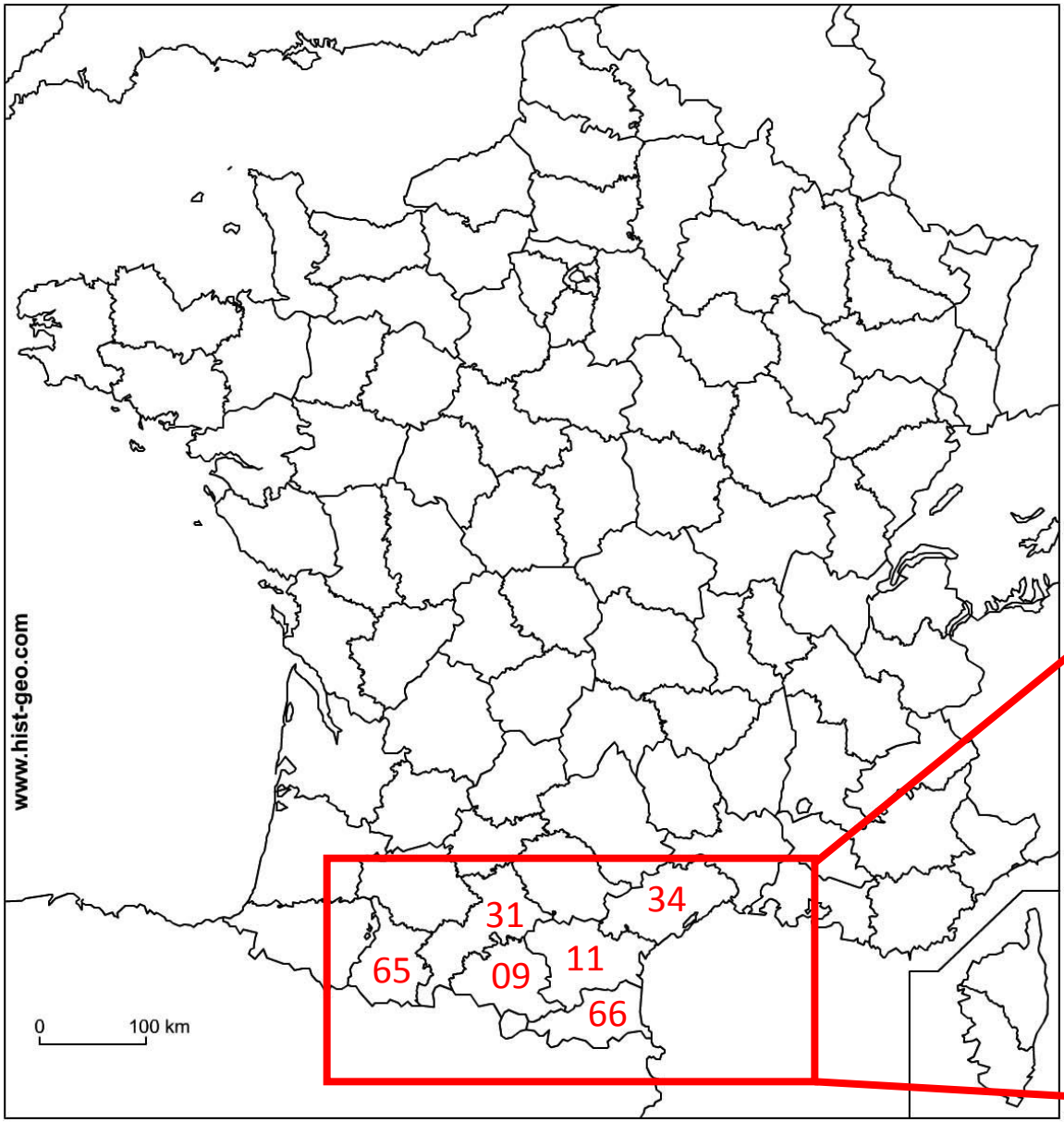
Ephippiger diurnus

Alternation + Synchrony

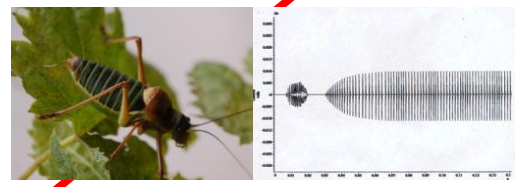


Females ignore following calls ;
Male song adjustment (inhibitory resetting) ;
Chorusing (alternation and synchrony)

Flightless ; negligible dispersal ;
narrow habitat preference ;
isolated, genetically differentiated populations



Ephippiger diurnus **(Tettigoniidae)**



Flightless ; negligible dispersal ;
narrow habitat preference ;
geographically isolated,
genetically differentiated populations

→

Application of comparative phylogenetic methods possible

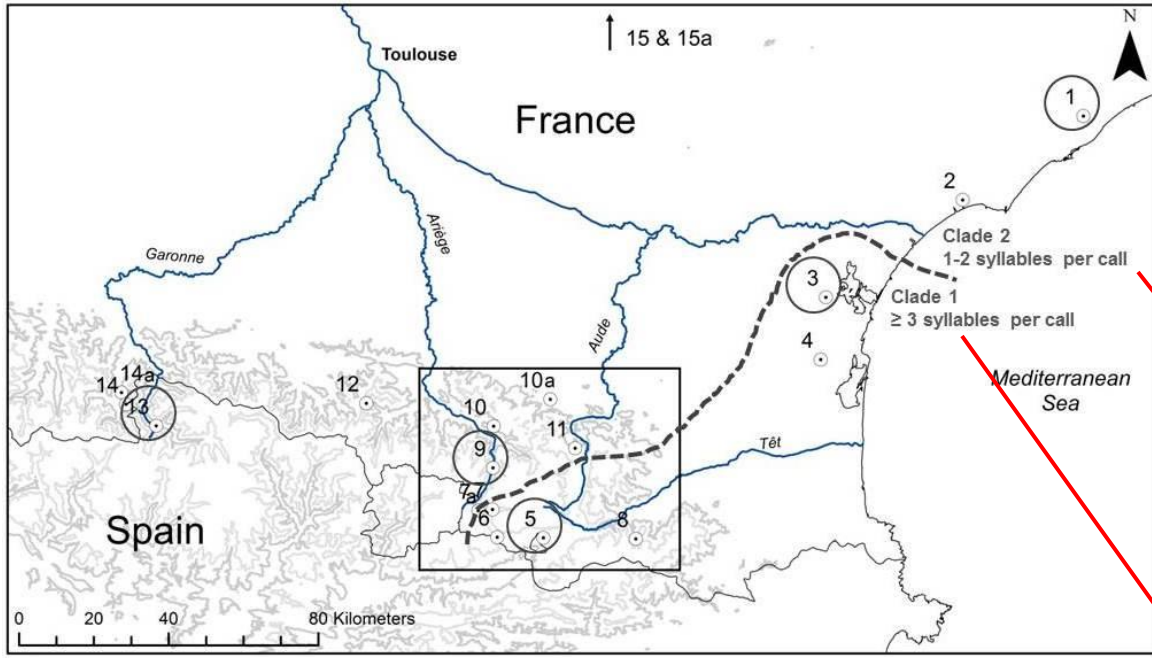
‘Comparative Method’ ;

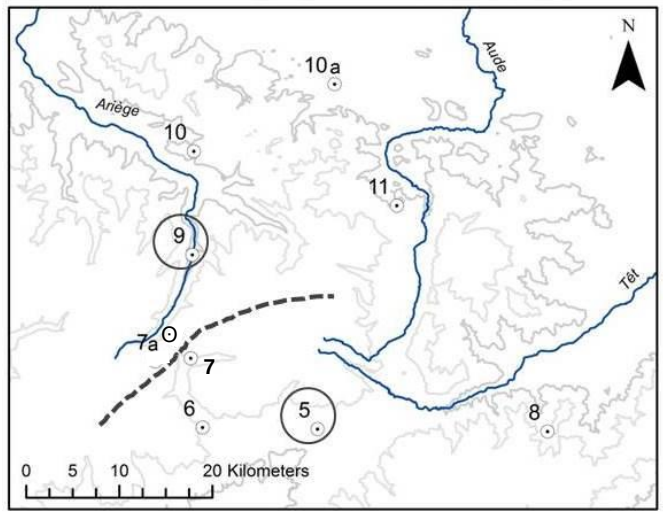
17 *E. diurnus* populations ‘sampled’ ;

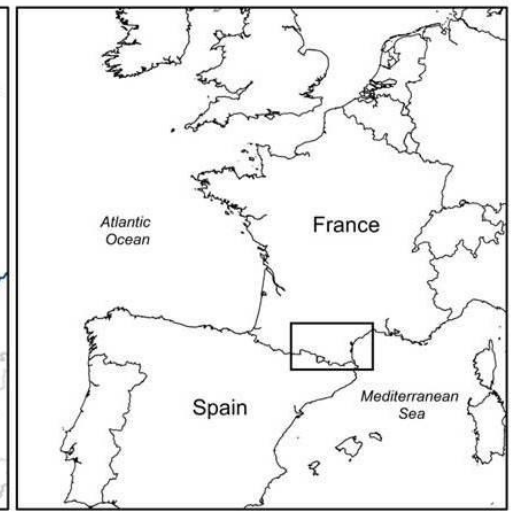
Phylogenetic analysis indicates branching topology ;

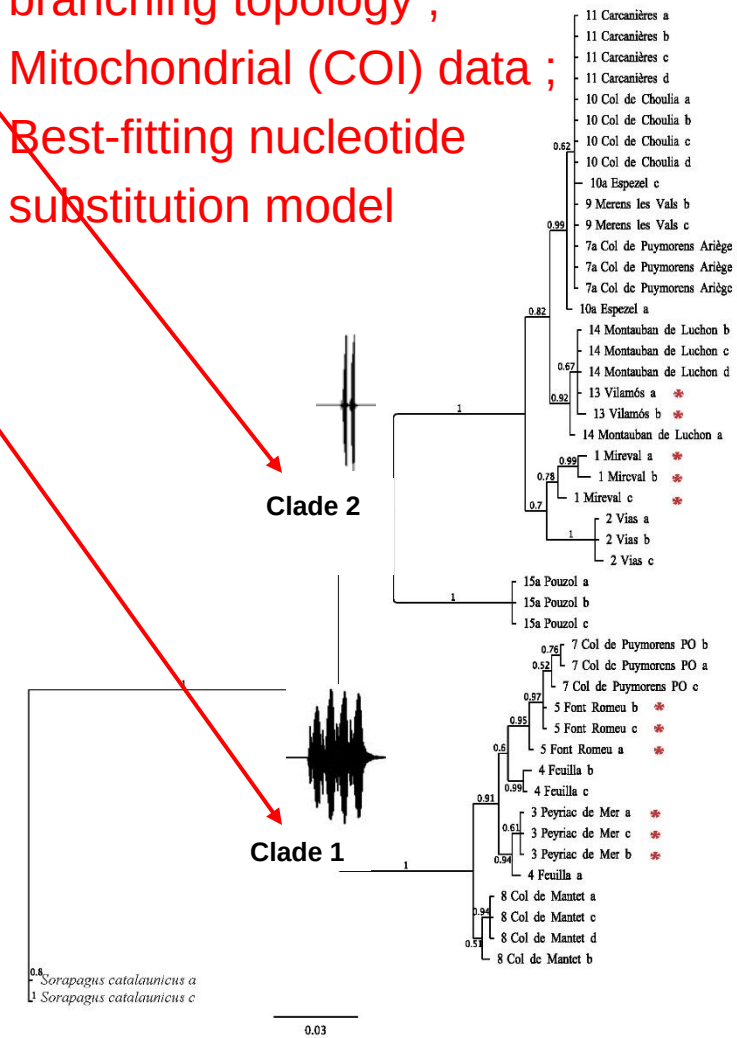
Mitochondrial (COI) data ;

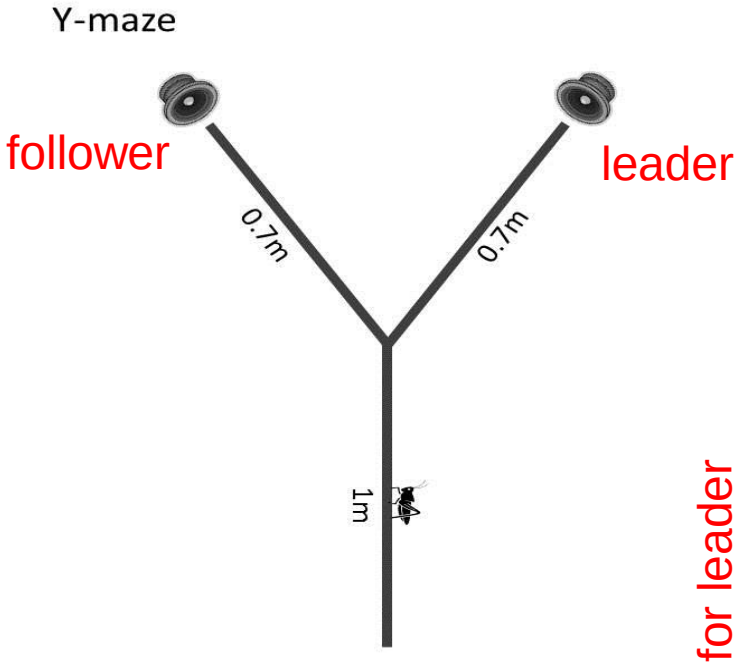
Best-fitting nucleotide substitution model



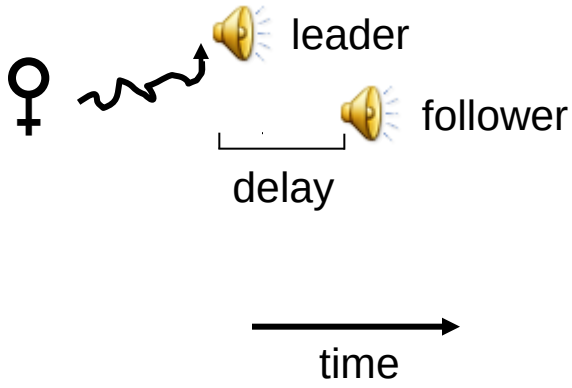


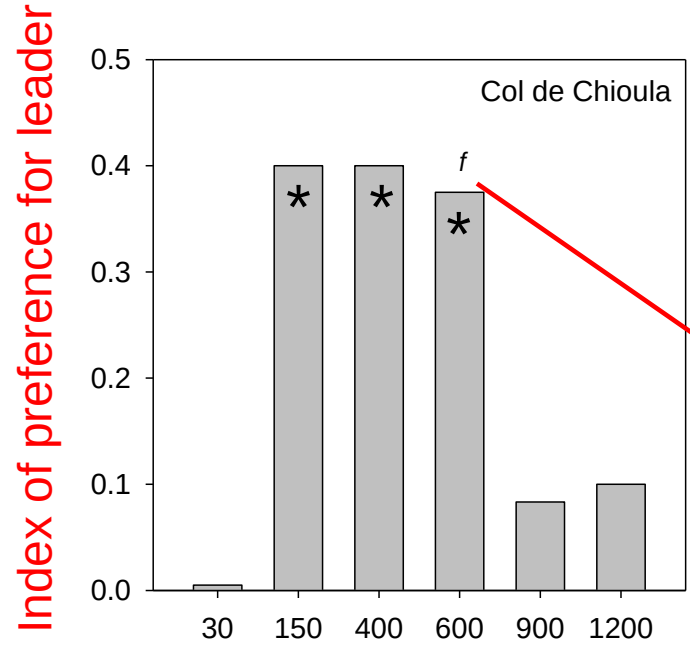






Measurement of female perceptual trait



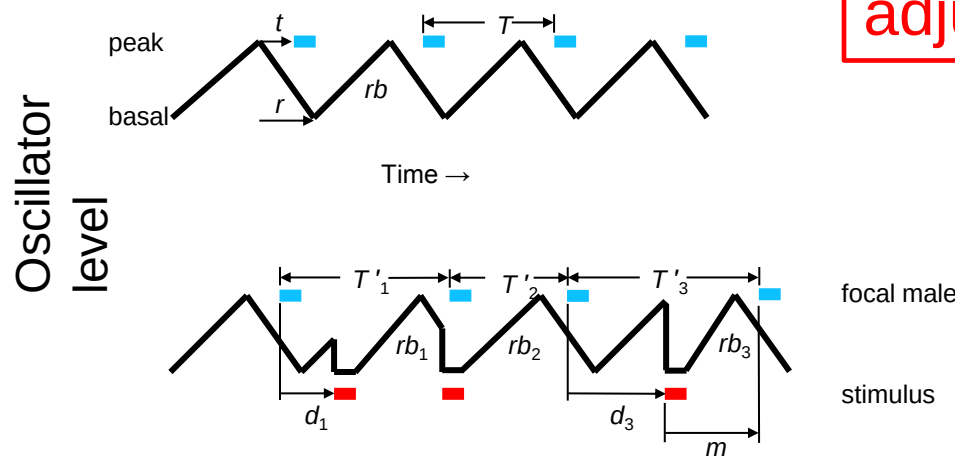


Col de Chioula population

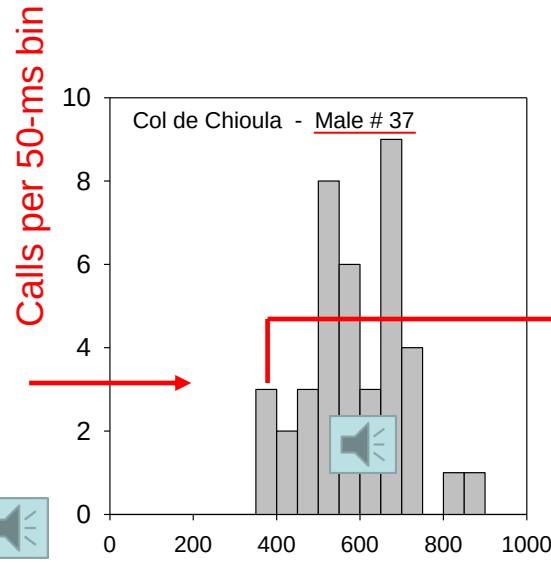
f – maximum separation at which females ignore follower

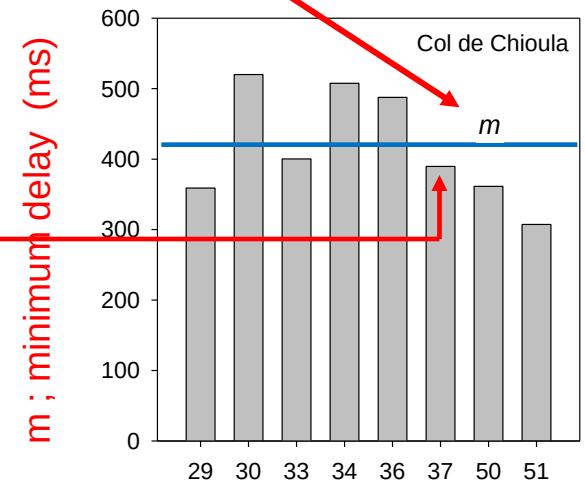
Leader – follower call separation (ms)

Measurement of male song adjustment trait



m – minimum delay before male resumes singing

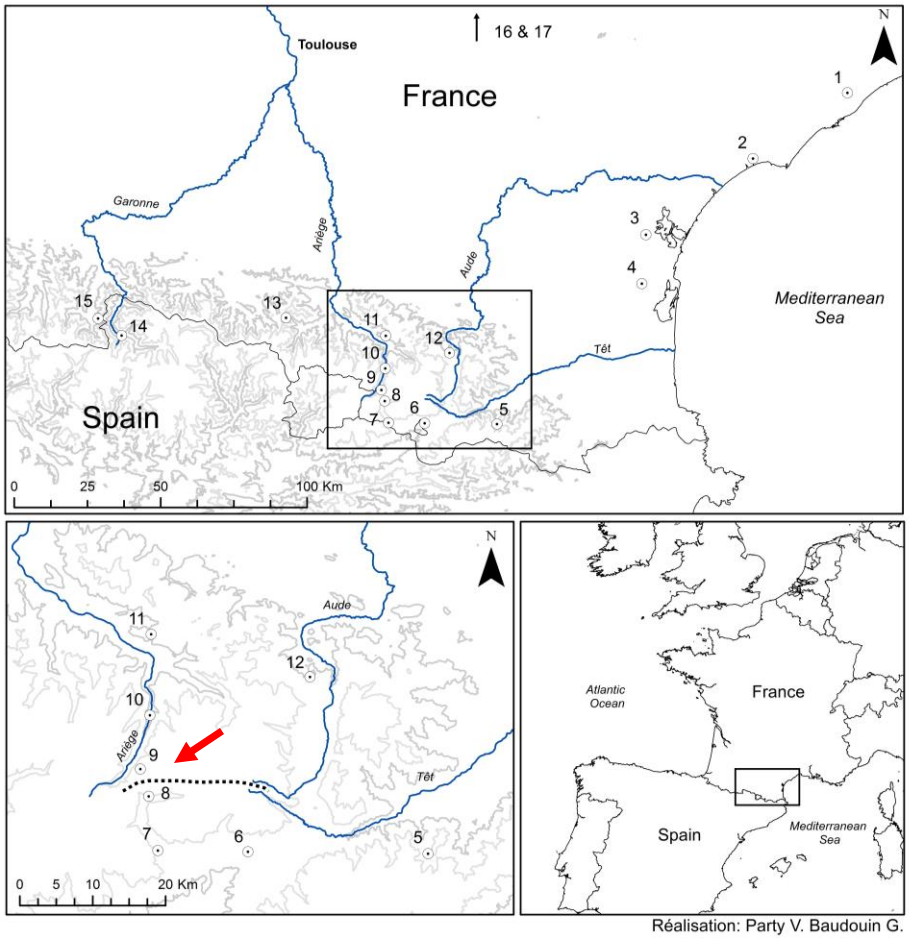




Col de Chioula population

Focal male does not call during post-stimulus interval

Synthetic song stimulus at t = 0



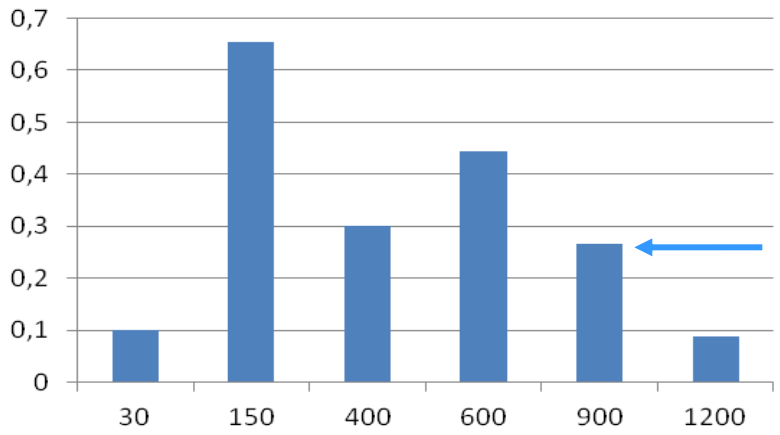
Populations: 1) Mireval, 2) Vias, 3) Peyriac de Mer, 4) Feuilla, 5) Col de Mantet, 6) Font Romeu, 7) Latour de Carol, 8) Col de Puymorens, 9) Hospitalet près l'Andorre, 10) Mérens-les-Vals, 11) Col de Chioula, 12) Carcanières, 13) Port de Lers, 14) Vilamòs, 15) Cigalère, 16) Le Lioran, 17) Pouzol.

Predictions :

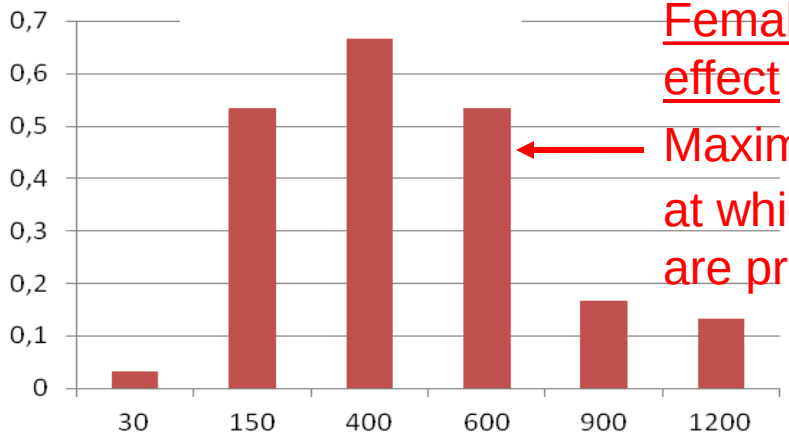
If male song adjustments have coevolved with female perception, *m* should be ≥ *f* such that males do not broadcast ineffective following calls.

Moreover, if *m* ≈ *f*, males will maximize their call rate while at the same time forgoing the broadcast of following calls.

Col de Puymorens ; 8

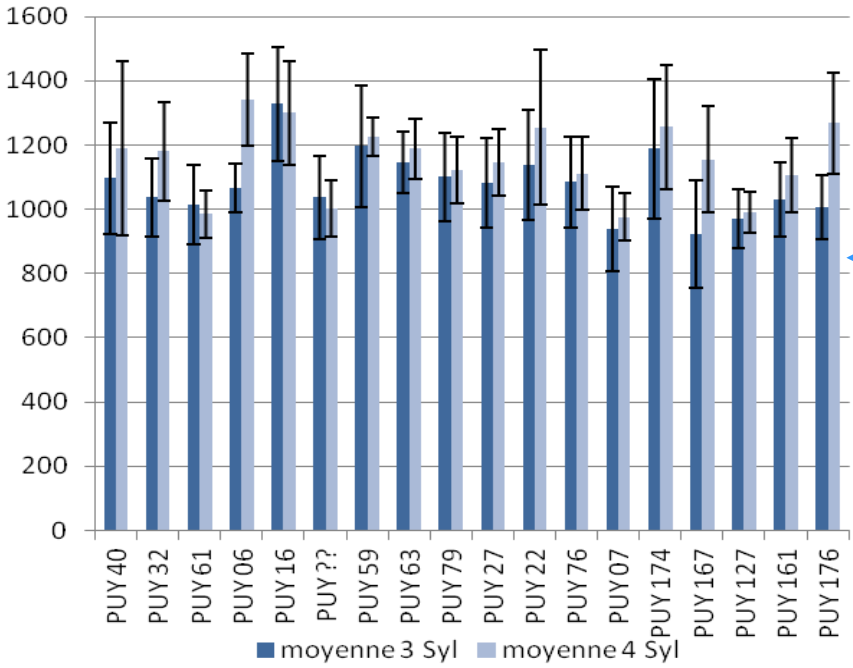


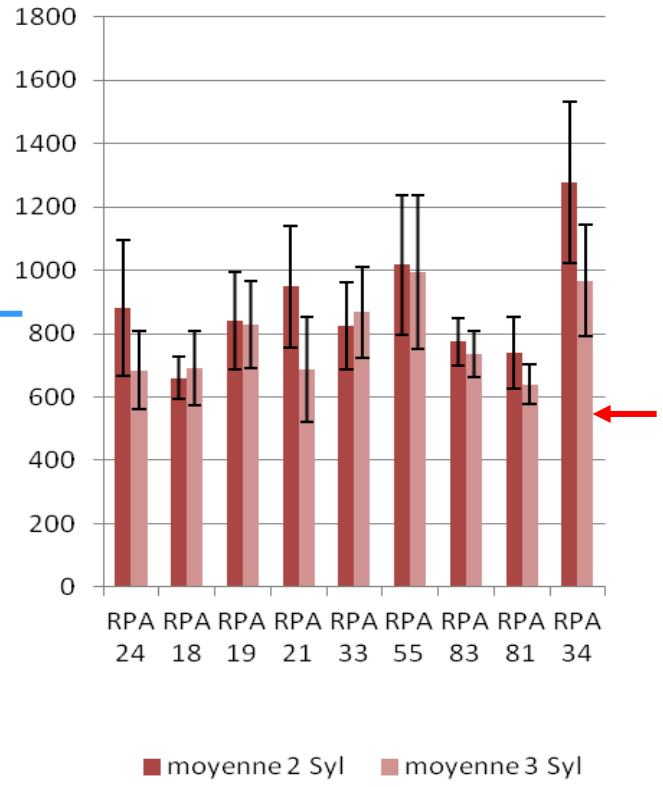
Hospitalet près l'Andorre ; 9



Female precedence effect ;

Maximum delay (msec) at which leading calls are preferred.

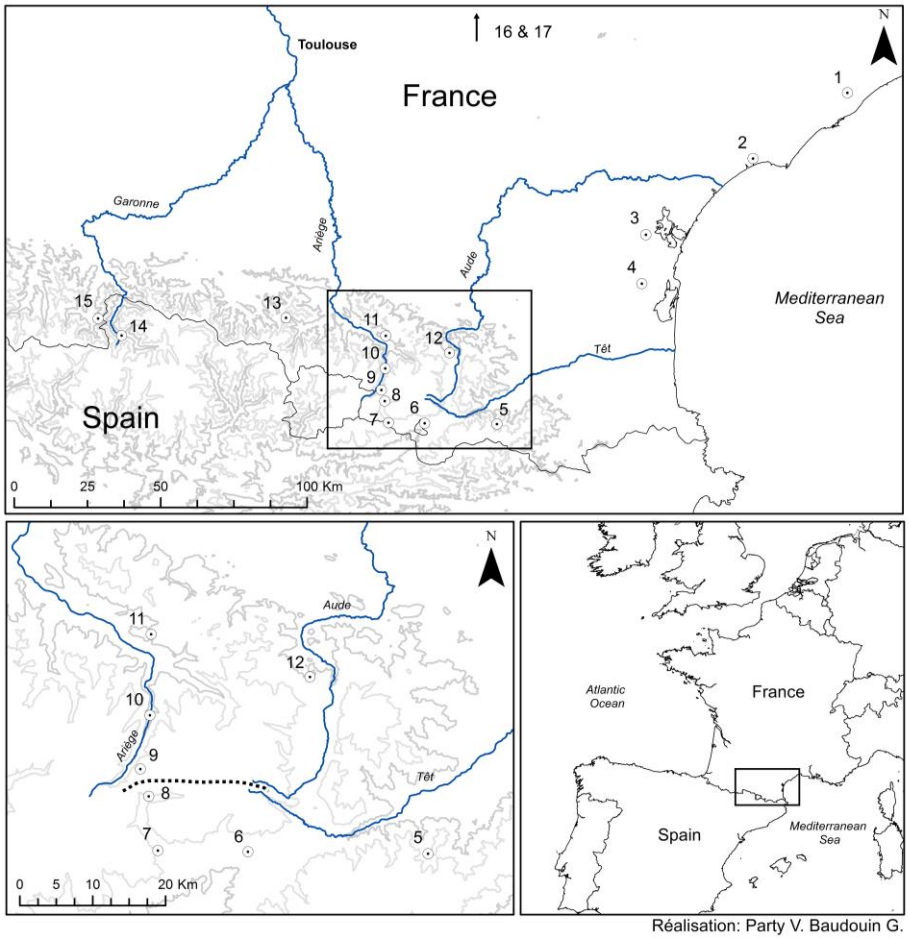




Male phase adjustment ;

Minimum delay (msec) before singing after a stimulus or neighbor.

A

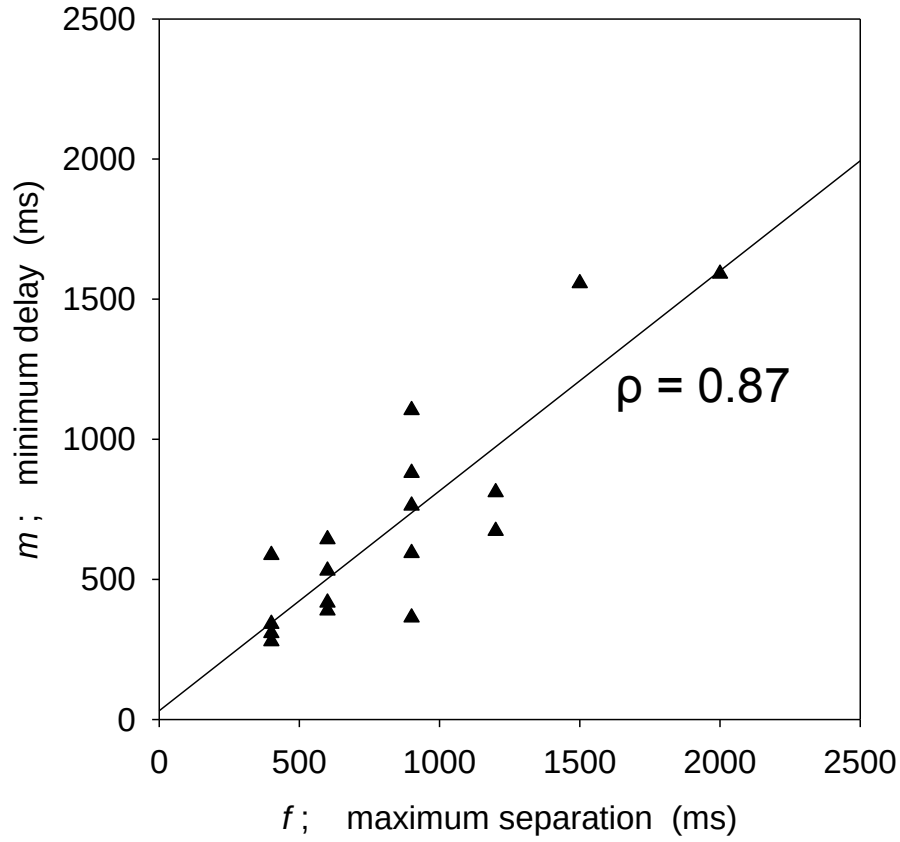


Populations: 1) Mireval, 2) Vias, 3) Peyriac de Mer, 4) Feuilla, 5) Col de Mantet, 6) Font Romeu, 7) Latour de Carol, 8) Col de Puymorens, 9) Hospitalet près l'Andorre, 10) Mérens-les-Vals, 11) Col de Chioula, 12) Carcanières, 13) Port de Lers, 14) Vilamòs, 15) Cigalère, 16) Le Lioran, 17) Pouzol.

For the 17 populations sampled,

$m \approx f$.

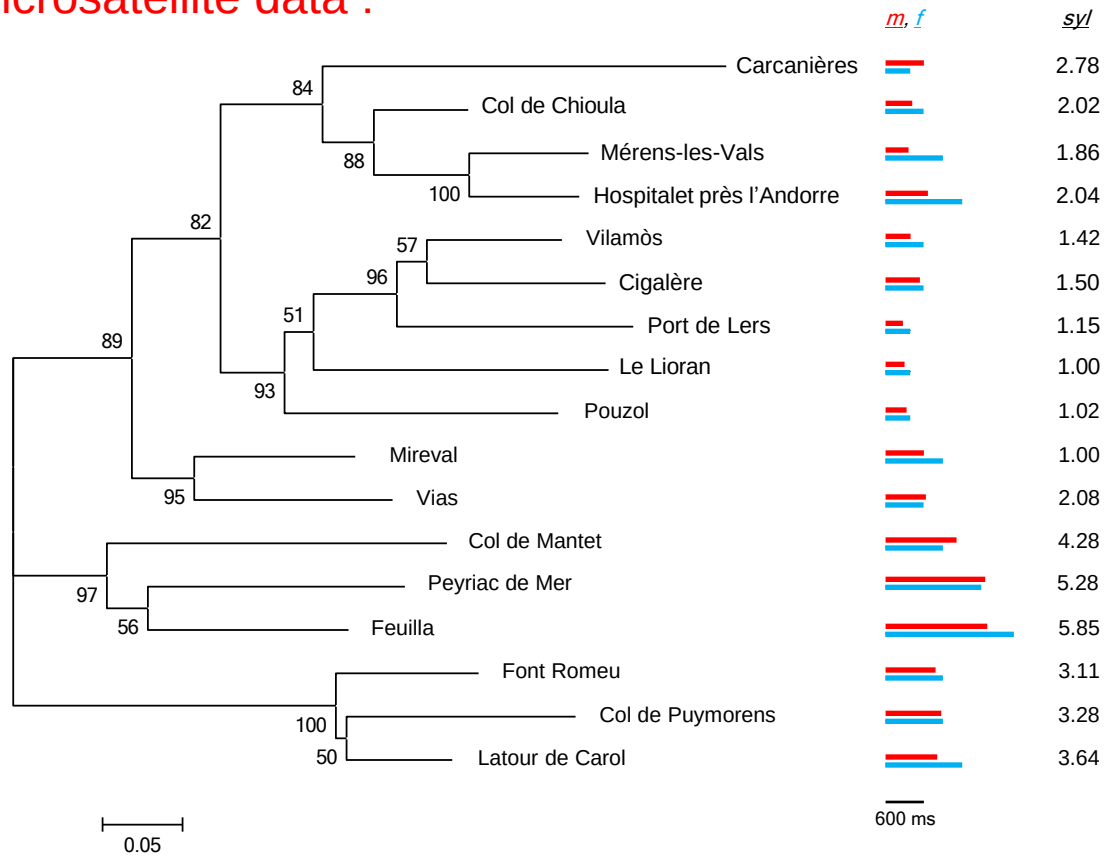
B



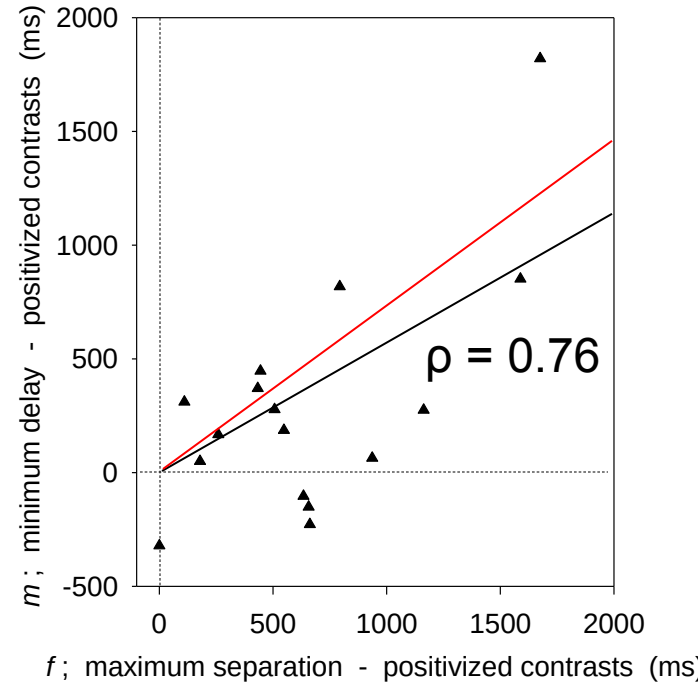
Is the *m* – *f* correlation among the 17 populations an artifact of sampling ?

a) Remove ‘phylogenetic signal’ by application of phylogenetic independent contrasts (PIC)

‘working phylogeny’ of sampled *E. diurnus* populations – unrooted neighbor-joining (NJ) tree based on microsatellite data :



m – *f* correlation following PIC correction



Is PIC justified for intra-specific comparison ?

Normally no, because gene flow resulting from inter-population migration will influence phenotypic vaues of a population. (Stone, Nee & Felsenstein 2011)

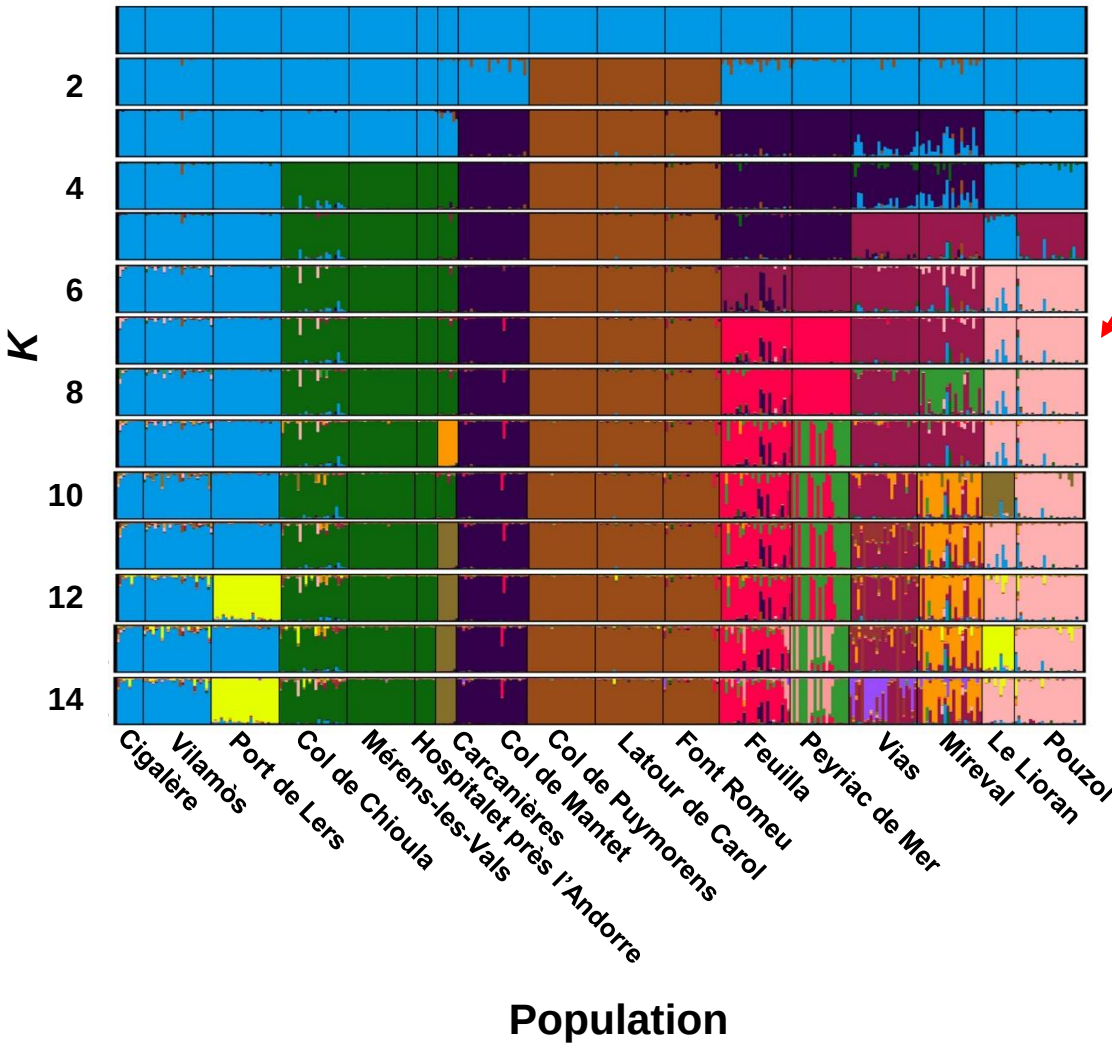
But, *E. diurnus* is a special case :

- Negligible dispersal ;
- Branching topology of population phylogeny ;
- Mitochondrial (COI) tree and microsatellite tree are very similar :
  - ‘working phylogeny’ is probably the correct one

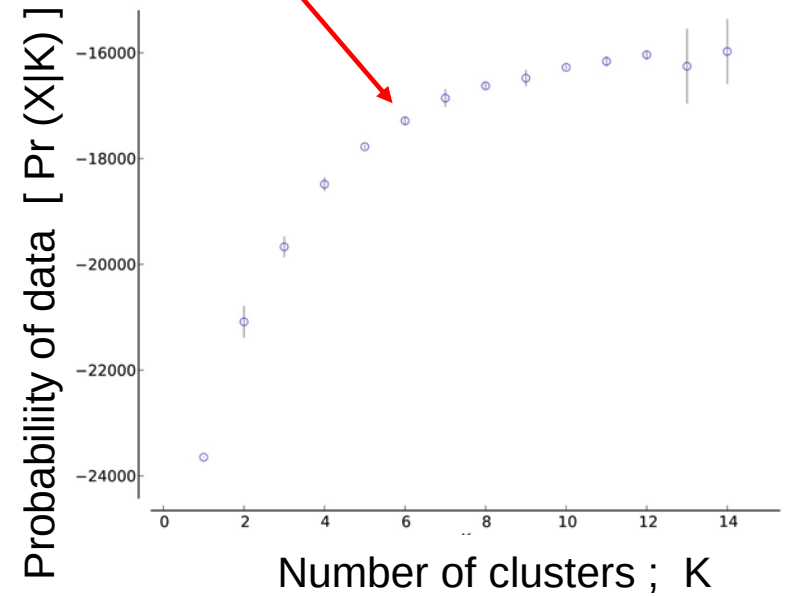
Nonetheless, we took a conservative approach :

- Identify genetically differentiated clusters of populations using a Bayesian clustering protocol (STRUCTURE) on microsatellite data

7 genetically differentiated clusters ; re-apply PIC on these 7 clusters

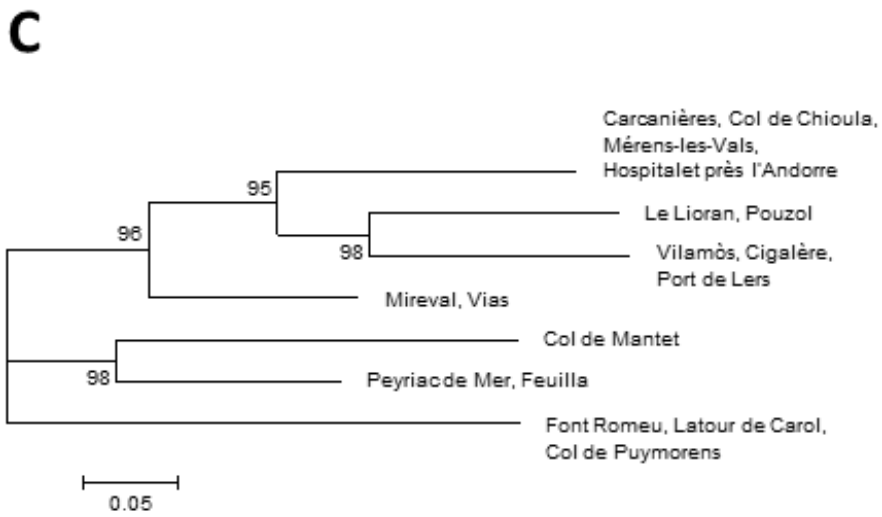

K
2
4
6
8
10
12
14
Cigalère
Vilamòs
Port de Lers
Col de Chioula
Mérens-les-Vals
Hospitalet près l'Andorre
Carcanières
Col de Mantet
Col de Puymorens
Latour de Carol
Font Romeu
Feuilla
Peyriac de Mer
Vias
Mireval
Le Lioran
Pouzol
Population

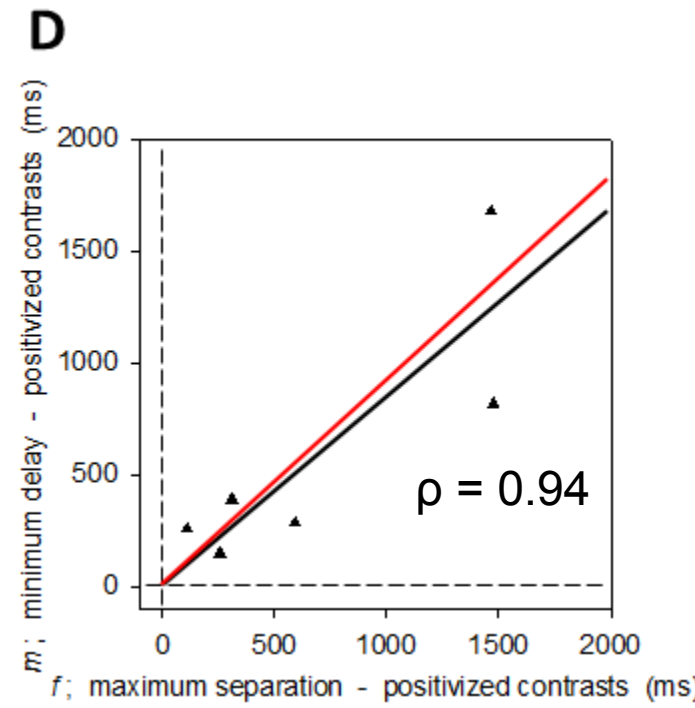
K = 7 clusters


Probability of data [Pr (X|K)]
−16000
−18000
−20000
−22000
−24000
0
2
4
6
8
10
12
14
Number of clusters ; K

Unrooted NJ tree of 7 clusters identified with STRUCTURE

m – *f* correlation following PIC correction



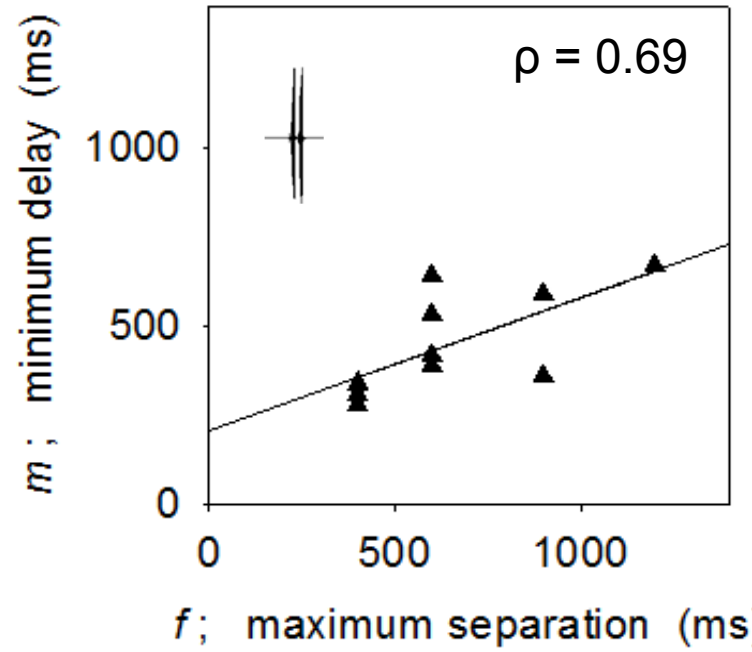


m – *f* correlation is not a phylogenetic artifact

Is the m – f correlation among the 17 populations an artifact of other correlations ?

b) Remove populations with long calls (≥ 3 syllables) ;
confounding correlations between *f* and *syl #* and between *m* and *syl #*

m – *f* correlation holds for the 10 populations having only 1-2 syllables per call ;
no influence of *syl #* on correlation



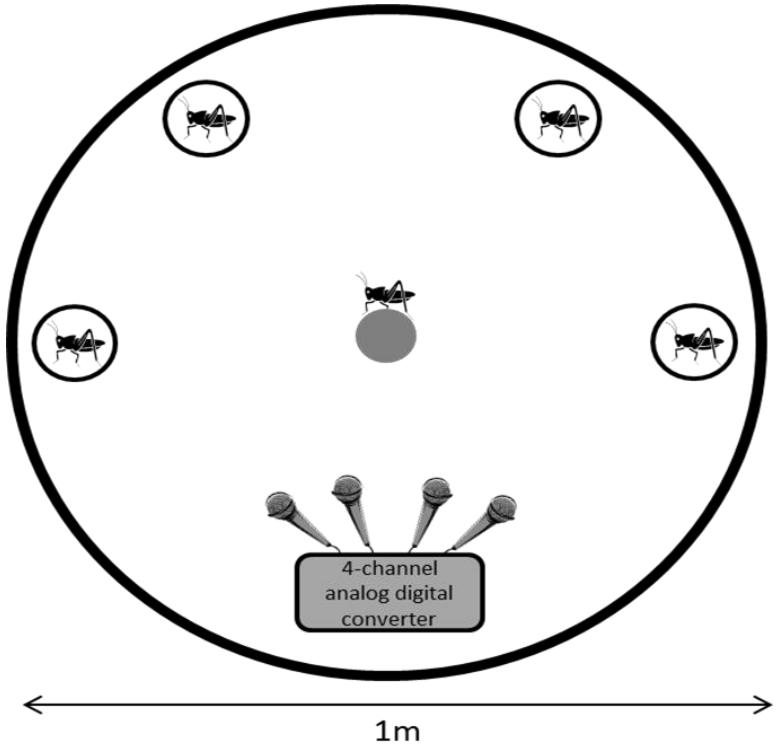
Conclusion : Male song adjustment (*m*) has coevolved with female perception (*f*)

Question 2 : Is receiver psychology (female perception of relative male call timing) important in the context of sexual selection within a chorus ?

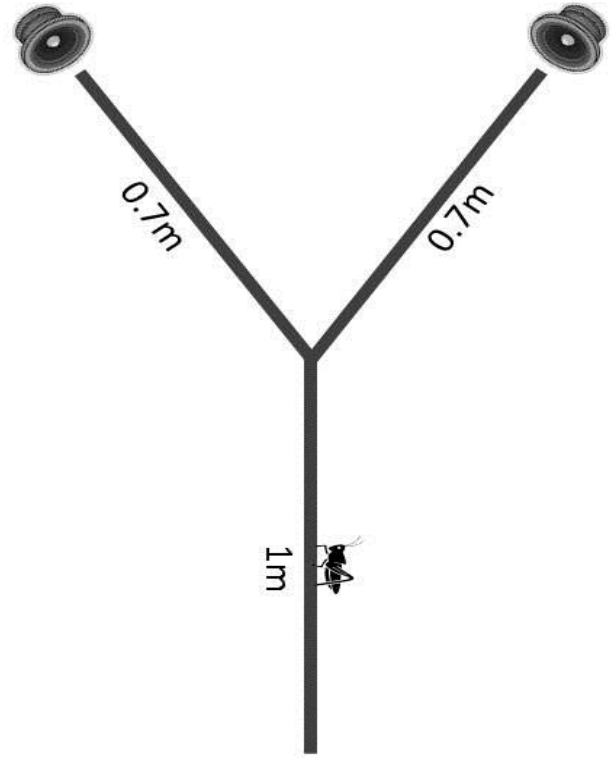
Method for testing female preferences for acoustic signal characters of males in a chorus.

The males differ in all 3 signal characters (leading calls, call rhythm, call length)

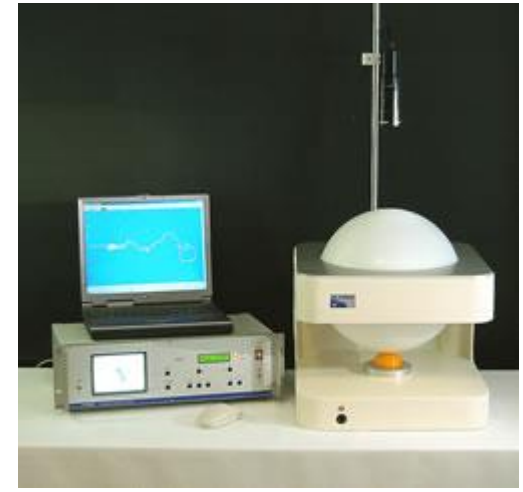
Do females pay attention to certain signal characters more than others ?

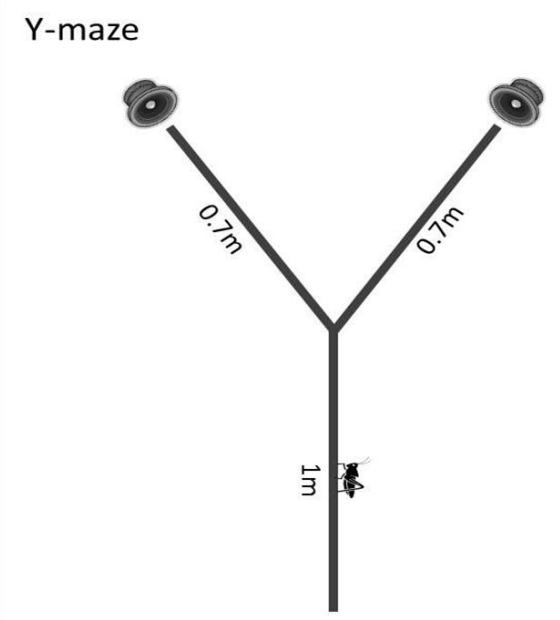


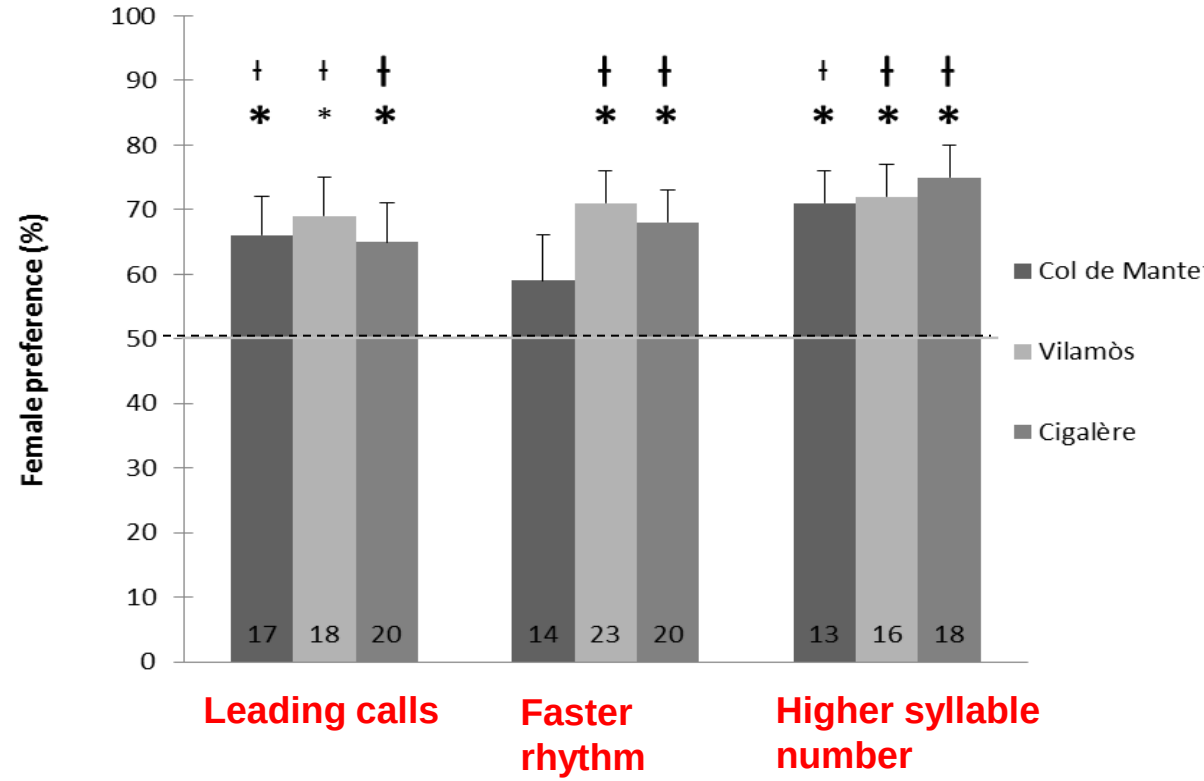
Y-maze



Kramer sphere
(open loop)

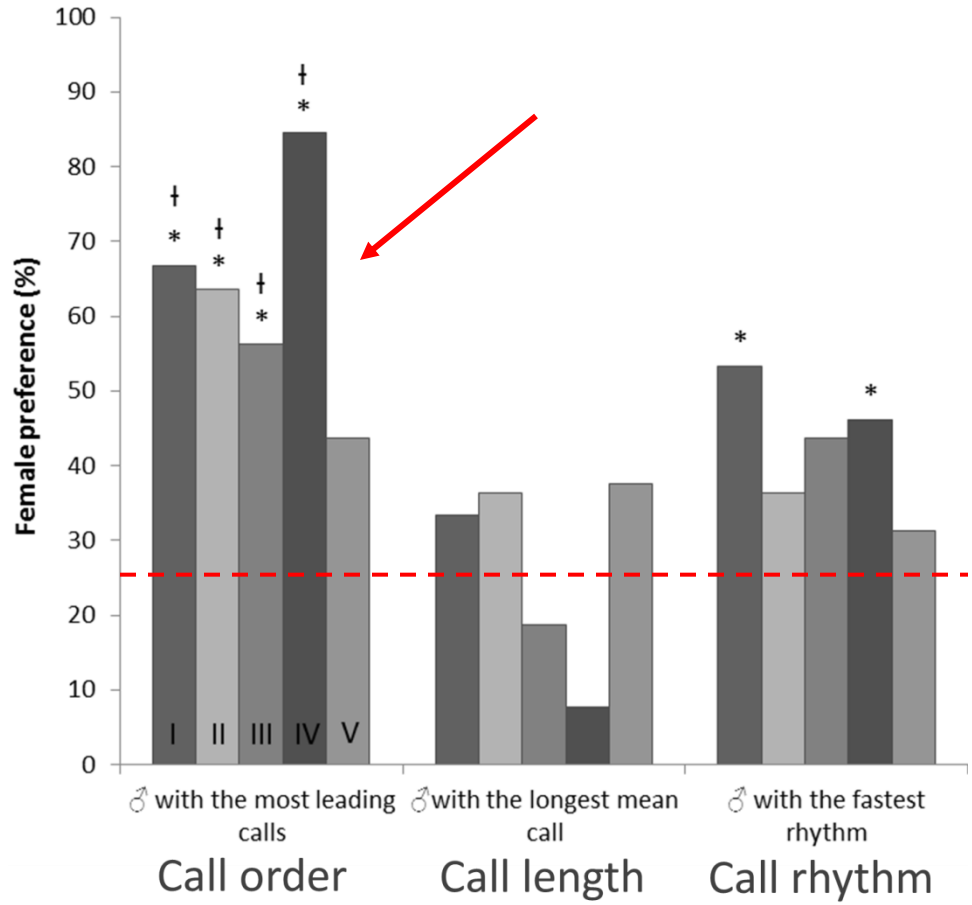






(Party, Brunel-Pons & Greenfield 2014)

Simple choice tests in 3 populations indicate female preferences for 1) leading calls, 2) faster rhythm, and 3) higher syllable number.



(Party et al. 2014)

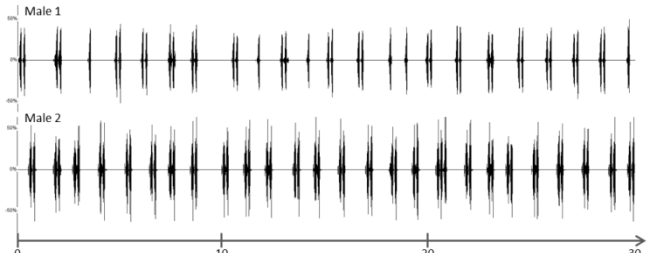
Priority of precedence : At a chorus females pay much more attention to call order than other signal characters.

Question 3 :

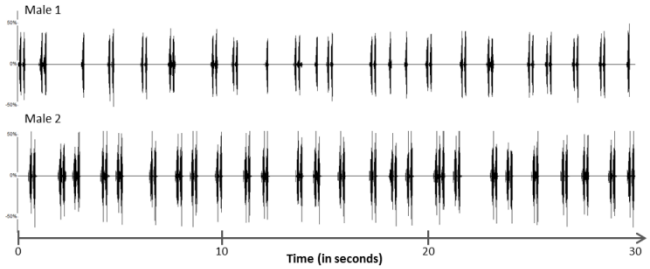
Do synchrony and alternation *per se* have adaptive value ?

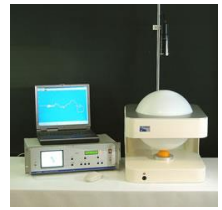
3 tests of synchrony, alternation, and overlapping calls, as broadcast by chorusing males, in the context of sexual selection :

Natural chorus stimulus (Merens-les-Vals)



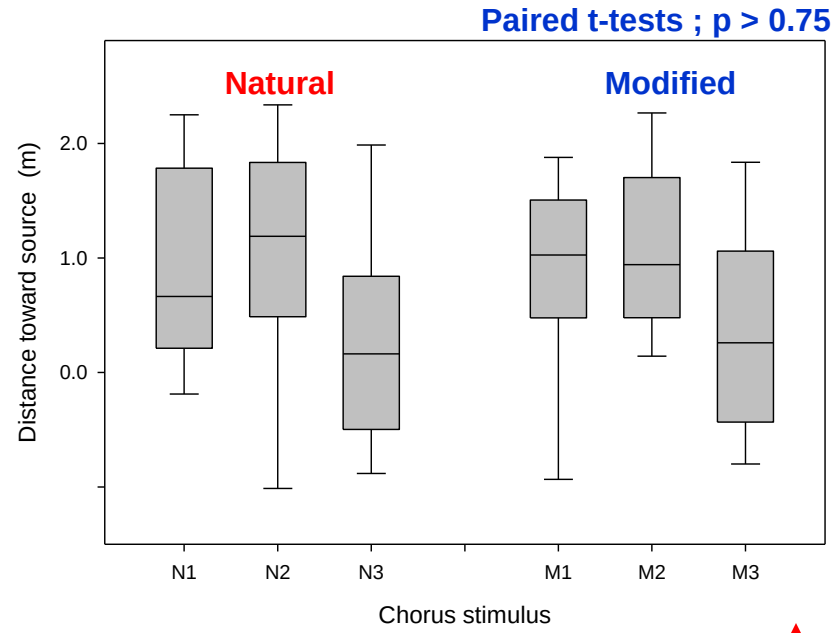
Modified chorus stimulus (Merens-les-Vals)



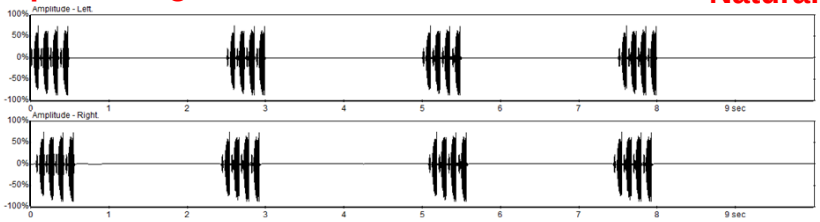


(Party, Streiff, Marin-Cudraz & Greenfield 2015)

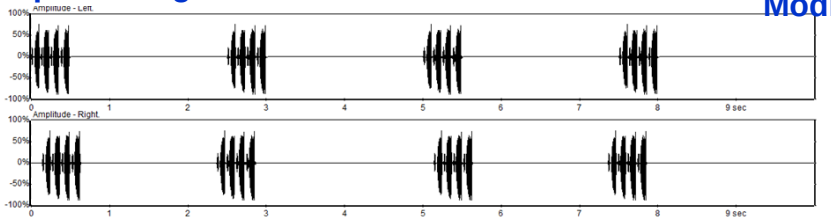
a. Merens-les-Vals



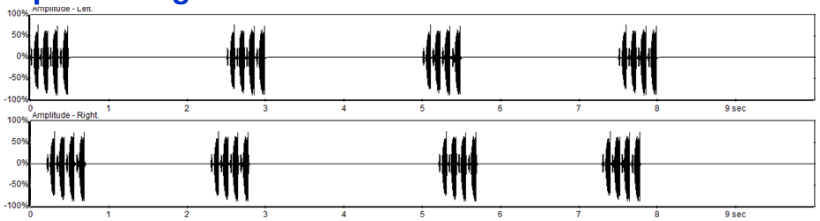
10° phase angle — Natural



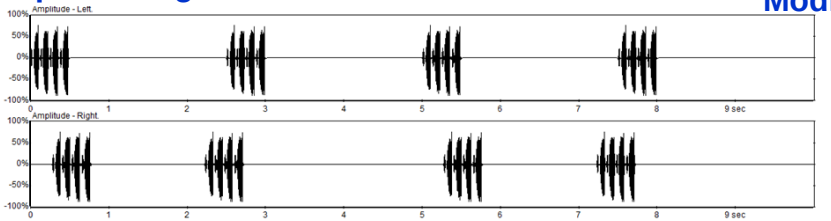
20° phase angle — Modified



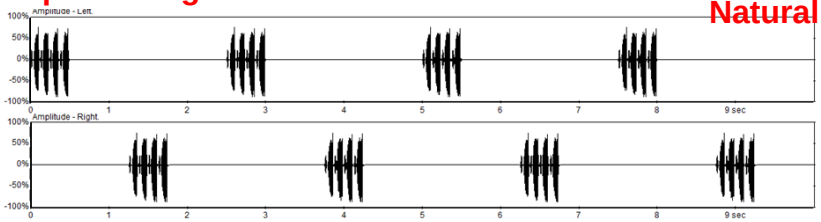
30° phase angle — Modified



40° phase angle — Modified

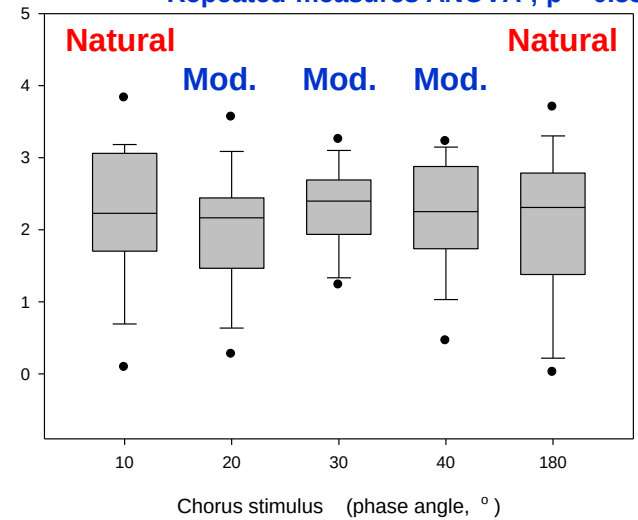


180° phase angle — Natural



b) Peyriac de Mer

Repeated-measures ANOVA ; p = 0.53

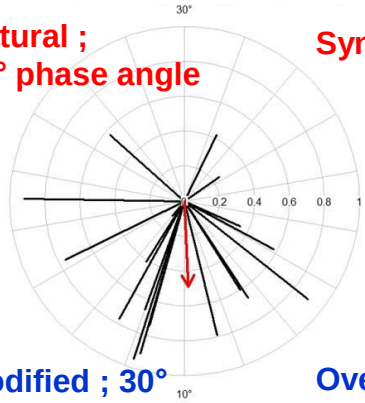


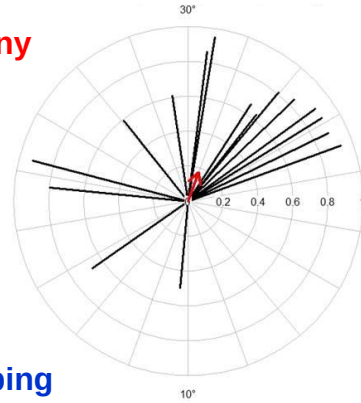
2. Levels of female response to natural (alternating and synchronous phase angles) and to modified chorus stimuli (overlapping phase angles) ;
single stimulus tests on Kramer sphere ;

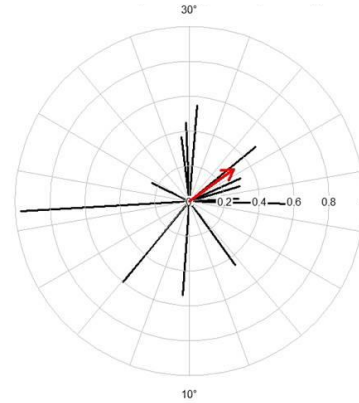
Result : Differential responses to natural and modified chorus stimuli not observed (power = 0.82)

Merens-les-Vals | **Mireval** | **Vilamòs**

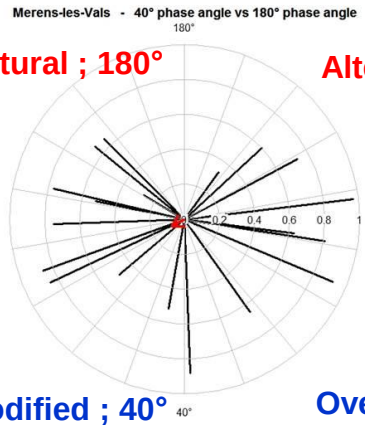
Natural ; 10° phase angle — **Synchrony**

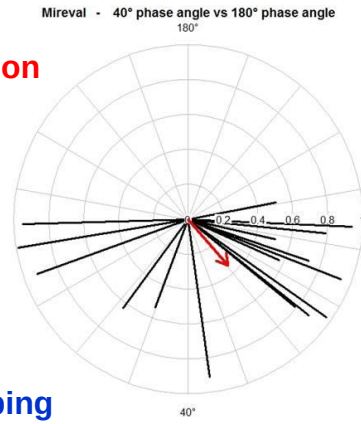


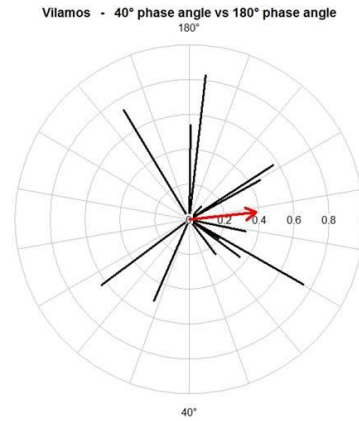




Modified ; 30° — **Overlapping**





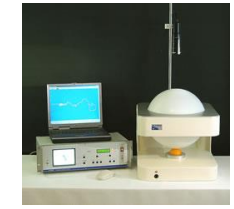


Natural ; 180° — **Alternation**

Modified ; 40° — **Overlapping**

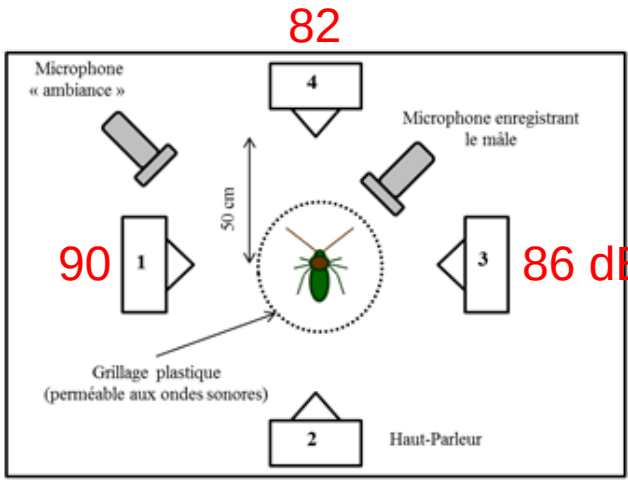
Result :
Overall preference for natural chorus stimuli not observed (Rayleigh and V-tests).

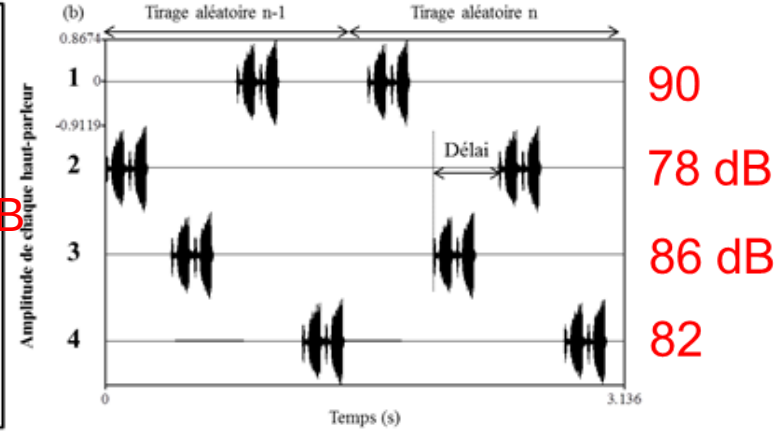
3. Female preference for natural (alternating or synchronous phase angles) vs modified chorus stimuli (overlapping phase angles) ; choice tests on Kramer sphere ;

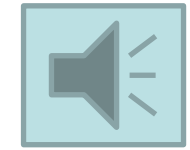


Question 4 :

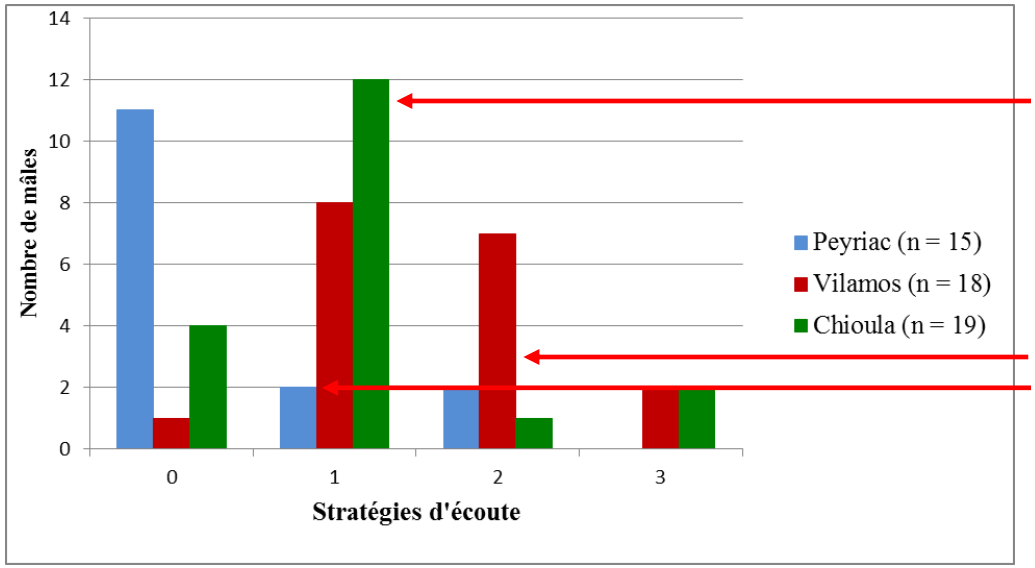
Is chorusing under central control ?





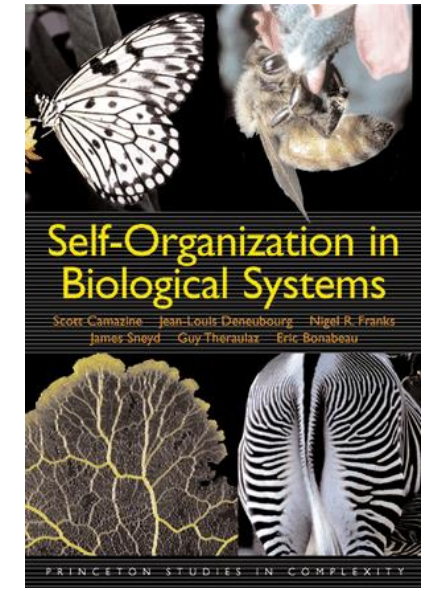


82 78 74 70 dB

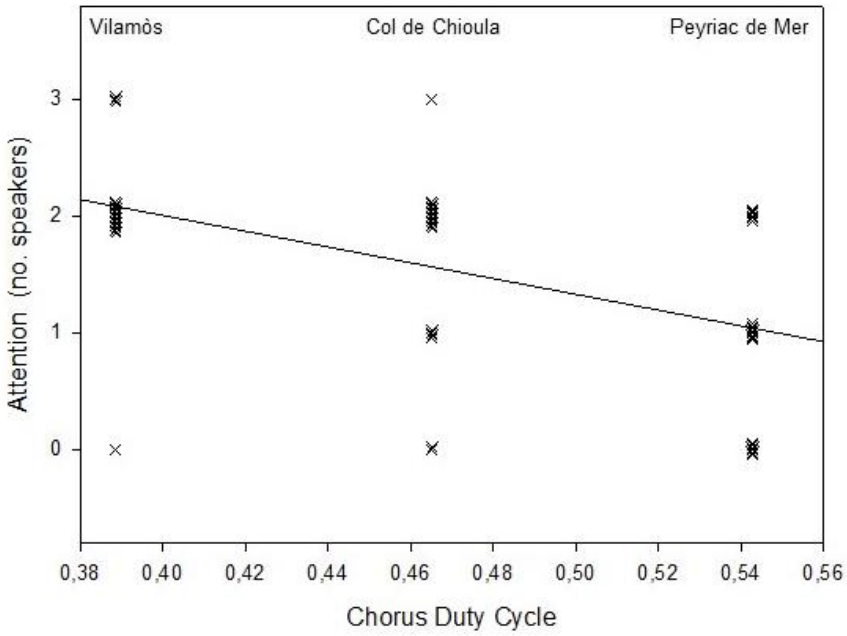


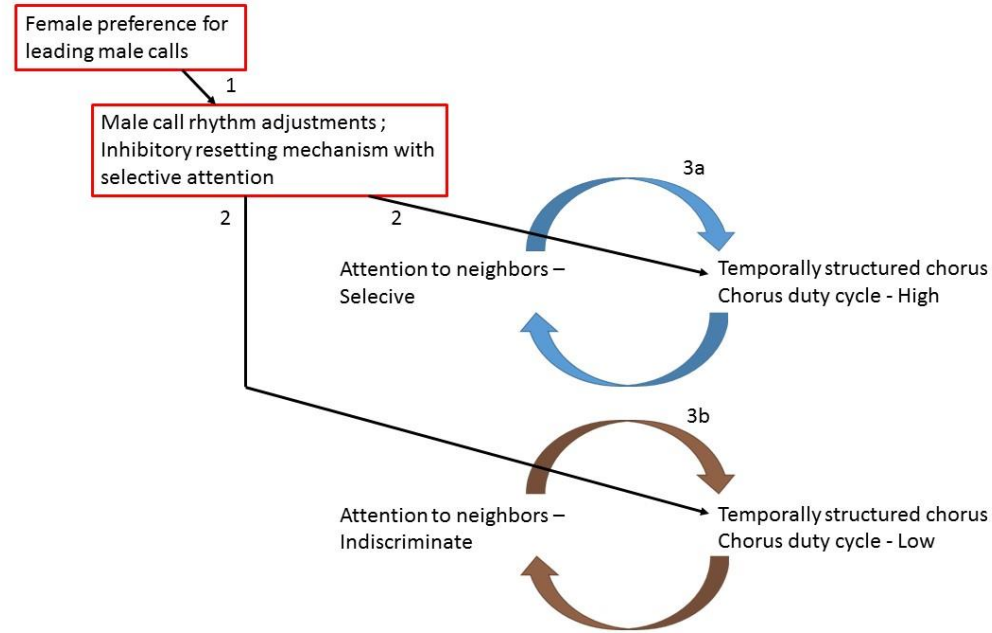
At Col de Chioula, most males pay attention to only one neighbor (90)

At Vilamós, most males pay attention to one or two neighbors (90, 86)

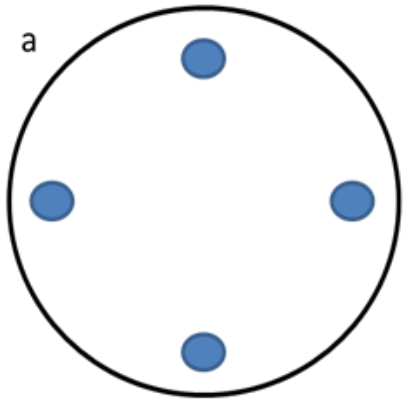


Order emerges from chaos !

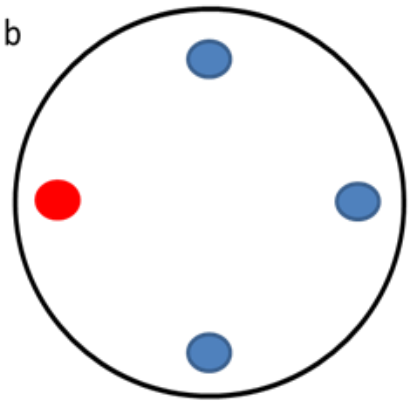

Vilamòs
Col de Chioula
Peyriac de Mer
Attention (no. speakers)
3
2
1
0
0,38
0,40
0,42
0,44
0,46
0,48
0,50
0,52
0,54
0,56
Chorus Duty Cycle


Female preference for leading male calls
1
Male call rhythm adjustments ; Inhibitory resetting mechanism with selective attention
2
2
3a
Attention to neighbors – Selecive
Temporally structured chorus ; Chorus duty cycle - High
3b
Attention to neighbors – Indiscriminate
Temporally structured chorus ; Chorus duty cycle - Low

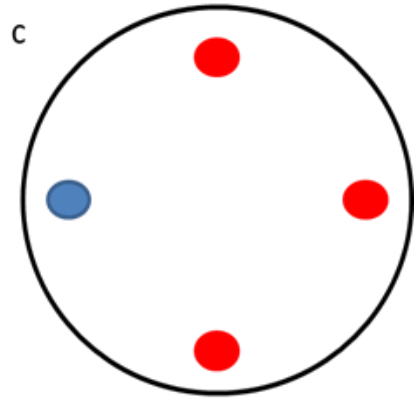
Question 5 : Will a population's chorusing format impede or enhance gene flow following secondary contact between populations ?



chorus: UNI



chorus: MAX

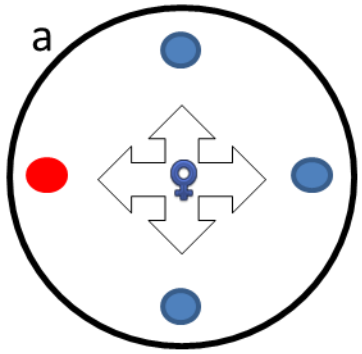


chorus: MIN

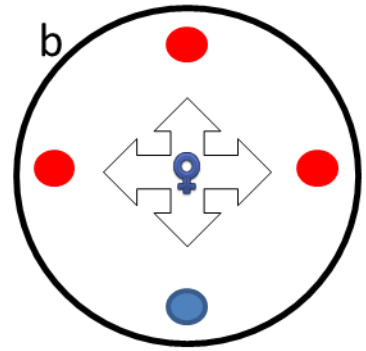
FR vs MER

Caractéristiques acoustiques

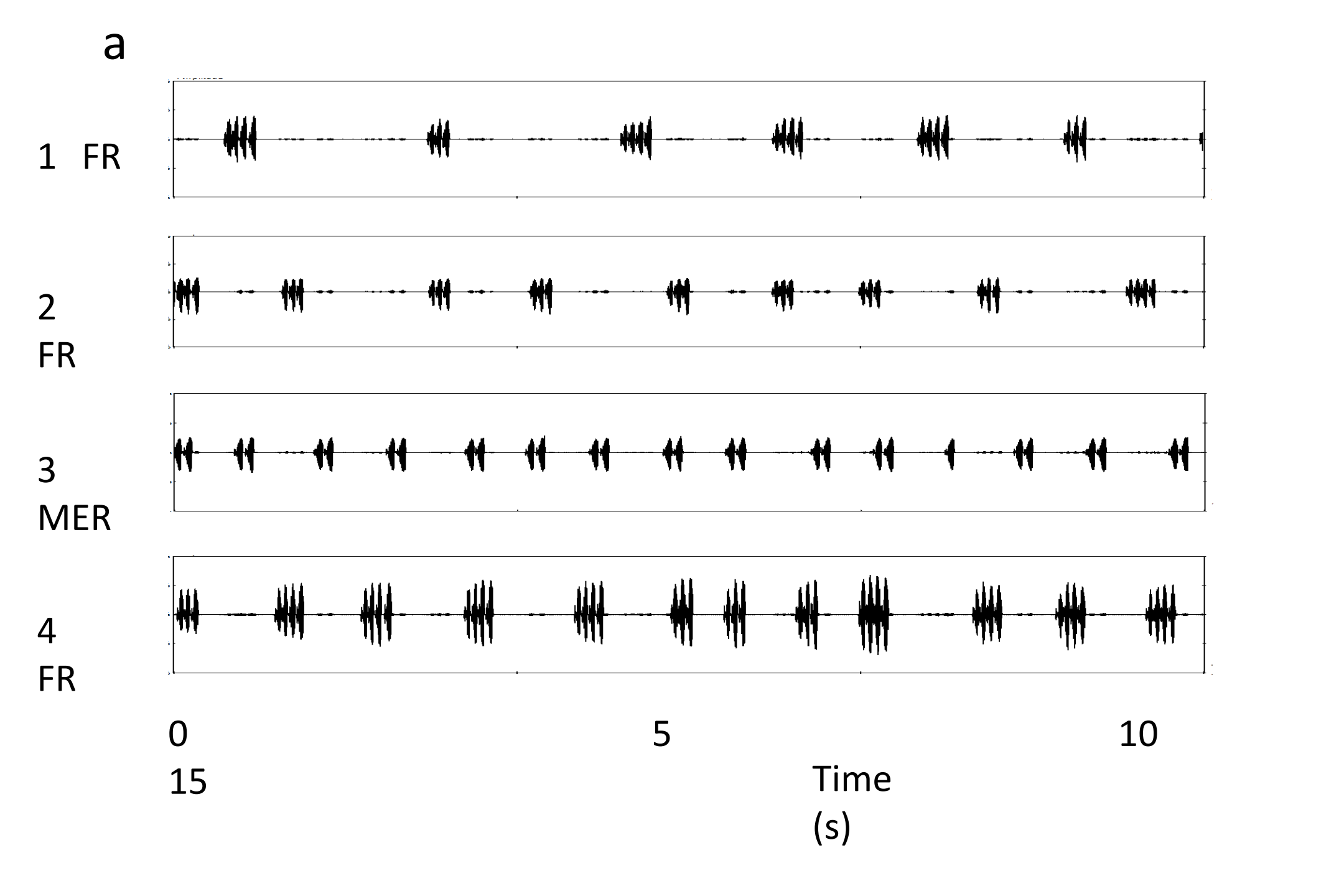
- Nombre de syllabes
- Durée moyenne des phrases (ms)
- Intervalle d'émission (ms)

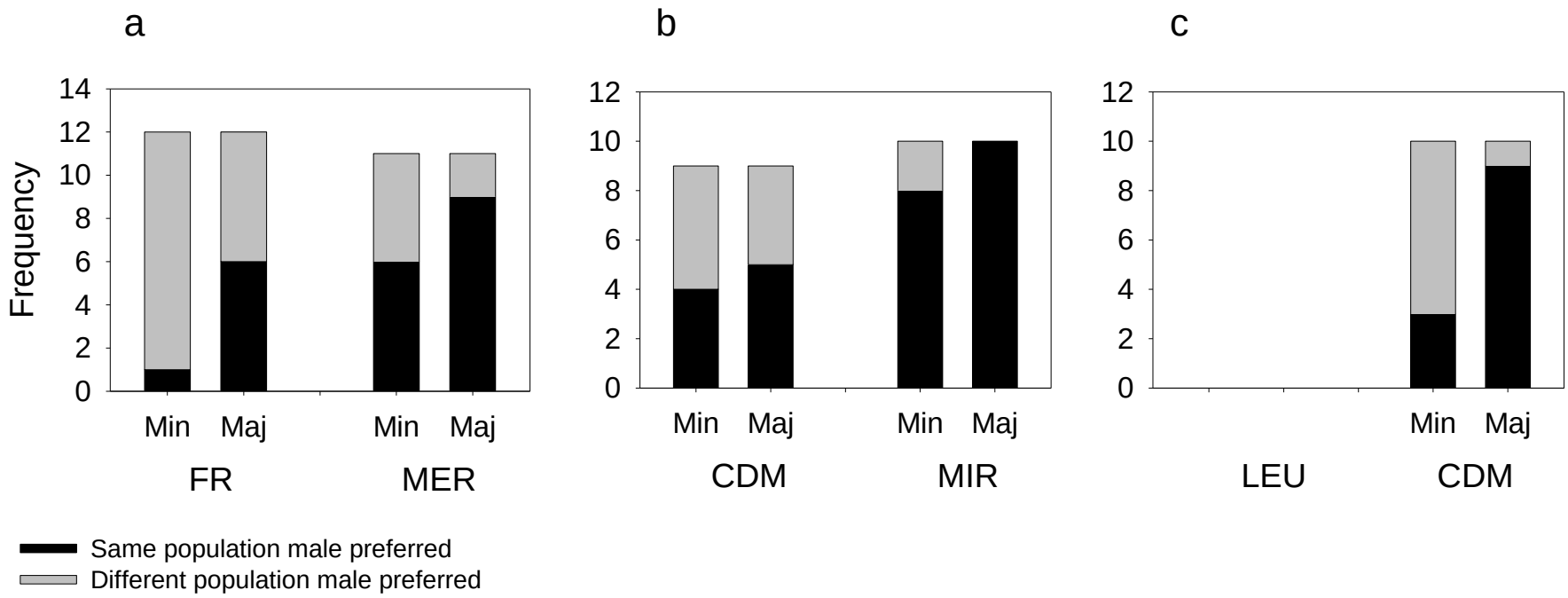


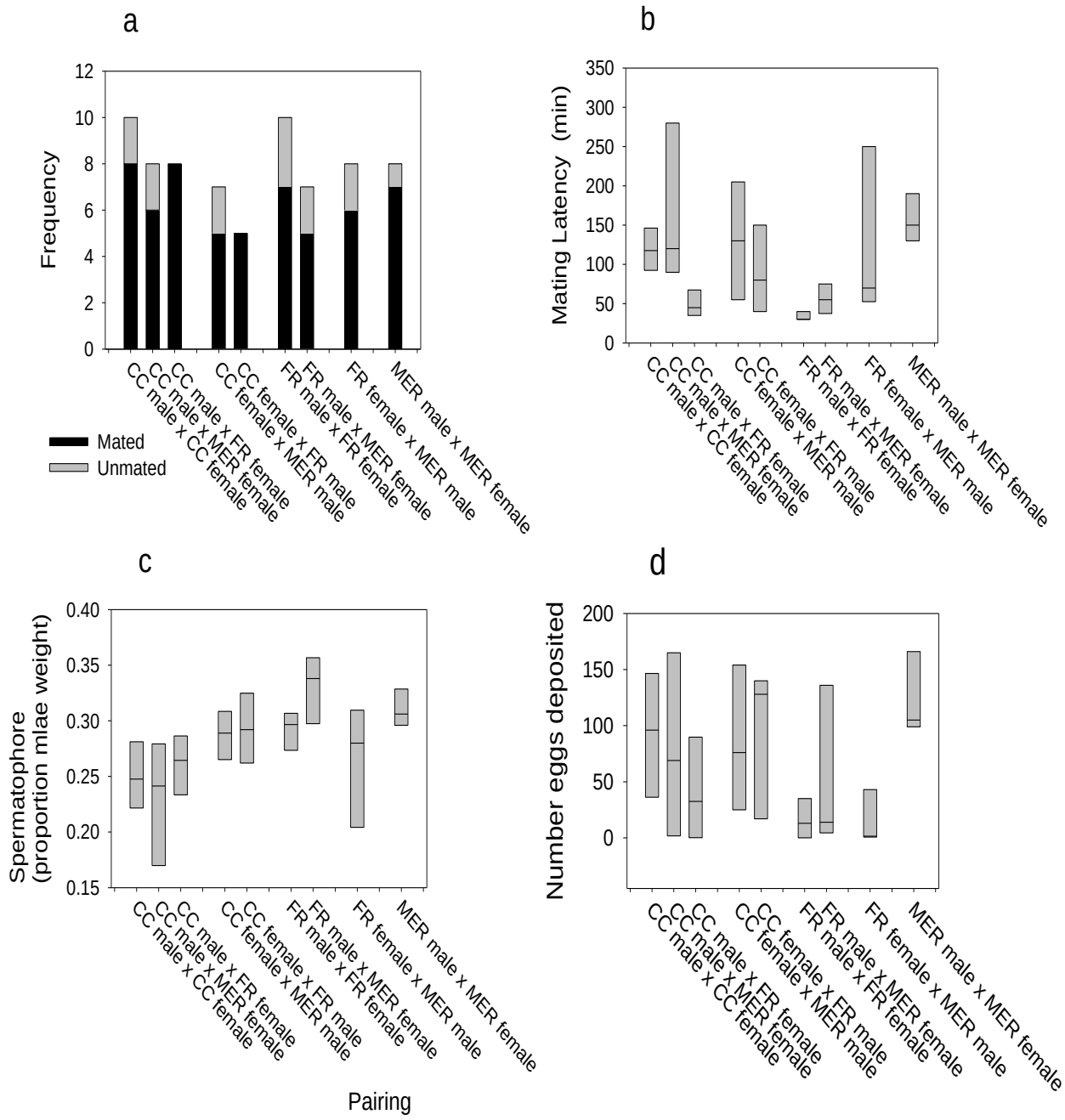
Choix femelle: Chorus MAX



Choix femelle: Chorus MIN

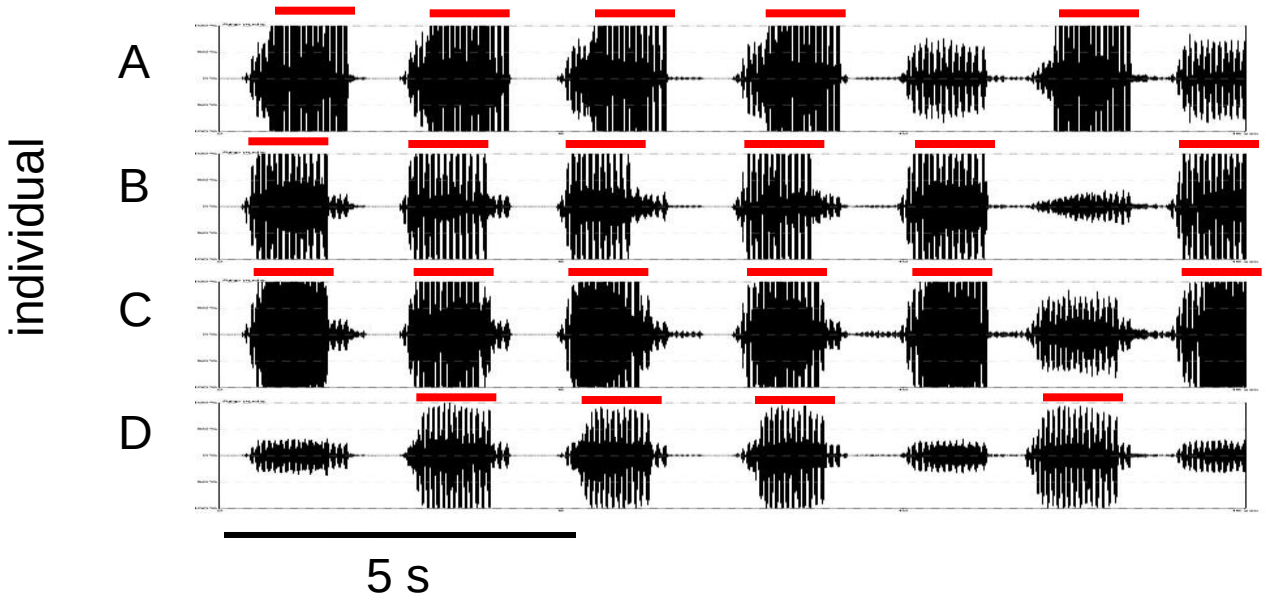

a
1 FR
2 FR
3 MER
4 FR
0
5
10
15
Time (s)


a
b
c
Frequency
14
12
10
8
6
4
2
0
Min
Maj
FR
MER
CDM
MIR
LEU
Same population male preferred
Different population male preferred


a
Frequency
Mated
Unmated
CC male x CC female
CC male x MER female
CC male x FR female
CC female x MER male
CC female x FR male
FR male x FR female
FR male x MER female
FR female x MER male
MER male x MER female
b
Mating Latency (min)
c
Spermatophore (proportion mlae weight)
Pairing
d
Number eggs deposited

Question 6 : What is true synchrony ? Does it exist ?

Tettigoniidae ; Bradyporinae

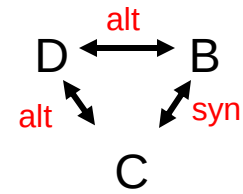


Sorapagus catalaunicus

Synchrony

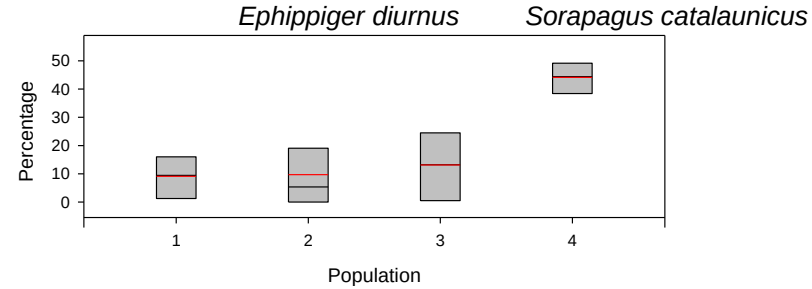
Ephippiger diurnus

Alternation + Synchrony

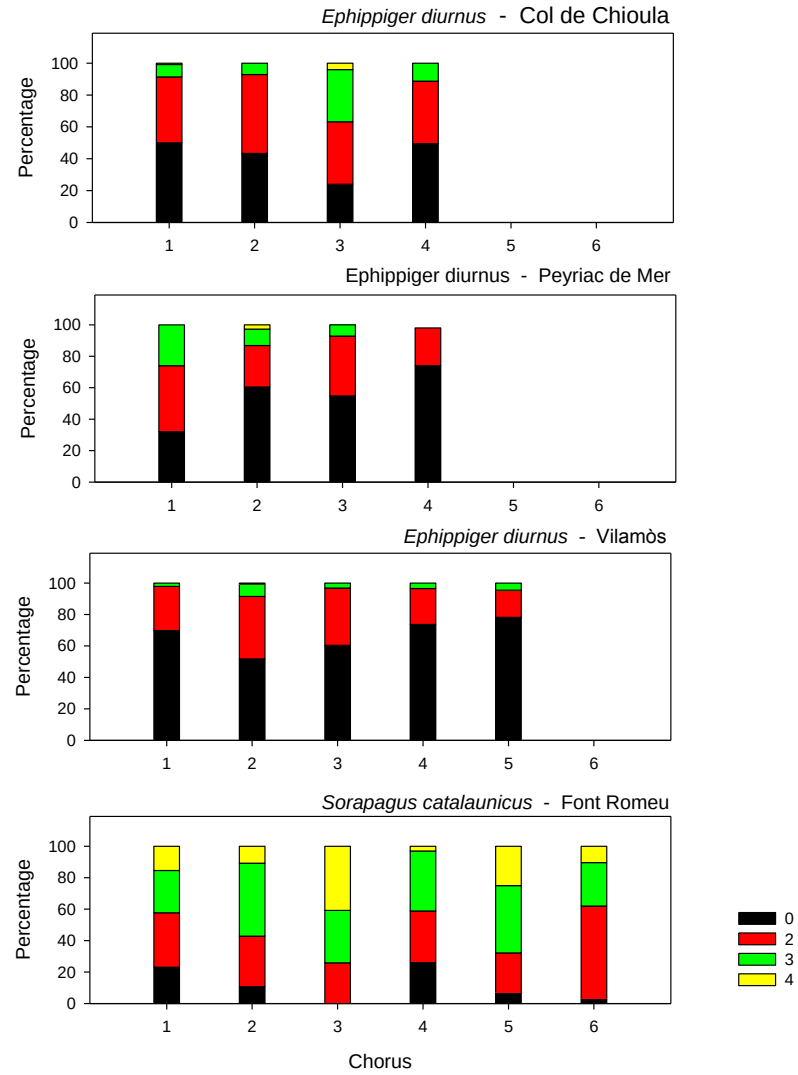


3 m

Synchrony - 2 male choruses

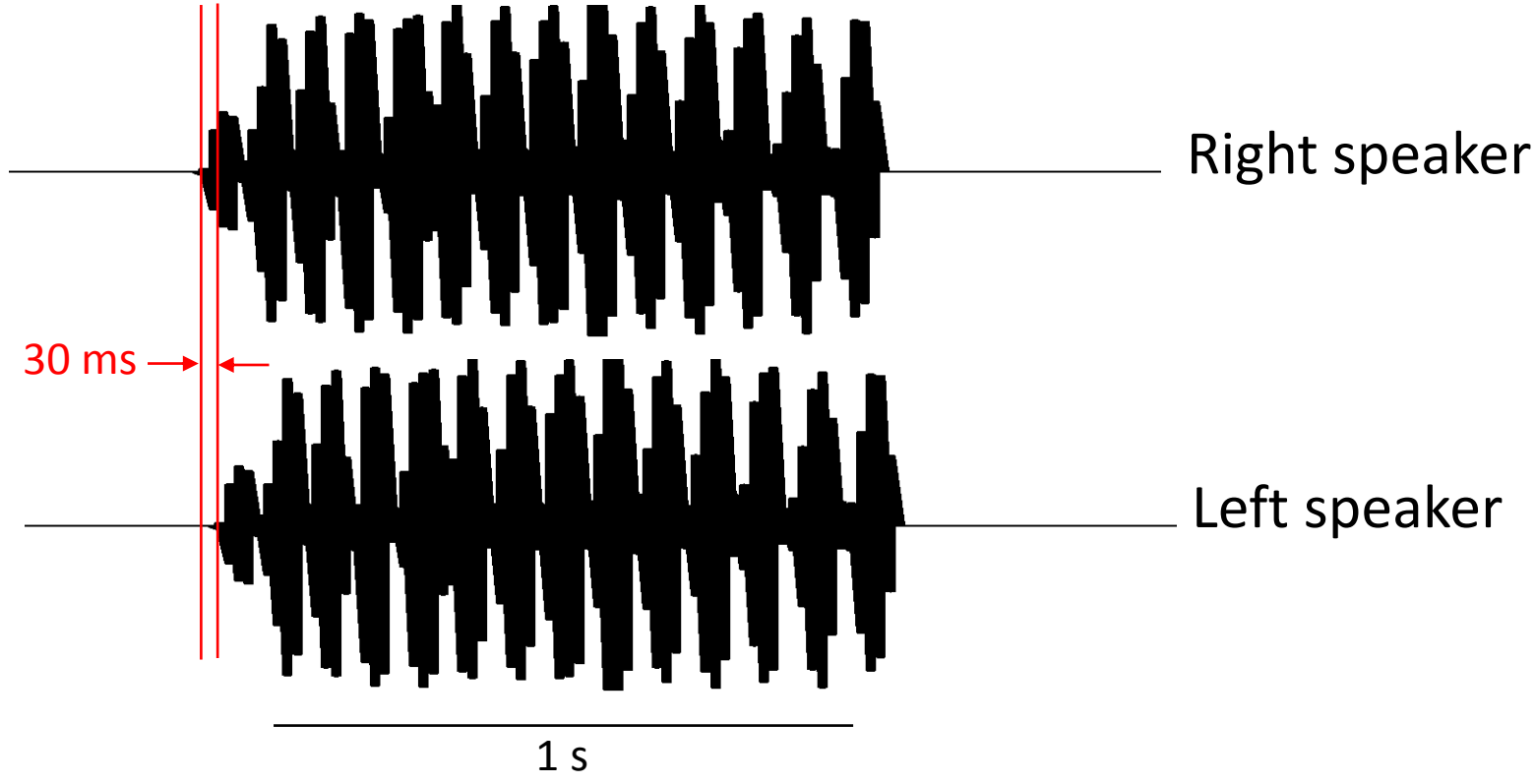


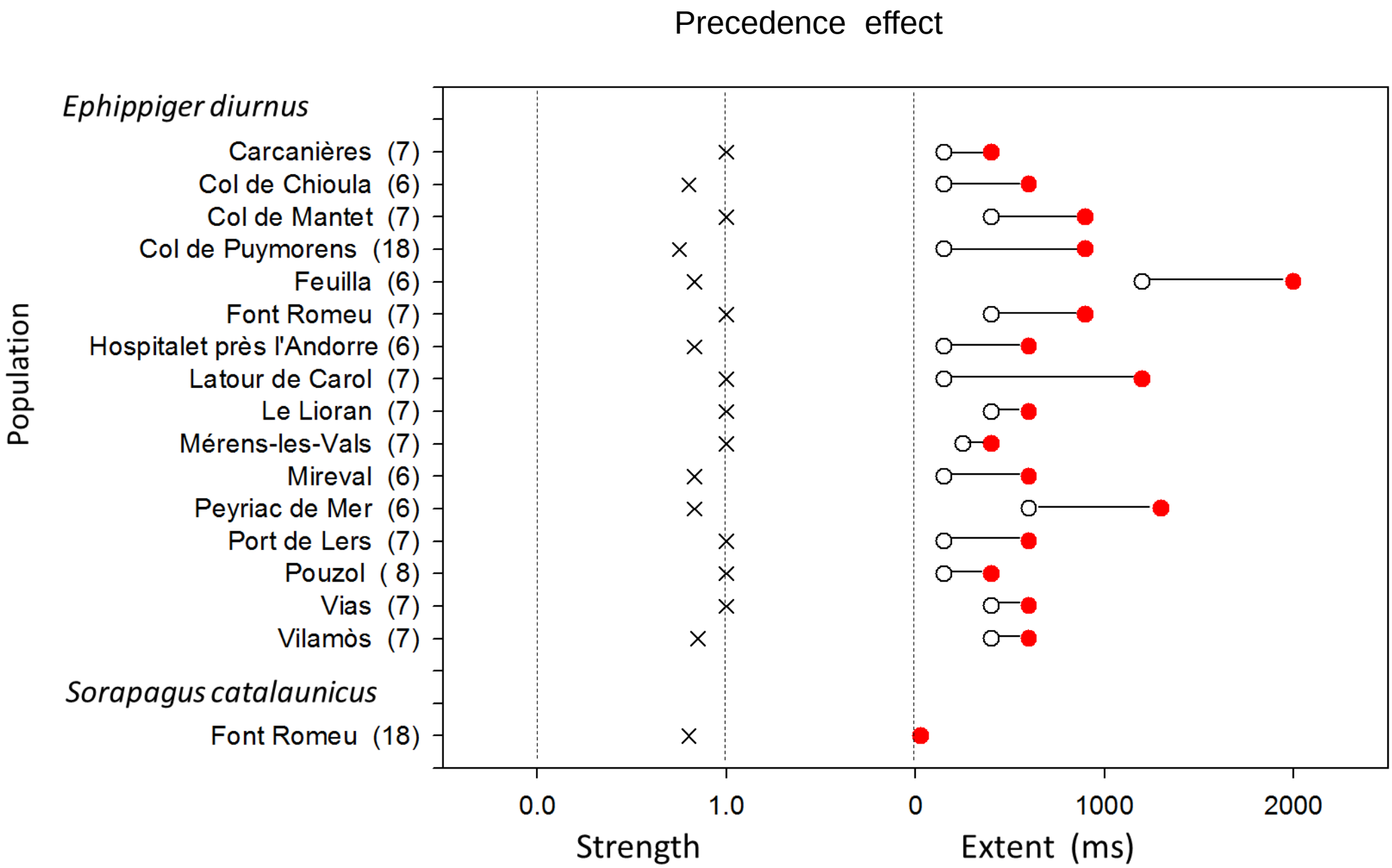
Synchrony - 4 male choruses



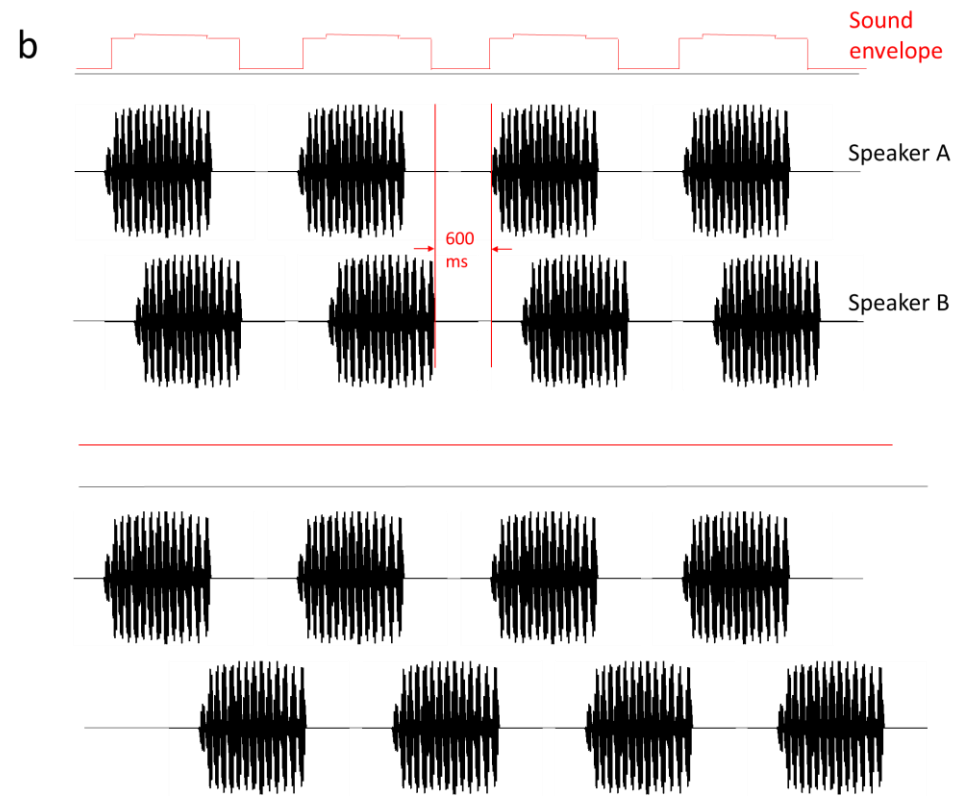
a

Playback - precedence effect - *Sorapagus catalaunicus*

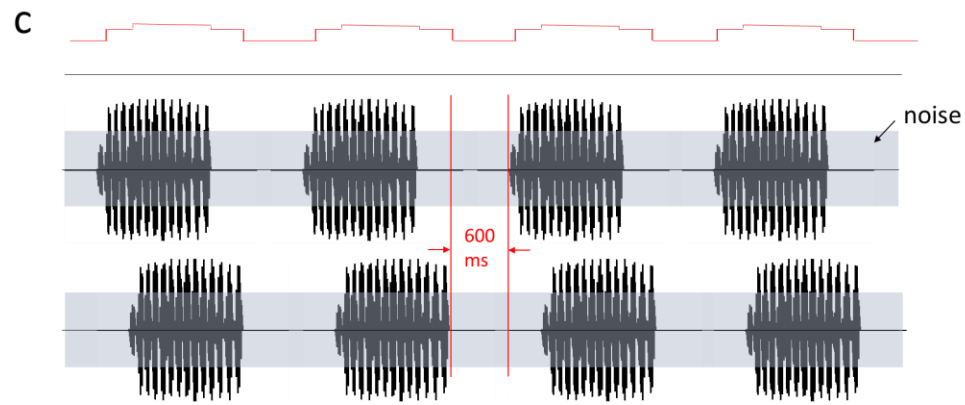



Precedence effect
Ephippiger diurnus
Carcanières (7)
Col de Chioula (6)
Col de Mantet (7)
Col de Puymorens (18)
Feuilla (6)
Font Romeu (7)
Hospitalet près l'Andorre (6)
Latour de Carol (7)
Le Lioran (7)
Mérens-les-Vals (7)
Mireval (6)
Peyriac de Mer (6)
Port de Lers (7)
Pouzol (8)
Vias (7)
Vilamòs (7)
Sorapagus catalaunicus
Font Romeu (18)
Population
0.0
1.0
0
1000
2000
Strength
Extent (ms)

Playback -
gap length



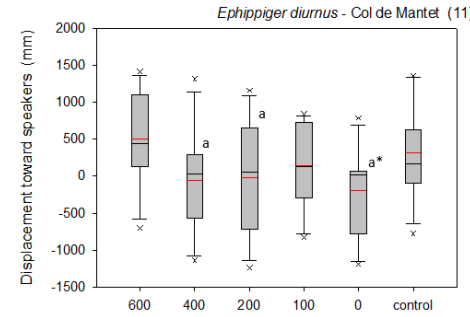
Playback -
gap depth

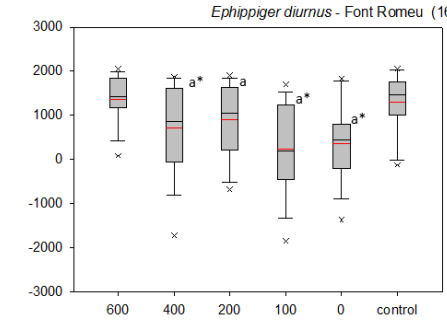


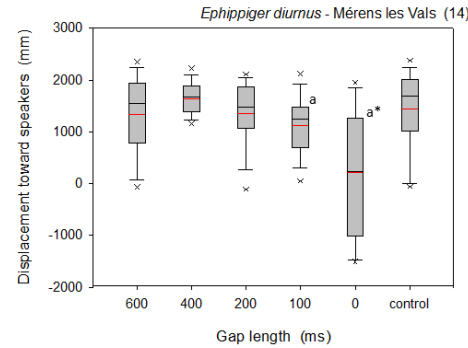
Gap Length

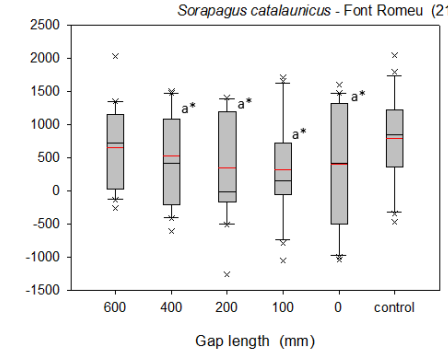
Gap Depth

a

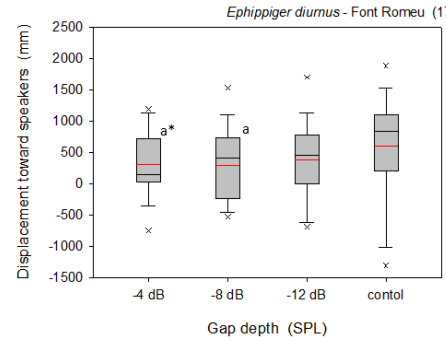


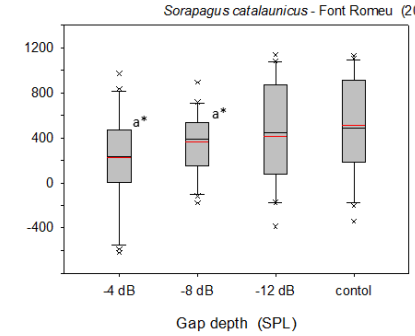






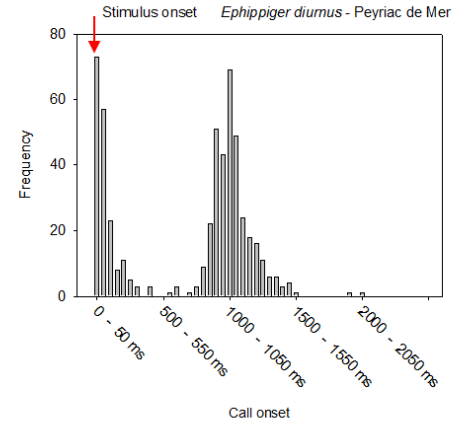
b

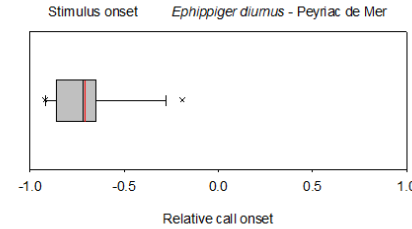




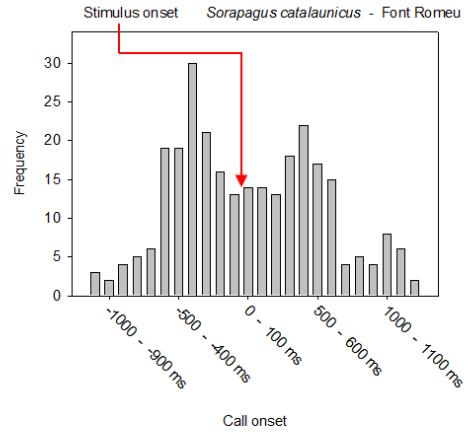
Relative call timing

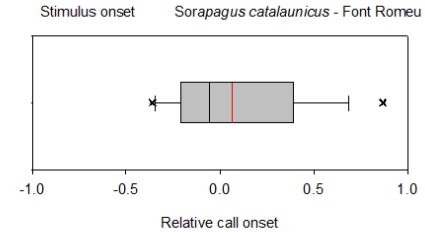
a



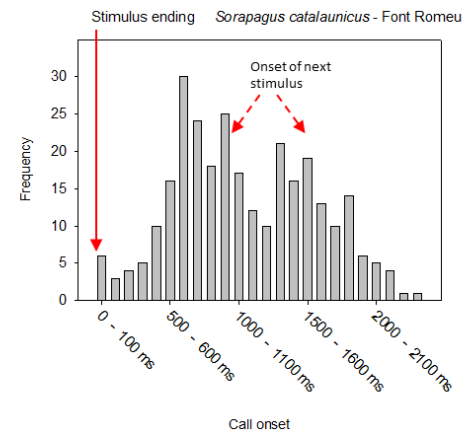


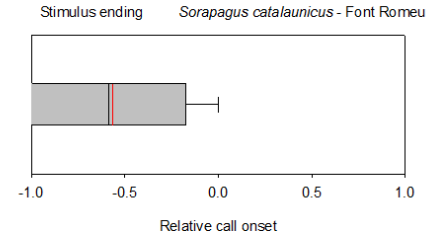
b

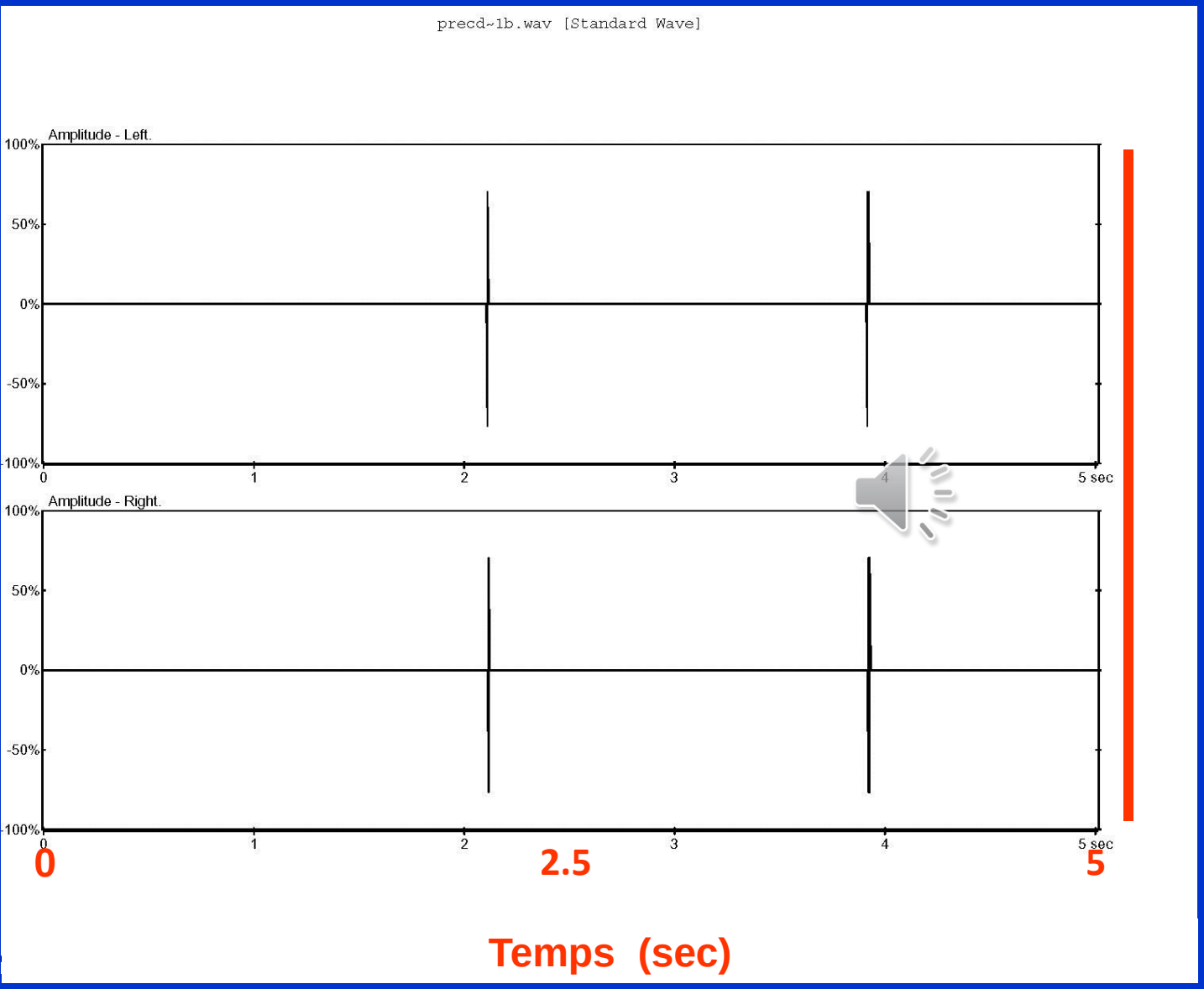




c

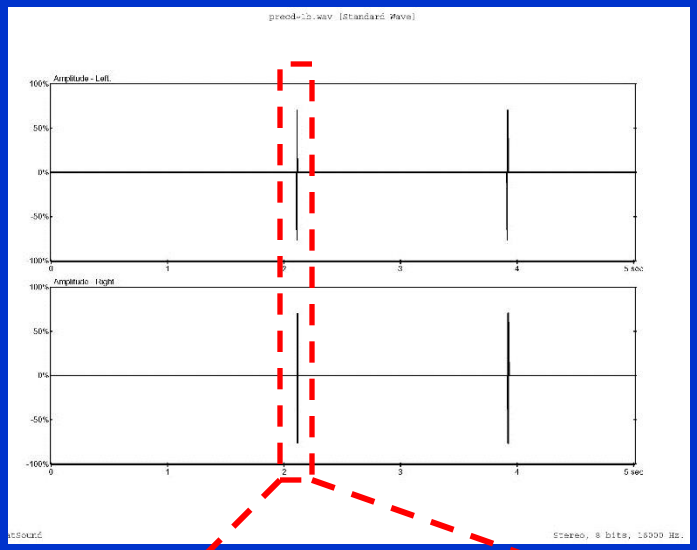


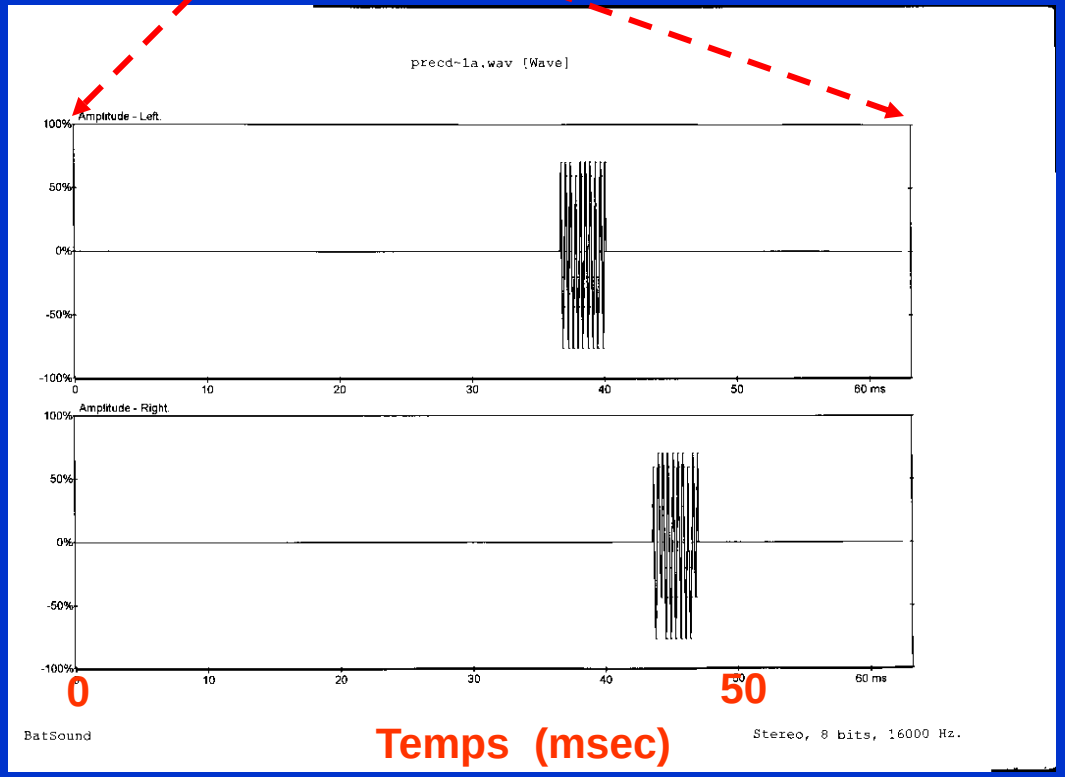



precd~1b.wav [Standard Wave]
Amplitude - Left.
100%
50%
0%
-50%
-100%
0
1
2
3
4
5 sec
Amplitude - Right.
100%
50%
0%
-50%
-100%
0
1
2
3
4
5 sec
0
2.5
5
Temps (sec)

G

D

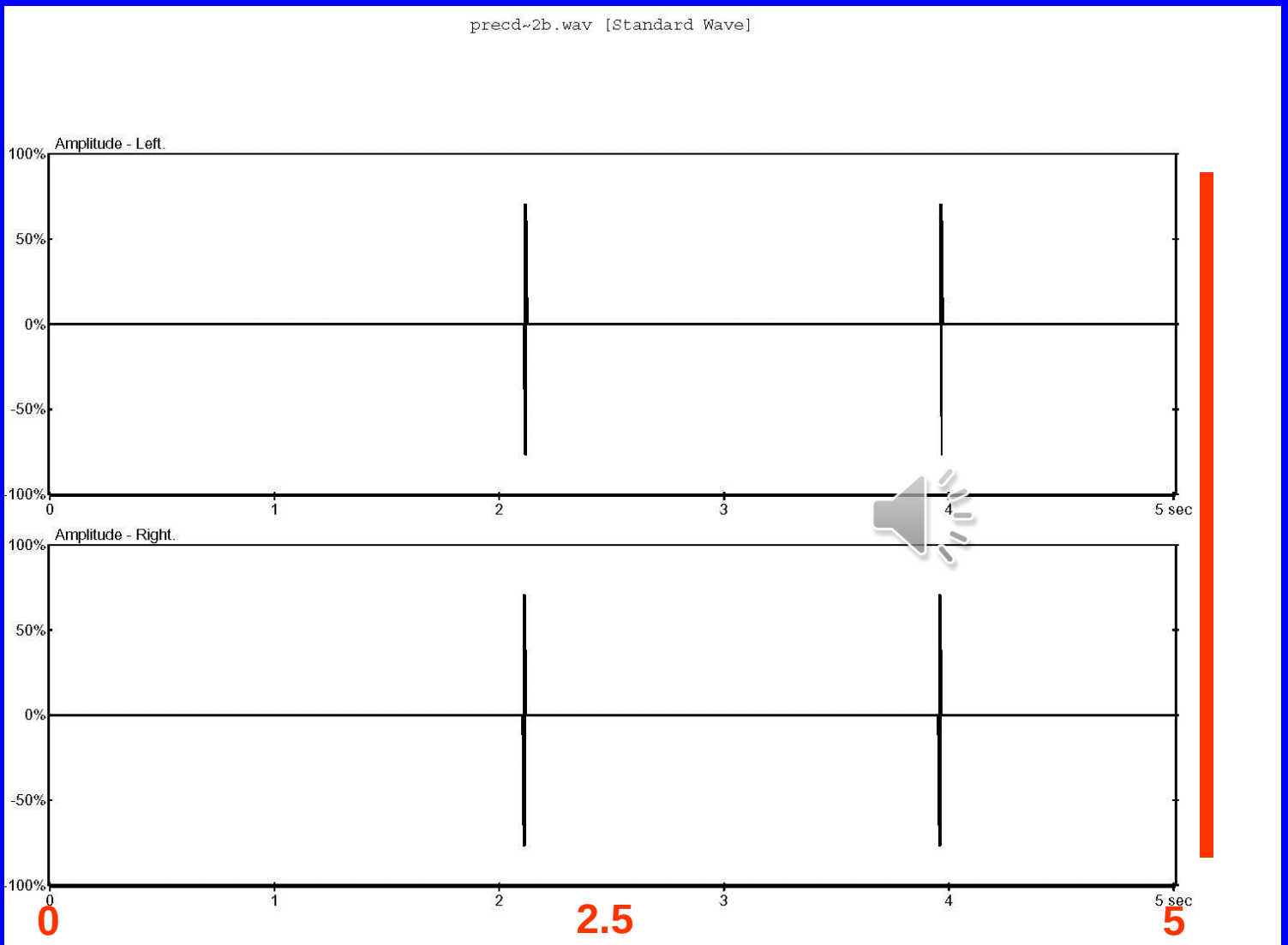




Precedence effect :

Localization of the first of 2 (or more) sounds that are separated by a brief interval.

Left channel is the leader (by 7 ms).



G

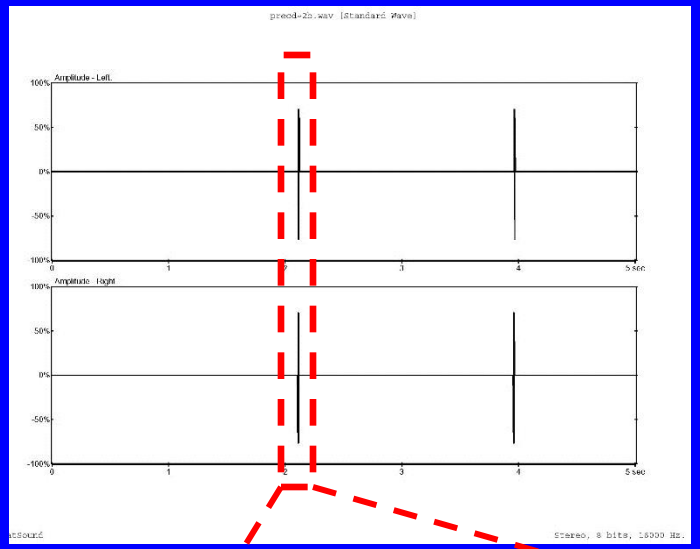
D

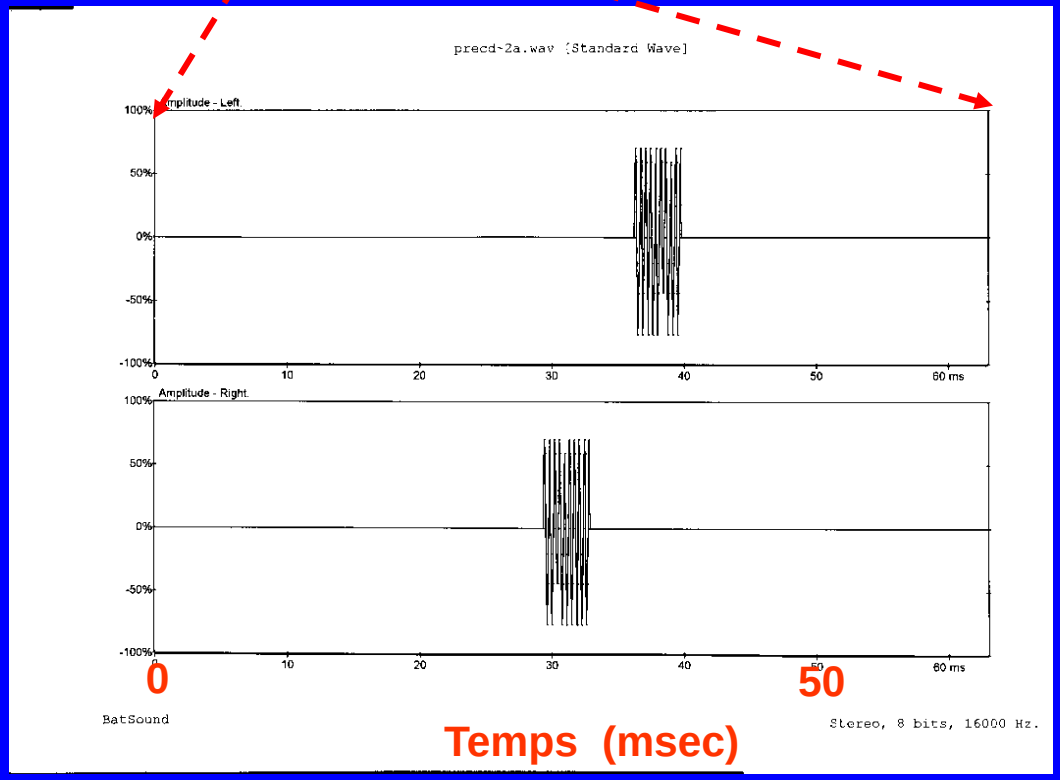
0

2.5

5

Temps (sec)

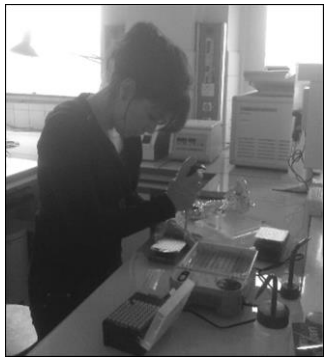




Canal à la droite est le premier

Le groupe ‘Montpellier’

Réjane Streiff (CBGP)

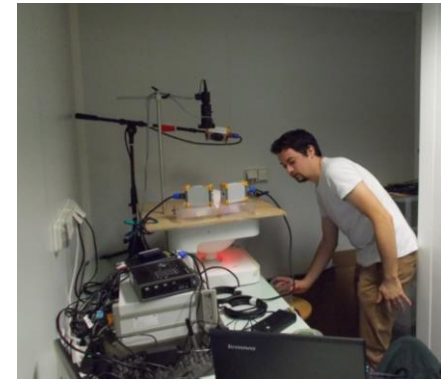


Yareli Esquer-Garrigos

Le groupe ‘Tours – St. Etienne’

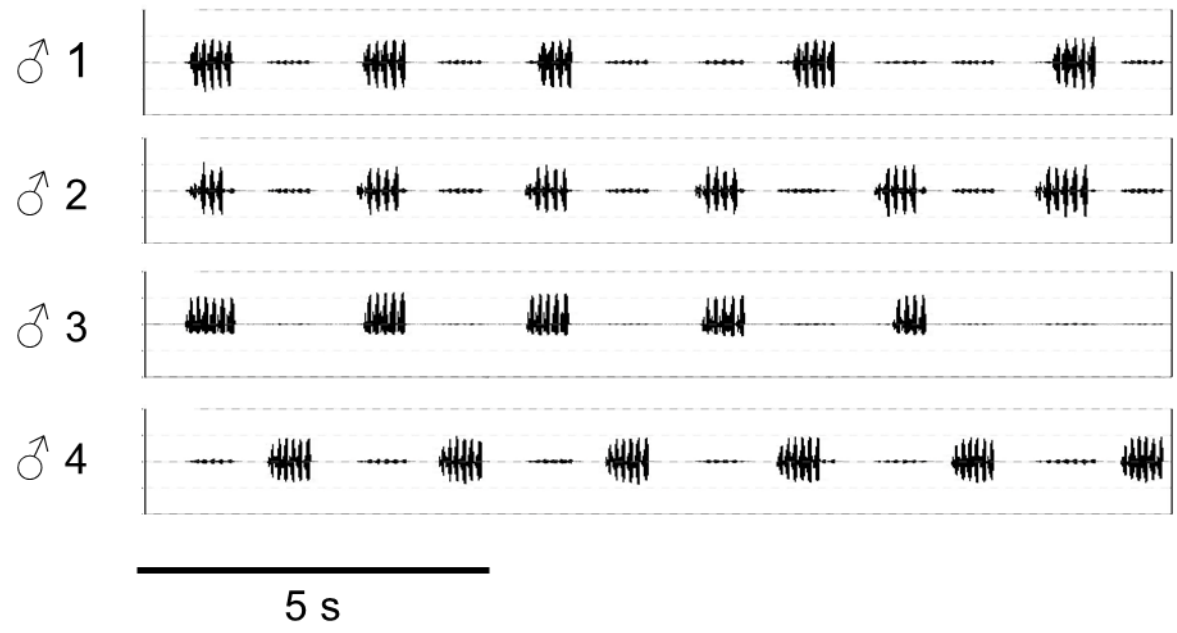
Virginie Party

Mathieu Mahamoud-Issa

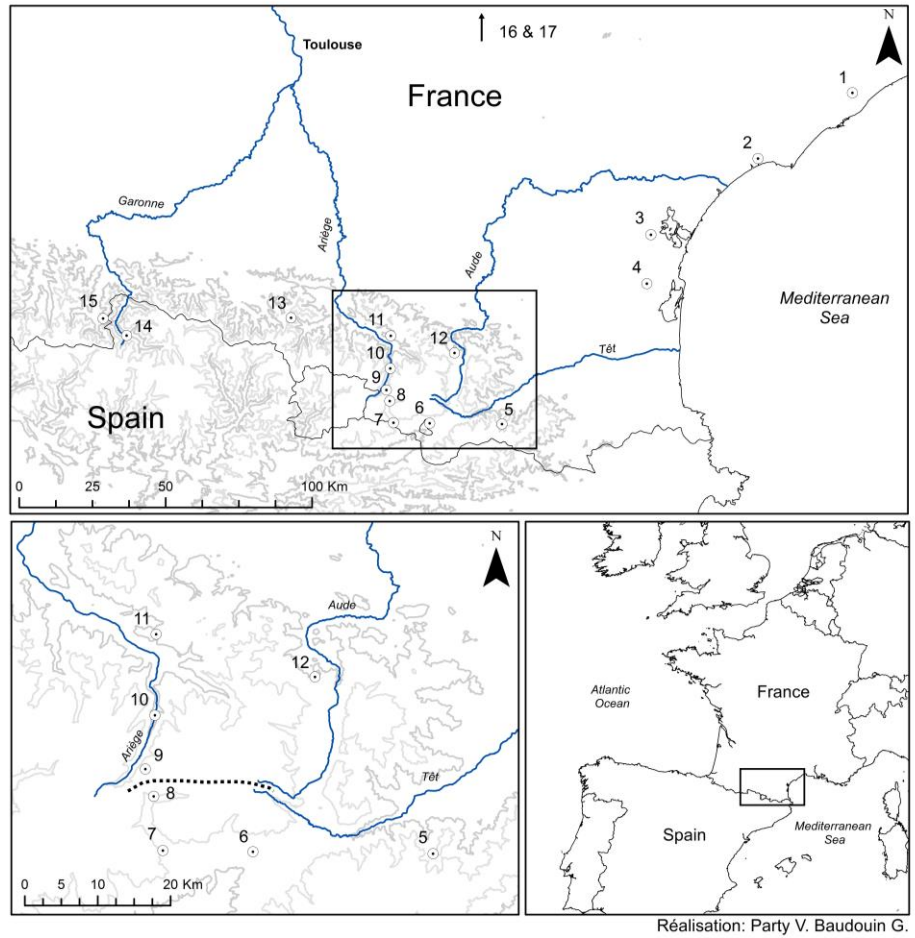


Thibaut Marin-Cudraz

And with thanks to :
Flavia Barbosa, Guillaume Baudouin, Guy Bourdais, Odette Brunel-Pons, Marine Deluen, Séverine Devers, Marlène Goubault, Caroline Hébert, Aurelien Kerbrat, Justine Penin, Florian Plault, Darren Rebar, and Valery Terwilliger

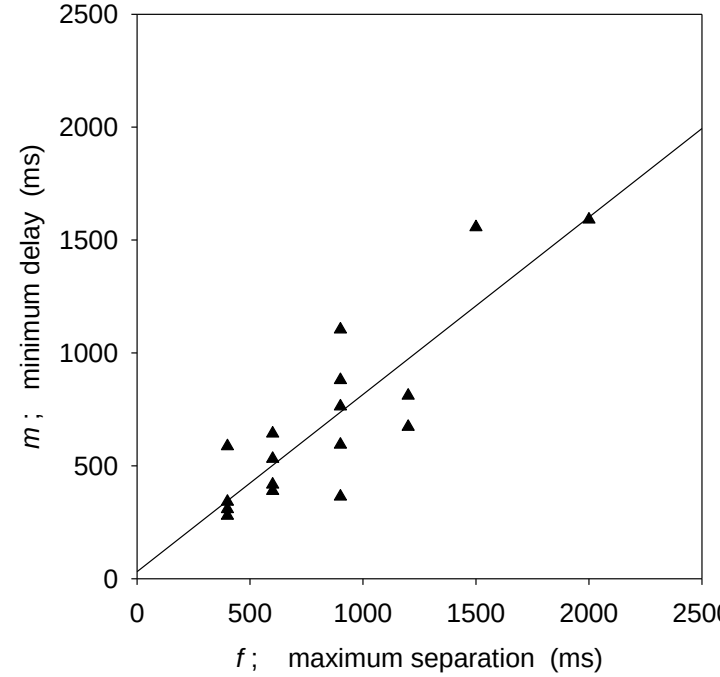

♂ 1
♂ 2
♂ 3
♂ 4
5 s

A

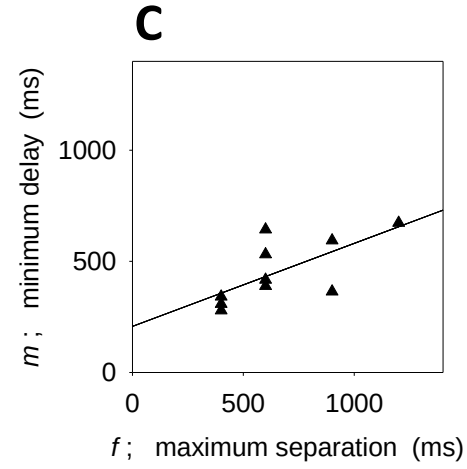


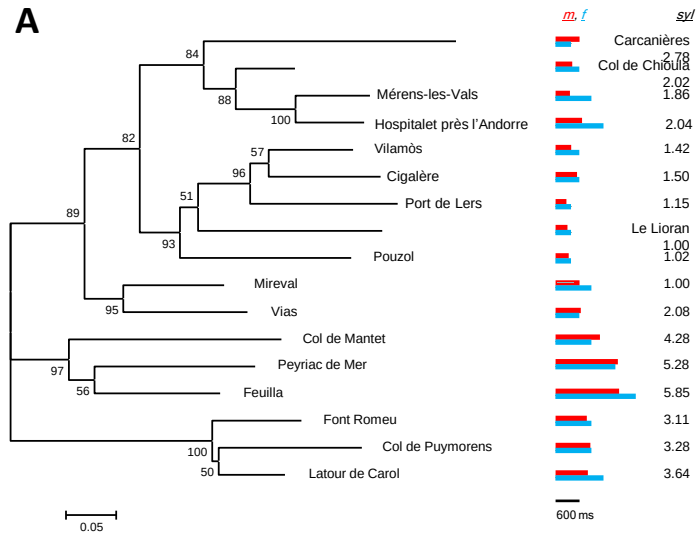
Populations: 1) Mireval, 2) Vias, 3) Peyriac de Mer, 4) Feuilla, 5) Col de Mantet, 6) Font Romeu, 7) Latour de Carol, 8) Col de Puymorens, 9) Hospitalet près l'Andorre, 10) Mérens-les-Vals, 11) Col de Chioula, 12) Carcanières, 13) Port de Lers, 14) Vilamòs, 15) Cigalère, 16) Le Lioran, 17) Pouzol.

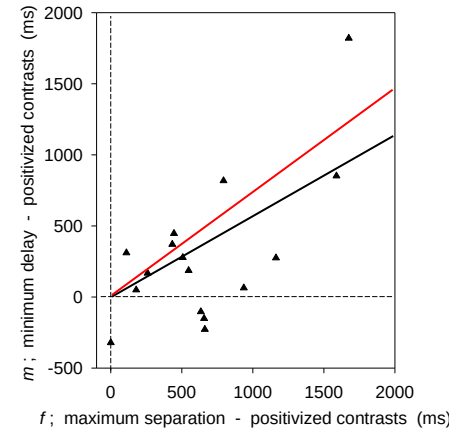
B

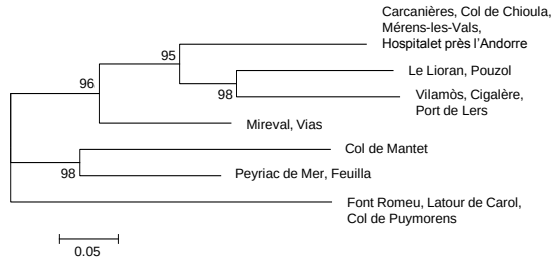


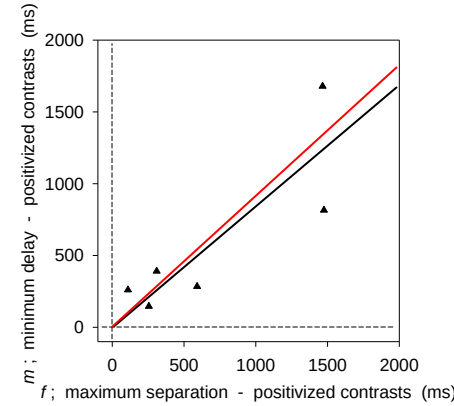
C

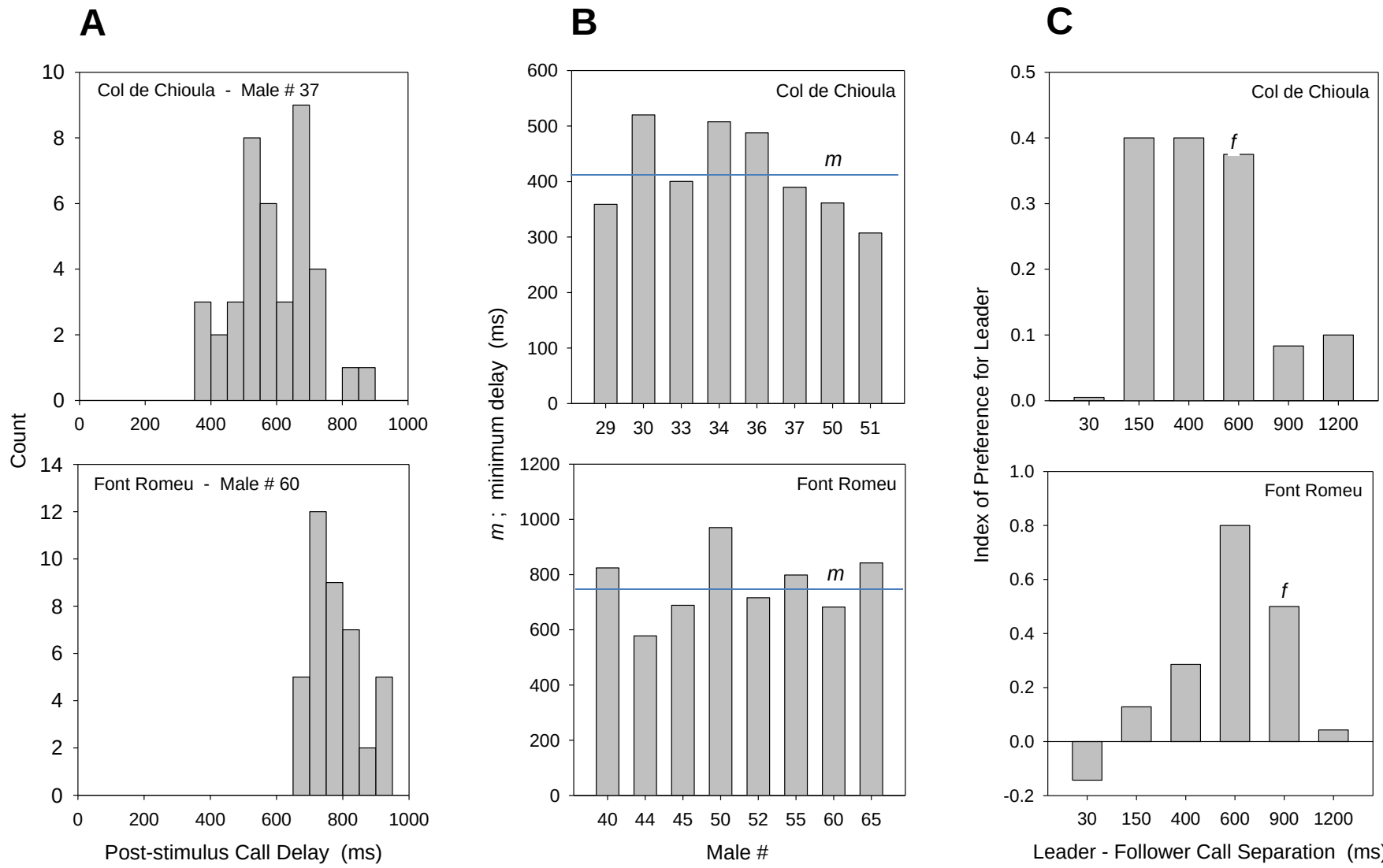



A
m, f
sv
Carcanières
Col de Chioula
Mérens-les-Vals
Hospitalet près l'Andorre
Vilamòs
Cigalère
Port de Lers
Le Lioran
Pouzol
Mireval
Vias
Col de Mantet
Peyriac de Mer
Feuilla
Font Romeu
Col de Puymorens
Latour de Carol
2.78
2.02
1.86
2.04
1.42
1.50
1.15
1.00
1.02
1.00
2.08
4.28
5.28
5.85
3.11
3.28
3.64
84
88
100
82
57
96
51
89
93
95
97
56
100
50
0.05
600 ms

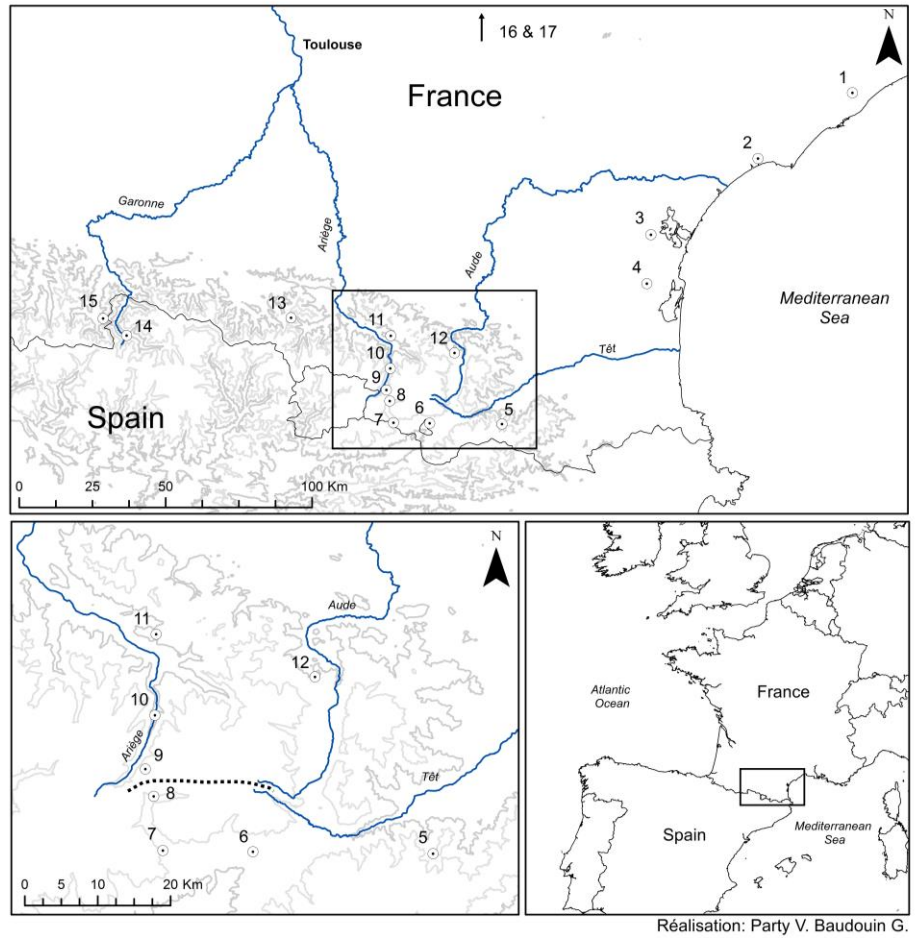

B
m ; minimum delay - positivized contrasts (ms)
f ; maximum separation - positivized contrasts (ms)
2000
1500
1000
500
0
-500
0
500
1000
1500
2000


C
Carcanières, Col de Chioula,
Mérens-les-Vals,
Hospitalet près l'Andorre
Le Lioran, Pouzol
Vilamòs, Cigalère,
Port de Lers
Mireval, Vias
Col de Mantet
Peyriac de Mer, Feuilla
Font Romeu, Latour de Carol,
Col de Puymorens
95
96
98
98
0.05


D
m ; minimum delay - positivized contrasts (ms)
f ; maximum separation - positivized contrasts (ms)
2000
1500
1000
500
0
0
500
1000
1500
2000

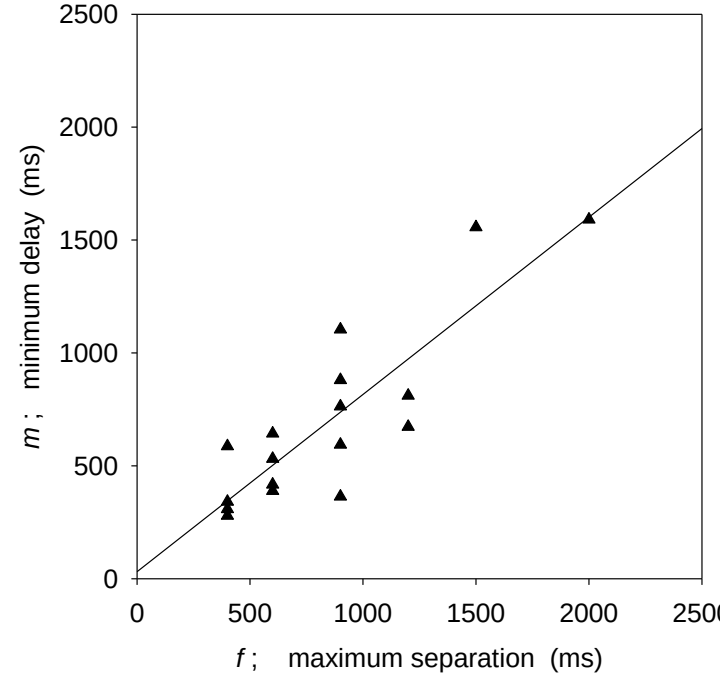

A
B
C
Col de Chioula - Male # 37
Font Romeu - Male # 60
Count
Post-stimulus Call Delay (ms)
Col de Chioula
Font Romeu
m
m ; minimum delay (ms)
Male #
Index of Preference for Leader
f
Leader - Follower Call Separation (ms)

A

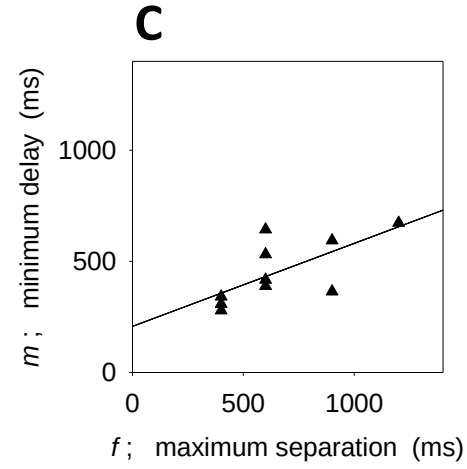


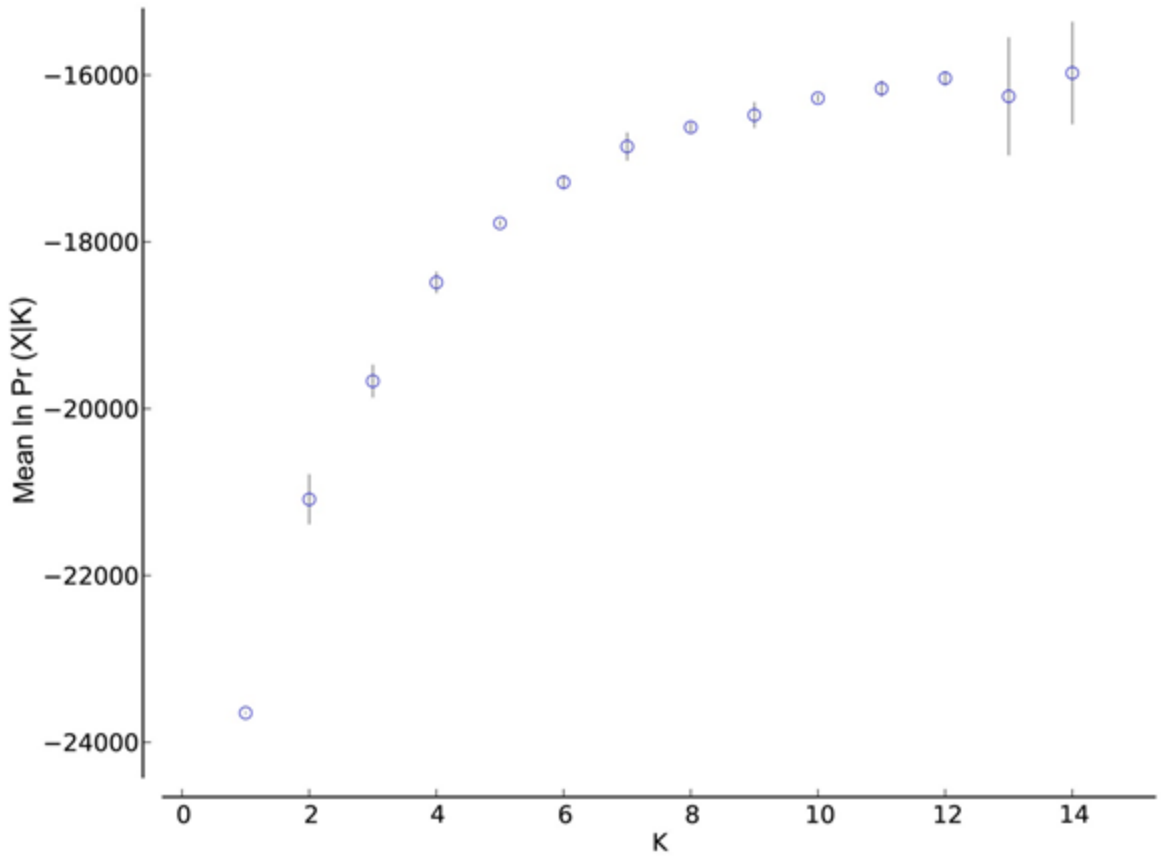
Populations: 1) Mireval, 2) Vias, 3) Peyriac de Mer, 4) Feuilla, 5) Col de Mantet, 6) Font Romeu, 7) Latour de Carol, 8) Col de Puymorens, 9) Hospitalet près l'Andorre, 10) Mérens-les-Vals, 11) Col de Chioula, 12) Carcanières, 13) Port de Lers, 14) Vilamòs, 15) Cigalère, 16) Le Lioran, 17) Pouzol.

B

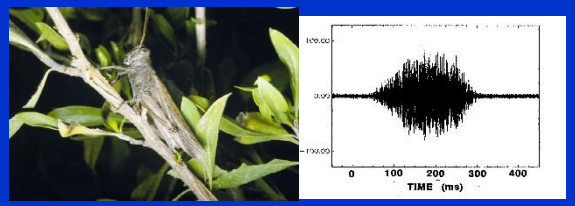


C

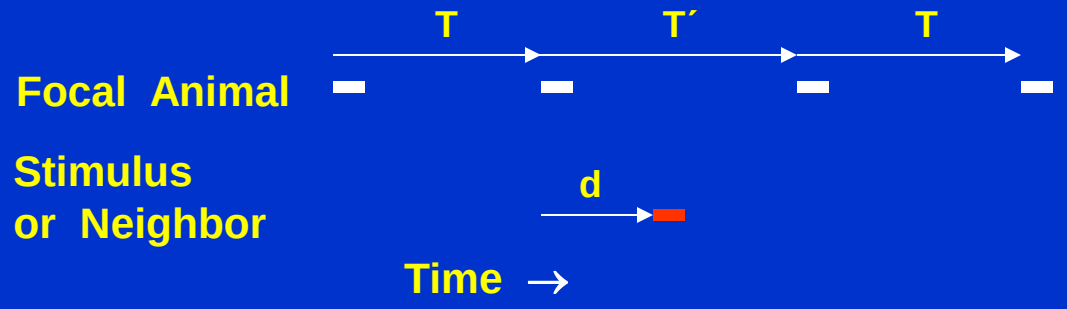



−16000
−18000
−20000
−22000
−24000
Mean ln Pr (X|K)
0
2
4
6
8
10
12
14
K

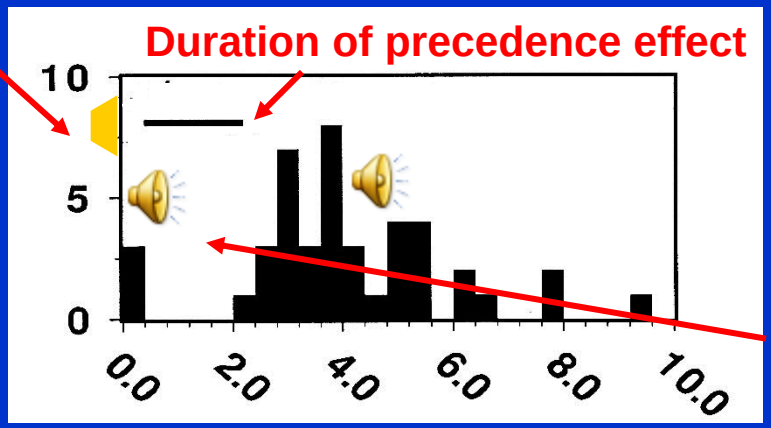
Hypothesis 1 : Inhibitory resetting mechanisms are favored by selection where psycho-acoustic precedence effects influence female receivers to prefer leading signals and to ignore following ones



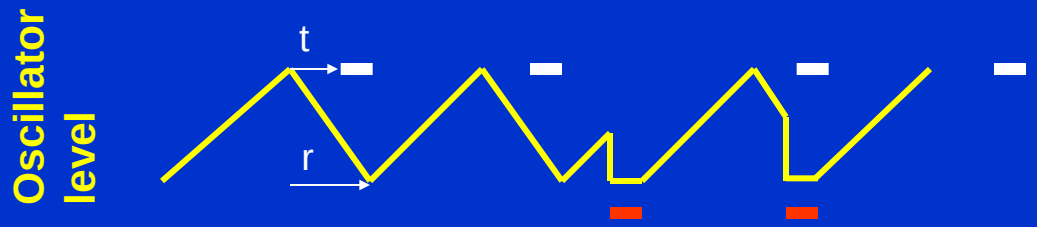
Ligurotettix planum **(Acrididae)**



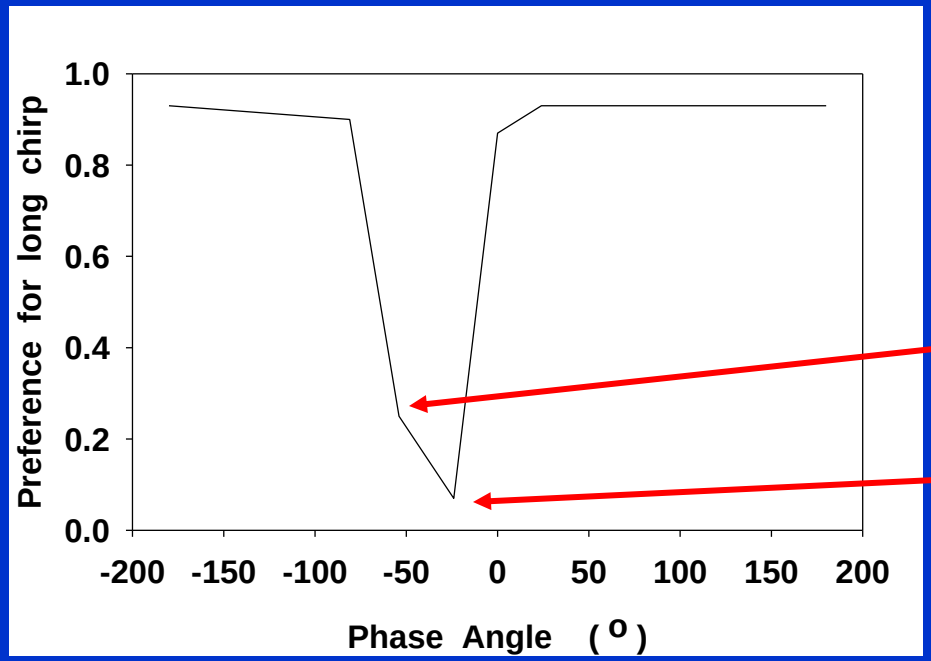
Stimulus or neighbor at 0 sec



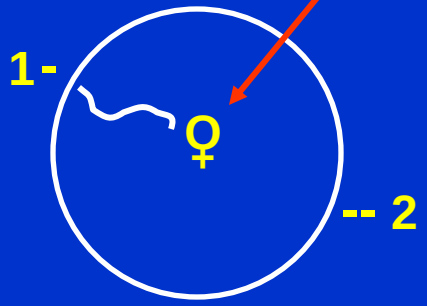
Call Delay (sec)

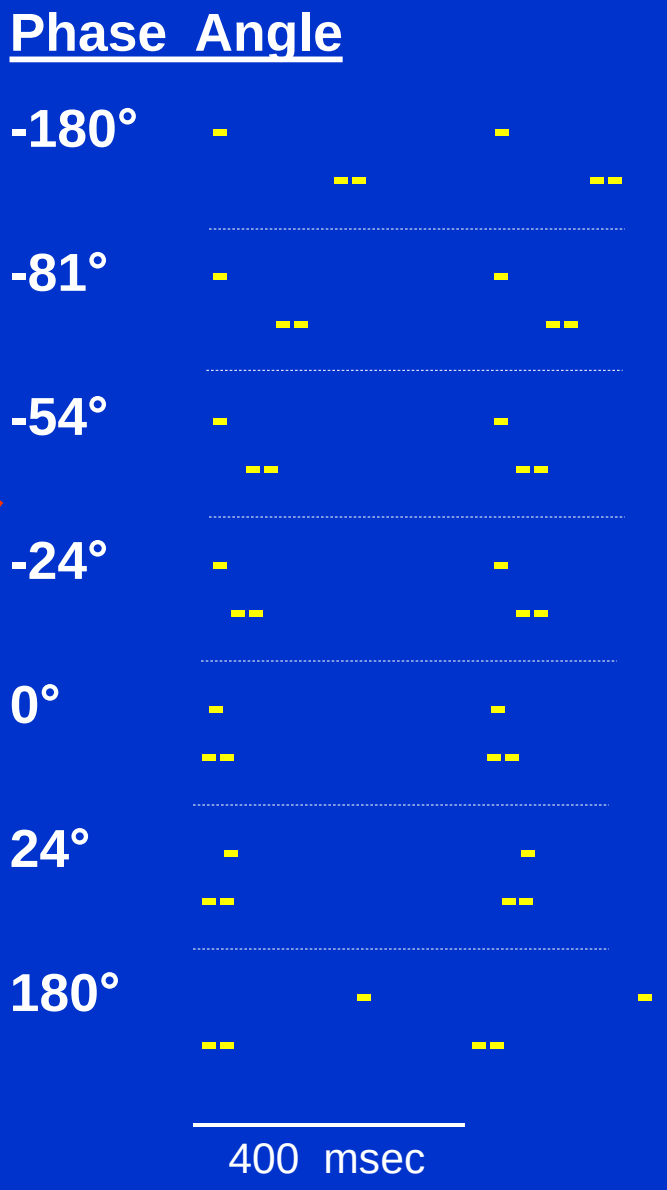


No signals by focal male during post-stimulus interval



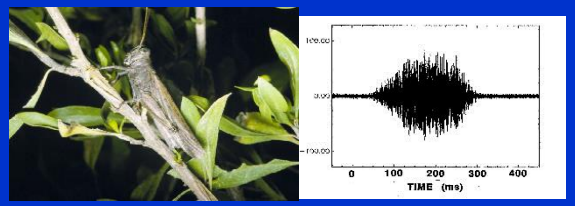
Greenfield & Roizen 1993



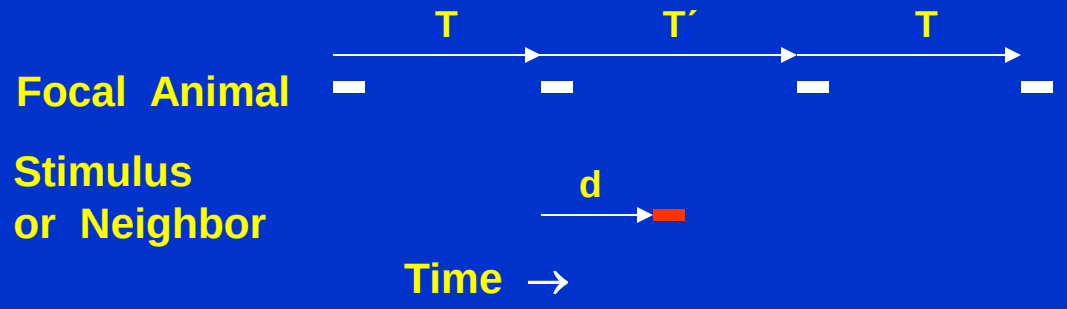


Neoconocephalus spiza **- precedence effect in female phonotaxis**

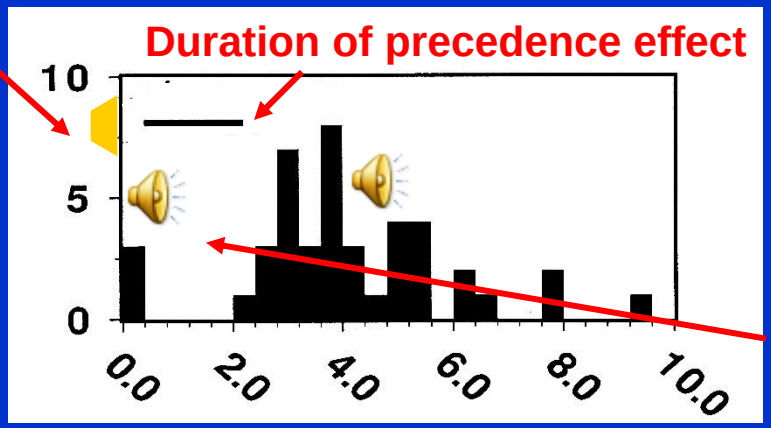
Hypothesis 1 : Inhibitory resetting mechanisms are favored by selection where psycho-acoustic precedence effects influence female receivers to prefer leading signals and to ignore following ones



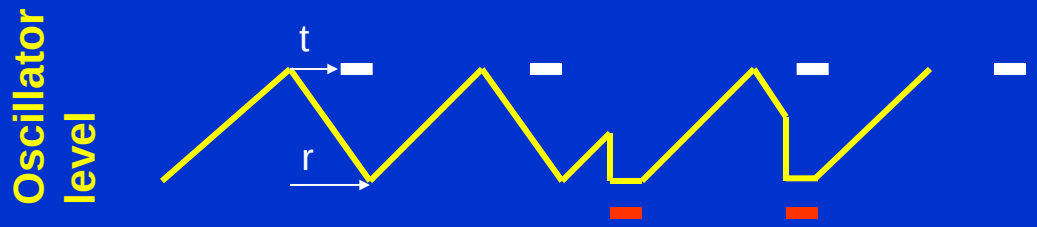
Ligurotettix planum **(Acrididae)**



Stimulus or neighbor at 0 sec



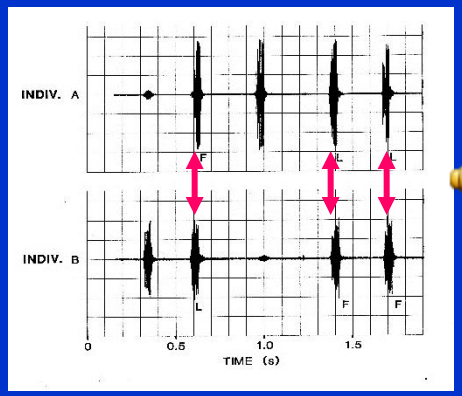
Call Delay (sec)



No signals by focal male during post-stimulus interval

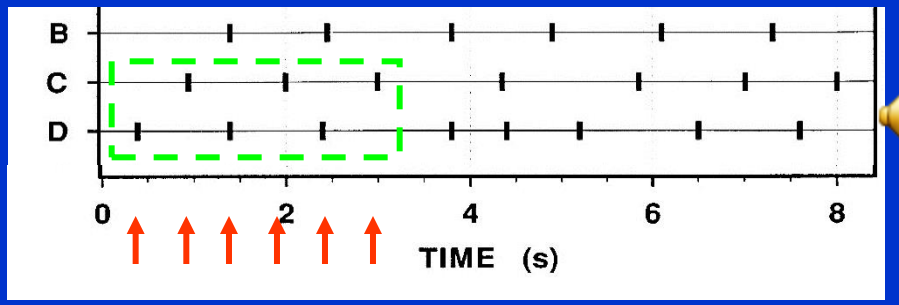
Hypothesis 2 : Synchrony and alternation may arise as emergent properties of pairwise inhibitory-resetting interactions between neighboring signalers.

Imperfect Synchrony

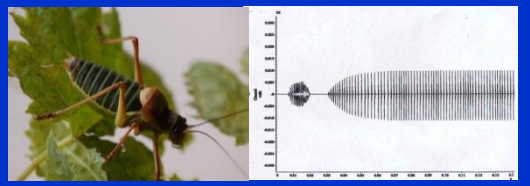


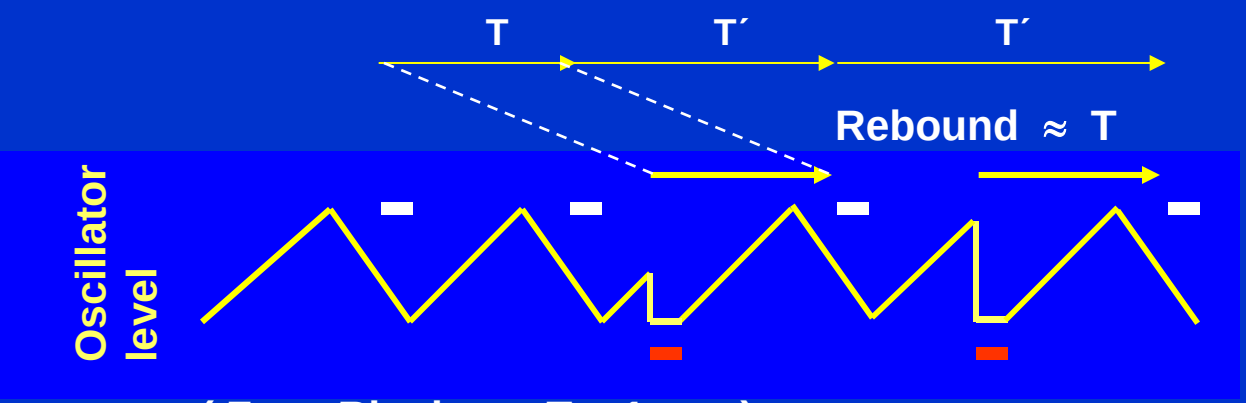
Neoconocephalus spiza **(Tettigoniidae)**

Alternation

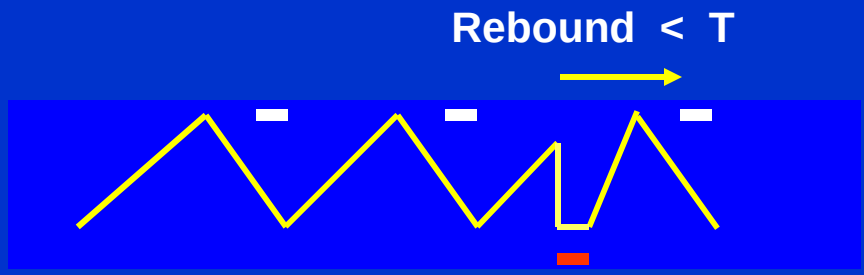


Ephippiger diurnus **(Tettigoniidae)**

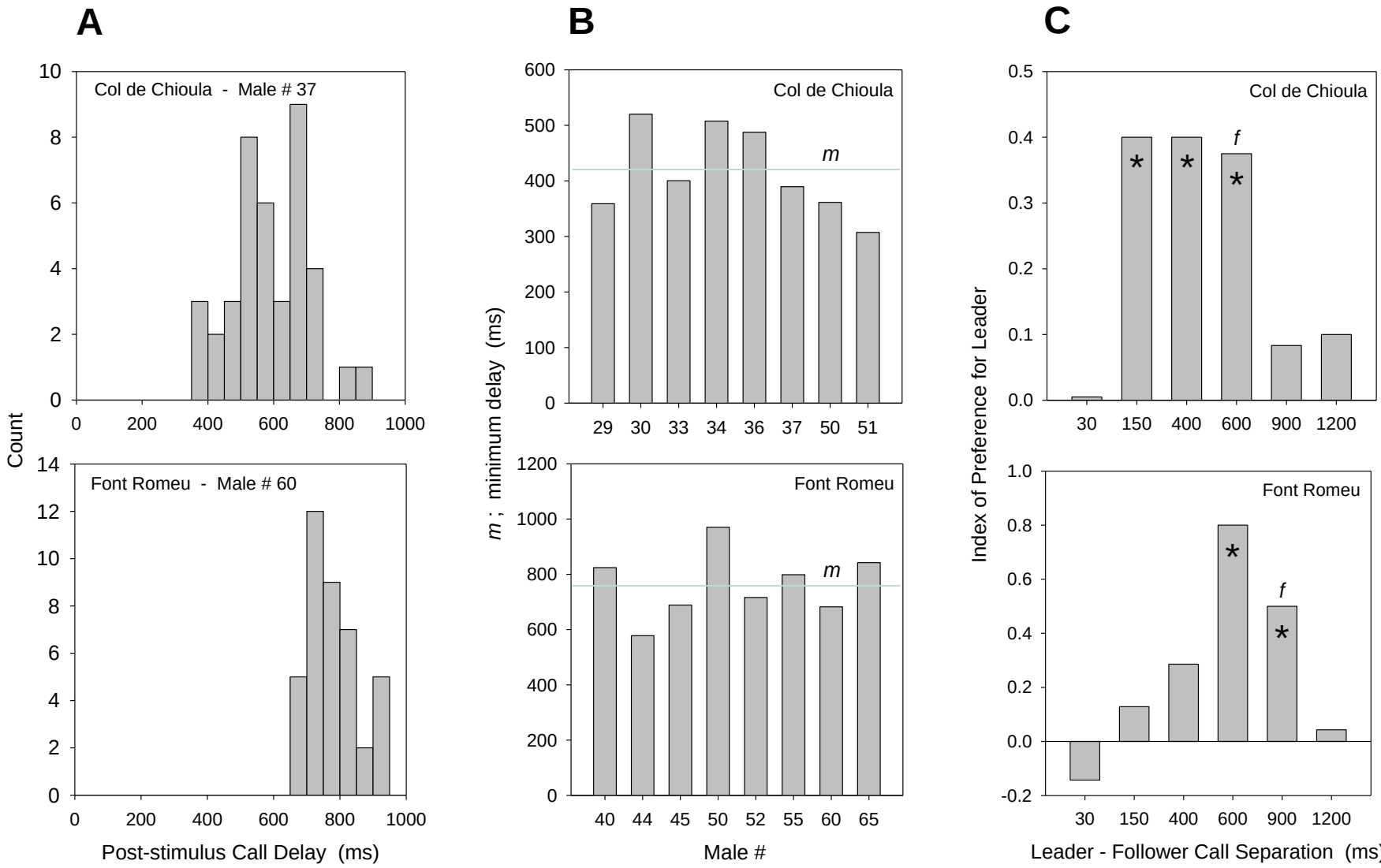




(Fast Rhythm ; T < 1 sec)



(Slow Rhythm ; T > 1 sec)


A
B
C
Col de Chioula - Male # 37
Font Romeu - Male # 60
Count
Post-stimulus Call Delay (ms)
Col de Chioula
Font Romeu
m
m ; minimum delay (ms)
Male #
Index of Preference for Leader
f
Leader - Follower Call Separation (ms)