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

Temporal adjustments in broadcasting at three levels of precision:

- **Individual**
  - a
  - b
  - c
  - d
  - e

- (an evening chorus)
  - 12
  - 18
  - 24
  - 6
  - 12 h

- (collective singing bouts)
  - 0
  - 5
  - 10
  - 15 min

- (regular rhythm and precise phase relationships)
  - 0
  - 1
  - 2
  - 3 sec

90° phase angle

* leader
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
**Uca annulipes**
(Crustacea: Ocypodidae);
Western Indo-Pacific;
Synchronized waving

Synchronized courtship in fiddler crabs;
Backwell et al. 1998
Female pheromonal chorusing in an arctiid moth, *Utetheisa ornatrix*

Hangyu Lim* and Michael D. Greenfield*✉

*Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045, USA*

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) signals attract 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 copulation and 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 non-related—females. **Key words:** Lepidoptera, mating system, operational sex ratio, sexual selection, signal competition. [BibTeX]
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.
Pulse Length (msec)

- 27.5
- 55.0

Number Females

- 0
- 2
- 4
- 6
- 8
- 10
- 12
- 14

Neoconocephalus spiza (Orthoptera: Tettigoniidae):

female preference for song length
**Neoconocephalus spiza:**
female preference for leading song overrides song length
*Neoconocephalus spiza* - precedence effect in female phonotaxis.
Inhibitory Resetting:

Stimulus Phase = \((d / T) \cdot 360^\circ\)

Response Phase = \(\{(T' - T) / T\} \cdot 360^\circ\)

Greenfield et al. 1997
Neoconocephalus spiza (Tettigoniidae):

PRC intercepts adjusted by stimulus length

Greenfield & Roizen 1993
Stimulus phase, \((d / T) \cdot 360^\circ\)

Response phase, \(\{(T' - T) / T\} \cdot 360^\circ\)

PRC slope = \(s\)

Basic model:
\[ T' = (T + \varepsilon) + (s \cdot d), \quad \text{where } \varepsilon \text{ is a stochastic element} \]

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

Calls of the 2 males; mostly synchronized

Male song adjustment parameters
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.

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.

No experimental evidence for coevolution between male and female traits.
Question 1:
Did male song adjustment (inhibitory resetting) coevolve with female response to relative call timing (leading vs. following calls)?

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.
Y-maze

follower

leader

Col de Chioula population

Measurement of female perceptual trait

Index of preference for leader

Leader – follower call separation (ms)

Col de Chioula

30 150 400 600 900 1200

0.0 0.1 0.2 0.3 0.4 0.5

†

f

Leader – follower call separation (ms)

f – maximum separation at which females ignore follower

leader

follower

delay

time

leader

follower
Measurement of male song adjustment trait

Focal male does not call during post-stimulus interval

Synthetic song stimulus at $t = 0$

Col de Chioula population

$m$ – minimum delay before male resumes singing
Predictions:

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

Moreover, if $m \approx f$, males will maximize their call rate while at the same time forgoing the broadcast of following calls.
Male phase adjustment; Minimum delay (msec) before singing after a stimulus or neighbor.

Female precedence effect; Maximum delay (msec) at which leading calls are preferred.

Col de Puymorens; 8

Hospitalet près l’Andorre; 9
For the 17 populations sampled, $m \approx f$.


\[ \rho = 0.87 \]
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

\[
\rho = 0.76
\]
Is PIC justified for intra-specific comparison?

Normally no, because gene flow resulting from inter-population migration will influence phenotypic values 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
Population

$K = 7$ clusters

Number of clusters ; $K$

Probability of data $[Pr(X|K)]$
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 ($\geq 3$ 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?
Kramer sphere
(open loop)
Simple choice tests in 3 populations indicate female preferences for 1) leading calls, 2) faster rhythm, and 3) higher syllable number.

(Party, Brunel-Pons & Greenfield 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:

(Party, Streiff, Marin-Cudraz & Greenfield 2015)
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)
3. Female preference for **natural** (alternating or synchronous phase angles) vs **modified** chorus stimuli (overlapping phase angles) ; choice tests on Kramer sphere ;

Result : Overall preference for **natural** chorus stimuli not observed (Rayleigh and V-tests).
Question 4:
Is chorusing under central control?

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

b) Mating Latency (min)

c) Spermatophore (proportion male weight)

d) Number eggs deposited

Pairing

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

Tettigoniidae; Bradyporinae

Sorapagus catalaunicus
Synchrony

Ephippiger diurnus
Alternation + Synchrony
Synchrony - 2 male choruses

Synchrony - 4 male choruses
Playback - precedence effect - *Sorapagus catalaunicus*
Ephippiger diurnus

Carcanières (7)
Col de Choula (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-Val (7)
Mireval (6)
Peyriac de Mer (6)
Port de Lers (7)
Pouzol (8)
Vias (7)
Vilamòs (7)

Sorapagus catalaunicus

Font Romeu (18)
Playback - gap length

Playback - gap depth
Relative call timing
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).
Canal à la droite est le premier
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
**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

**Duration of precedence effect**

**Call Delay (sec)**

**Oscillator level**

No signals by focal male during post-stimulus interval

(Focal Animal Stimulus or Neighbor)

**Stimulus or neighbor at 0 sec**

**Time**

**T**

**T’**

**T**
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.
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)

Rebound ≈ T

Rebound < T

Oscillator level

(Fast Rhythm; T < 1 sec)

(Slow Rhythm; T > 1 sec)