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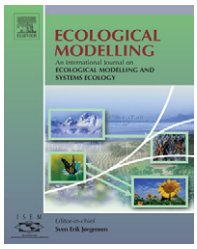

Chorus model of the synchronizing bushcricket species *Mecopoda elongata*

*Manfred Hartbauer**

Karl-Franzens University Graz, Department of Zoology, 8010 Graz, Universitätsplatz 2, Austria

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ABSTRACT

Males of the Malaysian bushcricket species *Mecopoda elongata* synchronize or alternate their cyclically occurring song elements (chirps) in a duet. The acoustic interaction of males interacting in a duet was successfully simulated by means of mutually coupled song oscillators, which respond to a disturbance by a phase shift which is known from the phase response curves (PRCs) of real males. However, little is known about the acoustic interaction of males in a complex chorus situation. Therefore, the aim of the current study was to extend the duet model to a chorus taking into account an inhomogeneous spacing of agents and a natural variability of oscillator properties. This chorus model was used to study oscillator coupling in a chorus consisting of 15 agents. Since such a computer model allows one to simulate chorus manipulations that far exceed the possibilities of behaviour experiments, the following scenarios were simulated: modification of chorus density, sensory bias during sound production, selective attention to only a subset of neighbors and males joining or leaving a chorus. Simulation results allow one to draw conclusions about the chorusing behavior of males in a real chorus and about signaler and receiver aspects influencing chorusing formation and mate choice.

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1. Introduction

The synchronization of communication signals in aggregations of many individuals has attracted the interest of many researchers throughout the last century. Near perfect synchrony of light signals can be found in some species of East-Asian fireflies (Buck, 1938; Buck and Buck, 1976; Buck, 1988). But also acoustic advertisement signals often show a high degree of synchrony. Such synchrony has been seen in the cricket *Oecanthus fultoni*, in the bushcricket species *Neoconocephalus spiza, Mecopoda elongata*, *Pterophylla camelliflora*, *Platycleis intermedia*, *Neoconocephalus caudellianus* in the genus Kawanaphila (Tettigoniidae: Zaprochilinae) and in the periodically occurring cicada *Magicicada cassini* and in the anuran species *Smilisca sila* (Alexander and Moore, 1958; Greenfield, 1994; Hartbauer et al., 2005; Mason and Bailey, 1998; Sismondo, 1990; Walker, 1969).

Synchrony within a population of biological oscillators is achieved by mutual entrainment. Similar mechanisms, responsible for the establishment of synchrony, were found in the pacemaker cells of the heart, circadian pacemakers, the hippocampus, insulin-secreting cells of the pancreas and the menstrual periods of women (for an overview see: (Winfree, 1967; Winfree, 1980)). Much theoretical work is based on the Peskin model (Peskin, 1975) of "integrate and fire" oscillators in which the interaction between two oscillators are either smooth or pulse like (Mirollo and Strogatz, 1990; Goel and Ermentrout, 2002). As Peskin (1975) already conjectured and Mirollo and Strogatz (1990) proved, for almost all initial conditions a steady-state evolves among a population of homogeneous "all to all" coupled oscillators in which all oscillators fire in synchrony. However, little work has been done so far considering the behavior of a population of biological oscillators with different natural frequencies and other

* Tel.: +43 316 380 8751; fax: +43 316 380 9875.
E-mail address: Manfred.Hartbauer@uni-graz.at.
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geometries different from "all to all" coupling or ring-like formations.

In a natural chorus situation the distances between signalers show a high degree of variability (e.g. Nityananda et al., 2007; Römer and Bailey, 1986; Thiele and Bailey, 1980) and the coupling strength of song oscillators strongly depends on the distance between individuals. This physical constraint together with an intrinsic variability of signalers with regard to solo chirp periods (solo CPs), signal level, cycle-to-cycle fluctuations and variability of phase change in response to a stimulus might result in an oscillator coupling which never results in global stable synchrony.

Males of the Malaysian bushcricket species *M. elongata* periodically display advertisement signals (called chirps) at a period of ~2 s. Males in a duet mutually couple their song oscillators by signals either displayed in synchrony or alternation. So far almost all investigations addressing the establishment of synchronization in this species were performed in real or simulated male duets (Sismondo, 1990; Hartbauer et al., 2005) neglecting the complexity that exists in a chorus situation. Multi-agent based simulations that consider transmission effects and a natural variability of signalers therefore constitute a useful approach for the investigation of chorusing in this species.

A so-called "inhibitory-resetting oscillator" (see Section 4) is often used to describe the underlying neural oscillator responsible for song oscillator coupling (Greenfield, 1994). However, the acoustic interaction of *M. elongata* males cannot be successfully described by this model, because a disturbance only affects the disturbed cycle but not the cycle subsequent to a disturbance in this species (Hartbauer et al., 2005). In addition, depending on stimulus phase the oscillator cycle is either shortened or prolonged. In order to account for these special oscillator properties in the current chorus model, agents mutually couple their song oscillators based on known phase response curves (PRCs) obtained from real males. This constitutes a more realistic modeling approach in comparison to an "inhibitory-resetting oscillator" model, which relies on several unknown variables. This modeling approach was successful in simulating firefly synchrony (Ermentrout, 1991) and in the simulation of the acoustic interaction of a male duet of a chirping Indian *M. elongata* species (Nityananda and Balakrishnan, 2007).

A chorus model not only allows one to study oscillator coupling in a reasonably realistic simulation of a chorus but it also allows one to investigate the influence of several receiver aspects on chorusing. Furthermore, the robustness of chorusing to influences arising from different chorus densities and agents that acoustically join or leave a chorus can also be studied.

Males of a chirping Indian *Mecopoda* species (Nityananda et al., 2007) and males of the bushcricket species *Neoconocephalus nebrascensis* (Meixner and Shaw, 1979) space themselves out in a way which preserves an average inter-male distance of about 5–6 m. The mean inter-male distance for *M. elongata* in the field is currently unknown and may vary in aggregations of different bushcricket species substantially (e.g. Thiele and Bailey, 1980; Römer and Bailey, 1986). Therefore, agents in the chorus model exhibit an uneven inter-male spacing. Simulations performed with different chorus densities offer the possibility to elucidate a minimum inter-male distance necessary for the establishment of steady-state oscillator coupling in a *M. elongata* chorus.

Apart from male density, chorus composition may also affect chorusing in a *M. elongata* chorus. Chorus attendance of a single male in a chorus of *M. elongata* is of limited duration (about 30 min) and individual males acoustically join or leave the chorus from time to time. This can be easily simulated in the computer model and allows one to draw inferences about the robustness of steady-state oscillator coupling to changes of chorus composition.

Some continuously signaling insects are known to hear while they sing. However, the rate of syllables in a chirp of *M. elongata* is quite high (125 Hz) and it is still unknown whether males hear while they produce a sound. This may result in a sensory bias that affects oscillator coupling and in consequence chorusing behavior. Simulations were therefore performed modeling a shift of the hearing threshold to a level which exceeds the current chirp level by 3 dB.

The attention of a male in a chorus may be influenced not only by self-generated sound but also by selective attention to a subset of neighbors in close proximity. In such a situation selective attention to agents close to a focal agent results in a higher coupling strength of their song oscillators compared to more distant agents. This however may neglect the probable existence of a selective response to only a few nearest neighbors as was found in insect choruses of *Ligurotettix planum*, *Ligurotettix coquilletti*, *Ephippiger ephippiger* and *Neoconocephalus spiza* (Snedden et al., 1998; Greenfield and Snedden, 2003) and also in an anuran chorus (*Physalaemus pustulosus* (Greenfield and Rand, 2000)). In the current chorus model, a selective response of agents can be simulated by forcing agents to ignore all signals except those of nearest neighbors.

All these chorus simulations may lead to a better understanding of signaler and receiver aspects influencing chorusing in *M. elongata*. Results will be discussed in the context of insect chorusing and female choice.

2. Methods

2.1. Biological background

Males of the species *Mecopoda elongata* (*M. elongata*) exhibit a chirp period (CP) of 1.75 to 2.3 s in songs displayed in isolation. Within such a song bout only little chirp-to-chirp variability is found and therefore fast and slow singing males can be discerned. Each chirp consists of syllables of increasing amplitude and are regarded as single oscillatory events displayed once in each cycle. In the current model agents couple their oscillators using acoustic signals which exhibit an amplitude profile that is similar to the increase of syllable amplitudes within a conspecific chirp (Fig. 1A). Individual agents were modeled on the basis of signal oscillators exhibiting the same properties as was found in 11 real *M. elongata* males. The phase response curves (PRCs) of these individual males were obtained from playback experiments using a conspecific stimulus, which was broadcast at 50, 60 and 70 dB SPL at random phases in the cycle of the song oscillator. All PRCs were already published in Hartbauer et al.

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