

# Pseudo-synchronization Leads the Pack:

A model examining pseudo-synchronization in *Pholidoptera griseoptera*, the dark bush cricket, as an evolutionary advantageous trait.

By: Charlie Chapman



# Dark Bush Cricket

*Pholidoptera griseoaptera*

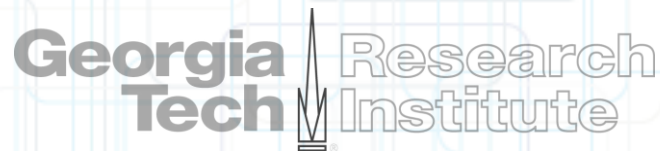
- Taxonomy: Orthoptera>> Ensifera>> Tettigoniodea>> Tettigoniidae>> Decticinae
- Appearance: Dark to red-brown, with a paler patch along the top of the thorax, and a yellow-green belly. The female has an up-curved ovipositor.
- Habitat: Southern and Central England and South Wales. Wasteland, bramble thickets, old hedges, woodland edges and rides, thickets on sea cliffs and scrub on the edges of saltmarshes and dunes.
- Food: Omnivorous, feeding on a range of vegetation and small insects.
- Fun Fact: They lay their eggs in 18 month cycles, resulting in odd-year and even-year crickets never meeting.



# Unique Behavior of the Dark Bush Cricket

The males of many species of insects are known to either synchronize or alternate their mating calls<sup>[1]</sup>. The dark bush cricket exhibits a unique behavior compared to other insects in this category, as not only will two male bush crickets alternate their chirps, they will also repetitively achieve temporary states of near synchronization <sup>[2]</sup>.

Most models of the synchronization and alternation behavior in insects, attribute it to simple integrate and fire variety response systems, in which the insects shift their phase. The basis of most models of this type is that the female insects have been shown to prefer the male which leads the chorus, so the males respond by attempting to shift their call into the lead position <sup>[3]</sup>.

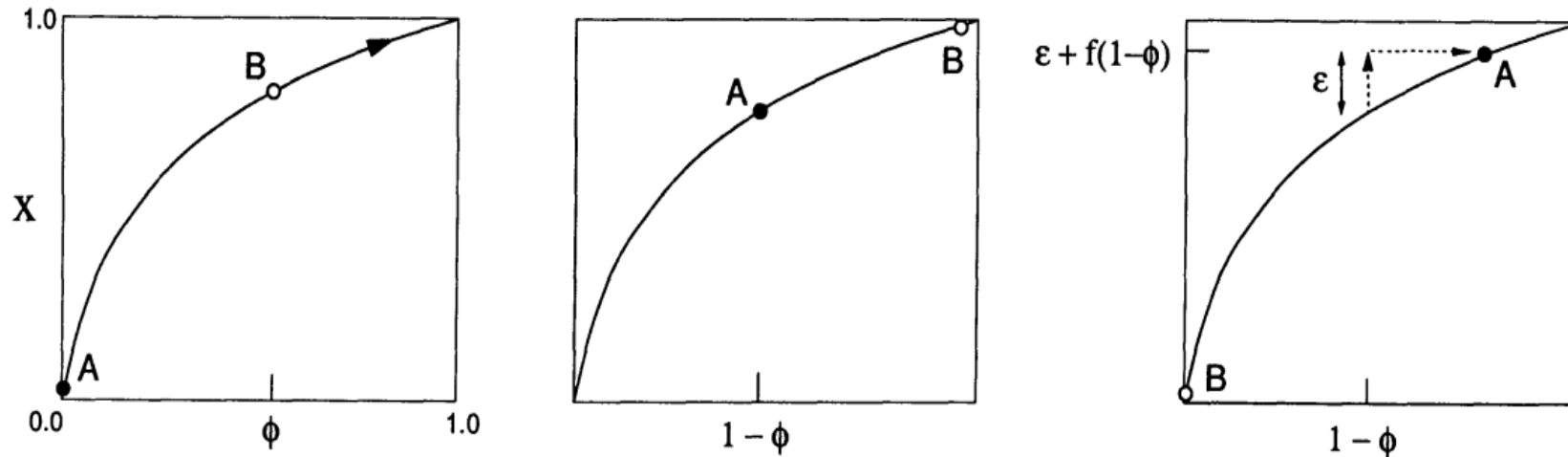


# Unique Behavior of the Dark Bush Cricket

It is believed that a simple integrate-fire system, as observed in other species of insects, does not adequately describe the unusual behavior of the bush cricket.

This behavior can not be due to two crickets simply drifting in and out of phase for several reasons. First of all, the shift from alternation to synchronization is done in clearly discrete steps, not continuously over a period. And second, the amount of chirps that a cricket remains synchronized with its partner is highly variable. In a 4 minute period, Jones was able to observe two crickets synchronize for between 1-6 iterations [2].

# Integrate-Fire Model



## Peskin's Model for the Cardiac Pacemaker

$$\frac{dx_i}{dt} = S_0 - \gamma x_i, \quad 0 \leq x_i \leq 1, \quad i = 1, \dots, N.$$

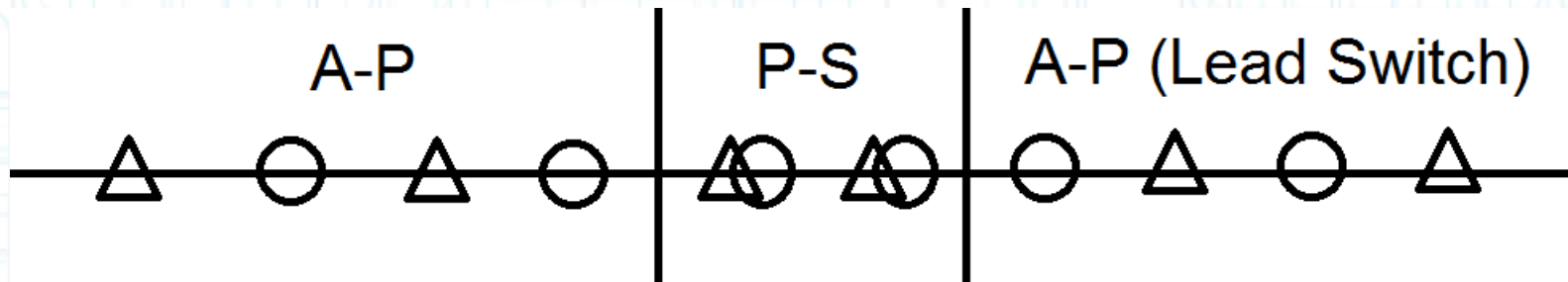
# Pseudo-Synchronization

A very interesting feature of the bush crickets behavior, is that bush crickets never achieve states of true synchronization. Two competing crickets will only ever become entrained in a state very close to synchronization, where their signals overlap <sup>[3]</sup>.

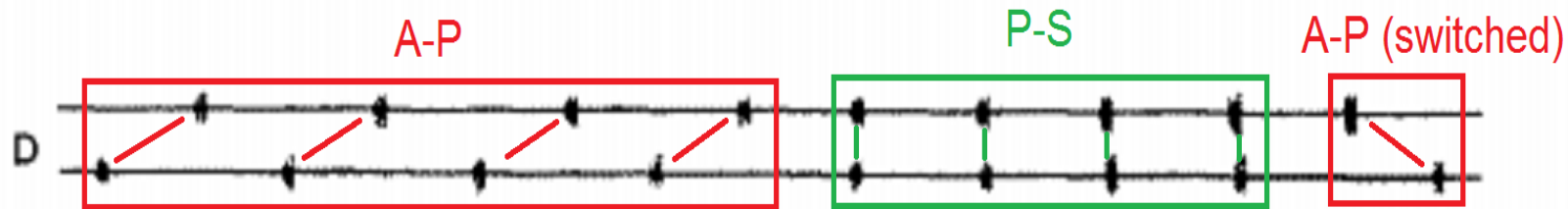
This state of near synchronization has been termed pseudo-synchronization (P-S), as auditorily it appears as if the two crickets have synchronized for the duration.

In the framework of a cricket trying to gain the lead position in the chorus, this P-S characteristic has valuable implications.

# Pseudo-Synchronization



General interaction behavior of *Pholidoptera griseoptera*, changing from an alternating phase (AP), to a phase of pseudo-synchronization (P-S), back to an alternating phase, where the lead has switched.



Observed interaction pattern between two dark bush crickets by M.D.R. Jones, exhibiting the described pattern [2].

# Advantages of P-S for Taking the Lead

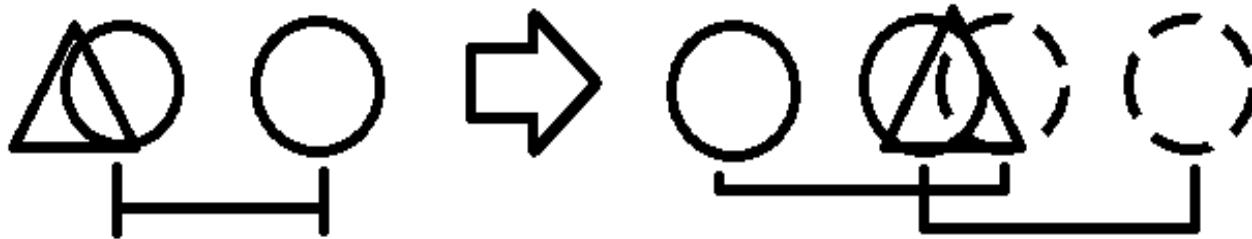
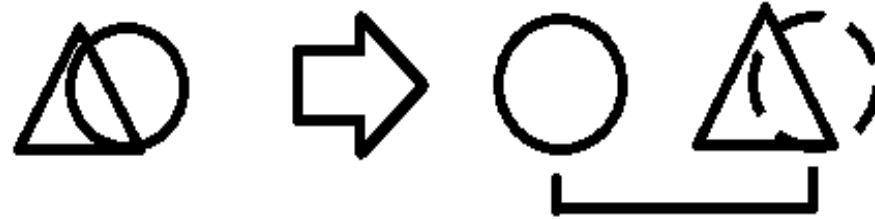
P-S potentially has several inherent advantages for insects which employ it, over the conventional model used to describe alternating and synchronizing behavior:

- The cricket can more reliably reach the lead position, as it isn't sporadically adjusting its chirp rate to try and take the lead. It can reach a state of P-S with the lead, and then simply shift its chirp forward slightly to take the lead.
- The cricket can gain a maximum lead over the previous lead. From a position of P-S, the cricket can shift its chirp forward a maximum amount over the current lead



# Advantages of P-S for Taking the Lead

P-S Outcome



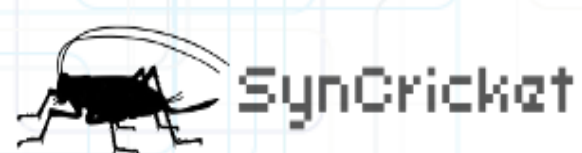
Integrate-Fire Outcome

# P-S Leads the Pack

Based on the information leading up to this point, I propose that this characteristic of P-S is in fact an evolutionary selected for trait in *Pholidoptera griseoptera*; allowing individuals which employ it to more effectively gain the lead position in a chorus, and thus propagate their genes.

The remainder of this talk will consist of a presentation of evidence regarding the quantitative favorability of a model employing the P-S characteristic, versus one employing the conventional integrate-fire model for alternation and synchronization.

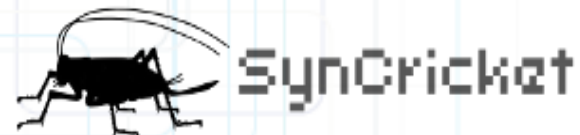
Favorability in this context, was defined on two fronts: the time it takes a cricket to gain the lead position from an alternating state ( $180^\circ$  out of phase with the leader), and the magnitude of the lead gained over the previous leader.



# The Plan

At first, the plan for this study was to quantitatively compare the favorability of a conventional integrate-fire model versus a P-S model, using both to control the response behavior of electronic crickets (SynCrickets).

However, defining the P-S model proved to be quite challenging, and as an alternative, the favorability of the P-S model was numerically calculated from Jones' data for live dark bush crickets, and compared to the favorability calculated from SynCrickets running an integrate-fire model.



# Say Hello to The SynCrickets



# Methodology

Two SynCrickets were bound in a Master-Slave relationship:

- Master: The master SynCricket was set to chirp at a constant rate, unresponsive to the slave.
- Slave: The slave responded to the chirps of the master, shifting its phase according to whichever response model it was told to follow. For the data in this presentation, a variant of the Peskin cardiac-pacemaker model, proposed by Mirolo and Strogatz, was used [4].

# Methodology

A base chirp rate of 12 chirps per minute was used for two reasons. Firstly, Matlab, which was used to control the behavior of the crickets, was unable to reliably process chirps rates of over 60 per minute (rates in live crickets can easily reach 120+ chirps per minute, varying with temperature). Secondly, this rate allowed for a higher relative precision when analyzing the favorability.

# Results from Live Crickets

From Jones' data of live cricket interactions, he notes the total duration of a recording, chirp rate of each cricket during this recording, the number of times a synchrony occurs between the pair, as well as the length of that synchrony (in chirps).

Using this data, a ratio of 0.088 was found for the synchrony occurrence rate in a sample of chirp interactions. Under the assumption that all synchrony events Jones' observed led to lead-switches, this ratio was used to define how quickly a cricket was able to take the lead.

For the lead gain of the live crickets, because discrete steps from alternation to synchronization were observed, the lead gain for all events of this type will be by a shift of  $180^\circ$ .

# Results from the SynCrickets

Much like with the live crickets, data collected from the SynCrickets was used to calculate the ratio of lead-switch events. For the Mirollo-Strogatz model this ratio was found to be 0.042. This value was calculated as an average of data taken over a range of possible coupling strengths for this model.

As expected, the range of gain in lead-switch events spanned from zero up to a maximum phase shift defined by the parameters of the model.





# Comparison of the Two Models

For a cricket responding according to a P-S model, there is a clear advantage over one which follows an integrate-fire model:

- A cricket following the P-S model will be able to gain the lead roughly 2.1 times faster. At 120 chirps per minute, we would expect 10-11 lead-switch events as opposed to only 5 from an integrate-fire model.
- The amount by which a cricket following the P-S model will lead, is potentially much greater.

Even accounting for the 7% error that arose between trials, this is still a significant difference.

# Future Possibilities

- Mathematically formulate the P-S model.
- Collect additional data from live crickets for comparison.
- Compare more models and their favorability.

# Citations

- [1] Dumortier, B. (1964). Ethological and physiological study of sound emissions in Arthropoda. In *Acoustic Behaviour of Animals*, ed. R.G. Busnel, 583-654. Amsterdam: Elsevier.
- [2] Jones, M. D. R. (1966). The acoustic behavior of the bush cricket pholidoptera griseoptera 1. alternation, synchronism and rivalry between males. In *J Exp Biol*, (45), 15-30.
- [3] Hartbauer, M., Kratzer, S., Steiner, K., & Romer, H. (2004). Mechanisms for synchrony and alternation in song interactions of the bushcricket mecopoda elongata (tettigoniidae: orthoptera). *J Comp Physiol A*, (191), 175–188.
- [4] Mirollo, R., & Strogatz, S. (1990). Synchronization of pulse-coupled biological oscillators. *SIAM J. Appl. Math.*, 50(6), 1645–1662.