MATHEMATICS

Chimera states among synchronous fireflies

Raphaël Sarfati[1]* and Orit Peleg[1,2,3,4,5,6]*

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Systems of oscillators often converge to a state of synchrony when sufficiently interconnected. Twenty years ago, the mathematical analysis of models of coupled oscillators revealed the possibility for complex phases that exhibit a coexistence of synchronous and asynchronous clusters, known as "chimera states." Beyond their recurrence in theoretical models, chimeras have been observed under specifically designed experimental conditions, yet their emergence in nature has remained elusive. Here, we report evidence for the occurrence of chimeras in a celebrated realization of natural synchrony: fireflies. In video recordings of *Photuris frontalis* fireflies, we observe, within a single swarm, the spontaneous emergence of different groups flashing with the same periodicity but with a constant delay between them. From the three-dimensional reconstruction of the swarm, we demonstrate that these states are stable over time and spatially intertwined. We discuss the implications of these findings on the synergy between mathematical models and collective behavior.

INTRODUCTION

Complex systems consisting of entities with internal periodicity often produce synchrony. This has been observed, demonstrated, and characterized across (spatial and temporal) scales and ensembles (*1*, *2*), animate or inanimate, from planetary orbits to ecosystems (*3*) to animal collectives (*4*, *5*) to cell tissues (cardiac or neuronal) and down to electronic structures. The underlying reason for this ubiquity is that interacting oscillators, even weakly coupled, tend to adjust their individual frequencies and drift toward a common phase. This is what the mathematical analysis of simple models of coupled oscillators has uncovered (*1*, *6*, *7*). However, even though these models converge to synchrony for a wide range of coupling schemes, the modalities of the resulting synchronous patterns can be quite complex and notably include different phases (*8*). Among them, recent research has focused on phases that exhibit a coexistence of synchronous and asynchronous dynamics (*9*), where constituting agents separate into different clusters aligned on different tempos. These phases have been named "chimera states" in reference to the Homeric hybrid creature made of parts of disparate animals (*10*). In a chimera state, coexisting subpopulations can either be synchronous and asynchronous or mutually synchronized on different tempos. While abundant in mathematical models, chimeras are rare in the real world. Certain chimera states have been observed in carefully designed experimental systems, yet they remain wildly elusive in nature and biological settings in particular (*11*).

Here, we present evidence for the occurrence of chimera states in natural swarms of *Photuris frontalis* fireflies. These fireflies are one of few species known for their precise and continuous synchrony (*12*, *13*), with coherent displays that can span several tens of meters. Synchronous fireflies, wherein congregating males flash in unison possibly to optimize courtship communication with grounded females (*14*), have long been considered a picturesque paragon of natural synchrony and an inspiration for theoretical developments (*2*). However, until recently, little had been known about the details of their collective dynamics, particularly their spatiotemporal patterns (*15*). On the basis of high-resolution stereoscopic video recordings, we demonstrate the existence and persistence of synchronized chimera states within *P. frontalis* swarms. We characterize their spatial distribution and movement and find that chimeras appear spatially intertwined, albeit slightly clustered, but without enhanced correlations in their displacement, and generally stable in their phase distribution. We conclude by discussing the theoretical conditions for the emergence of these chimeras, possible implications about the structure of firefly interactions, and how the natural system might further inform future mathematical models.

RESULTS

In late May in Congaree National Park, *P. frontalis* displays ardently across a forest of loblolly pines spreading along the convergence line between a bluff and the Congaree River floodplain (*16*). While the swarm stretches across hundreds of meters, most fireflies tend to coalesce into localized leks hovering above smaller parcels. Many fireflies were observed to swarm in an area at the outskirt of the pine forest forming roughly a quadrilateral of side length of ~40 m (Fig. 1A). Two cameras were recording at 60 frames per second toward the center and above a clear ground (Fig. 1B). From stereo recording, a portion of the swarm could be reconstructed three-dimensionally (3D), corresponding to a cone of aperture of ~35° and length of ~40 m (Fig. 1A). Recording started at dusk every night, just when the first flashes could be observed, and continued for about 150 min.

P. frontalis fireflies produce brief flashes lasting 20 to 30 ms (Fig. 1C), owning them the nickname of "snappies" (*17*). After image binarization by intensity thresholding, each flash is generally detected in a single frame of the movie, sometimes two. Snappies are known for their precise, collectively continuous synchrony (*12*). The time series of the number N of flashes per frame reveals a chorus of sharp spikes of up to 20 concurrent flashes repeated with great regularity (Fig. 1D). Here, the duration between these collective flashes is narrowly distributed around 39 ± 1 frames (Fig. 1D, inset) or 0.65 ± 0.02 s, although this period is inversely correlated with temperature (*13*, *17*), and hence varies over time (typically between 0.5 and 1 s; fig. S1).

[1]BioFrontiers Institute, University of Colorado Boulder, Boulder, CO, USA. [2]Department of Computer Science, University of Colorado Boulder, Boulder, CO, USA. [3]Department of Applied Math, University of Colorado Boulder, Boulder, CO, USA. [4]Department of Physics, University of Colorado Boulder, Boulder, CO, USA. [5]Department of Ecology and Evolutionary Biology, University of Colorado Boulder, Boulder, CO, USA. [6]Santa Fe Institute, Santa Fe, NM, USA.
*Corresponding author. Email: raphael.sarfati@colorado.edu (R.S.); orit.peleg@colorado.edu (O.P.)

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