MATHEMATICS

Chimera states among synchronous fireflies

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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).

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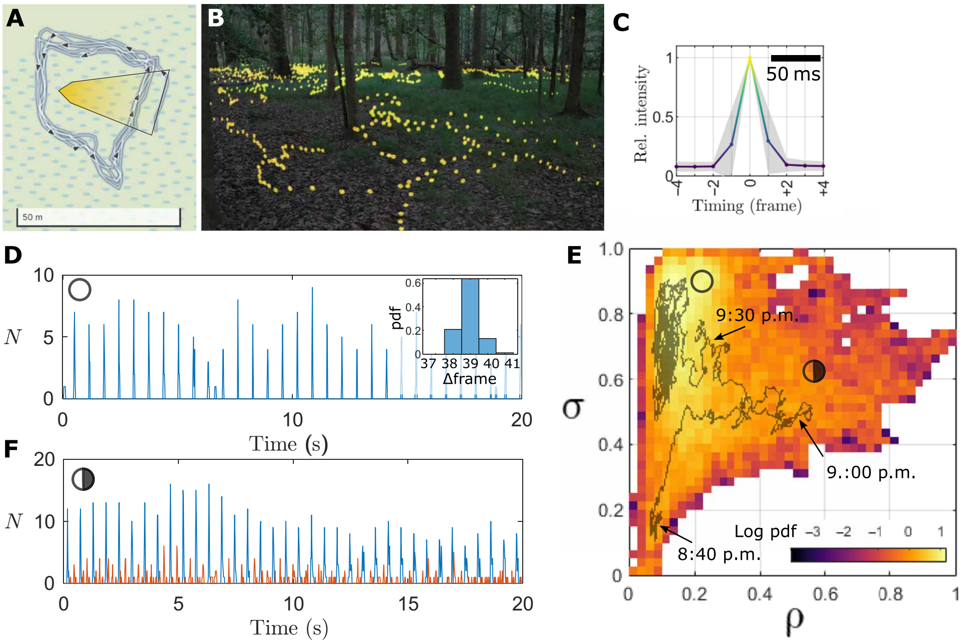

Fig. 1. Recording of collective display. (**A**) Approximate contour of swarming area and overlap of both cameras' fields of view (yellow cone). (**B**) Composite image showing the swarming environment as seen from left camera and firefly flashes over 20 s. (**C**) Intensity profile of a single flash over a 150-ms time window (average from 100 separate flashes, normalized by maximum value; SD in gray). After thresholding, each flash is typically detected in a single frame because of the narrow profile. (**D**) Time series of the number of flashes per frame, N, revealing a chorus of synchronous flashes occurring with great regularity every 0.65 s. Inset: Distribution of peak-to-peak intervals. (**E**) Distribution of synchrony σ versus density ρ, representing respectively the fraction of flashes in the chorus and the average number of flashes per frame (data from every night, 20 to 30 May, 140 to 180 min). The gray trace represents the (ρ, σ) trajectory for 29 May. Approximate corresponding times (EDT) indicated with arrows. The circular markers correspond to the approximate locations of the time series in (D) and (F). (**F**) Time series showing two concurrent and interlaced synchronized groups: the chorus (blue) and dissonant characters (orange). From 23 May around 8:55 p.m. (*28*). pdf, probability distribution function.

Over the course of the evening, the collective flashing density ρ, quantified as the moving average of the number of flashes per frame, increases rapidly for 15 min, then decreases slowly, and eventually plateaus from 9:30 p.m. until after 11:00 p.m. (fig. S2). In prior studies of synchronous fireflies, a high degree of synchronization is reached only at high flashing density (*18*, *19*). However, we remark that this is not the case here. We define the degree of synchronization $\sigma \in [0,1]$ as the number of flashes in the chorus over the total number of flashes within 1-min time intervals (Materials and Methods). The distribution of σ versus ρ in Fig. 1E shows a noticeable pattern, as the collective display transitions between three different states. Early in the evening, the density is low, and flashes tend to be uncorrelated ($\sigma \simeq 0.2$), while later, the same low density produces a highly synchronized display ($\sigma \simeq 0.6$ to 1). The difference might be due to residual ambient light at earlier times, which can impede visual interactions (fig. S2). Unexpectedly, when ρ is at its peak ($\rho \geq 0.35$), the group is only partially synchronized, with $\sigma \simeq 0.5$. We remark from the time series that while a majority of flashes concur with the chorus (χ_O), a substantial portion occur off-beat, often mutually in unison (Fig. 1F). These nonconformist characters (χ_a) form an eclectic ensemble consisting of both independent flashers and sporadic synchronized clusters. In other words, the swarms appear to produce a natural occurrence of a chimera state. We resolve to further investigate this type of anecdotal realizations of ambivalent states by looking at 11 nights of data (20 to 30 May 2021) in intervals where $\rho > 0.35$.

To study these two interlaced populations, we identify the chorus as those in the immediate temporal vicinity of local maxima in N (see Materials and Methods) and set apart the characters as all other flashes. Frequency spectra reveal that both χ_O and χ_a exhibit the same periodicity (Fig. 2A). This suggests that the collective dynamics consists of distinct groups of similar oscillators with different phases. While the term "chimera states" broadly designates the coexistence of synchrony and asynchrony (*11*), we find that a significant proportion of characters are also synchronized between them. The distribution of $N(\chi_a)$ shows that about 25% of character flashes occur concurrently with at least one other within the camera's field of view (Fig. 2B). These statistical signatures suggest the existence of chimera states consisting of at least two mutually exclusive synchronous clusters.

Are these chimera states stable? In other words, do off-phase synchronous clusters tend to drift back toward the chorus' tempo over time or rather maintain their phase difference? To investigate, we look at the temporal evolution of character time delays, defined as the time τ between a flash and the closest preceding or following chorus beat. Flash localization in 3D combined with a distance-based linking algorithm allows to track individuals for the duration of their wanderings within the field of view (Materials and Methods). For each trajectory, we evaluate the difference in time delay $\Delta\tau = \tau_{k+1} - \tau_k$ between flash k and succeeding flash $k + 1$. For all initial τ, the distribution is sharply distributed around $\Delta\tau = 0$ (Fig. 2C), indicating that most characters maintain their phase difference with the chorus between flashes. This remains true over several successive flashes, as shown in Fig. 2D. This is strong evidence for chimera persistence, at least over time scales of about 20 oscillations, corresponding to about 10 s. Individual fireflies can rarely be tracked over longer durations as they quickly traverse and exit the field of view.

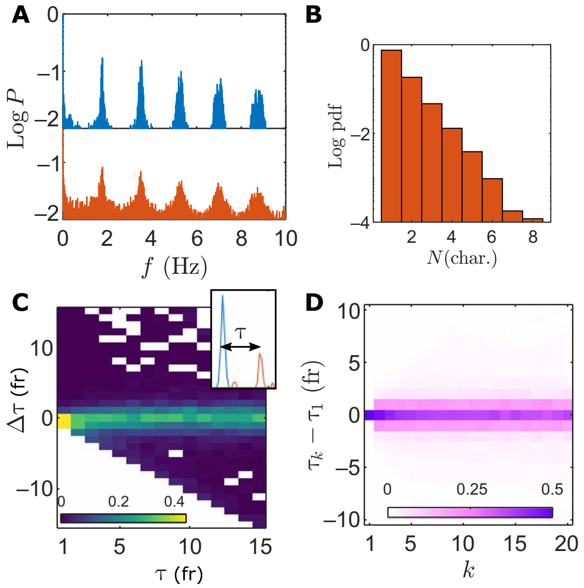

Fig. 2. Periodicity and persistence of characters. (**A**) Power spectra *P* shows that both chorus and characters have the same periodicity (23 May, over 1 hour). (**B**) Distribution of the number of concurrent character flashes. About 25% of them have $N \geq 2$. (**C**) Using 3D reconstruction, individual trajectories can be tracked. Every flash *k* can be assigned a delay τ_k with respect to the nearest chorus beat (inset). The following flash within the same trajectory has delay τ_{k+1}. The distribution of flash differences $\Delta\tau = \tau_{k+1} - \tau_k$ shows that most trajectories maintain the same delay compared to the chorus, independently of what that delay is. (**D**) Changes in time delay for the k^{th} flash compared to the first flash in the trajectory remain narrowly distributed around 0 ± 1 frame even after 20 successive flashes in the trajectory.

Having established the existence and temporal stability of chimera states, we characterize their spatial self-organization. Characters and chorus appear generally intertwined, occupying the same space without clear partitioning (Fig. 3A). To demonstrate the absence of topological structure, we consider instances when at least three synchronized characters populate the field of view. In about 20% of these occurrences, at least one member of the chorus is located within the convex hull defined by the group of characters (Fig. 3B). This demonstrates the absence of separation more accurately than looking, for example, at nearest neighbors, which may be situated outside of the field of view. However, despite the spatial blending of χ_O and χ_a, we find weak signatures of group aggregation. For synchronous groups of characters, the distribution of pairwise distances shows that characters are closer together than members of the chorus (Fig. 3C). The largest distances happen between synchronized characters and the embedding chorus. These distance distributions are statistically distinct, per two-sample Kolmogorov-Smirnov tests with *P* values < 0.001.

Last, we consider firefly kinematics and examine whether separate synchronous groups exhibit correlations in their movement. Because of the geometry of the lek and the positioning of our cameras (Fig. 1A), there appears to be a systematic centripetal bias in firefly displacement that is not merely an artifact of the imaging setup (fig. S3). Therefore, individual velocities $\vec{v}_i$ are inherently correlated, but we investigate whether they tend to be more correlated among individuals of the same subpopulation. We first look at alignment terms $\vec{u}_i \cdot \vec{u}_j$, where $\vec{u}_i = \vec{v}_i / |\vec{v}_i|$. We find no significant difference in the distribution of alignment terms among the chorus or the characters compared to the baseline across populations (Fig. 3D). Similarly, considering $\vec{u}_i \cdot \vec{s}_{ij}$, where $\vec{s}_{ij} = (\vec{r}_j - \vec{r}_i) / |\vec{r}_j - \vec{r}_i|$ is the separation vector between pairs of fireflies, we find no preferential attraction toward individuals of the same subpopulation. These findings, although perhaps unexpected, further suggest that spatial and temporal dynamics in natural chimeras need not be correlated.

DISCUSSION

Twenty years after chimera states were first noticed in mathematical models by Kuramoto and Battogtokh (*9*), we unearth the existence of comparable states of coexistence between phase-mismatched synchronous clusters in swarms of *P. frontalis* fireflies. Besides the spatially divided phenomenon of unihemispheric sleep (*20*–*22*), this may be one of the only known occurrences of chimera states in natural or animate systems. Unlike prior experimental realizations of chimeras in systems designed specifically for that purpose (*23*–*25*), firefly chimeras are spontaneous and self-organized. They presumably emerge thanks to a particular type of interactions between individuals and the underlying topology of their connectivity.

One caveat to consider, however, is that while the macroscopic realization is akin to a chimera state, the microscopic details of the natural swarm (as of any natural system) might slightly differ from those of an idealized theoretical model. In particular, fireflies present some degree of individual variability, and their interaction network may not be fully symmetric. We show nonetheless that chorus and characters all have the same periodicity (Fig. 2A), which is the variable of interest here, and that their spatial distribution suggests that their interactions are likely similar in their (time-averaged) structure. Therefore, there is arguably a solid rationale to include these synchronous fireflies into the broader concept of natural-world chimeras (*11*).

Using high-resolution, 3D reconstructions of the swarm, we show that these chimeras are persistent and that different synchronous groups are spatially intertwined, although slightly clustered. In the current state, our investigation is somewhat impeded by the fact that only a portion of the swarm can be observed, because of its spread, with fireflies constantly entering and exiting the field of view. Multicamera systems may be able to improve on this issue and reconstruct the entire lek. This would notably allow observing the bifurcation toward several phase-delayed clusters and further characterize the dynamics between subpopulations (e.g., whether individuals switch between groups).

What might the presence of chimera states in firefly swarms reveal about the network of their interactions? Initially, chimeras were believed to only emerge in systems with nonlocal interactions (*22*). More recently, they have been found in other connectivity structures, namely, global or local coupling (*26*). All-to-all coupling, where each individual interacts with all others, is evidently not a reasonable assumption in a sprawling group of fireflies with limited field of view. Purely local interactions, where each entity interacts with strictly nearest neighbors, typically require convoluted, delayed, and nonlinear types of interactions to result in fragmentation (*27*). Nonlocal interactions, designating weaker or less likely coupling at increasing distances, are the most adequate to produce chimeras (*11*). They also reflect a probable social structure in firefly swarms, as supported by simple considerations regarding the extent of line-of-sight

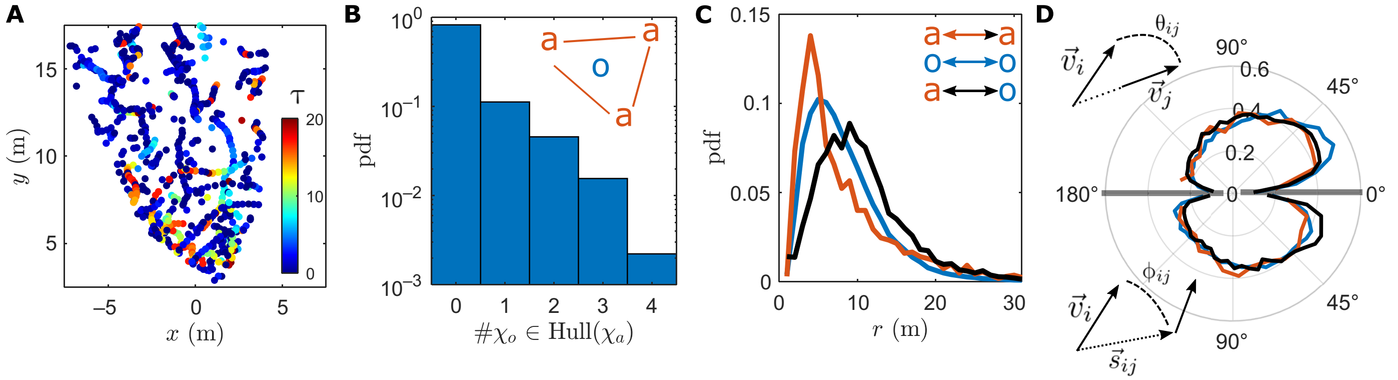

Fig. 3. Spatial organization and dynamics of chimeras. (**A**) Reconstructed top-down view of the swarm in a chimera state (2-min interval). Each dot represents a flash, with colors indicating the relative delay τ (in frames). Characters appear spatially intertwined with the chorus (dark blue). (**B**) Distribution of the number of chorus flashes occurring inside a convex hull of synchronized characters (when at least three). The proportion of $\#\chi_o \geq 1$ is about 20%. (**C**) Distribution of pairwise distances, among the chorus (blue), characters (orange), and between chorus and characters (black). (**D**) Top: Distribution of angles θ between two simultaneous flashers' instantaneous velocities, $\theta = \arccos \vec{\boldsymbol{u}}_i \cdot \vec{\boldsymbol{u}}_j$. Bottom: Distribution of angles ϕ between the velocity of flasher *i* and its direction toward a simultaneous flasher *j*, $\vec{\boldsymbol{s}}_{ij} = \vec{\boldsymbol{x}}_j - \vec{\boldsymbol{x}}_i$. Same colors as in (C).

interactions and prior results in a different synchronous species, *Photinus carolinus* (*18*).

Reciprocally, spatiotemporal patterns of real-world chimeras may be able to inform and instigate new theoretical paradigms. In particular, current chimera-generating models traditionally involve continuous coupling and a static network of interactions, two assumptions that are evidently at odds with the reality of firefly swarms. Even more perplexing, perhaps, fireflies presumably use cognition in their interactions with each other, a process substantially more complex than the typical functional relations that link abstract oscillators. Natural chimeras, while certainly not malicious, may have de facto opened up a Pandora's box of intriguing new problems for mathematicians to consider.

MATERIALS AND METHODS

Field recordings

Field experiments took place at Congaree National Park, SC, USA between 15 and 30 May 2021 (permit #CONG-2021-SCI-0002). As previously described (*18*), we used two Sony α7R4 cameras mounted with a wide-angle objective and recording at maximum ISO (32,000) at 60 frames per second. The cameras were about 4 m apart, situated and oriented in the same way every night to a very good approximation. Recording started at 8:38 p.m. Eastern Daylight Time (EDT) every night.

Movie processing

Each night, relative camera pose was estimated from 10 to 15 pairs of images of a checkerboard poster (25-cm squares) using MATLAB's stereoCameraCalibrator interface, which returned the fundamental matrix for the bifocal system. Frame matching was obtained from the cross-correlation of time series of *N*. Flashes were detected in each frame by intensity thresholding after adaptive background subtraction. 3D reconstruction of the swarm was performed as described previously (*15*, *18*). Briefly, flash planar coordinates in complementary frames were matched on the basis of the distance to their reciprocal epipoles and resolved through an assignment problem solver. The 3D location of flashes was subsequently obtained by triangulation of the complementary coordinates based on prior estimation of the fundamental matrix (MATLAB's triangulate function).

Chorus flashes

The times of the swarm's main beat were computed from the local maxima in the time series. To account for flash persistence, the chorus was defined as all flashes mutually overlapping with beat times (i.e., connected components). The characters were defined as the complementary set (all other flashers).

Trajectories

Thanks to the low density of active fireflies and the short displacements between flashes from the same individual, trajectories were simply obtained from a distance-based linkage method: Two flashes detected within both a time span of 1 s and a distance of 1 m from one another were connected as belonging to the same trajectory. Reconstructed trajectories appear visually consistent with those captured with infrared binoculars (movie S1). Individual "instantaneous" velocities $\vec{\boldsymbol{v}}_i$. are simply defined as the displacement between two successive flashes within the same trajectory, divided by the time interval between them: $\vec{\boldsymbol{v}}_i = (\vec{\boldsymbol{r}}_i(t_{k+1}) - \vec{\boldsymbol{r}}_i(t_k))/(t_{k+1} - t_k)$

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at https://science.org/doi/10.1126/sciadv.add6690

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