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A new chapter in the physics of firefly swarms

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Orit Peleg describes how a blend of models and experiments are revealing new insights about the intricate physics of firefly swarms.

In some species of firefly, males take flight and synchronize their radiant displays, turning the night sky into a captivating spectacle[1–4]. At the heart of these glowing sequences is a courtship ritual: as these males hover, they emit a species-specific on–off light pattern, signalling to stationary females below (Fig. 1a). Females show a preference for males that produce an 'optimal' light pattern, as judged from the standpoint of that species. Upon a female's responsive flash that aligns with his species, a male firefly might further engage, continuing their bioluminescent conversation until they meet.

However, thousands of fireflies flashing within a swarm can create visual clutter that makes it difficult to find potential mates. The clutter is exacerbated by the presence of multiple species emitting different patterns. This visual cacophony mirrors the 'cocktail party problem' in neuroscience, where one attempts to hone in on specific auditory inputs amidst background noise. Synchronization among males of the same species flashing in unison is an effective way to maximize signal-to-noise ratios and simplify the signal detection process.

The phenomenon of firefly synchronization has catalysed numerous mathematical frameworks, most notably the Kuramoto model, alongside its variants and applications[1]. To rigorously test such mathematical models of synchronization, more intricate data detailing firefly flashing patterns, both spatially and temporally, are essential. With the advent of advanced field recording techniques, there has been a renewed interest in the physics of firefly swarms. To understand the new data, there is a growing need for, and expansion of, more tailored and context-specific mathematical models of firefly and firefly-like synchronization.

Historical overview

Although fireflies have a widespread geographical distribution, species that exhibit synchrony are less common. Historically, scientists examining accounts of synchronized firefly behaviours were often sceptical, attributing perceived synchrony to optical illusions, observational biases or even inadvertent synchronization due to external factors such as wind[1]. The rarity and intricate nature of these displays intensified this scepticism. Though the phenomenon was conclusively documented in Thailand in 1968, it remained unrecorded in the western hemisphere until the latter part of the twentieth century. However, research in recent decades has ascertained that the occurrence of synchronous fireflies is greater than previously acknowledged. Presently, North America is known to host three such synchronous species, and further discoveries remain a possibility.

The best-known model for firefly synchronization is the Kuramoto model, first introduced by physicist Yoshiki Kuramoto in the 1970s. This model characterizes the anticipated behaviour of a large ensemble of coupled oscillators — entities that transition between two states, analogous to the fireflies' 'on' and 'off' luminescence (Fig. 1b). This model operates on various assumptions, addressing how the oscillators are coupled, how similar their frequency is, how far oscillators are from each other in space, and so on. Whereas this set of models was aligned with empirical data in fields such as solid-state physics and neuroscience, only recently have behavioural observations of fireflies provided sufficient data for comparable analysis.

New observations

The synchronized displays of *Photinus carolinus* fireflies have been documented in recent years using stereoscopic cameras[3,4], which allow for the capture of 3D images to precisely depict spatial arrangements. It is noteworthy that this species exhibits discrete synchronization, manifesting in a distinct burst structure. Males of this species engage in synchronized flashing every $T_f \simeq 0.5$ s, creating bursts that last for several seconds. Following this, they pause collectively, plunging their environment into darkness. These flash bursts occur periodically every $T_b \simeq 12$–14 s. This first-ever 3D reconstruction of flashes within a firefly swarm revealed layers of complexity beneath the surface (Fig. 1c).

Observations in natural environments with varying firefly densities yield distinct patterns (Fig. 1c). At lower densities, flashes are largely uncorrelated, with a signature of a Poisson process. At higher densities, synchronous flashes occur within periodic bursts. 3D reconstructions show that these flash bursts initiate at specific points and then propagate throughout the swarm in a relay-like manner[3]. Flash occurrences are correlated over several metres, indicating interactions possibly facilitated by a dynamic network of visual connections influenced by visual occlusion from terrain and vegetation. In controlled settings with regulated firefly numbers[4], results indicate that even small groups of interacting males synchronize their flashes within a burst (on a time scale of T_f), but periodic flash bursts are observed only in groups with more than 15 males (on a time scale of T_b).

Further analysis of the data reveals trajectories of individual fireflies, offering insights into their specific roles within the swarm and the potential of information storage via movement patterns. Notably, fireflies that flash early within a collective burst exhibit increased mobility and elongated flash durations relative to subsequent fireflies, suggesting a nuanced communication system beyond simple temporal synchronization[3].

Within these firefly swarms lies another revelation: the manifestation of chimaera states. Traditional understanding posited that densely connected oscillators, analogous to fireflies in dense swarms, would gravitate towards synchronization. However, more recent research on coupled oscillators revealed the possibility of chimaera states[1]. In these scenarios, synchronous and asynchronous clusters coexist within a larger, ostensibly synchronized system. While these states

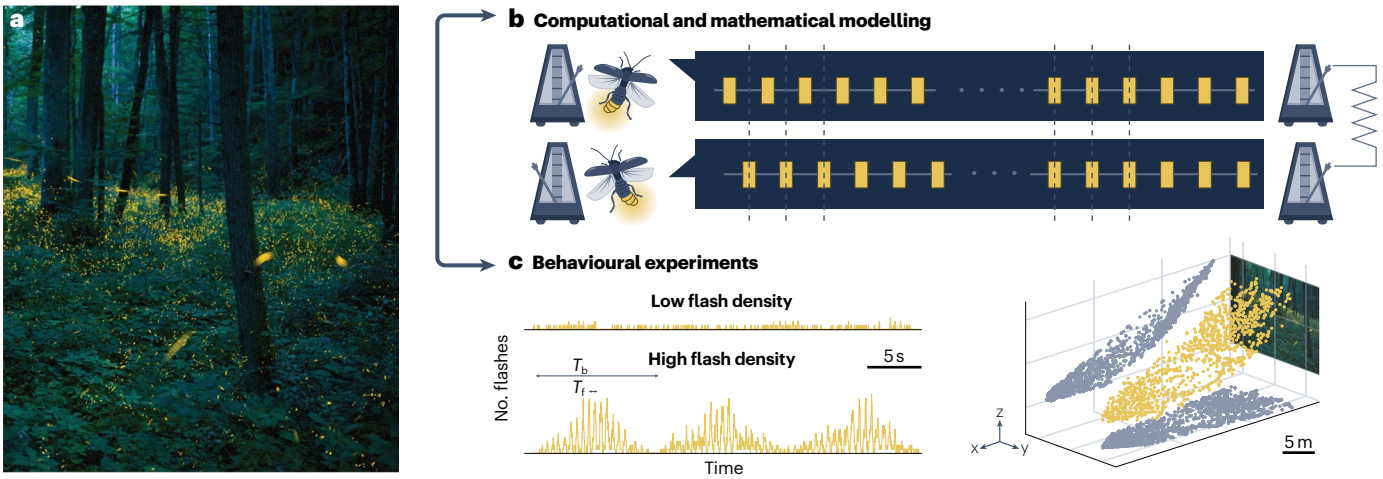

Fig. 1 | Physics of firefly synchronization through models and experiments. **a**, Synchronous fireflies (*Photinus carolinus*) illuminate the lush forests of the Great Smoky Mountains National Park, Tennesse, USA. **b**, Fireflies are depicted as coupled oscillators to model their synchronized flashing patterns. **c**, Behavioural experiments with *P. carolinus* synchronous fireflies[3,4] yield temporal data (left) highlighting the sequence and timing of flashes, and spatial data (right) illustrating the distribution and positioning of fireflies during synchronized displays. T_f is the time between the start of consecutive flashes, and T_b is the time between the start of consecutive bursts. Part **a**, Nature Picture Library/Alamy Stock Photo. Part **b**, TEDx. Part **c**, adapted with permission from ref. 3, AAAS.

had been theorized and observed in controlled experimental environments, empirical evidence from natural settings remained elusive. This gap was bridged by studies on *Photuris frontalis* fireflies[2]. Unlike the *P. carolinus* fireflies, which exhibit synchronization in a burst pattern, groups of *P. frontalis* fireflies demonstrate continuous synchronization without characteristic bursts. While the swarm appeared cohesive, many homogeneously distributed fireflies flashed with noticeable temporal offsets, confirming the existence and stability of chimaera states.

A burst of new models

The complexities of the observations above highlight an increasing need for refined, context-specific mathematical models of firefly synchronization. One study[5] modelled firefly synchronization as a system of pulse-coupled oscillators (the oscillators are coupled only during a flash and do not interact when the flash is off) while enabling excitatory and inhibitory interactions. This model qualitatively produces the collective synchronization of *P. carolinus*, and has been used to quantify the importance of the initial conditions in reaching synchronization and the time required to do so. In another study[6], the dynamics of *P. carolinus* flash displays were modelled using an elliptic burster, a slow–fast dynamical system producing a repeating pattern of multiple flashes followed by a quiet period, with added noise terms to capture the behavioural variability of individual fireflies. With a small amount of noise, the temporal oscillation of fireflies was irregular, but interaction through flashes induced more periodic behaviour, aligning qualitatively with experimental findings. By distributing fireflies in a 2D spatial domain with varying interaction ranges, diverse spatiotemporal patterns, including ripples and spirals, were observed, qualitatively reflective of observed real-world behaviours. Transitioning from qualitative to quantitative model–experiment comparisons, a modified integrate-and-fire model has been used to represent *P. carolinus*[7]. In this model, individual fireflies display random flash patterns drawn from an empirically obtained distribution. After each flash event, values were reset, resulting in the emergent rhythmicity and synchronization observed within the group empirically. The experimentally measured inter-burst (T_b) distributions were in quantitative agreement with the distributions predicted by the model, accommodating varying numbers of fireflies in the group.

Extending to broader firefly-like synchronization phenomena, model systems with multiplicative interactions between two parent shot-noise processes have been explored[8], drawing parallels to neural networks. This model shows that edge plasticity influences connectivity in networks of pulsing agents, ensuring both efficient learning and stable edge strength distribution. Transitioning from motile agents to mobile ones, swarmalators have been developed as mobile agents with intertwined phase and spatial degrees of freedom[9], allowing them to synchronize and swarm. Owing to the inherent coupling of their phase, often modelled using the Kuramoto model, and spatial dynamics (such as phase similarity leading to spatial attraction), swarmalators exhibit rich spatiotemporal patterns. These patterns persist across varied conditions (including different spatial motions and natural frequencies), are resilient to interaction noise, and might manifest in both natural and technological systems.

Challenges and future directions

As the field of the physics of firefly synchronization advances, both opportunities and challenges continuously emerge. One approach to bridge the experiment–model gap involves experiments in which fireflies interact with LED mimics. This technique allows for the design of interspecies and intraspecies mating calls in real-time based on observed firefly behaviour. Such quantitative behavioural assays could pave the way for delivering specific stimuli tailored to test underlying hypotheses. However, the transient nature of firefly displays, existing predominantly as flashing adults for only a few weeks annually, presents a challenge for data collection. Although there are now abundant data on well-established synchronous firefly species, a richer understanding necessitates insights into less well-documented species. To address these challenges, some research strategies are converging on integrating crowdsourcing with advanced machine-learning techniques to enhance data collection and analysis[10].

These comprehensive data could deepen our understanding of the physics of firefly synchronization and support conservation initiatives, especially as numerous firefly species confront environmental challenges. Given that synchronization is central to their mating displays, preserving this phenomenon is crucial to mitigate the threats to firefly populations and ensure the survival of the species. As the field continues to advance, it is plausible that the intertwining of in-depth understanding and conservation principles will gain more prominence, enabling the development of informed and targeted conservation interventions, such as habitat preservation efforts, policy advocacy, and community-based conservation initiatives. Ultimately,

the delicate equilibrium between scientific inquiry and ecological commitment could very well influence the trajectory of future research in this intriguing domain.

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Competing interests

The author declares no competing interests.