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THE ROYAL SOCIETY

Statistical analysis reveals the onset of synchrony in sparse swarms of *Photinus* knulli fireflies

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Flash synchrony within firefly swarms is an elegant but elusive manifestation of collective animal behaviour. It has been observed, and sometimes demonstrated, in a few populations across the world, but exactly which species are capable of large-scale synchronization remains unclear, especially for low-density swarms. The underlying question which we address here is: how does one qualify a collective flashing display as synchronous, given that the only information available is the time and location of flashes? We propose different statistical approaches and apply them to high-resolution stereoscopic video recordings of the collective flashing of Photinus knulli fireflies, hence establishing the occurrence of synchrony in this species. These results substantiate detailed visual observations published in the early 1980s and made at the same experimental site: Peña Blanca Canyon, Coronado National Forest, AZ, USA. We also remark that P. knulli's collective flashing patterns mirror those observed in Photinus carolinus fireflies in the Eastern USA, consisting of synchronous flashes in periodic bursts with rapid accretion and quick decay.

1. Introduction

Many animal species are capable of, and benefit from, behaving collectively, from insects forming rigid aggregates, such as ants and bees, to large mammals migrating as herds over thousands of kilometres. Although in some cases the emergence of collective dynamics is intuitively evident, for example in collective turns of flocking birds or swirling schools of fish, in other instances characterizing the ensemble structure or dynamics as collective requires a much finer analysis than simple visual observations. This is the case, for example, in disorganized midge swarms [1]. In fact, despite a growing interest for large-scale patterns in animal groups, a clear definition of which behaviour qualifies as collective is still lacking [2].

To address this broad and complex question, it may be easier to start with a simple subset of collective behaviour: synchrony. Animal synchronization manifests itself in many different ways and across various time scales [3], and it is certainly a signature of how social interactions produce system-wide patterns. An inspiring and readily accessible example of biological synchrony is seen sometimes on summer nights in firefly swarms, when most flashes occur at specific instants.

Firefly flashing is primarily a courtship dialogue. In some species, advertising males flash in unison while females respond independently. Initially observed in Southeast Asia, synchronous fireflies were first reported in North America in the 1910s [4]. Observations were rare and sporadic, and often

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