Mechanisms of Transition from Discrete to Continuous Synchronization in Firefly Swarms

by

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The final copy of this thesis has been examined by the signatories, and we find that both the content and the form meet acceptable presentation standards of scholarly work in the above mentioned discipline.

Ranjan, Anurag (Bachelors of Arts in Physics)

Mechanisms of Transition from Discrete to Continuous Synchronization in Firefly Swarms

Directed by Prof. Orit Peleg
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Abstract

Many biological systems tend to display self-organization; one such system is swarms of fireflies. Self-organization for systems of fireflies is manifested as synchronization of the flashes in a melody of light. As the volume of data amassed has increased, our observations indicate that conventional modeling approaches are inadequate for accurately representing them. A different method of studying these models has arisen: Agent-Based Modeling. This thesis aims to study one emergent phenomenon of fireflies using this method, that of the transition from discrete to continuous synchronization. By using this Agent-Based Model, we show that the transition from discrete to continuous synchronization should occur around seven flashes per burst. Furthermore, we validate this model by using observational data from firefly species that display discrete synchronization and a species that displays continuous synchronization.

Dedication

This thesis is dedicated to my mom and dad.

Acknowledgements

I would like to thank my advisor Professor Orit Peleg for giving me the opportunity to join her lab and work on this project. Her valuable advice over the past year has been invaluable to the completion of this project as well as my understanding of computational modeling of biological systems. She has always been invested in my success and I could not have imagined a better advisor.

I would also like to thank my thesis committee members: Professor Nuris Figueroa Morales and Professor Michael Ritzwoller for taking their time for my thesis. Next, I must thank Owen Martin for his availability in answering my questions as well as providing critical data needed for this project.

Finally, I would like to extend my gratitude towards my family and friends for their unconditional support for me throughout this process. They really made the last four years enjoyable for me.

Contents

Chapter

Chapter 1

Introduction

1.1 Self-Organization in Biological Systems

The complex patterns arising from interacting parts have long fascinated scientists. The phenomena of individual parts coming together to create something bigger can be seen everywhere, from gears in a clock, members of a music band, coupled metronomes, to buyers and sellers in a market [1, 3, 6, 18]. One such area of interest for observing these collective patterns is in the case of biological systems. These systems consist of individuals of the same species interacting visually, chemically, or mechanically to create groups that can help the individuals survive better in their environment.

Biological systems tend to self-organize, altering individual behavior to better fit in the group, as a measure of survival and reproduction. Some examples include a school of fish coordinating movement [14] (Fig. 1.1A), cells forming tissues [10] (Fig. 1.1B), or termites forming mounds [11] (Fig. 1.1C). A key characteristic of these systems is that their collective behavior is not commanded by central controls (an example would be a corporation whose board/CEO may decide the direction or blueprints with roles for individuals). There are many definitions of self-organization, but one such is “self-organization is a process in which patterns at the global level emerge solely from numerous interactions among the lower-level components of the system. Moreover, the rules specifying interactions among the system’s components are executed using only local information, without reference to the global pattern” [4]. Using this definition, we see that self-organization in biological systems is not innate to them; instead, it emerges from groups. Thus, to truly model these systems, we must not just consider isolated individuals but rather how they interact with the rest of the group.

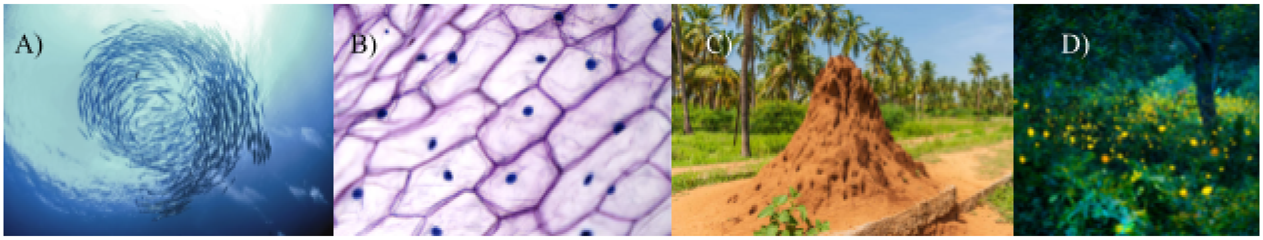


Figure 1.1: Examples of biological systems exhibiting self-organization. A) A school of great barracuda (Sphyraena barracuda) fish. B) Onion epidermis with large cells under light microscope. Each cell has a wall, membrane, cytoplasm, nucleus and large vacuole. C) Termite Mound. D) Fireflies flashing and flying in the bush at night at Prachinburi, Thailand. Photo & Caption credit: iStock (A), E. Haggart (B), PeterHermesFurian (C) , Chandrasekhar Velayudhan (D) WUT789

1.2 Fireflies as Self-Organizing Systems

One such biological system that exhibits self-organization is swarms of fireflies (Fig. 1.1D). Lampyridae, known as fireflies, are a family of beetles with about 2,200 species [7]. Firefly species are widespread globally; however, not all of them exhibit flashing as adults, and not all species synchronize. In the past, researchers believed that synchronization of firefly swarming was due to optical illusions, biases, or external factors [20]. Eventually, there was verifiable documentation of this behavior, first in 1968 in Thailand and then later in the West.

Self-organization in the context of fireflies occurs when individuals change their flash patterns to better sync with their neighbors [7]. The reason why fireflies may want to synchronize with the group is for better chances of reproduction. In general, both male and female fireflies flash [20]. If the flash of the male is different from the rest of the group, its mating success may decrease significantly. This provides an incentive for individuals to conform to group behavior.

The act of individuals synchronizing with their neighbors creates collective swarm flash behaviors. Two such swarm patterns are discrete synchronization and continuous synchronization. Continuous synchronization is characterized by no distinctive breaks between collective flashes (Fig. 1.2A), while discrete synchronization is characterized by breaks in collective flashes where light is not emitted (Fig. 1.2B).

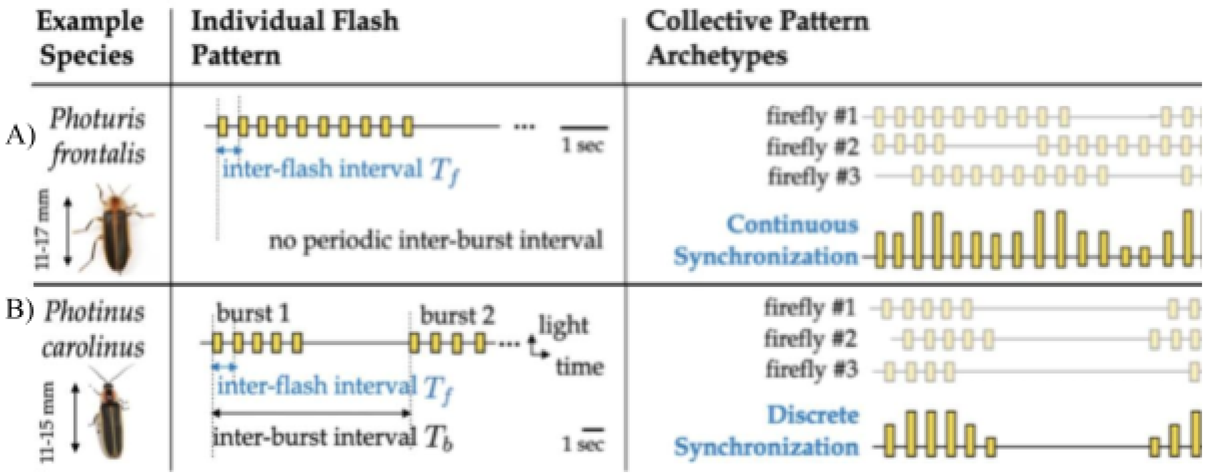


Figure 1.2: Example of two species of Fireflies. Individuals flash pattern and collective flash pattern shown. A) Photuris Frontalis, species displays continuous synchronization in swarms B) Photinus

Carolinus, with periodic inter-burst interval for individuals, displays discrete synchronization in swarms.

1.3 Modeling Fireflies

Firefly synchronization has been a long standing interest in the fields of nonlinear dynamics and synchronized systems. This has led to the development of different methods of modeling collective behavior of fireflies. One such method is to model them as coupled oscillators [19]. This method is similar to the classical mechanics approach to modeling coupled systems such as pendulums (Fig. 1.3A) or masses attached to springs (Fig. 1.3B). Changes have to be considered to the classical mechanics approach to solving these systems as they display much more complexity. Oftentimes, synchronization in biological systems consists of many more oscillators and the method of coupling can be expressed in different ways such as visual, chemical, or hydrodynamical.

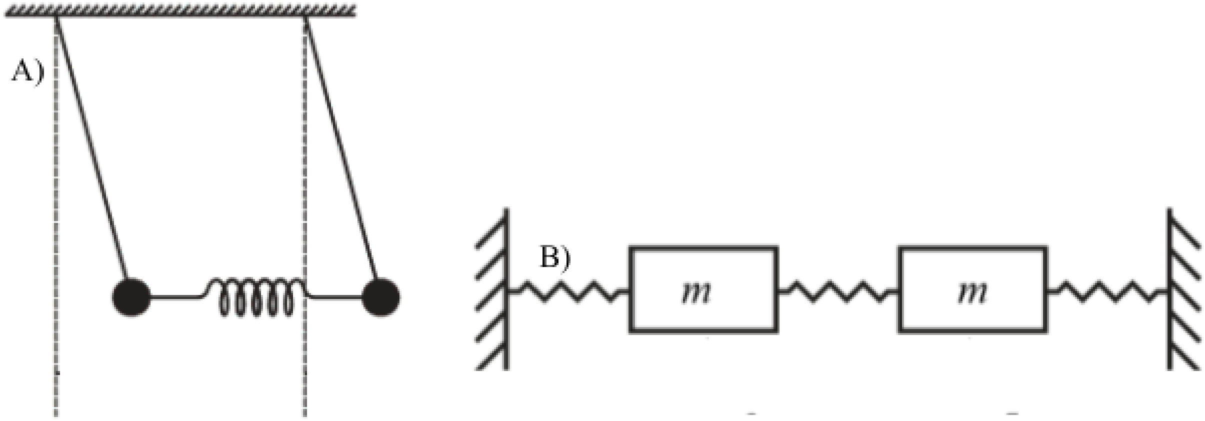


Figure 1.3: Two Examples of Coupled Oscillators. A) Two pendulums connected via a spring, B) Two masses connected to each other and the wall via springs. Photo credit: John Taylor, *Classical Mechanics*

1.3.1 Kuramoto Model

One method used to model more complex coupled oscillator systems is by employing the Kuramoto model. This model, first proposed by Yoshiki Kuramoto, a Japanese physicist, explains how systems with many oscillators behave. It has become instrumental in studying synchronization in neural networks, Josephson junctions, and chemical oscillators [2].

The Kuramoto model consists of N coupled phase oscillators $\boldsymbol{\theta}_i(t)$, where a phase oscillator is defined as a simple oscillator with periodic solutions, such as a metronome. Each oscillator has a natural frequency ω_i. The coupling constant (K_{ij}) attempts to synchronize oscillators to each other while they try to oscillate at their own frequency. The dynamics of this system are governed by

$$\frac{d\theta_i}{dt} = \omega_i + \sum_{j=1}^{N} K_{ij} sin(\theta_j - \theta_i),\ i = 1, . . . , N \qquad \text{(Eq. 1)}$$

This model has also had success in describing some species of fireflies such as *Pteroptyx malaccae* [13], where individuals fire regularly but with different periods. However, these models fail to describe systems in which individual inter-burst intervals are not periodic, e.g. the Photuris Frontalis or Photinus Carolinus firefly species (Fig 1.4) [15]. Thus, when applying the Kuramoto model to such systems, they are unable to converge to a well-defined interflash period as a function of N, the number of fireflies. To address this, a different method of modeling these systems must be used.

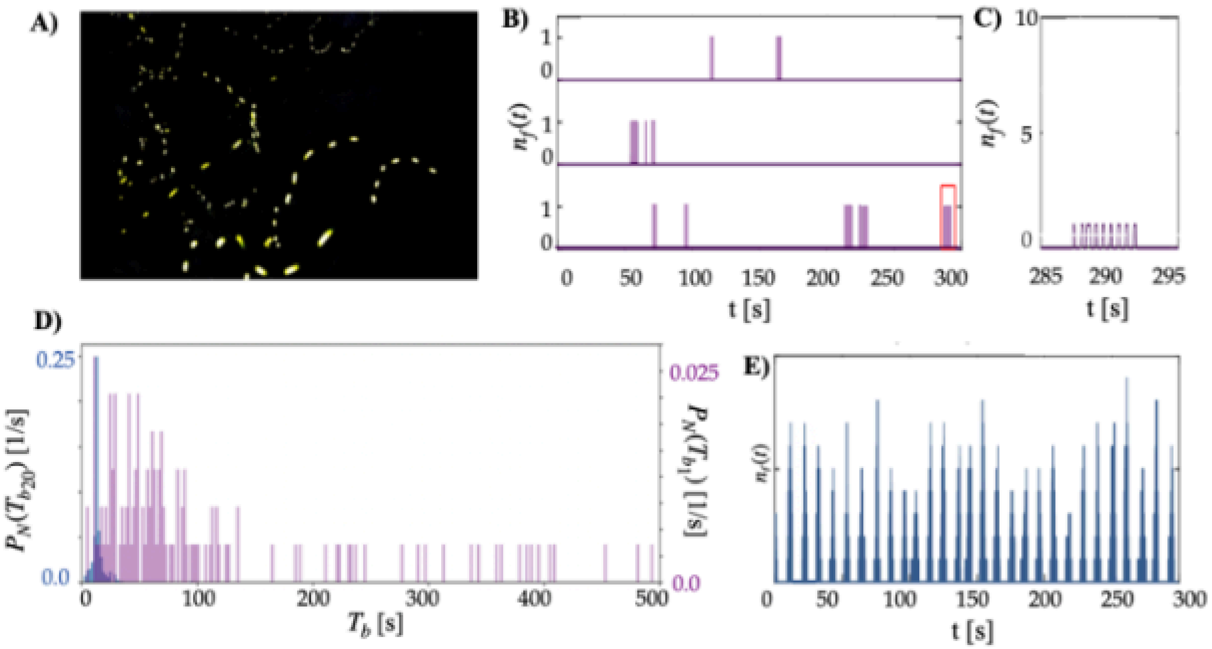


Figure 1.4: Experimentally collected data of *Photinus Carolinus*: (A) Long exposure photograph illustrating flashes in a *P. Carolinus* natural swarm. (B) Overlaid time series of three isolated individual fireflies emitting flash bursts which appear random. The inset (C) shows the burst-like nature of *P. Carolinus* flash events. (D) Interburst distributions b(t) for one firefly (purple) and twenty fireflies (blue) insulated from the rest of the swarm. (E) Twenty *P. Carolinus* fireflies flashing in a tent exhibiting the periodic nature of their collective flashing. Photo & Caption credits: [15].

To represent biological systems such as the one present in Fig. 1.4, it is important to create stochastic models that can mimic the random nature of individuals. These models must be able to converge onto experimentally obtained statistics.

1.3.2 Agent Based Modeling

Another approach to modeling synchronous systems is by using agent-based models (ABMs), which are primarily computational representations of how interactions between autonomous agents affect the whole system. There are numerous advantages to using ABMs as a method of studying systems with emergent phenomena such as firefly swarms. ABMs allow us to not have to pre-define emergent properties, such as synchronization. ABM representations are often more intuitive and easier to understand than mathematical models, as simulated individuals have to follow simple rules [21].

One of the most famous and earliest examples of an ABM is Conway's Game of Life, created by British mathematician John Horton Conway in 1970. This system consists of tiles that can either be alive (colored) or dead (gray), following four simple rules:

1) Any live cell with fewer than two neighbors dies (due to underpopulation).
2) Any live cell with two or three neighbors survives.
3) Any live cell with more than three neighbors dies (due to overpopulation).
4) Any dead cell with exactly three live neighbors becomes alive (due to reproduction).

These four simple rules give rise to very complex behavior, where a simple pattern (Fig 1.5A) can become very interesting geometrically (Fig 1.5b, Fig 1.5C).

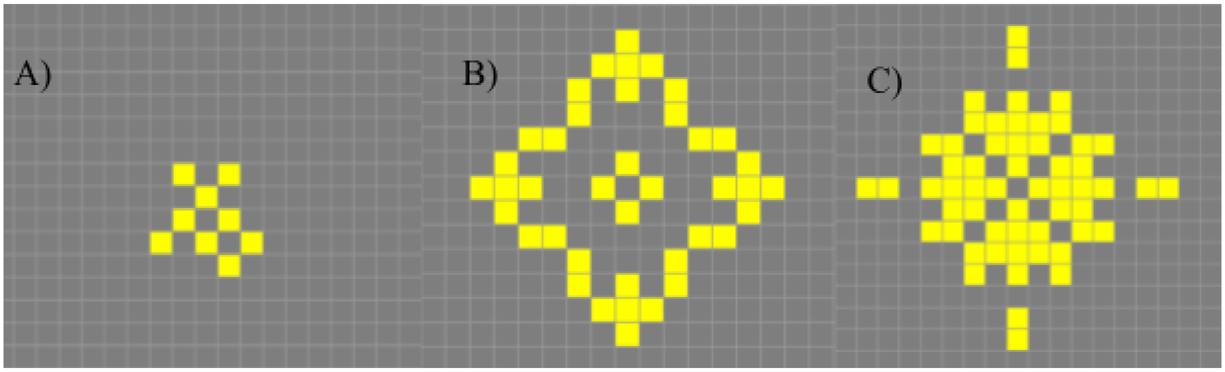


Figure 1.5: Example images of emergent patterns from random initial state and simple rules (Yellow means alive, Grey means dead). A) A random pattern of live cells. B) A flower pattern created after 10 generations, C) A pattern created after 12 generations.

The measurement and analysis of ABMs pose distinct challenges compared to Equation-Based Models (EBMs). These challenges arise due to the large number of inputs and outputs in the model. Even in simple models, such as one with 100 agents, each with 5 characteristics that can be true or false, there are 1024^{100} possible populations of individuals [9]. In more complicated models, a combinatorial explosion could occur, making it almost impossible to examine all scenarios [21]. To address these challenges, it is crucial to start with the simplest possible models and then increase complexity gradually.

The correctness of a model is also a source of concern, as the usefulness of the model depends on its accuracy. To ensure accuracy, the model must undergo evaluation through different modeling processes: validation, verification, and replication (Fig 1.6). Validation is the process of determining if the model corresponds to a real-world phenomenon [21]. Verification is the process of ensuring that the implemented model corresponds to the conceptual model. Replication is the process of other researchers using the model to answer their own questions. By undergoing these processes, the chances of "bugs" being present and impacting the results are significantly reduced [9].

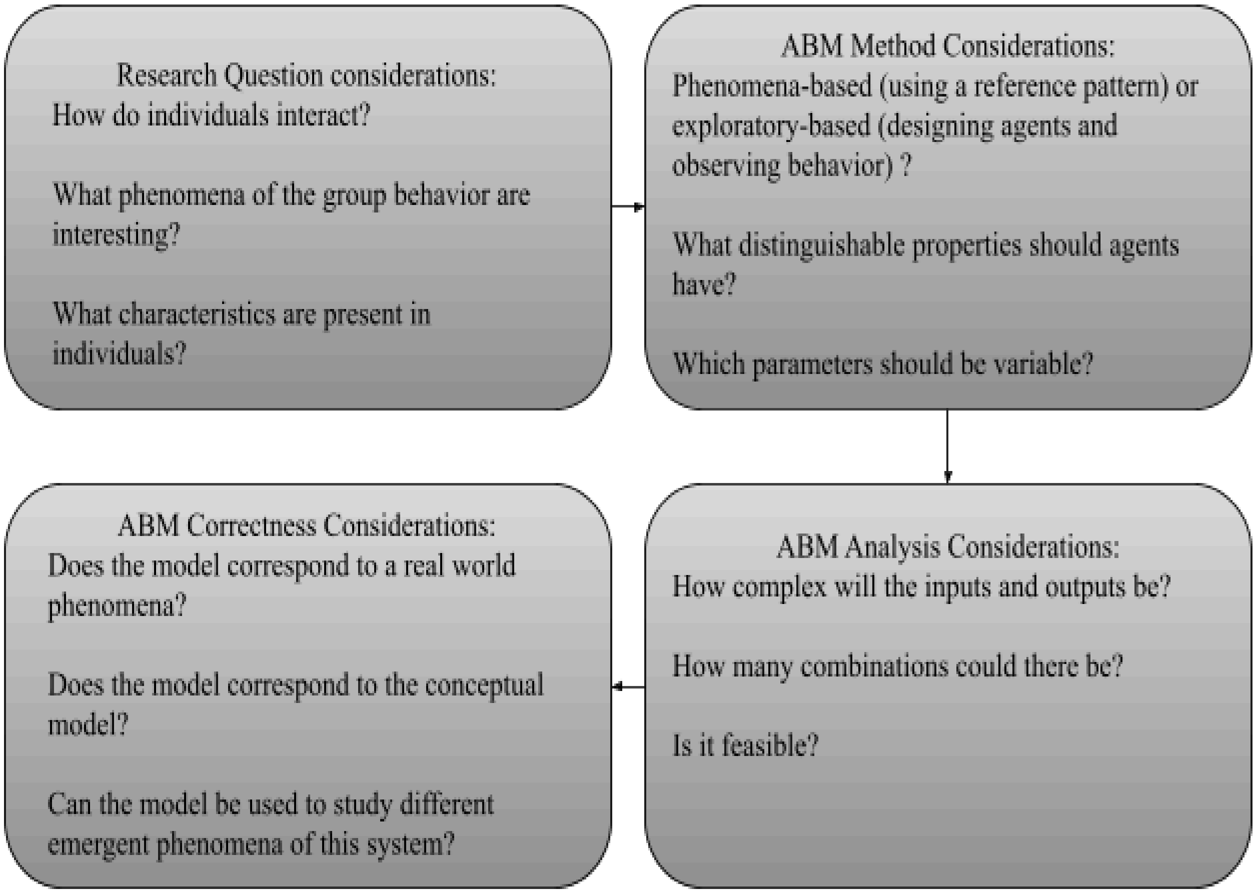


Figure 1.6: Flow chart of crucial questions to ask during the construction of an Agent based model. Starts at the Research question considerations and ends at correctness.

1.4 Literature Review of Modeling Fireflies

One firefly species of interest for modeling has been the *Photinus Carolinus*, this has been due to recent documentation of their synchronization patterns using stereoscopic cameras [16, 17]. The data has revealed that males synchronize in discrete bursts (Fig. 1.2B) every (T_f) 0.5s. The collective bursts occur periodically every (T_b) 12-14s. These studies have revealed that groups of fireflies may manifest chimera states. These are states consisting of a large number of oscillators and when sufficient coupling is present, group synchronization takes place.

These observations have led to a flurry of context-specific models of firefly synchronization [13]. One model represented firefly synchronization as consisting of a set of pulse-coupled oscillators [14]. These types of oscillators only couple during the flash and become uncoupled when not flashing. This study was able to qualitatively reproduce the group behavior of *P. carolinus*, and provides quantitative importance of initial conditions. Another model, represented firefly systems as elliptic bursters [21], a slow-fast system which produces repeating patterns of multiple flashes followed by periods of no flashes. This model also has some noise to recreate the stochastic nature of real fireflies. This model showed that at smaller noise, more periodic group behavior emerged.

One study gave quantitative results for modeling *P. carolinus* [15]. In this study, firefly behavior was drawn from experimental data to display flash patterns. They proposed a theoretical framework for modeling the observed *P. carolinus* behavior. Their formulation for the state of a was governed by the integrate-and-fire (IF) scheme equation

$$\frac{dVi}{dt} = \frac{1}{Tsi}\epsilon_i(t) - \frac{1}{Tdi}[1 - \epsilon_i(t)] + \epsilon_i(t)\sum_{i,j}^{N}\beta_{ij}\delta_{ij}[1 - \epsilon_j(t)] \ . \ \text{(Eq.2)}$$

The internal state of firefly i is characterized by V and ϵ, ϵ_i is a binary variable that is 1 when the individual is charging and 0 when it is flashing. ϵ_i turns to 0 when the firefly's voltage (V) is 1 and switches to 1 when the voltage is 0. T_{di} represents the flash length, obtained from observed data. T_{si} represents the end-to-start interflash interval calculated as $T_{si} = T_{bi} - T_{di}$ where T_{bi} is a variable drawn randomly from experimental distributions of interburst intervals. This variable introduces stochasticity into the model which makes Eq. 2 different from non-stochastic IF schemes. This model was able to recreate the observations of *P. carolinus* group behavior. In Fig. 1.7, we see as beta increases the systems collective period Tb tends to cluster and as the number of fireflies are increased the peak of Tb distribution dresses. With N = 20 fireflies and a beta value of 1.0, the group has a peak in the period distribution around 12s, which agrees with observed data.

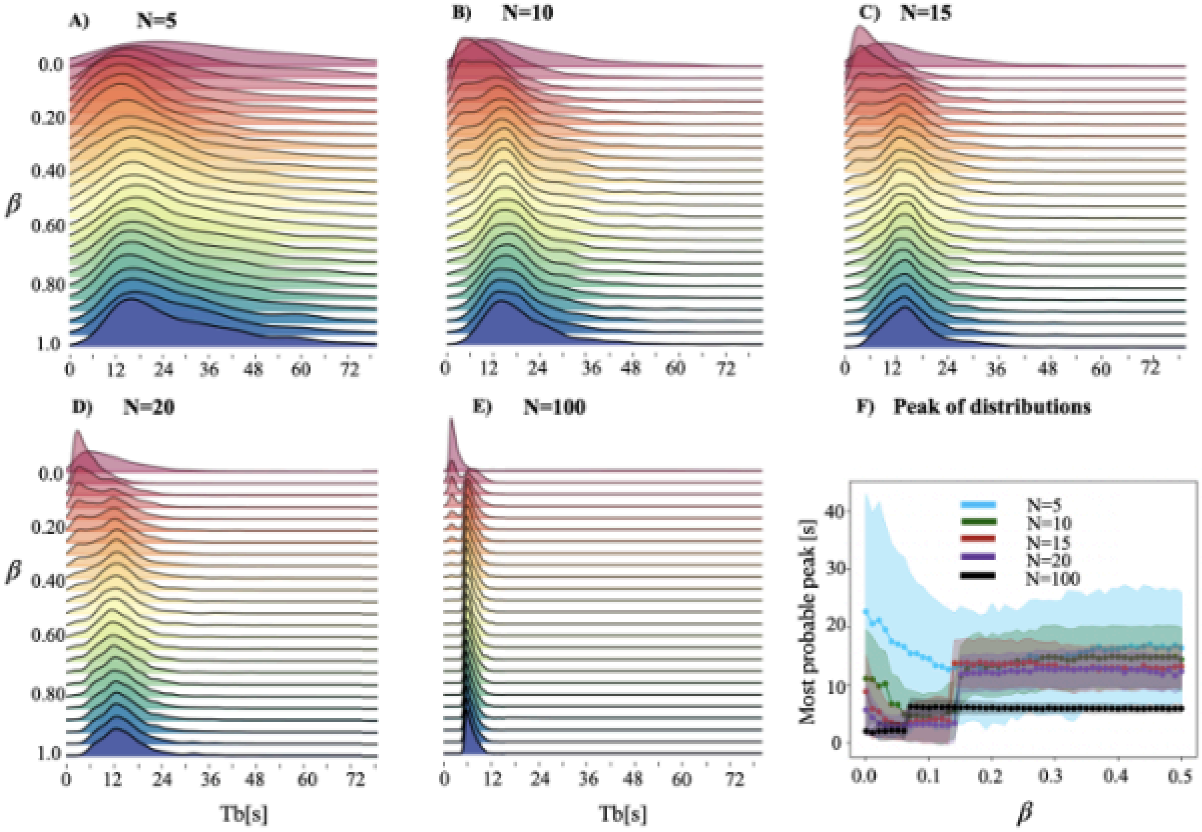


Figure 1.7: Results from IF model. (A-E) Visual demonstration of the emergence of a collective periodicity above T_{b0} as β ranges between 0-1 for different values of N, (E) shows N = 100, a value outside the scope of experimental observations but relevant for model validation. The lack of coupling in the first few rows produces noisy and cluttered collective interburst intervals as flashes from any individual are uncorrelated with those from its neighbors. As the coupling constant (β) increases, a consistent interburst interval emerges at the peak of each distribution. (F) The relationship between the most probable interburst

interval (the distribution peak) as β and N vary. The shaded regions represent the standard error of the distributions for each density. For small values of beta, the collective group produces noisy distributions where the pulsatile coupling of flashes is not quite enough to pull the starts of bursts into alignment. However, as the coupling constant β increases, individual flashes begin to trigger subsequent flashes in neighboring fireflies, causing the quiet periods of the individuals to line up and the emergence of a collective frequency at the fastest interval in each burst cycle. Each higher density simulated causes the peak of the distribution to both shift slightly downwards and become less variant, as it is progressively more likely for one individual in the swarm to drive the collective frequency towards intervals on the short end of the input distribution. Figure and caption credit: [15].

Chapter 2

Model

2.1 Formulation

The model used to run parameter sweeps and then test observational data is an integrate and fire (IF) scheme. There are two parts to IF schemes as suggested by the name. The integration component where an agent builds up information (voltage in our case) and once the threshold is met it fires (flashes in our case). Thus the equation is the standard equation for these schemes (Eq. 2) with some alterations. As this study is aimed towards understanding how the transition of discrete to continuous synchronization is the number of flashes in a burst (nf), β is kept at 1 to ensure sufficient coupling. δij, representing the connectivity between agents, is also kept at 1 as all fireflies should be coupled to each other since this model assumes that fireflies are close to each other. This simplifies Eq. 2 to

$$\frac{dVi(t)}{dt} = \frac{1}{T_{si}} \epsilon_i(t) - \frac{1}{T_{di}} [1 - \epsilon_i(t)] \qquad \text{Eq. 3}$$

For the parameter sweep T_{si}, is set for 5.0 s (end-to-start interval) and the flash length (T_{di}) is set to 0.1s. These values are chosen based on experimental observations collected [15]. In this way we keep with best practices of keeping ABM's as simple as possible. Eq. 3 with the T_s is used for parameter sweeps. But when looking at data from observational studies of *P. carolinus* and *P. frontalis*, the model uses values of T_{si} and T_{di}, from the means of observational data. This way a general understanding of these systems will be learned.

2.2 Algorithm Description

After we have determined the model for the internal state of each firefly, it is time to set up the ABM for our system. The aim of this study is to model the transition of synchronization, so we assume that this transition does not depend on the environment (e.g., obstacles in the vision path of fireflies). Therefore, for this model, only interactions between agents are simulated. Since it is crucial to keep the ABM as simple as possible to avoid overconsumption of computational resources, another assumption made is that except for the initial voltage of each agent, all other parameters are the same among all the agents. These parameters include nf, the number of flashes within a burst, Ts, the end-to-start interval between bursts of multiple flashes, and Td, the duration of each flash.

The model operates as follows: it simulates the behavior of an individual firefly's flash in a swarm of other fireflies. The main parameter varied for all simulations in this model was nf. Initially, each firefly's internal voltage level is decided randomly, and each firefly is set as charging. After this, the simulation starts and runs for all the steps. At each step, for each firefly, it detects if the current firefly is within a burst or not. Then, Eq. 3 is used to update the voltage value for the firefly. Following that, the effect of other fireflies on the voltage of the current firefly is determined. This process is then repeated for each firefly in the system.

Pseudocode for this algorithm is written below:

```
emergent_sync_w_bursts(nf, s)
```

```
Initialize variables:
    N = 20, Tf = 0.2, Td = 0.1, beta = 1.0, dt = 0.01, STEPS = 100000000,
    Initialize arrays: flashed_status, V, epsilon, flashes_left_in_current_burst, within_burst
Set initial conditions for fireflies:
    Generate random initial voltage and set charging status for each firefly
Main simulation loop:
    For each time step from 1 to STEPS:
        Update firefly dynamics based on their current state:
            - Calculate dV_ff_i based on charging or flashing condition
            - Update voltage V for each firefly

        Update flash status within bursts or charging based on conditions:
            - Update flash status and number of flashes left in current burst
            - Handle transitions between charging and flashing states
        Update flashed status array based on epsilon values
```

The flashed_status array monitors which fireflies have flashed in the current time step. Alongside, the V array denotes the voltage of each firefly at every time step, while epsilon distinguishes whether each firefly is charging (1) or flashing (0). Additionally, the flashes_left_in_current_burst array tracks the remaining flashes for each firefly within its current burst, while the within_burstarray specifies whether each firefly is currently within a burst or not.

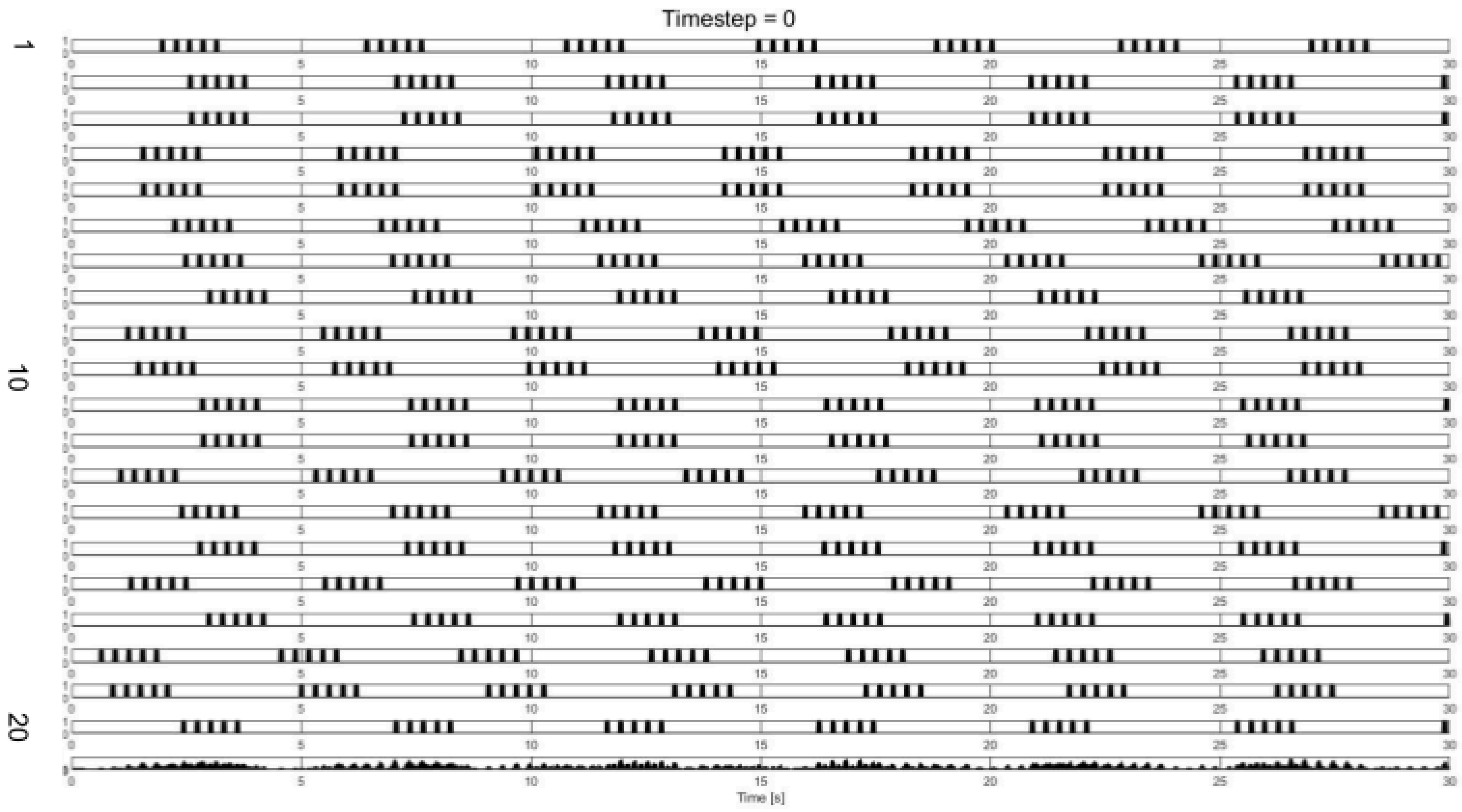
Chapter 3

Results

3.1 Parameter Sweeps

First, a qualitative exploration of the systems is undertaken. To this end, raster plots of different nf values and initial conditions are examined. One such raster plot is Fig. 3.1A, here the initial state of nf = 5 has some level of continuous synchronization, but at the end of the run the group behavior becomes discrete (Fig. 3.2A). This suggests that at an nf = 5 value, the system has not made the transition. The zoomed in plots are also shown for an individual firefly (Fig. 3.1B, 3.2B) and the summed values for all the systems.

A)



B)

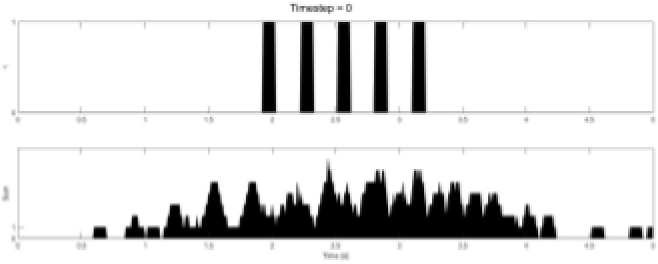
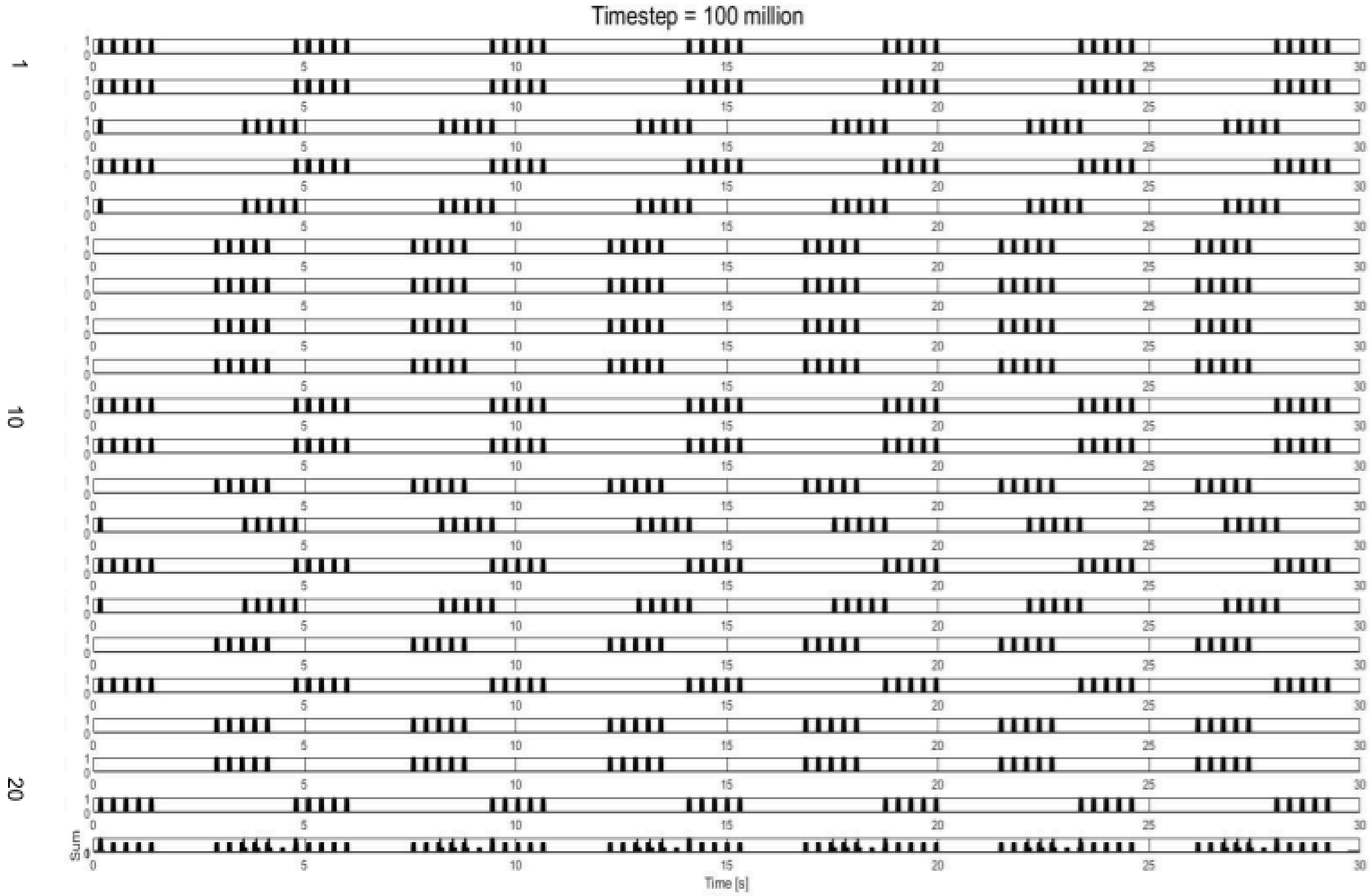


Figure 3.1: Raster Plots. A) Raster plot displaying flash patterns for individuals and the group. An example of a starting configuration of a simulation of 20 fireflies, representing the first 30s of the simulation. Each raster plot shows the number of flashes vs. time for individual fireflies (first 20 rows), and in the bottom "Sum" subplot, the collective flash pattern is illustrated. Each black vertical bar represents a flash. Input values: nf=5, $T_s = 5.0$ s (end-to-start interval), Td = 0.1s (Flash length). B) Zoomed in raster plot for individual and collective for the first 5 sec, bar width is flash length.

A)



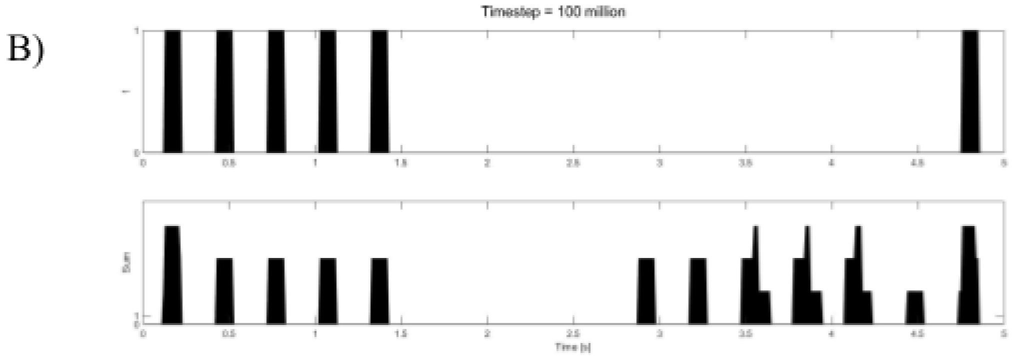


Figure 3.2: Raster Plots. A) Raster plot displaying flash patterns for individuals and the group. An example of a starting configuration of a simulation of 20 fireflies, representing the last 30s of the simulation. Each raster plot shows the number of flashes vs. time for individual fireflies (first 20 rows), and in the bottom "Sum" subplot, the collective flash pattern is illustrated. Each black vertical bar represents a flash. Input values: nf=5, T_s = 5.0 s (end-to-start interval), Td = 0.1s (Flash length). B) Zoomed in raster plot for individual and collective for the last 5 sec, bar width is flash length.

Different runs with the same nf value tend to have different initial and final flash patterns. This is due to them having different initial states (such as initial flash state), by running different random states we see that different initial states should converge to a similar type of synchronization. We see this in Fig. 3.3, 3.4 and 3.5 and 3.6, each set has different initial states yet they converge on to a discrete synchronization regime.

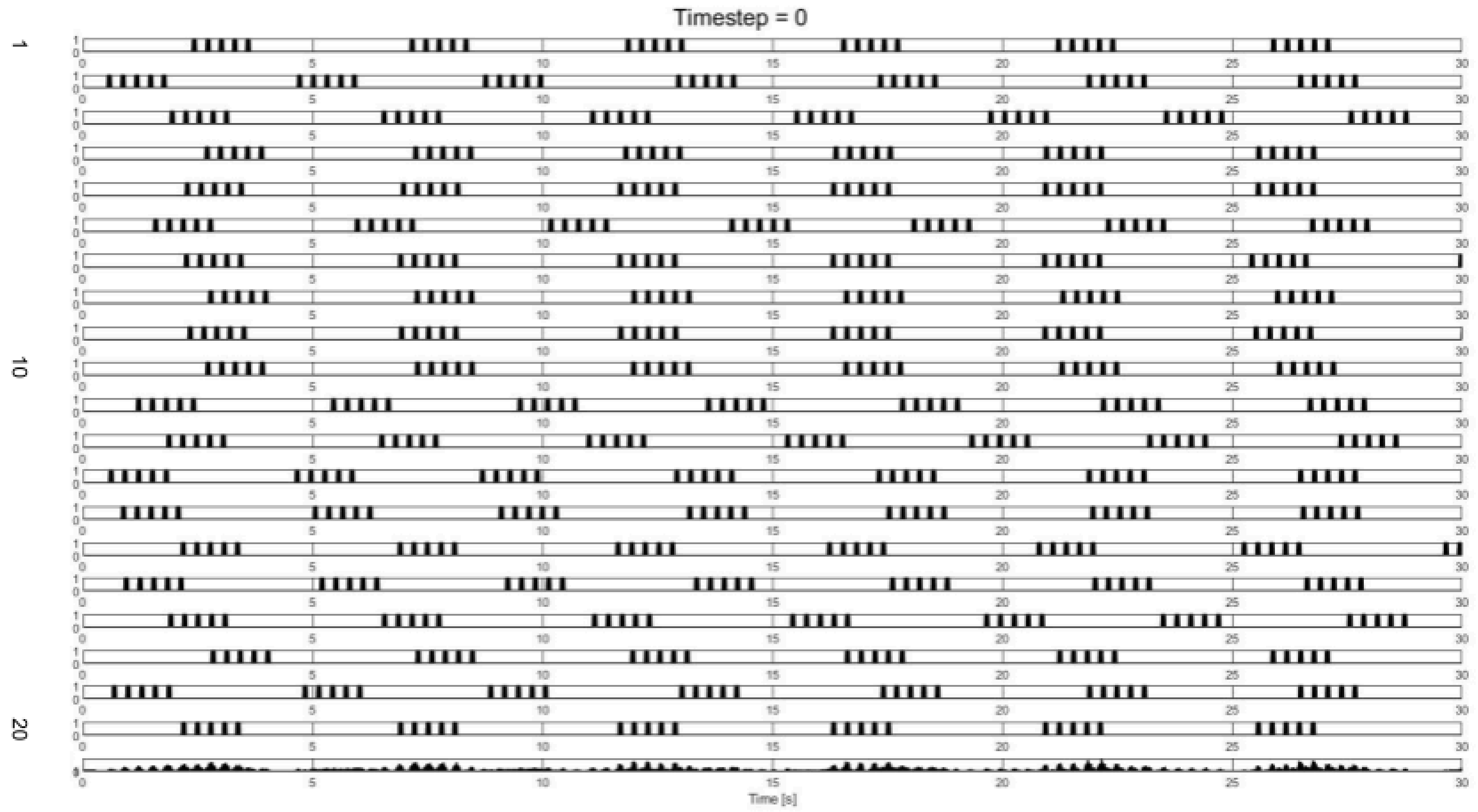
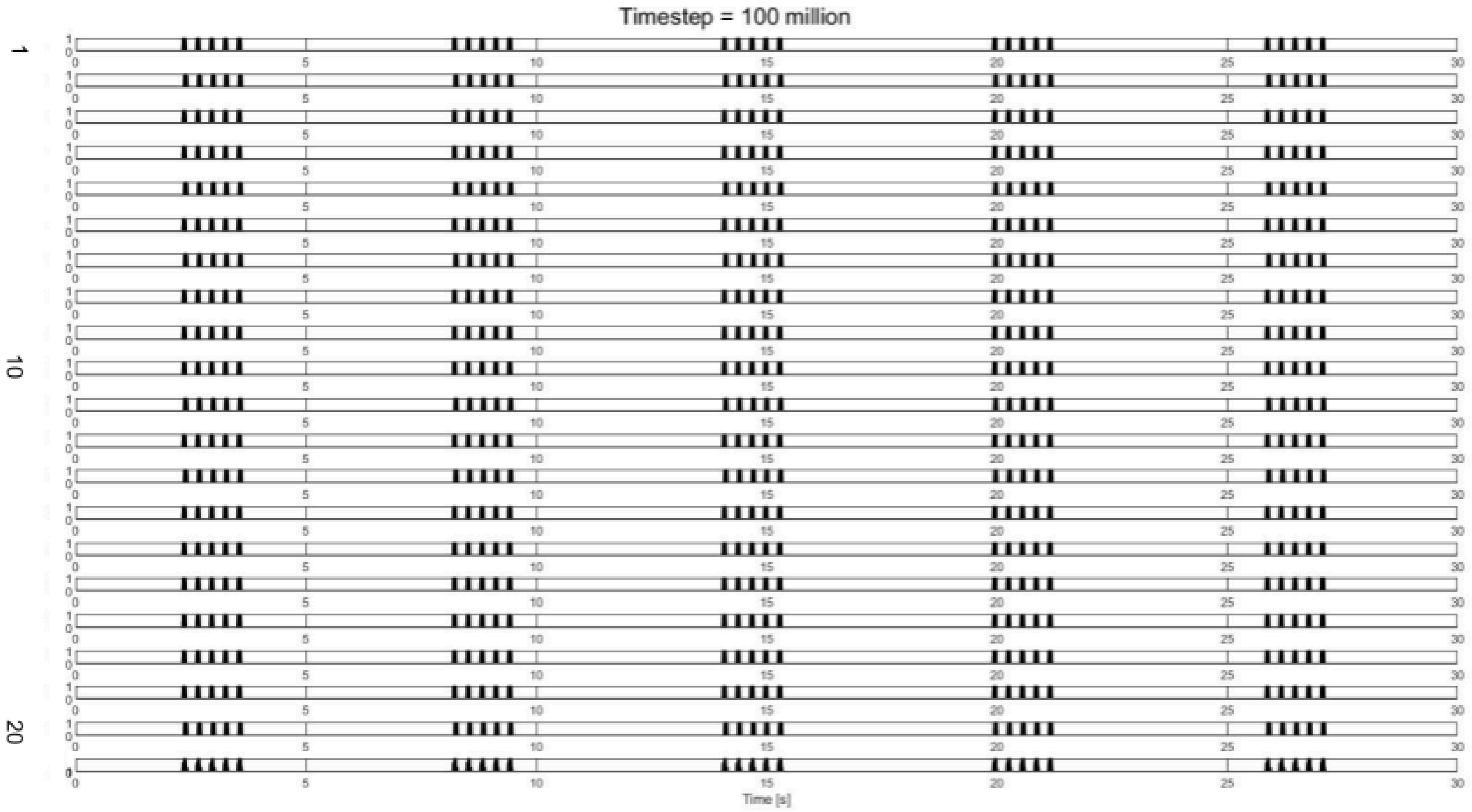

Timestep = 0
1
10
20
0
5
10
15
20
25
30
Time [s]

Figure 3.3: Raster plots. Display flash patterns for individuals and the group. An example of a starting configuration of a simulation of 20 fireflies (different initial state), representing the first 30s of the simulation. Each raster plot shows the number of flashes vs. time for individual fireflies (first 20 rows), and in the bottom “Sum” subplot, the collective flash pattern (summed) is illustrated. Each black vertical bar represents a flash. Input values: nf=5, Ts = 5.0 s (end-to-start interval), Td = 0.1s (Flash length).


Timestep = 100 million
1
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20
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0
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5
10
15
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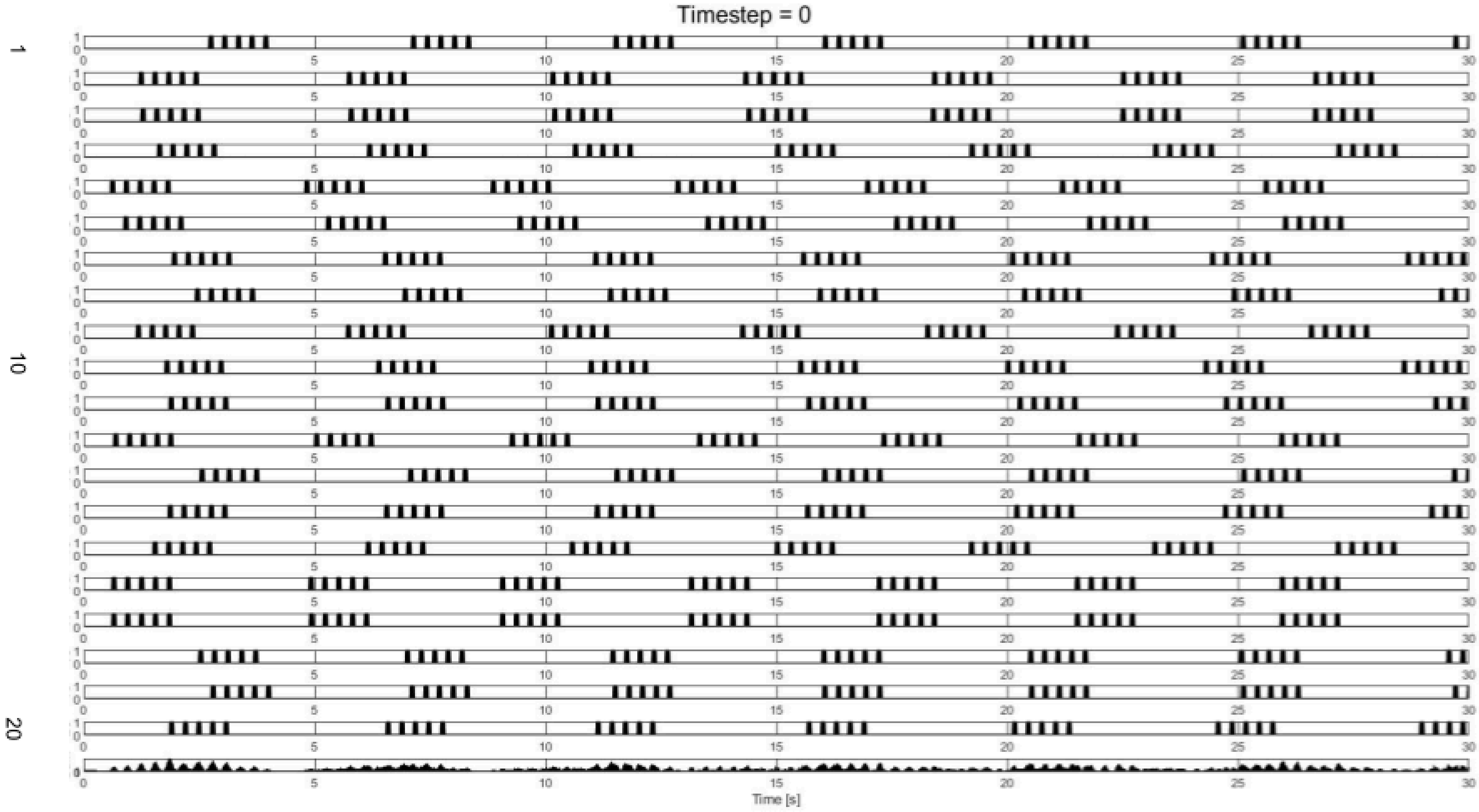
Time [s]

Figure 3.4: Raster plots. Display flash patterns for individuals and the group. An example of a starting configuration of a simulation of 20 fireflies (different initial state), representing the last 30s of the simulation. Each raster plot shows the number of flashes vs. time for individual fireflies (first 20 rows), and in the bottom "Sum" subplot, the collective flash pattern is illustrated. Each black vertical bar represents a flash. Input values: nf=5, $T_s = 5.0$ s (end-to-start interval), Td = 0.1s (Flash length).


Timestep = 0
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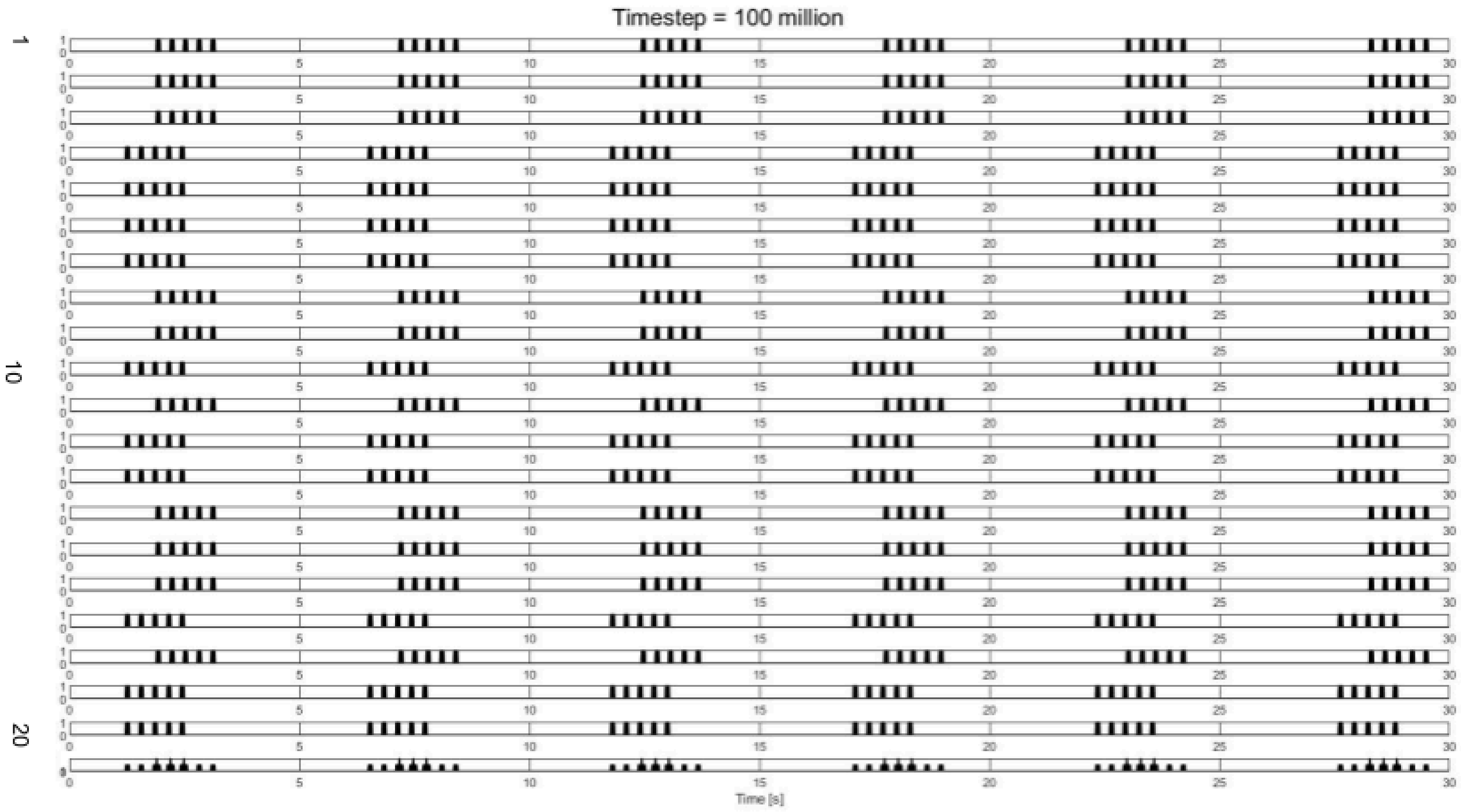
Time [s]

Figure 3.5: Raster plots. Display flash patterns for individuals and the group. An example of a starting configuration of a simulation of 20 fireflies (different initial state), representing the first 30s of the simulation. Each raster plot shows the number of flashes vs. time for individual fireflies (first 20 rows), and in the bottom "Sum" subplot, the collective flash pattern is illustrated. Each black vertical bar represents a flash. Input values: nf=5, T_s = 5.0 s (end-to-start interval), Td = 0.1s (Flash length).


Timestep = 100 million
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Time [s]

Figure 3.6: Raster plots. Display flash patterns for individuals and the group. An example of a starting configuration of a simulation of 20 fireflies (different initial state), representing the last 30s of the simulation. Each raster plot shows the number of flashes vs. time for individual fireflies (first 20 rows), and in the bottom "Sum" subplot, the collective flash pattern is illustrated. Each black vertical bar represents a flash. Input values: nf=5, T_s = 5.0 s (end-to-start interval), Td = 0.1s (Flash length).

After this, the group raster plots for various nf values were examined. It seems that between an nf value of 5 and nf value of 10 the transition takes place (Fig. 3.7). This is characterized by having no discernible gaps between subsequent flashes.

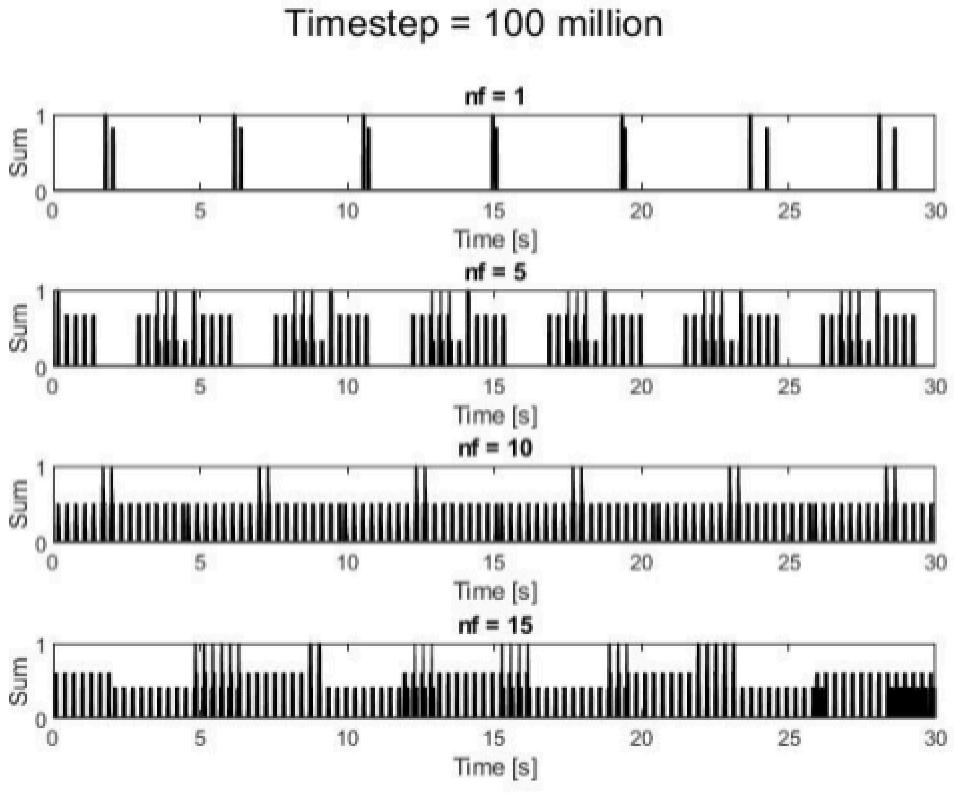

Figure 3.7: Collective Raster Plots for nf = 1, nf = 5, nf = 10 and nf = 15. A flash value of 1 represents the maximum luminosity of the system and 0 represents no luminosity.

To verify that the model was transitioning from discrete to continuous synchronization was by looking at histograms of gap saves over the last five minutes of simulation time. Two peaks should be present at lower nf values and only one should be present at higher ones.The first peak corresponds to the time between flashes in a burst while the second represents the time between bursts. This is the one that should disappear at higher nf values as the transition from a series of bursts with time interval between them to one continuous burst takes place. When looking at the data, we can indeed see that this is the case. As nf values increase from 1 to nf the second peak decreases in size when compared to the first peak.

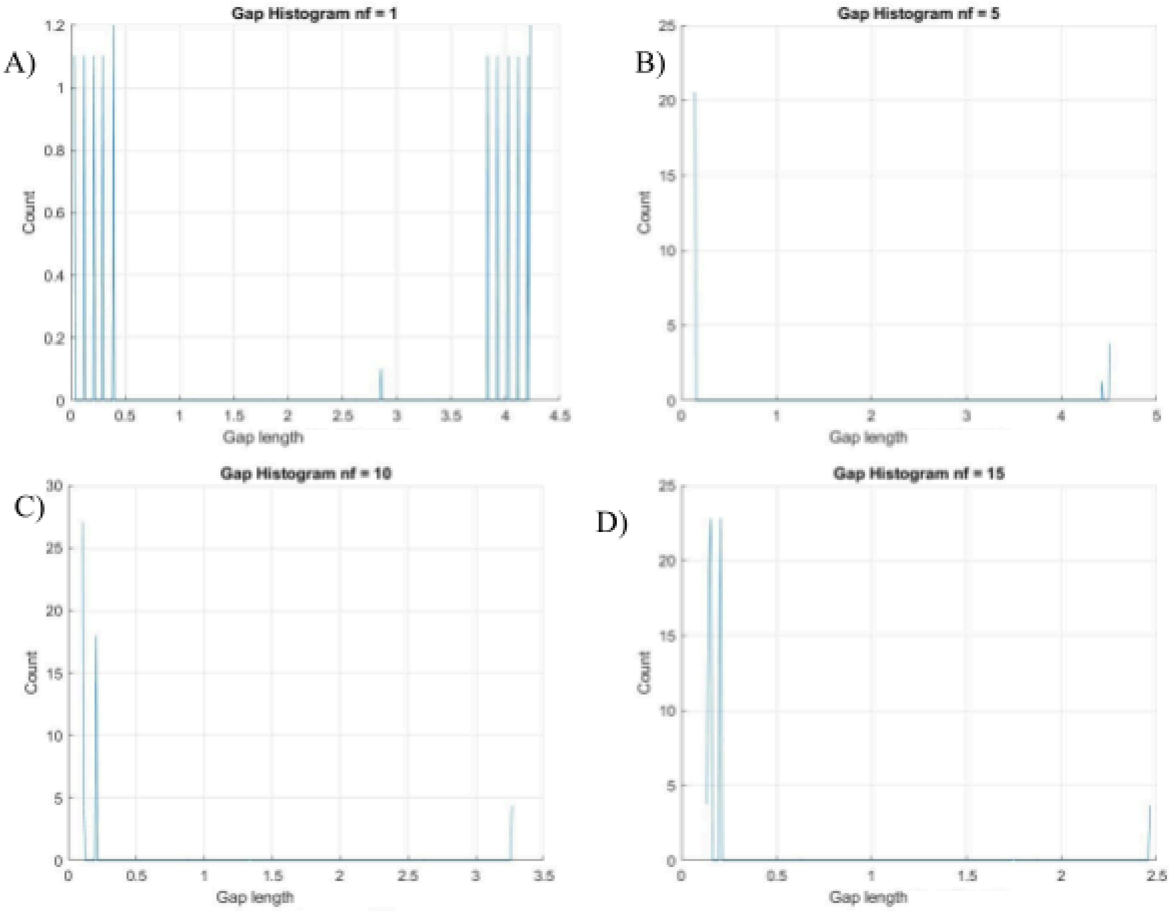

Figure 3.8: Histograms of Gap lengths [s]. A) nf = 1, B) nf = 5, C) nf = 10, D) nf = 15

The plots present in Fig. 3.8, show that after nf = 5 the count of the first peaks remains largely the same. One interesting feature here is that the placement of the second peak changes slightly and actually gets closer to the first peak. In Fig 3.8A, the second peak is at roughly 4s around the 5 s set in the initial conditions. While in Fig 3.8D, the peak is around 2.5 s, half the initial end-to-start length. This suggests that as nf increases, the second peak does not just decrease in size, but it also shifts and gets closer to the first peak. And at a high enough nf value, the peak disappears (Fig 3.8).

For this model, it is important to ensure that the simulations reach equilibrium by the end of run time. In particular, it is important that the average gap length reaches stability. This way, the simulations do not become computationally expensive and analysis of the transition is characterized properly. Plots of gap length through simulation are seen in Fig. 3.9, it is notable that by the end of 50 million steps, simulations for various numbers of flashes do stabilize.

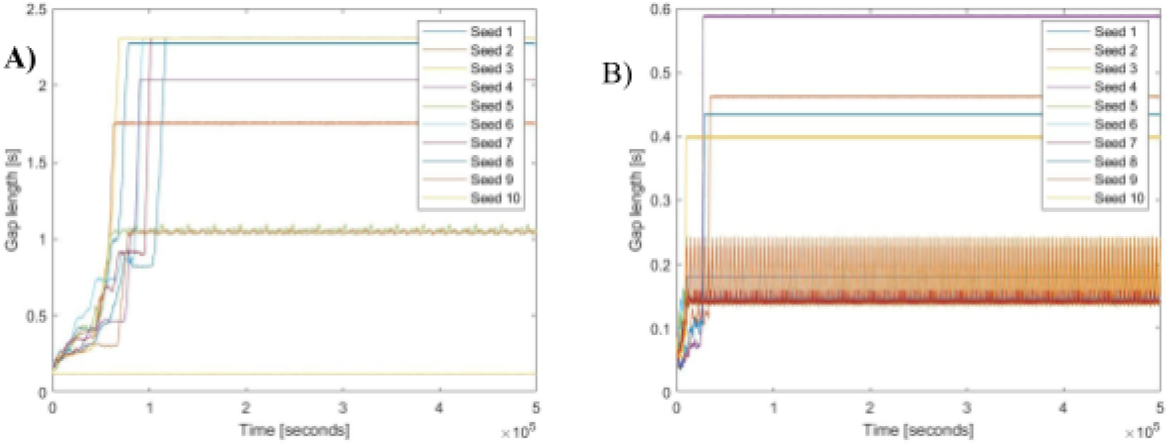

Figure 3.9: Moving average of Gap lengths**.** A) nf = 1, B) nf = 10.

One interesting observation is that as nf values increase, the equilibrium gap length decreases. This suggests an inverse relationship between nf value and gap length, which aligns with the conclusions drawn from the histograms and hypothesized.

Another intriguing behavior is that in some simulations, the gap length oscillates around a certain value. While this behavior may seem concerning, the oscillations remain around the same value with deviations of at most 0.1. The oscillatory behavior can be explained by several possible reasons. First, ABMs can exhibit feedback loops where even small fluctuations can be amplified, leading to system-wide oscillatory behavior. Second, these systems can demonstrate nonlinear dynamics, where one property may be oscillations. Third, ABMs are highly sensitive to initial conditions, so certain seed values may cause this type of behavior. However, these oscillations should not significantly impact the transition from discrete to continuous synchronization, so further investigation into their cause is not necessary.

After qualitatively validating and verifying the model, it is important to perform quantitative measurements. To achieve this, the burstiness of the simulation is calculated. Burstiness is characterized by short periods of intense activity followed by periods of little to no activity, a phenomenon observed in various systems from emails to earthquakes. Although the exact origins of burstiness are unknown, its prevalence is widespread. The definition of burstiness for this paper, is the tendency of the system to exhibit periods of activity followed by periods of inactivity. As the system transitions from discrete to continuous synchronization, burstiness should go down.

There are several methods to quantify burstiness, but for this model, a simple procedure is used. The area under the averaged histograms of gap sizes is integrated (Eq. 5), where peaks at longer times contribute to a higher burstiness level for a given nf value. Fig. 3.11, shows the rapid decrease in burstiness as a function of nf value. A continuous system is defined as one in which the burstiness is 0.1 seconds or less, which is smaller than the 0.1-second interflash interval.

$$Burstiness = \int_0^\infty P_{gap}(T_b)\, dT \qquad \text{Eq. 5}$$

In this equation $P_{gap}(T)$ is the probability density of gap time as a function of time.

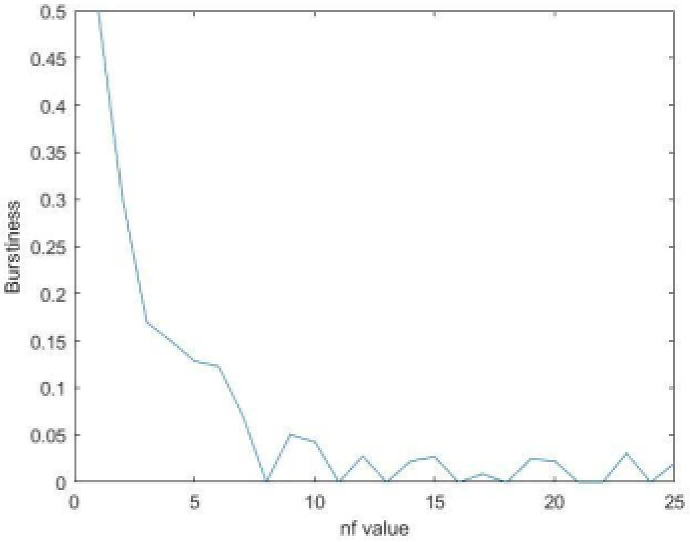

Figure 3.11: Burstiness as a function of nf value.

In Fig. 3.11, we see that around nf equals seven the burstiness level is 0.07 s which is the predetermined cutoff for a continuous system. After nf equals seven, no other nf value raises above 0.1s further instilling confidence in the model. A key feature of this table is the at nf = 8, burstiness is actually 0. This suggests that there was some local equilibrium the model found itself in, this does not suggest that 0 is the end equilibrium. At nf values larger than 8, burstiness raises again but seems to level out around 0.02s . Since this value is much smaller than the 0.1 s for the period between flashes per firefly set initially, this suggests that fireflies are coordinating in such a way that they do overlap.

3.2 Simulation Results from Observational Data

In [17], the procedure for collecting observational data is described. The results of these measurements are seen in Figure 3.12. Some key characteristic differences in the behavior between *P. carolinus* and *P. frontalis* are that the flash duration of the *frontalis* species displays remarkably lower flash duration than the *carolinus* species. The interflash gap of the *carolinus* and *frontalis* species is on the same order of magnitude, however the *frontalis* species interflash gap is shifted slightly to the right. *Frontalis* individuals also have a much higher number of flashes (nf) than that of the *carolinus* species.

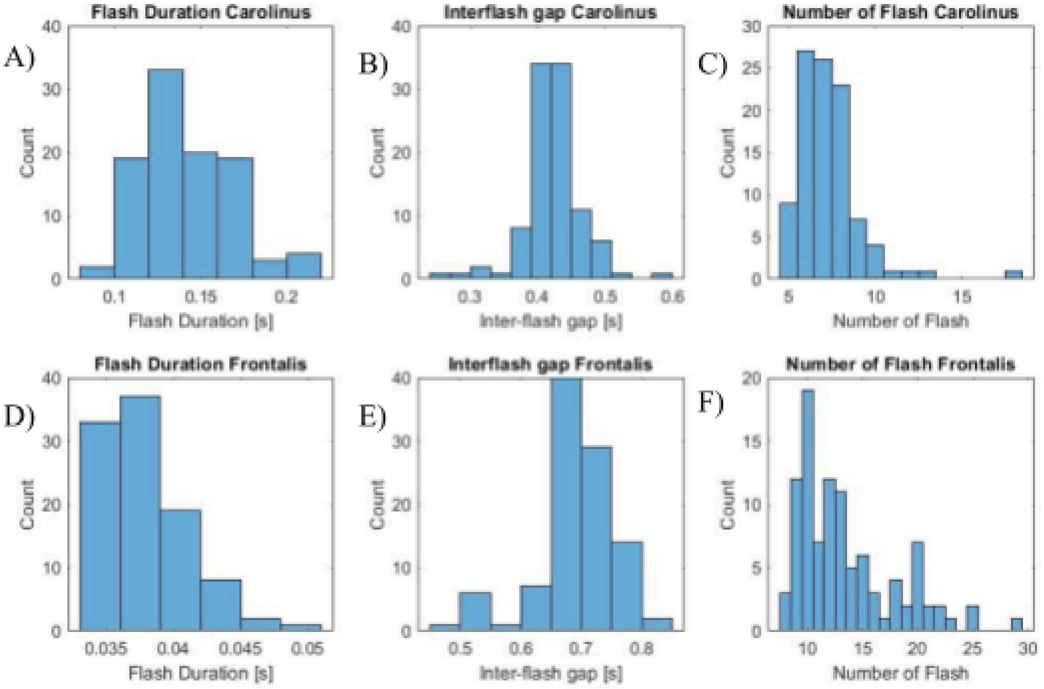

Figure 3.12: Histograms of observational data of *P. Carolinus* and *P. Frontalis* species. A) Flash duration for *Carolinus* species. B) Interflash gap for *Carolinus* species. C) Number of flashes (nf) individuals display for *Carolinus* species. D) Flash duration for *Frontalis* species. B) Interflash gap for *Frontalis* species. C) Number of flashes (nf) individuals display for *Frontalis* species. Credits: Histograms created from data from [17].

For the model, only the means for flash duration and interflash gap along with the mode for number of flashes were used as they serve as a general test. In the parameter sweep we had already studied how nf values affect this model. The next set of parameters are run as a method of validation of the model with real world data. In Table 1, we see that *carolinus* on average display a mean flash duration about 3.7x more than *frontalis*. However, *frontalis* interflash gap length is larger than that of *carolinus* and has a higher nf per burst as well. This data suggests that *frontalis* individuals tend to flash more frequently with shorter flashes and a larger refractory(charging) period than individuals of the *carolinus* species.

	P. carolinus	P. frontalis
Mean Flash Duration [s]	0.1415	0.0375
Mean interflash gap [s]	0.4210	0.6906
Mode nf	4	10

Table 1: Statistics of interest from observational data. Data collected from [8]

Using these as inputs, we ran the simulations once again. Fig 3.13 and Fig. 3.14 raster plots show that from the initial to final state *carolinus* species exhibit discrete synchronization. Fig. 3.15 and Fig. 3.16 show that *frontalis* species display continuous synchronization. A notable characteristic is that the *carolinus* system starts at continuous synchronization and ends in a discrete state. This reiterates the validity of the model as even if given the opposite initial states, the simulations converge to the right end behavior. Using the definition of burstiness (Eq. 5), we see that *carolinus* species exhibit burstiness of 0.1316s and *frontalis* of 0s. This suggests that the *carolinus* species displays discrete synchronization while the *frontalis* displays perfectly continuous synchronization. These results agree with the observations, thus we can conclude that this model is valid for characterizing the transition from discrete to continuous synchronization, and that this transition should occur around equals seven.

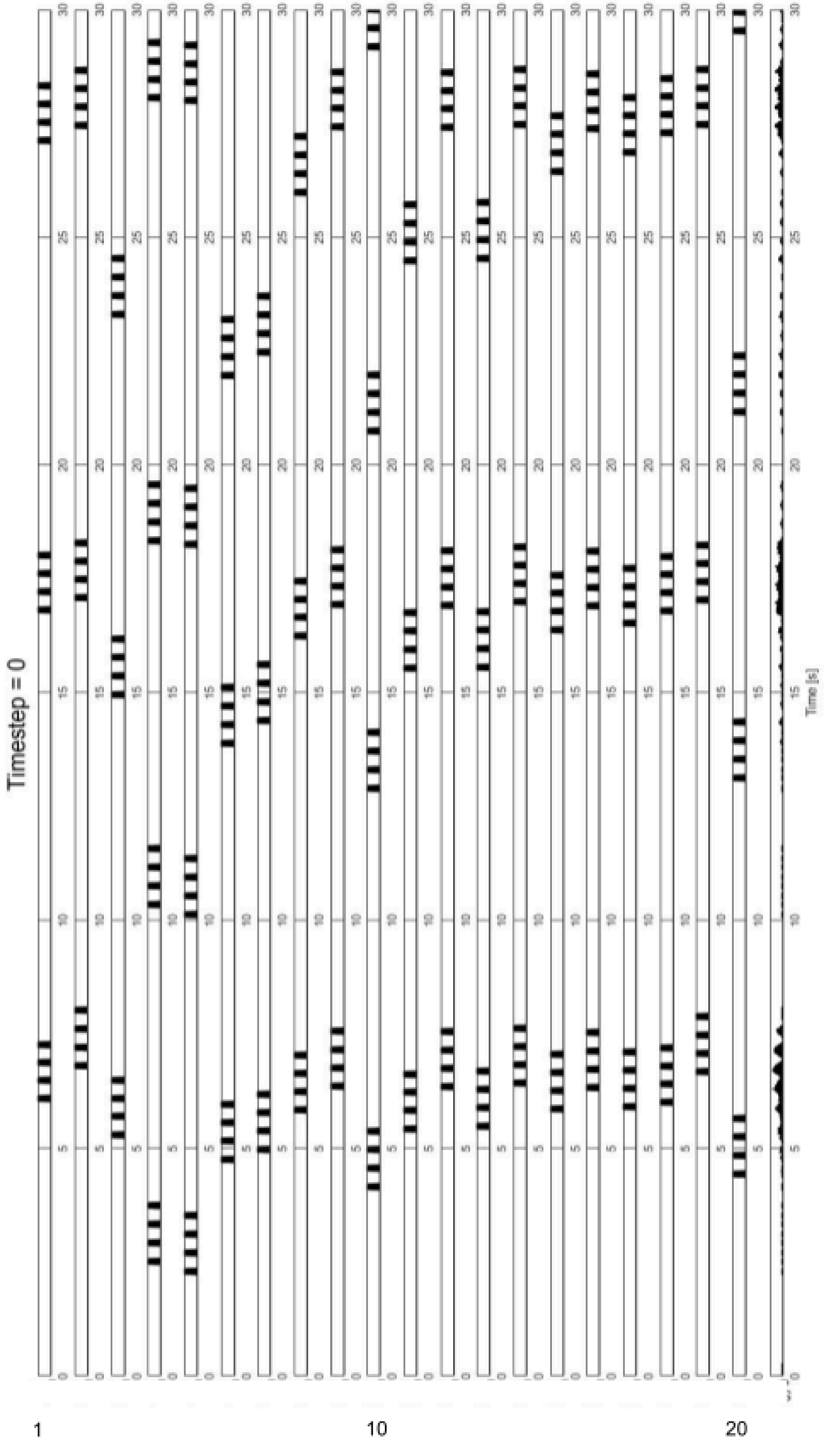
Timestep = 0
Time [s]
0
5
10
15
20
25
30
1
10
20

Figure 3.13: Raster plots. *carolinus* for the first 30 seconds of simulation time. Individual flashes shown and in the “Sum” subplot, collective flash pattern is illustrated. Black vertical bar represents a flash.

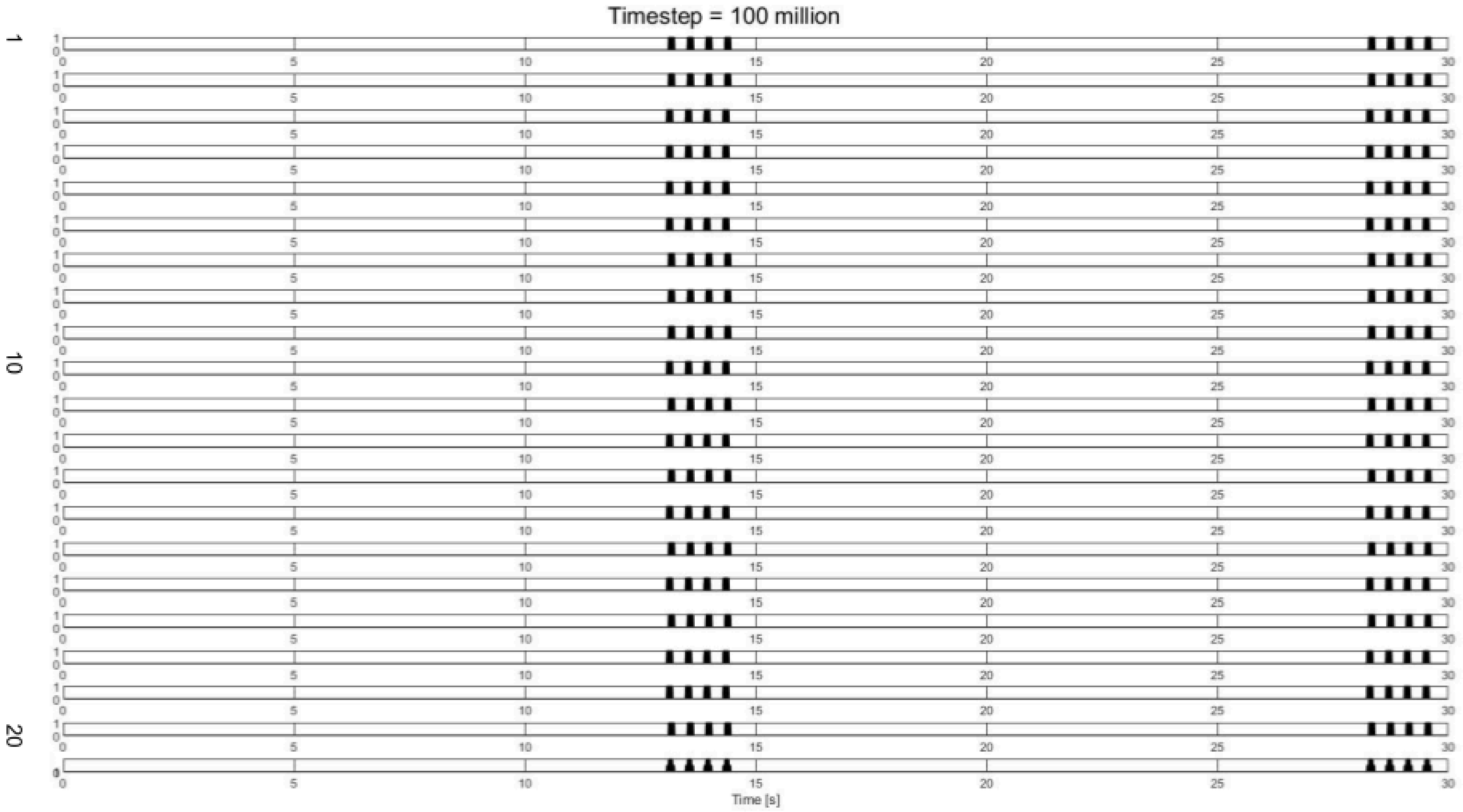
Timestep = 100 million
Time [s]
0
5
10
15
20
25
30
1
0
1
10
20

Figure 3.14: Raster plots. *carolinus* for the last 30 seconds of simulation time. Individual flashes shown and in the “Sum” subplot, collective flash pattern is illustrated. Black vertical bar represents a flash.

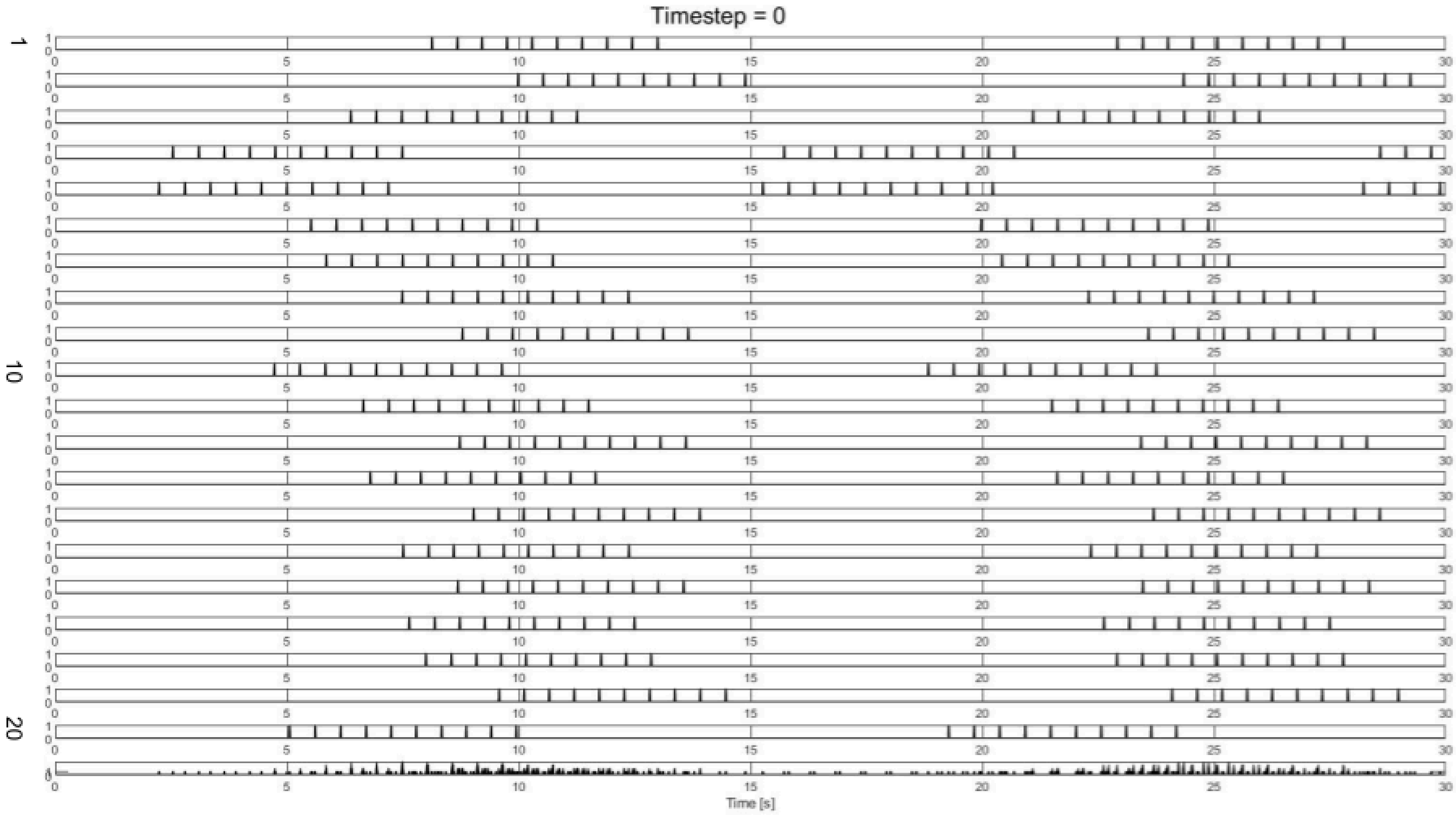
Timestep = 0
1
10
20
1
0
0
5
10
15
20
25
30
Time [s]

Figure 3.15: Raster plots. *frontalis* for the first 30 seconds of simulation time. Individual flashes shown and in the “Sum” subplot, collective flash pattern is illustrated. Blue vertical bar represents a flash.

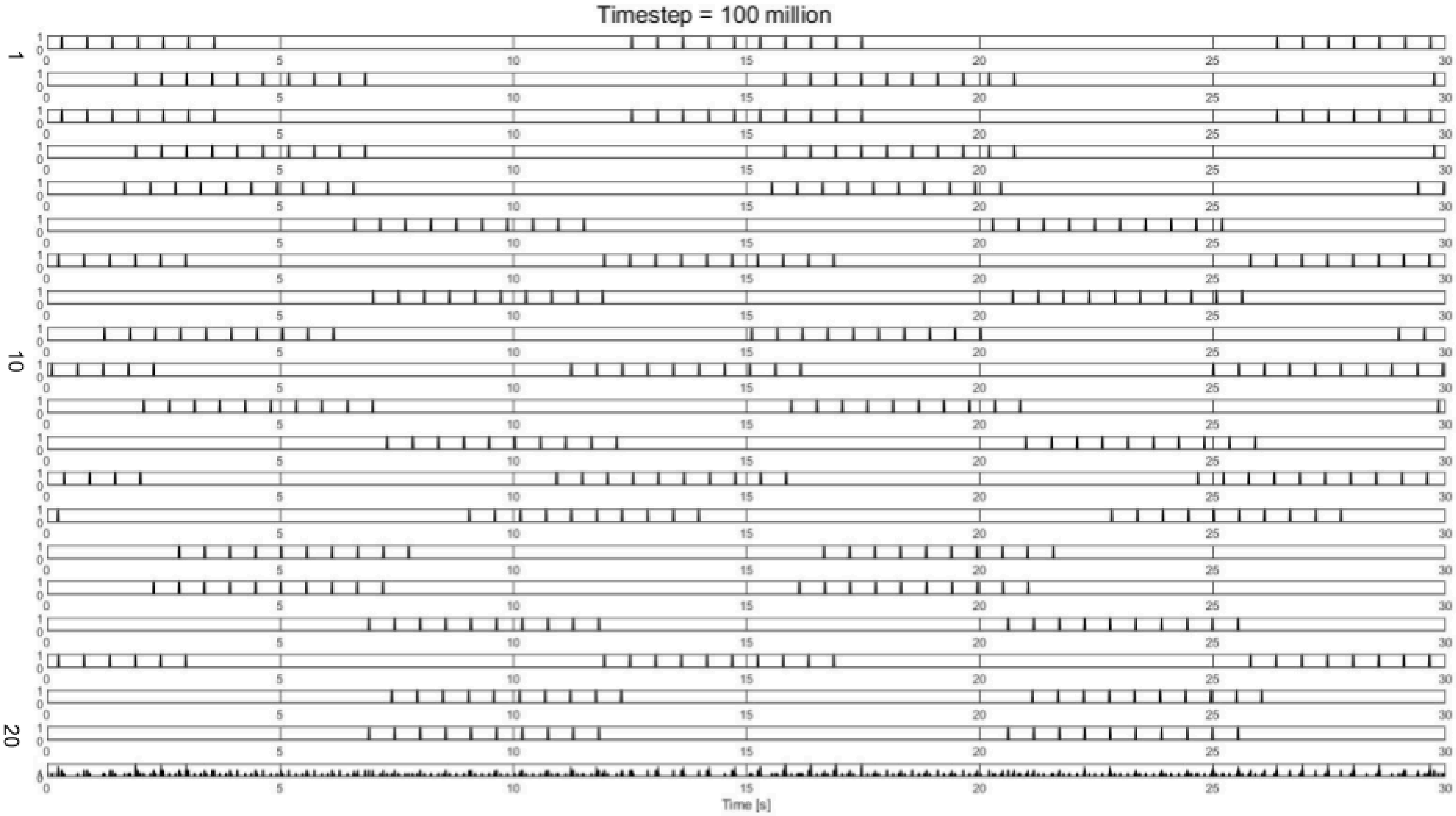
Timestep = 100 million
1
10
20
1
0
0
5
10
15
20
25
30
Time [s]

Figure 3.16: Raster plots. *frontalis* for the last 30 seconds of simulation time. Individual flashes shown and in the “Sum” subplot, collective flash pattern is illustrated. Black vertical bar represents a flash.

Chapter 4

Conclusion and Discussion

In this work, we model the transition from discrete to continuous synchronization for fireflies, and show that the number of flashes per burst (nf) is key to the transition. We show through numerical simulations of an Agent Based Model, that as the number of flashes increase, the length between collective bursts decreases. In particular, systems of 20 fireflies transitioned from discrete to continuous synchronization at an nf value of seven. Further, we validated our model by using observational data of two representative species *Photuris Frontalis* (continuous) and *Photinus Carolinus* (discrete), and saw that the results from the simulations were consistent with observational data from previous studies.

Future work could involve exploring non-homogeneous parameters between fireflies. All firefly agents in a system had the same input parameters, namely number of flashes per burst (nf), flash duration, interflash interval and interval between bursts and coupling strength. It would be interesting to study if this model converges to similar final states under such conditions.

Exploring the variability among individual fireflies and how it influences the overall synchronization pattern could unveil new insights into the collective behavior of biological systems. By integrating diverse behaviors and characteristics, future studies could provide a more comprehensive understanding of the mechanisms driving synchronization in nature, bridging the gap between mathematical models and the complex dynamics of the natural world.

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