

How the Firefly Got His Flash: Modelling sympatric *Photinus* flash signal evolution through naming games

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1 Introduction

Warm summer nights in North America are often decorated with the mesmerizing light displays of fireflies. Flashes serve as the firefly’s sexual signal during mate search and provide a proto-language for study.

We consider the flash communication system of *Photinus* fireflies, a genus which contains 35 described species. The simplicity of these visual binary firefly communication signals lends themselves to study through simple computer modelling.

Previous studies have considered the dual evolutionary processes of sexual selection (mate choice) and natural selection (predation) with respect to the shaping of firefly flash signals. Fireflies use flashes to identify the species and sex of the signaler. Specifically, males, typically airborne, will signal with their species-specific patterns. Females, upon recognition of the correct signal, will respond to the male flashes with a species-specific response delay. Based on the delay, males will either continue searching or approach physical contact, leading to mating.

This simplistic overview of the courtship process highlights the necessity of distinguishable flash signals, as it is often the case that more than 10 flashing species of fireflies occupy a geographic area. While previous studies have considered selective pressures with respect to a specific species of firefly in shaping its own signal, it is unclear how these pressures interplay with the sympatric nature of the species. Indeed, Stanger-Hall and Lloyd (2015) conclude that reproductive character displacement was a main factor for signal divergence among sympatric *Photinus* species, but their findings fail to address the way in which that pressure shapes the signal itself beyond correlational values.

We thus seek to understand how various selection factors such as predation risk interact with the need for sympatric species to have mutually distinguishable signals and thus shape the evolution of firefly flash patterns.

2 Approach

2.1 Overview of Naming Game

We approach our question through the lens of language evolution. In this case, we view the language in question to consist of the flash patterns of each species, with the caveat that each firefly only has knowledge of its own species’ flash signal. We model the evolution of this language of firefly flash patterns through a modified minimal naming game, in which the objects to be named are the firefly species, and the words are a fixed length binary sequence. A naming game broadly conceived proceeds as follows: a population of agents, connected in a certain topology, start with empty memories and follow simple protocols of game rules to achieve consensus on the name of an object.

In our naming game, the population of agents is a set of individual fireflies. We view the objects to be named as the firefly species themselves. We simplify the problem space by specifying the underlying topology as a complete graph. In each time step, either a learning or comparison step is taken for each edge of the graph, as described as follows.

2.2 Learning and Comparison Steps

In the full signal naming game, a learning step is executed between fireflies of the same species and a comparison step is executed between fireflies of different species. The comparison step of two different species of fireflies is a calculation of a similarity metric with respect to the patterns held in

the memory of the fireflies involved. The fireflies keep a running mean of the similarity scores they receive in the comparison step. The learning step between two fireflies of the same species is a comparison of that running mean. The firefly with the higher (thus worse) score then adopts the pattern of the firefly with the lower score, with a chance of mutation. The learning step essentially replicates the better flash pattern with respect to the similarity metric, allowing the population to achieve consensus upon the “name” that is the most different from the known flash patterns of other species. We introduce a chance of mutation to facilitate the exploration of the pattern space.

Acknowledging that visual communication in the environment is lossy, we also developed a partial signal naming game in which fireflies converge upon a signal that is not only distinguishable from the known patterns of the other species but also robust to missing bits. We designed the comparison step to account for this type of robustness with inspiration from the female responses observed in *Photinus* fireflies. Instead of simply calculating a similarity metric, one firefly in the pair will send a contiguous subsequence of its pattern. Given this subsequence, the other firefly must make a decision of whether the two are of the same or different species, based upon the similarity of the received subsequence to its own pattern. A reward or penalty discounted by the length of the subsequence upon which the decision was made is given to both fireflies based upon the accuracy of the decision.

Note that the comparison step is taken for all edges in the graph. The learning step is thus only executed in a following round for all pairs of fireflies of the same species. This learning step is essentially the same as in the full signal naming game, using the aggregate rewards and penalties to compare and replicate based on the fitness of the flash patterns. In this case with positive rewards and negative penalties, a higher aggregate score indicates a higher fitness.

2.3 Similarity Metric

While previous studies (Stanger-Hall and Lloyd 2015) have characterized the periodic flash patterns with four parameters – flash duration, flash pattern interval, interpulse interval, and female response delay, we relaxed some of those assumptions and chose to characterize flash patterns bit

by bit. To ensure we capture the periodic nature of the flash signals, we consider the patterns cyclically. That is, we essentially consider the equivalence classes with respect to the permutation cycle $(123\dots n)$, where n is the fixed length of the flash pattern.

We propose two different similarity metrics, the first being more straightforward to calculate, while the second better captures our intuitions regarding distinctiveness.

The first similarity metric counts bit-wise similarity for every possible alignment of the two patterns with respect to the permutation cycle $(123\dots n)$. That is, for two patterns p_1, p_2 , we define the similarity score as

$$\text{sim}(p_1, p_2) = \sum_{i=0}^n \sum_{j=0}^n \mathbb{1}[p_1[i + j \bmod n], p_2[j]],$$

where

$$\mathbb{1}[x, y] = \begin{cases} 1 & \text{if } x = y; \\ 0 & \text{otherwise,} \end{cases}$$

and $p[i]$ refers to the i^{th} bit in the pattern p , with indexing starting at 0. We can understand the index i as representing the number of permutation cycles applied to the pattern p_i .

As an example, given two flash sequences of length 5 $[1, 0, 0, 0, 0]$ and $[1, 0, 1, 0, 0]$, we get a score of 14 using this bit-wise comparison similarity metric. If we require at least one bit to be “on” in the sequence, then the lowest possible score is 5, realized by the two sequences $[1, 0, 0, 0, 0]$ and $[1, 1, 1, 1, 1]$. Generalizing to sequences of length n , the minimum score is thus n . The highest possible score – that is, two identical patterns – is 25, or n^2 .

The second similarity metric we use simply measures the length of the longest common subsequence. Here, we compare shared subsequences between doubled flash patterns, that is we consider subsequences that are “wrapped.” Mathematically, we can define our second similarity metric as follows,

$$\text{sim}(p_1, p_2) = \max_{i \in [0, 2n-1], j \in [0, 2n-1]} T[i][j],$$

where

$$T[i][j] = \begin{cases} T[i-1][j-1] + 1 & \text{if } p_1[i-1 \bmod n] = p_2[j-1 \bmod n] \\ 0 & \text{otherwise.} \end{cases}$$

Revisiting the previous examples, the longest contiguous subsequence shared between $[1, 0, 0, 0, 0]$ and $[1, 0, 1, 0, 0]$ is $[0, 1, 0, 0]$, giving a similarity score of 4. The lowest possible score using this metric is 1, again instantiated in patterns of length 5 by the two sequences $[1, 0, 0, 0, 0]$ and $[1, 1, 1, 1, 1]$. The highest possible score for two identical patterns is 9, or $2n - 1$, where n is the length of the pattern. We see an immediate difference in range for these two similarity metrics and how they differ in capturing degrees of similarity.

This second similarity metric can be modified for a partial sequence and is used in the partial signal naming game in order to decide whether a subsequence belongs to the same species. That is, we find the longest common substring between the full pattern of one firefly and the subpattern of the other and use that length divided by the length of the subsequence with a constant decision threshold. Specifically, let p_2 be a partial sequence with length m . Then, the decision score is

$$d(p_1, p_2) = \max_{i \in [0, 2n-1], j \in [0, m]} T[i][j],$$

where

$$T[i][j] = \begin{cases} T[i-1][j-1] + 1 & \text{if } p_1[i-1 \bmod n] = p_2[j-1] \\ 0 & \text{otherwise.} \end{cases}$$

We note that we “wrap” the full pattern but do not do so for the partial pattern.

2.4 Risk of Flashing – Score Discounting

To address the physiological cost of producing a flash and the predation risk of flashing, we discount scores with respect to the number of flashes in the signal in order to select towards more limited time spent flashing. In the full signal naming game, in which a lower score indicates a fitter flash pattern, the score that is compared during the learning step is multiplied by the number of flashes divided by 3. Specifically, the similarity score between two patterns p_1 and p_2 from the perspective of the firefly with pattern p_1 is,

$$\text{score}(p_1, p_2) = \frac{\sum_{i=1}^n p_1[i]}{3} \text{sim}(p_1, p_2).$$

Conversely, in the partial signal naming game, in which a higher aggregate reward indicates more success in the comparison step, the reward used in the learning step is divided by the total number of flashes in the pattern.

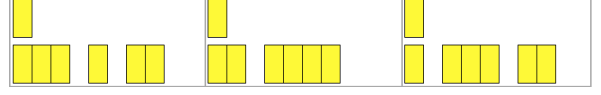


Figure 1: Top results for 2 species full pattern naming game, with similarity scores from left to right of 3, 4, and 4.

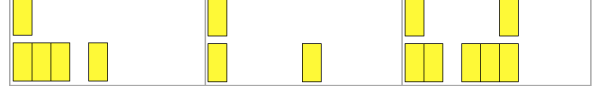


Figure 2: Top results for 2 species partial pattern naming game, with similarity scores from left to right of 7, 9 and 12.

2.5 Methods Summary

In both naming games, fireflies seek to find a flash pattern that is distinctive from the patterns seen in other firefly species, while limiting the number of flashes used to create such differences. Distinctiveness is measured through one of two similarity scores or by the ability to make the correct decision with respect to partial signal recognition. We can thus understand the objective function of the simulation as finding the pattern that either minimizes or maximizes (depending on type of naming game) the score function with discounting.

3 Experimental Results

We experimentally simulated both types of naming games, varying the similarity metric used and the number of species in the simulation. Each naming game simulation was populated with 15 fireflies of each species and ran for 1000 time steps. For each set of parameters, we ran 20 different trials. We present some of the resulting patterns of the trials with the best discounted similarity scores using the longest common substring metric.

For simplicity, we set the pattern length to 10 – that is, we defined the flash patterns as a sequence of ten 0s or 1s, with a 1 indicating a flash and a 0 indicating no flash for one time unit. Because we view the patterns cyclically, there is no inherent starting index with which to present the signals. Consequentially, we chose to display the resulting patterns of the naming game as ending with the longest contiguous sequence of 0s, emulating the “waiting” time observed in firefly signals. When there are two or more sequences of 0s of the same

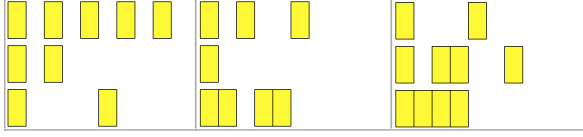


Figure 3: Top results for 3 species full pattern naming game, with similarity scores from left to right of 17.3, 21.7, and 24.

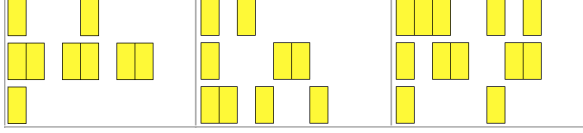


Figure 4: Top results for 3 species partial pattern naming game, with similarity scores from left to right of 18, 24.7, and 25 .

length, we present the patterns starting with the longest contiguous sequence of 1s possible.

In each figure, we include the resulting patterns from the top three trials of one specification of the naming game. Each set of patterns from one trial is contained in its grey bounding box. Note that the fitness of a flash signal is inherently dependent upon those other patterns with which it evolved, which can be found in the same column. We indicate a 1 by a yellow block and a 0 with white space. Contiguous yellow blocks should be interpreted as a single flash of that duration. In each figure’s caption, we include a score for each trial. This reported score is a mean of the similarity scores of each pair of patterns for species i and j ,

$$\frac{1}{\binom{N}{2}} \sum_{(i,j)} \text{sim}(p_i, p_j)$$

3.1 Simulations with Two Species

We use the toy setting of two species to ensure that our similarity metric and rules of the naming game capture our intentions on a basic level. In the full pattern naming game, we see that one species almost always converges upon the simplest pattern $[1, 0, 0, 0, 0, 0, 0, 0, 0, 0]$, while the other species converges upon patterns with more flashes. We note this tendency to find the simplest pattern as evidence that the naming game instantiates an approximation of our intended selective pressures. We see a similar pattern in the partial pattern naming game. Interestingly, the second, more complex patterns, generally use fewer flashes in the partial

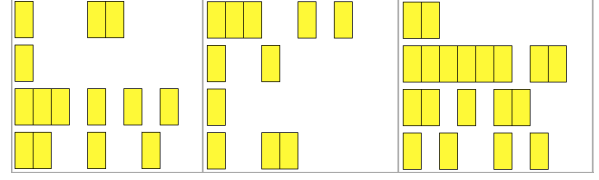


Figure 5: Top results for 4 species full pattern naming game, with similarity scores from left to right of 20.3, 21.3, and 26.3.

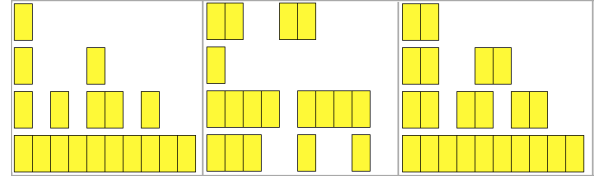


Figure 6: Top results for 4 species partial pattern naming game, with similarity scores from left to right of 16.3, 25, 28.3.

pattern naming game.

3.2 Simulations with More Species

We then increased the number of species within the simulation up to 5, an upper bound imposed by room to differentiate within the pattern space. As we increase the number of species within the naming game, it seems that one species is likely to err on the side of more flashes in the trade-off between distinguishability and penalty for flashing, with some opting to keep their flash on at all times. While species in simulations with three species seem to be able to manage this trade-off, it seems that as the number of species in the naming game increases, it becomes harder for fireflies to find a distinguishable pattern with a low number of flashes. Indeed, as any one species will often have multiple contenders for the best pattern, the search space is quite constrained.

4 Discussion

Upon visual inspection of the flash patterns, those patterns emerging from the partial sequence naming game seem to exhibit pseudo-periodic properties. Given that observed firefly flash signals are periodic in nature, that is, they can be fully described by the flash duration (length of a contiguous “on”), interpulse interval, and flash pattern interval, we proffer that periodic sequences are efficient solutions to the problem of distinguishability.

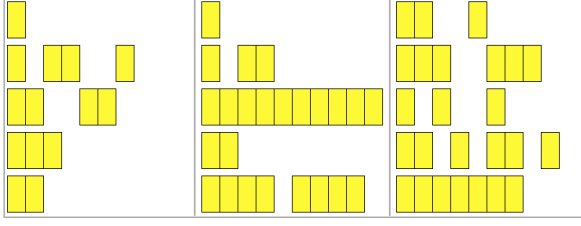


Figure 7: Top results for 5 species full pattern naming game, with similarity scores from left to right of 22.9, 23.1, and 26.3.

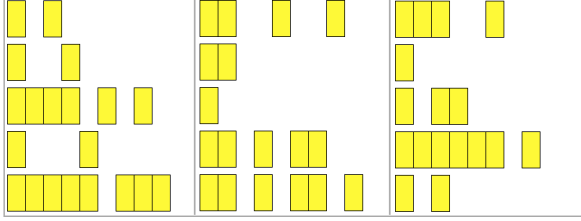


Figure 8: Top results for 5 species partial pattern naming game, with similarity scores from left to right of 24, 25.7, 26.

Additionally, the simulation selection pressures of interrupted signals as seen in the partial sequence naming game pose a better imitation of the selection pressures. This poses a question of how we might quantify efficiency with metrics other than simply counting the number of flashes in a pattern.

Indeed, we observe that the resultant patterns from our simulations are much more complicated – with variable flash durations and interpulse intervals within one signal – than those observed and catalogued by (Stanger-Hall and Lloyd). A better efficiency metric might be needed to impose more realistic selective pressures in order to better inform our model. Moreover, imposing a more complex metric on efficiency would limit the pattern space more, which may allow certain combinations of patterns to stand out as fitter. We note that within our 20 trials of each simulation, we never obtained the same set of final patterns more than once.

We present the final patterns that emerge from the naming games after a few time steps of the game without individual patterns mutating. Tracking the evolution of patterns with respect to other patterns in all agents’ memories might better inform how the space of patterns is searched and explored. This may lead to a better understanding of what types of patterns are ultimately fitter and

more distinguishable.

Moreover, if we track how patterns change throughout the naming game, it would be interesting to introduce, remove, and/or merge species during the game. Such a dynamic simulation would better highlight how the presence of a specific pattern affects distinguishability.

We acknowledge that only the male flash patterns were studied in our analysis of the evolutionary pressures of the flash signal. However, with inspiration from reinforcement learning and policy learning, our partial pattern naming game lends itself easily to incorporate female response times within the model. Indeed, if we require the fireflies to make a second decision encapsulating a correct response delay, we can also follow the way in which the current selection pressures considered shape how females learn an optimal response delay time.

Our model is simplified with the use of a complete graph as the underlying topology of the naming game. While this choice in topology allows for quick consensus to be reached, different types of random graphs or geographically inspired graphs may better encapsulate environmental factors that affect speciation.