Firefly courtship as the basis of the synchronization-response principle

G. M. Ramírez Ávila[1,2,3] [(a)], J.-L. Deneubourg[4], J.-L. Guisset[4], N. Wessel[1] and J. Kurths[1,2]

[1] *Institut für Physik, Humboldt-Universität zu Berlin - Robert-Koch-Platz 4, 10115 Berlin, Germany, EU*
[2] *Potsdam Institut für Klimafolgenforschung - P.O. Box 60 12 03, 14412 Potsdam, Germany, EU*
[3] *Instituto de Investigaciones Físicas, Universidad Mayor de San Andrés - Casilla 8635, La Paz, Bolivia*
[4] *Interdisciplinary Center for Nonlinear Phenomena and Complex Systems and Unité d'Ecologie Sociale, CP 231, Université Libre de Bruxelles - Campus de la Plaine, Bld. du Triomphe, Brussels, Belgium, EU*

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Abstract – Response to synchronization seems to be a widespread phenomenon specially in biological systems. We highlight this phenomenon studying the courtship of flashing fireflies in which arises a typical collective rhythm occurring only among the males and it is followed by a response of the females. Based on a model issued from electronic fireflies, we explain the synchronization of the males and the active responses of the females in the courtship of mingled (both sexes) populations of fireflies. The model also explains the courtship behavior of other species whose interactions follow the same logic even if their physical features are different. Moreover, the model can make predictions on the behavior of mingled and mixed (natural and artificial) groups of such animals. This finding could be considered as the basis of a new principle, namely the synchronization-response.

Introduction . – Synchronization has been extensively studied as an ubiquitous phenomenon which occurs due to the coupling of self-sustained oscillators [1]. Many biological systems exhibit synchronous behavior that could constitute a manifestation of functional processes such as in cardiac cells [2] or pathological ones such as in the neurons triggering epileptic seizures [3]. On the other hand, numerous species use synchronization as a form of communication that allows the accomplishment of certain tasks and more important, it is an essential ingredient in their reproduction as a first step in the courtship. Animals have different strategies in order to attract conspecifics of opposite sex. One of these strategies consists in the aggregation of males performing displays which constitute a signal to communicate with the females. There are abundant examples of species using this strategy. Among the courtship displays performed by the males, synchronization is one of the most well-known [4]. In several species the males synchronize their physical signals as a preliminary step in the courtship. Synchronization in crickets [5, 6], katydids [7–10], cicadas [11], frogs [12, 13], and crabs [14, 15] among others, constitute examples in which males use their mechanical signals for this purpose. In each case, the communication occurs with different types of signals but exhibiting similar features for their courtship. On the other hand, fireflies use electromagnetic signals (light pulses) to communicate and they are able to synchronize their flashes. Synchronization in ensembles of fireflies is one of the most attractive biological phenomena and it was described mostly in Asian [16–18] and in American species [19–23]. Some mathematical models have attempted to explain the synchronous behavior in certain species, in particular in *Photinus pyralis* [24, 25] and *Pteroptyx malaccae* [26]. In all these models, the authors considered relaxation oscillators coupled by pulses or slight stimuli. Although the obtained results describe quite well the observations, all these models considered several simplifications and even some unrealistic features such as instantaneous flashes, thus describing only "a partial" story concerning the fireflies' courtship: how the males are able to synchronize. However, it is crucial to include the females' active role and its implications as Moi-

[(a)] E-mail: `gramirez@ulb.ac.be`

seff and Copeland have recently stated in [27]. They have shown that a *Photinus carolinus* female responds better to synchronous artificial males, than to asynchronous ones. This fact demonstrates the essential role of synchronous flashes in furthering female recognition of its conspecifics.

In this Letter, we address the problem of how a response arises in a subgroup of a population of oscillators as a result of the synchronization of another subgroup. For this, we study the courtship in which are involved two types of individuals (males and females) considering their oscillatory features related to the phenomenon. We study the courtship as a whole and we present a model which describes the two important steps of the fireflies courtship: (i) the synchronization of the males and (ii) the response of the female facilitated by the synchronous behavior of the males. This is the first time that both steps are explained by a model which should also have promising further applications in systems exhibiting synchronous behavior.

The model . – Our results come from an experimentally validated model based on simple electronic devices that mimic the fireflies' behavior in the sense that they interact only by pulses of light and they may exhibit synchronous behavior. We have studied experimentally, theoretically and numerically the synchronization of these electronic fireflies or Light-Controlled Oscillators (LCOs) [28–31], taking into account the modern definition of synchronization as adjustment of rhythms of oscillators due to their weak interaction [1]. One of the most remarkable features of LCOs is that the mechanism of synchronization includes excitation and inhibition of an LCO due to the light of other LCOs. The dynamics of an isolated LCO comprises a charging and a discharging (when the flash is emitted) stage whose durations are respectively T_{c0} and T_{d0}.

In order to explain the courtship in mingled groups of males and females in a population of fireflies, we consider that both males and females have the same oscillatory features but they differ in their reaction to the flashes of other individuals. Thus, the light acts on a male in an excitatory manner during the interflash interval (charging stage), and in an inhibitory manner when he is flashing (discharging stage). On the contrary, the light acts on a female inhibiting the charge and exciting the discharge. Due to the above mentioned features, the model can be written as:

$$\begin{aligned}\frac{\mathrm{d}V_i(t)}{\mathrm{d}t} &= \frac{\ln 2}{T_{c0i}}[(V_{Mi}-V_i(t)]\epsilon_i(t)-\frac{\ln 2}{T_{d0i}}V_i(t)[1-\epsilon_i(t)]\\ &\quad +\theta_i\sum_{i,j}^{N}\beta_{ij}\delta_{ij}[1-\epsilon_j(t)]\ ,\end{aligned}\tag{1}$$

where ϵ_i is a binary variable which defines whether the firefly is charging ($\epsilon_i = 1$) or discharging ($\epsilon_i = 0$); δ_{ij} indicates whether or not the individuals i and j are coupled ($\delta_{ij} = 1$ when fireflies i and j are coupled and $\delta_{ij} = 0$ otherwise); and β_{ij} is the coupling strength and represents the pulsatile action of the firefly j's flash over the firefly i that occurs during the discharging of the firefly j [1]. Finally, we include the factor θ_i which determines the sign of the sum term according to the firefly's sex: $\theta_i = +1$ for males (N_M, the number of males) and $\theta_i = -1$ for females (N_F, the number of females; $N = N_M + N_F$).In this form, eq. (1) describes oscillators flashing continuously as it occurs in the LCOs and in some firefly species (e.g. *Pteroptyx malaccae*) [16]. Nevertheless, there exist other firefly species such as *Photinus carolinus* in which the oscillations are not continuous and the males exhibit bursts with n_f flashes per burst, followed by a silent interval $T_s = T_p - n_f(T_c + T_d)$, being T_p the duration of a phrase. Moreover, it is possible to consider a phase delay $\Delta\phi$ playing the role of initial condition. The flash pattern, the form of the oscillation and the parameters are represented in fig. 1.

Taking the features of *Photinus carolinus* as the parameters of our model, i.e., phrases of six flashes, with the flash width, the interflash interval, and the interval between the beginning of each phrase with durations of the order of respectively 200 ms, 500 ms, and 10 s for the males; and phrases of one flash with 100 ms, 6 s, and 10 s for the females. Synchronization of the males and the consequent response of the female can be obtained using eq. (1) in two main forms: (i) *All-to-all coupling*, in which, the fireflies are coupled each other with the same coupling strength. In this case, the coupling term can be expressed as $\beta_{ij} = \beta/N$. (ii) *Distance dependent coupling*, in which the coupling between the fireflies depends on the distance and its strength decays following a power-law: $\beta(r_{ij}) = \beta_{\mathrm{ref}}/r_{ij}^{\alpha}$, where $\beta(r_{ij})$ stands for the coupling dependence on the distance r_{ij}. The parameters β_{ref} and α must be determined experimentally [2].

Results . – Considering situations in which the number of males is small, e.g. 8 males and one female and using the parameters values above mentioned, distance dependent coupling, and random initial conditions, we observe that males easily synchronize and when it occurs, the female responds with a flash as shown in fig. 2. We observe that in a certain way, the female anticipates the behavior of the males and estimates their degree of synchrony.

Now, we focus on the experimental results obtained in [27], where the authors carried out experiments with 8 light-emitting diodes (LEDs) acting as virtual *P. carolinus* males and stimulating a female. They have observed that the female response (FR) occurs according to the stimulus generated by the 8 males. They have used 4 types of stimuli: A (unison synchrony); B (near unison) with phase delays $\Delta\phi_i$ for the LEDs varying from 2 to 150 ms;

[1]The binary variable ϵ_i changes its value from 1 to 0 or from 0 to 1 when V_i reaches the upper or the lower threshold respectively. For an LCO, these thresholds are related to the source voltage V_M as $V_{\mathrm{upper}} = 2V_M/3$ and $V_{\mathrm{lower}} = V_M/3$.

[2]In the case of the LCOs, $\beta_{\mathrm{ref}} \approx 0.415$ when $r_{ij} = 4.85$ cm and $T_d = 200$ ms, and α being approximately 2, i.e. the coupling strength falls roughly with the square of the distance.

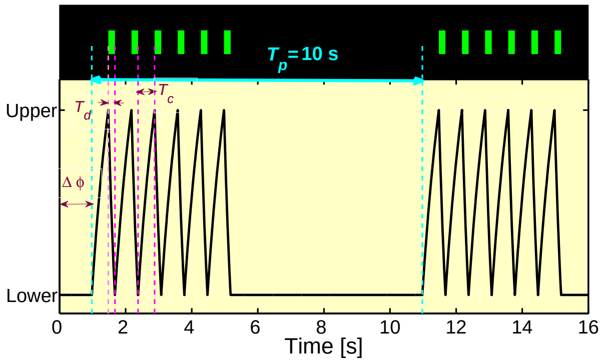

Fig. 1: (Color online) Parameters used in the model explained by means of two phrases of the *P. carolinus* male flash-pattern (top) and signal (bottom). The elapsed time between the first flashes of each phrase is $T_p = 10\,\mathrm{s}$; the phase delay is $\Delta\phi$; the duration of a flash and the interflash interval are respectively T_d and T_c.

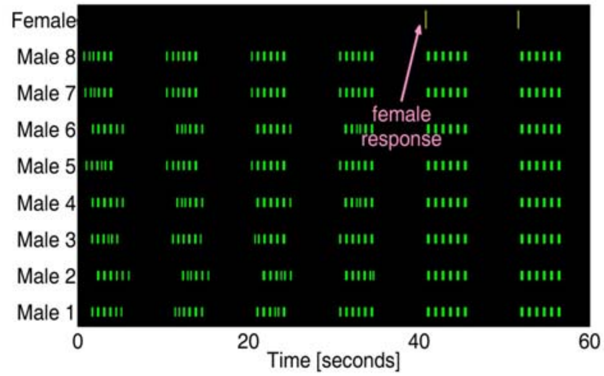

Fig. 2: (Color online) Flash sequences of eight males and one female when all are mutually interacting, obtained according to eq. (1), considering a distance dependent coupling with the parameters that mimics *P. carolinus*, i.e. phrases of $n_f = 6$ flashes, $T_{d0} = 200\,\mathrm{ms}$, and $T_{c0} = 500\,\mathrm{ms}$ for the males; and phrases of $n_f = 1$ flash, $T_{d0} = 100\,\mathrm{ms}$, and $T_{c0} = 6.0\,\mathrm{s}$ for the females. In both cases, the duration of a phrase is the same $T_p = 10\,\mathrm{s}$, and the initial conditions $\Delta\phi_i$ are chosen randomly.

C and D correspond to nonsynchronous stimuli with $\Delta\phi_i$ ranging from 4 to 4560 ms and from 7 to 4900 ms respectively. We performed numerical experiments using eq. (1) with the experimental parameters and features issued from [27], i.e. the LED signals are not modified ($\beta_{ij} = 0$), and only the female (index 9) is affected by the light of the 8 LEDs ($\beta_{9j} \neq 0$ and $\beta_{i9} = 0$), with $i, j = 1, \ldots, 8$. Fig. 3 shows the average response of the female computed over 100 numerical experiments for each stimulus A, B, C, and D. The error bars correspond to the standard deviation. As is shown, the numerical results are in good agreement with the experimental ones.

Synchronization in the population of males depends in general on the initial conditions, the number of individuals, the type of coupling and its strength. The results obtained using the all-to-all coupling show that the synchronization of the whole population of males with the consequent response in the females is more easily achieved than in the case of distance dependent coupling. This is due to the fact that the latter introduces a strong heterogeneity in the system and contrary to the former case, the synchronization of the whole population is not commonly achieved. Nevertheless, synchronized clusters emerge in the population and depending on the males' synchrony degree, the female could eventually respond. This is an interesting point since it shows that the complete synchrony of males is not mandatory in order to induce a female response (FR). Fig. 4 shows the evolution of the flashes of 499 slightly different males and one female coupled according to the distance dependent schema. The random initial conditions tend to evolve toward ordered situations as shown in fig. 4(b) but the degree of synchrony in the males is not still enough to induce a FR. Depending on the degree of synchrony of the males, FR can be sporadic or permanent as shown in fig. 4(c) and in fig. 4(d) respectively. In the sporadic case, at determined times, there exist FR despite the fact that not all the males are synchronized, contrary to the permanent case, in which all the males are synchronized. Thus, our results support the hypothesis of the role of males' synchronization on females recognition of its conspecifics, and also predict that the greater the initial number of males, the slower the female's response.

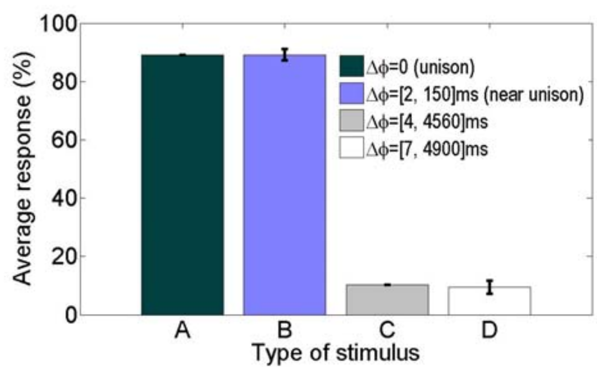

Fig. 3: (Color online) Percent female response to stimulus when applying the model to the cases presented by Moiseff and Copeland [27] (no interaction between males and no action of the female on males). The stimuli A, B, C and D correspond to the same LED configurations used in [27].

An exploration of our model allows us to describe situations that as far as we know, have not been yet described. For instance, in a situation in which the population is constituted only by females, they do not achieve synchronization when interacting. On the contrary, when the population is constituted both by males and females, synchronization-response occurs as described above but it is interesting that females can synchronize their responses due to the interaction between them and to the action of males on them. As an example, we consider in fig. 5

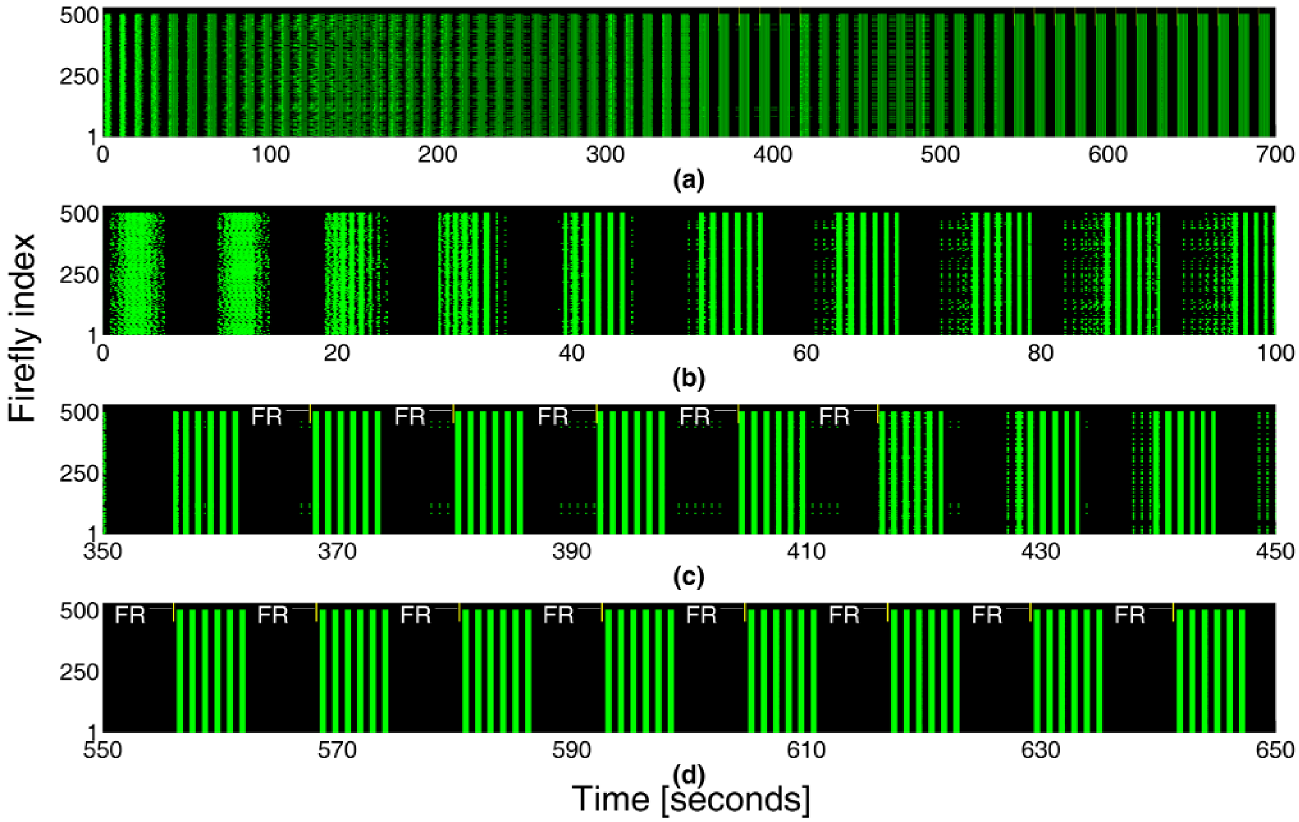

Fig. 4: (Color online) Evolution of the flashes in a population of 499 slightly different males and one female considering similar parameters and features as in fig. 2. (a) Whole sequence (700 s), from which are selected three regions: (b) Random initial conditions with the tendency to become ordered. Female response (FR) is not observed. (c) Phrases with almost total synchronization giving rise to sporadic FR. (d) Total synchronization with the consequent permanent FR. The FRs are indicated by means of a white line directed to the female flash (yellow flash corresponding to the index 500).

a population consisting of 15 males and 5 females with the characteristic that the individuals of the same sex are not identical and exhibit slight differences between them. When almost all the males are synchronized, some of the females can anticipate a synchronous but sporadic response as shown fig. 5(b). On the contrary, all the females respond synchronous and permanently when all the males are synchronized (fig. 5(c)). Finally, it is interesting to note that the males achieve the total synchronization more rapidly and permanently when considering the natural situation of mutual coupling between all the individuals (males and females). In order to highlight this fact, we consider a situation in which the population of males and females have the same features and parameters (same initial conditions and spatial disposition) as in fig. 5 but assuming that the coupling is unidirectional in the sense that only the males can influence the females. As a result of the aforementioned condition, the synchronization of the males takes more time and occurs first sporadically, followed by a loss of synchrony (fig. 6(a)) before becoming permanent (fig. 6(b)); therefore, the females' responses also follow this behavior. This fact reflects the existence of a reinforced action on the synchronization of the males when those perceive the response of the females. Thus, there is a kind of feedback since the males' synchronization enhances the females' response and these responses stabilize the synchronous regime of the males.

Summary and perspectives . – We proposed a model which explains the two main steps in fireflies' courtship. We obtained good agreement applying our model to experimental situations. We explored other aspects related to the interaction of mingled populations of fireflies. In summary, we showed the importance of a new concept: the response to synchronization which is stated as follows: considering two groups of oscillators, the oscillator(s) of one of the groups might respond when the most of the oscillators of the other group are synchronized. Interestingly, the experiments of Moiseff and Copeland involve mixed groups (artificial males and a real female) in a similar spirit as the integration of robots into groups of cockroaches by Halloy *et al.* [32]. A great challenge is to study mingled and mixed dynamical groups of fireflies and LCOs (as shown pictorically in Fig. 7). In this case, LCOs playing the role of artificial males might interact with mingled groups of fireflies, affecting their dynamics and also being affected by them, i.e. synchronizing with real males and inducing responses in real females. More-

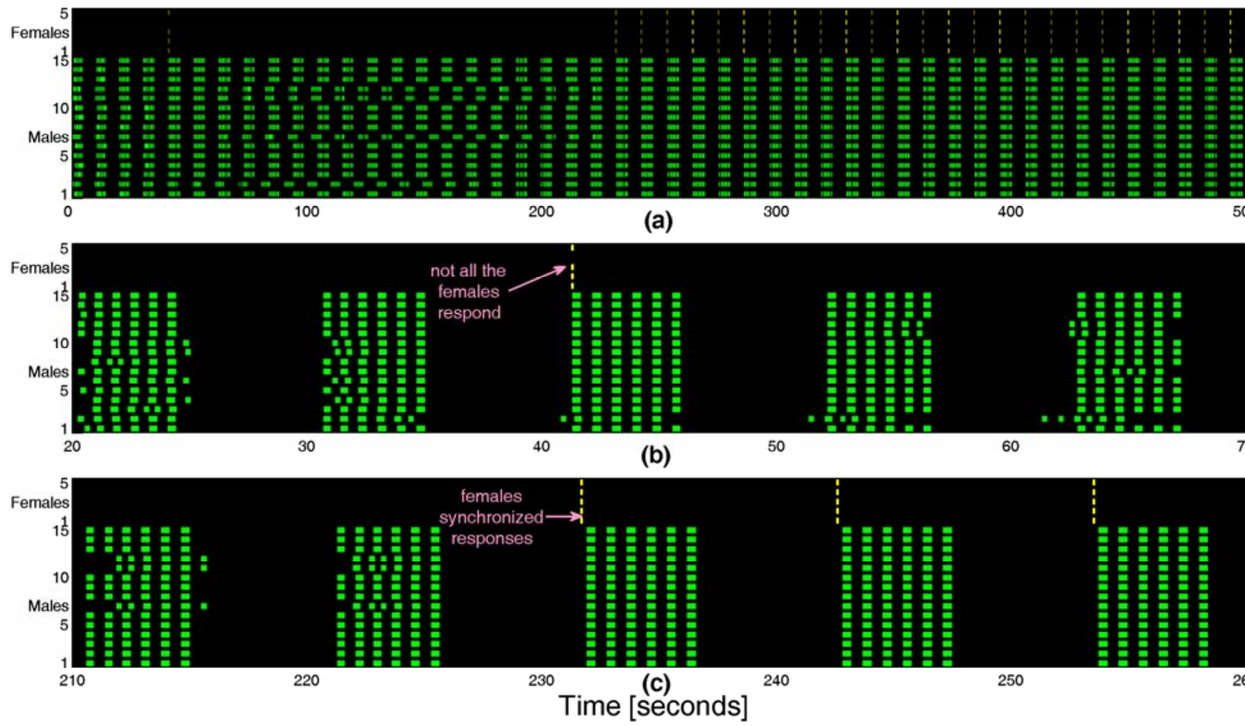

Fig. 5: (Color online) Evolution of the flashes in a population of 15 slightly different males and 5 slightly different females considering similar parameters and features as in fig. 2. (a) Whole sequence (500 s), from which are selected two regions: (b) Phrases with almost total males synchronization giving rise to sporadic FR but not in all the females. (d) Total males synchronization with the consequent permanent and synchronous FR of all the females.

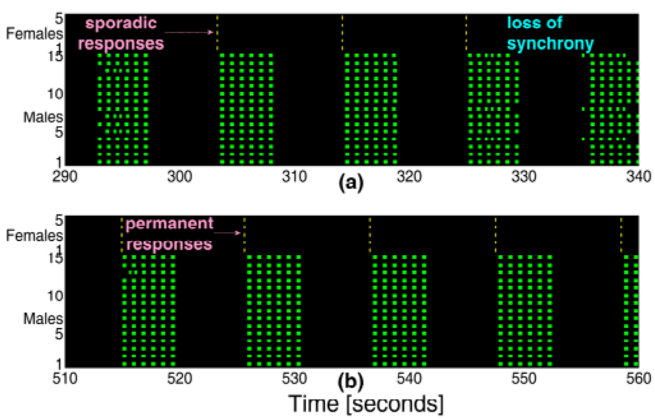

Fig. 6: (Color online) (a) Sporadic females' responses and (b) permanent females' responses when considering a similar situation as in fig. 5 (same parameters, initial conditions and spatial disposition of the males and females) but assuming that there is no action of the females on the males.

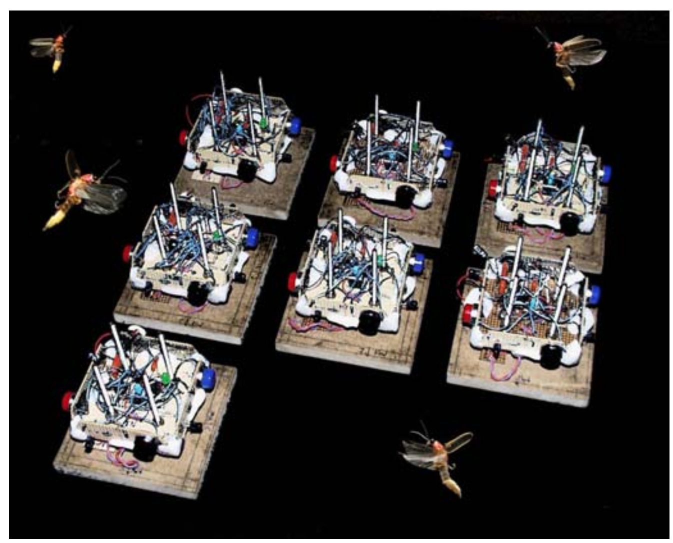

Fig. 7: (Color) A pictorial view of the interaction between LCOs and real fireflies. (Use of fireflies images with permission of Terry Priest.)

over, the study of mixed societies (animals-automata) can reveal further interesting details and also assess the hypothesis of self-organized courtship behavior of other fireflies' species and other species such as crickets, katydids and crabs in which similar processes are involved. Both the experimental issues and the model are complementary and might thus help in the design of the experiments with mingled and mixed groups. These results could also find application in systems in which synchronization triggers episodes requiring further response. Based on the principle of synchronization-response developed here, it is possible to conceive some devices which are capable to anticipate and respond to synchronization. The latter could be useful in synchronous neurons triggering epileptic seizures; the response to high levels of synchrony may have the ability to thwart the synchronous process.

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