Biology of Behaviour, 1977, 2, 143-158

Synchrony in Texas fireflies with a consideration of male interaction models

Daniel OTTE*, John SMILEY**

* *The Academy of Natural Sciences, Philadelphia, Pennsylvania, 19103.*
** *Department of Zoology, University of Texas, Austin, Texas, 78712.*

Key words : Fireflies, synchronous signaling.

RESUME

Un cas de synchronisation de groupe chez une luciole du nouveau monde est décrit

Lorsqu'ils sont en densité élevée, les mâles de *Photinus concisus* synchronisent leurs émissions lumineuses. Ils diffèrent des espèces de Nouvelle Guinée en ne formant pas d'agrégation sédentaires et semi-permanentes. Plusieurs modèles qui pourraient expliquer les avantages de ce synchronisme sont proposés.

Mots clés : Lucioles, Synchronisme, Signaux.

INTRODUCTION

We report here on a case of mass synchronization of flashes in a New World firefly, *Photinus concisus* Lloyd and use several simple models to explain the possible significance of synchrony. Most firefly species which are known to synchronize are Southeast Asian in distribution (Buck and Buck, 1966). In that region, and especially in the genus *Pteroptyx* Oliver, males form leks (all-male reproductive aggregations) in certain trees (swarm trees) where many thousands of individuals congregate and synchronize their flashes (Buck, 1938 ; Buck and Buck, 1966,

---

Reçu le : 10.8.1976 ; *Accepté le :* 18.10.1976.
Tirés à part : D. OTTE, adresse ci-dessus.

1976 ; Lloyd, 1973a, b). Females also fly to these trees and mating occurs there. Synchronous flashing is not as common among New World species and evidently rarely involves tight congregations of males (Buck, 1935, 1937b, 1938 ; Buck and Buck, 1966).

In the United States synchrony has been reported in *Photinus pyralis* Linn (Mast, 1912 ; Richmond, 1930 ; Rau, 1933 ; Buck, 1938), a close relative of *P. concisus*, but Lloyd (1969a) has caused males of *Photinus lineaticollis* and *P. greeni* Lloyd to synchronize with an artificial light which simulates the female answer, and has also showed (1969b) that males of *Photuris brunnipennis* synchronize when put together in the same jar. In Europe, Baldicini, Fiaschi and Papi (1969) occasionally observed synchrony in flying males of *Luciola mingrelica* Men. when males cruised near one another. Physiological mechanisms of synchronization have been discussed by Buck and Buck (1968, 1976), Hansen, Case, Buck and Buck (1971) and Baldicini, Fiaschi and Papi (1969).

OBSERVATIONS

On a wooded hillside just west of Austin, in central Texas, males of *P. concisus* flashed synchronously while flying. This population was observed in previous years (1972, 1973) in much lower densities, and no mass synchrony was observed. Between 15 and 30 May, 1974, and again in 1975 this same population was comparatively speaking very dense. Animals were most abundant and showed a high degree of synchrony in a thick stand of cedar, spanish oak, and yaupon along and above Madrone Road.

Synchronized flashing in *P. concisus* is similar to that observed in *Photinus pyralis* (Linn.) (Buck, 1935 ; Alexander, 1975) and differs from that of Southeast Asian *Pteroptyx* species in the following ways :

(1) No tight aggregations of males of the *Pteroptyx* types were discernible. In *P. concisus* synchrony sometimes extended across a whole woods, with waves of flashing proceeding from one section of the woods to another over distances up to 50 meters or more. Groups of more closely spaced males were often asynchronous with other such groups, but wave-like synchrony extending as far as one could see through the underbrush was common. Interactions between clusters of synchronizing males also produced wave-like action in *Photinus pyralis* (Alexander, 1975) and in *Pteroptyx* (Buck and Buck, 1968 ; Lloyd, pers. comm.). Shortly after males of *P. concisus* began to flash some minutes after sundown, synchronous flashing involved only neighboring males. Within the woods, greater cohesion of flashing among certain males could here and there be discerned, but we observed nothing fitting the description of swarm trees. Since males were more abundant inside the woods than outside, a very loose kind of aggregation imposed by the patchy nature of suitable habitat could be recognized, but such aggregations may not involve mutual attraction of males.

(2) Males of *P. concisus* synchronize while flying, whereas congregating New Guinea *Pteroptyx* usually synchronize while perched on vegetation.

(3) In *Pteroptyx* both sexes are capable of flight. Males are attracted to the flashes of other males and aggregate in certain trees, and females fly to these male aggregations (Buck and Buck, 1968 ; Lloyd, 1937 a, b). Females can also flash rhythmically although not in the male cadence, and once in the swarm tree their emissions are "relatively dim, long duration flashes or glows given both while perched and in flight" (Buck and Buck, unpub. manuscript). In *Photinus*, where

males are capable of flight and females rarely fly (Buck, 1935; Lloyd, 1966, 1968), pairs are formed when sedentary females (sitting on leaf litter or vegetation) answer the flashes of flying males. The males thereupon alight near the female and approach her on foot. An important difference between these two modes of pair-formation may be that in *Pteroptyx* the species-typical signal pattern is coded principally in the flashes of males, whereas in *Photinus* the males possess species-typical flash patterns, and the females answer in a species-typical fashion (Lloyd, 1966). Lloyd (1968) found that although male flash periods of *P. concisus* and its sympatric sibling *P. pyralis* are different, females of each species may answer male flashes of both species. But the delay between the male flash and the female answer was very different and is probably sufficient to prevent interspecific matings (*Table I*).

Table I: *Comparison of flash characteristics of* Photinus concisus *and* P. pyralis *(after Lloyd, 1968). These two species are sympatric in central Texas and are therefore likely to interact sexually. N, number of females or males observed.*

Tableau I: *Comparaison des caractéristiques des émissions lumineuses de* Photinus concisus *et* P. pyralis *(d'après Lloyd, 1968). Ces deux espèces sont synyatriques dans le centre du Texas et sont donc susceptibles d'interagir au plan sexuel. N désigne le nombre de ♀ ou ♂ observés.*

Female

	Delay (sec.)	Flash length	N	Temp.	Locality
P. concisus	0.57	0.61	5	22.7° C	Kerrville Texas
P. pyralis	2.15	0.38	8	26.5° C	Kerrville

Male

	Flash interval (sec.)	Flash length (sec.)	N	Temp.	Locality
P. concisus	2.2	0.3-0.4	many	23° C	Kerrville Texas
P. pyralis	5.9	ca. 0.6	many	22.7° C	Lake Lure N. C.

Time of Activity

P. concisus	starts about 30 minutes after sunset
P. pyralis	peak activity about 30 min. after sunset

CINEMATOGRAPHIC ANALYSIS

A movie was made of flashing males at 21°C (Beaulieu 4008 ZM II movie camera; Angenieux 8-64 Zoom lens; Tri-X super 8 film). Film speed was 8 frames per second. Not more than three fireflies were recorded at one time because of distance or scatter. Nevertheless, the movie was used to document synchrony between pairs and triplets. The number of flashes per frame in 2000 frames was counted. A flash was counted only once if it occured in two successive frames.

Distribution of flashes among frames was compared to a Poisson distribution and flashes were shown to be highly clumped. *Figure 1A* represents the flashing pattern in one 48-second sequence. Clearly there are few scattered, non-synchronous flashes. The same train is further analyzed by superimposing every 16th frame (*Fig. 1B*). The interflash

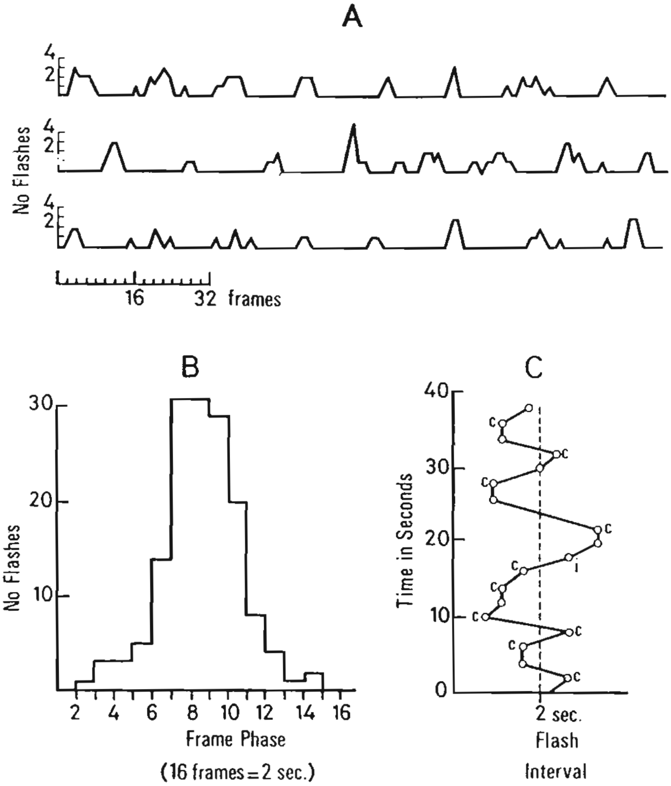

Fig. 1 :
A) Filmed flashing pattern in a 48-second sequence. Dots indicate midpoints in each pulse group.
B) Histogram of flash period, with every 16th frame of the movie superimposed, beginning with the center frame between the first two flash sequences.
C) Fluctuation in the flash interval around a 2-seconds flash period over a 40-second period (read from bottom upwards). Points to the left and right indicate longer and shorter flash periods. A *c* indicates a correct resetting towards the mean 2-second period and *i* indicate an incorrect resetting.

Fig. 1 :
A) Enregistrement cinématographique des émissions lumineuses lors d'une séquence de 48 secondes.
B) Histogramme de périodes d'émissions avec superposition de chaque 16ᵉ image, en commençant par l'image centrale entre la première et la seconde séquence d'émissions.
C) Fluctuation de l'intervalle d'émission autour d'une période de 2 secondes pendant un temps de 40 secondes (lire de bas en haut). Les points à gauche et à droite indiquent des périodes d'émission plus longues et plus courtes. Un « c » indique un ajustement correct vers la période moyenne de 2 secondes et un « i » un ajustement incorrect.

period varied little around 16 frames. The 16-frames period was determined by estimating for each synchronous pulse of flashes the center point or mean time that the pulse occurred. These points were estimated and summed to give an average which by chance equalled an integral number (interval mean averaged over 21 intervals = 16.0, with standard deviation 1.3). At other temperatures the flash period would be expected to be different (Buck, 1937a).

The constancy of the period seen in *Fig. 1B* can be shown to be greater than one would expect simply on the basis of a two-second (16 frame) flash interval with a given standard deviation. If the local group being photographed were flashing synchronously among themselves, but were isolated from other fireflies, then the flash periods would conform to a random variable, with mean 16 and S. D. 1.3. However, the steps are not random, as shown in *Fig. 1C*. When the peak begins to change phase with respect to the 16-frame period, there is a strong tendency for the next flash interval to be lengthened or shortened so as to bring the next flash peak back into phase. A series of random steps on the other hand should give an approximately equal number of correct and incorrects steps. As shown *Fig. 1C* there were 10 correct steps, one incorrect step, and five neutral steps. The probability of this occuring by chance alone is less than 0.006 (Binomial distribution, $N = 11$, $p = 0.5$). Apparently the larger aggregation of males is operating to re-set the flash period of the local group to the observed 2-second period.

DISCUSSION

Lloyd (1973b) proposed two models to account for synchronous flashing in *Pteroptyx*. We shall review and build on these, but our models will relate primarily to *Photinus* fireflies, species in which males do not form tight, sedentary aggregations. Because synchrony is correlated with the density of individuals (see Buck, 1935 ; Buck and Buck, 1966) we have also attempted to model the possible effects of density on flash behavior.

It is important at the outset to consider the distances over which males and females perceive and begin to interact with one another. We do not know what the precise distances are, but existing data (Lloyd, 1966) suggest what the signs of the major inequalities are.

A. Interaction Distances

We believe that the following interaction distances are the most important in a consideration of a *Photinus*-like signaling system :

1. *dmsf* : distance at which males can see females (determined mainly by male vision, conspicuousness of female flash, and prevalence of physical obstructions to vision). In firefly genera in which mobile, roving

males seek sedentary females, the eyes of the male are much larger than those of the female. But in species in which females are also mobile and fly to males, the eyes in the two sexes are more nearly equal (Buck and Buck, 1966).
Consequently we expect *dmsf* to be greater in *Photinus*-types species than in *Pteroptyx*-type species.

2. *dmdf :* distance at which males can distinguish the flashes of females from those of males. This distance will probably vary greatly with male population density, but at low densities *dmsf* and *dmdf* should be nearly equal.
3. *dmrf :* distance at which males respond to females by approaching (this distance is probably equal to *dmsf* because male reproductive success is likely to be proportional to the number of times he mates. Therefore the larger the value of *dmsf* and therefore of *dmrf* the more females can be encountered per unit time). This distance is likely to be less in *Pteroptyx* than in *Photinus* (see 1 above).
4. *dfsm :* distance at which females can see males (determined by female vision, conspicuousness of male flash and the incidence of physical obstructions to vision). When males are aggregated (*Pteroptyx*), *dfsm* is greatly increased and Lloyd (1937b) showed that both *dfrm* and *dmrm* is increased as size of male aggregation, and hence of the overall light intensity, increases.
5. *dfrm :* distance at which females respond to males ; *dfrm* is probably less than *dfsm* for two reasons : (a) female flashes are less conspicuous than male flashes ; females might therefore tend to reduce predation* risks by flashing only when males are very near. (b) Females are more likely to be choosy than males (for reasons given by Trivers, 1972) and are likely to respond only when the chances of mating with a suitable male are high. Her reproductive success is more likely to be determined by the quality of her mate than by the number of times she copulates. When a female's urge to mate is very high, as under very low population densities, then *dfrm* might even exceed *dmsf*. the higher the density and therefore the probability of encountering males, the more choosy she can afford to be.
6. *dmsm :* distance at which males can see males (determined by male vision, conspicuousness of male flash and vegetation density).
7. *dmrsm :* distance at which males respond to other males by synchonizing (determined by unknown factors, but possibly by the probability of signal interference by another male or by the chances of interloping (see following models).

---

* Lloyd (1973 c) has compiled a list of firefly predators. He notes that fireflies may be distasteful to some predators, but that other predators such as goatsuckers (*Caprimulgidae*), potoos (*Nyctibiidae*), spiders, certain lizards and frogs may specialize on firefly prey at times.

B. SYNCHRONY MODELS (NOISE REDUCTION)

Most firefly pair-formation involves an exchange of signals between males and females. When many individuals are simultaneously active the noise-to-signal ratio is high, thus interfering with the exchange of signals between a male and female. Three different models explain how synchrony might reduce the noise level and increase the probability of pairing.

1. *The rhythm-preserving model* (*Fig. 2A*).—If females select males on the basis of flash repetition rate, and respond only to the correct (conspecific) flash period, then cloasely spaced males of the same species which flash synchronously would not disrupt the species-specific rhythm. However, males would be under selection to synchronize their flashes only if females responded less to an asynchronously flashing male than to a synchronizing male, which they might be selected to do if there was some chance of coupling with males of another species. The model applies only to species in which male species-specificity is coded in the flash repetition rate.

2. *Delay recognition model* (*Fig. 2B*).—If males need to compute the delay of female answers in order to distinguish between conspecific and heterospecific females, then selection may favor males which synchronize their flashes. We surmise that this would be especially likely if asynchronously flashing males could not properly distinguish between the delays of conspecific females following their own flashes and the delays of heterospecific females following the flashes of their males ; or if males could not distinguish between flashes of females and those of other conspecific males. Since females of *P. pyralis* sometimes also answer males of *P. concisus* (in the laboratory) and the two species are sympatric (Lloyd, 1968), the ability to correctly compute delay may be important. Each male would then benefit by synchronizing if this improved his ability to compute female delay time. This model could only apply to those species in which the species-specificity in male signals is coded in the flash repetition rate and that of females is coded in delay time. Buck (pers. comm.) has claimed that simulation of the flash repetition rate of male *P. pyralis* can be varied considerably without affecting the answering response of females. If this is true, it would appear that model 1, which calls for a preservation of rhythm, is a less likely explanation than model 2.

3. *The female detection model* (*Fig. 2C*).—In a field crowded with flashing males and a few answering females, picking out the occasional female flashes from the mass of asynchronously blinking lights may be a difficult feat. The noise-to-signal ratio would be greatest under conditions where males attempt to flash during dark periods, would be less when males are flashing at random, and would be least when they are flashing synchronously (see *Fig. 2C*). This model would be most appropriate for those species in which males are watching for female answers. In *Fig. 3*

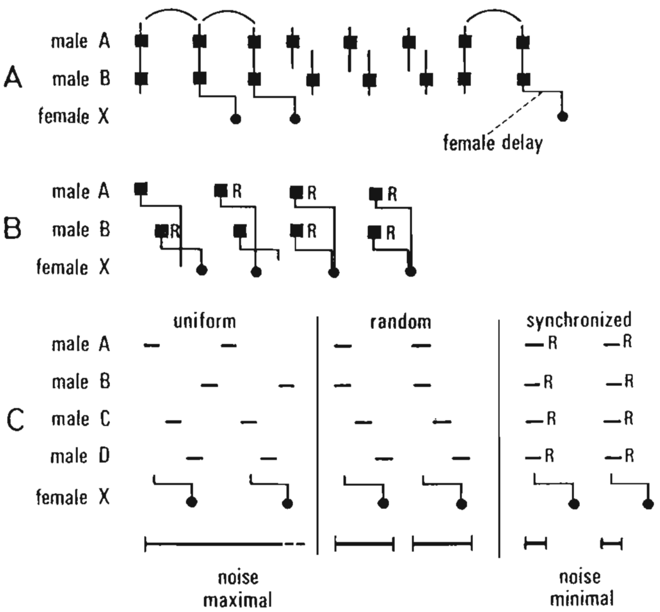

Fig. 2 :
A) Female X observes at least one interflash period and when that period agrees with the species-typical pattern, she answers. When males flash asynchronously that pattern is more likely to be disrupted.
B) Female X responds alternately to several males, but males respond to the female only when the delay corresponds to the species-typical pattern. When males A and B synchronize they can detect the species-typical delay each time they flash (R stands for a positive male response following the female flash).
C) A hyperdispersed or uniform spacing of males flashes maximizes the noise-to-signal ratio, making it difficult for males to see female flashes. Synchronized flashing reduces the noise level for all males to a minimal level.

Fig. 2 :
A) La femelle X observe au moins une période interémission et si cette période correspond à celle caractéristique de l'espèce, elle répond. Lorsque le mâle émet de manière asynchrome, cette période a tendance à être interrompue.
B) La femelle X répond alternativement à plusieurs mâles, ceux-ci ne répondent à la femelle que lorsque le délai correspond à la caractéristique de l'espèce. Lorsque les mâles A et B se synchronisent, ils peuvent à chaque émission détecter le délai caractéristique (R indique la réponse positive du mâle à la suite d'une émission femelle).
C) Un espacement uniforme ou une dispersion extrême des émissions des mâles accroît au maximum le rapport « signal/bruit » rendant difficile pour les mâles de percevoir les émissions des femelles. La synchronisation des émissions réduit pour tous les mâles le « bruit » à un niveau minimum.

we plot hypothetical relations between noise level and number of males signaling. With few males (two or three) the hyperdispersed and random patterns should be similar, with noise levels rising linearly. At some point, random flashes begin to overlap with each other, while hyperdispersed flashes do not. The result is a divergence of random and hyperdispersed curves. The synchrony curve, in the meantime, remains near zero.

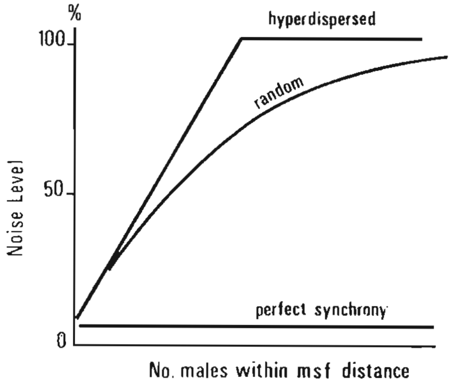

Fig. 3 : *Theoretical noise levels as a function of male density.*

Fig. 3 : *Niveaux théoriques de « bruit » en fonction de la densité des mâles.*

INTERLOPING

Males could conceivably use the flashes of other males to find females, and synchrony could improve this ability. Such exploitation could be achieved in two ways :

4. *Interloping model.*—Consider the behaviour of a set of individuals all belonging to the same species (*Fig. 4*). Male A is flashing periodically and is attempting to locate females ; female X is nearby and responds to him directly. Female Y, who is more distant, responds only to male B, but A can see her when she does so, since she is within his *dmsf*. If female delay time is important to males (as in species where males are mobile and females are sedentary) then the only way A can known if Y's delay time is appropriate is if he is synchronized with B.

This model assumes that a male computes delay time between his own flash and that of the female, rather than the delay between another male's flash and a female's answer.

5. *Conspecific cuing model.*—If male A cannot see a female (Z) directly (she is outside his *dmsf* or is hidden), male A could conceivably tell, through changes in behaviour of male B, if B is interacting with her (a case of conspecific cuing—Kiester and Slatkin, 1974). On intuitive grounds, it seems likely that A will be better able to visually track the behaviour of several males and to detect behavioural changes in such males if he is synchronous with them. Some evidence exists for conspecific cuing in fireflies. Buck (1935) showed that males of *Photinus pyralis* frequently approach females who are responding to other males. He describes the interaction as follows : "... the exchange of signals is initiated by a single pair of insects (male and female), and other males within range of the female (10 feet) often join in . . . so that at times as many as five males may fly simultaneously toward the same female, and . . . under these conditions all these males flash in unison. Here, obviously, there is

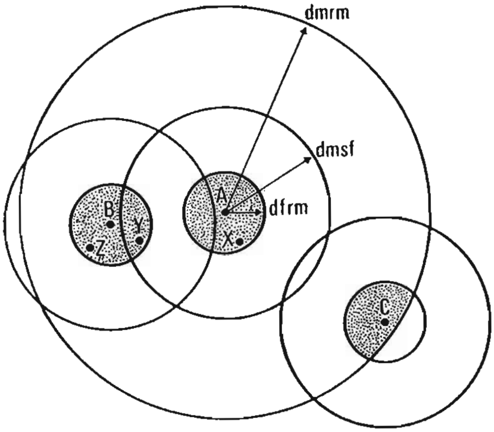

Fig. 4 : *Interloping model of male interactions.* Male A can respond to female X directly. But A can see female Y only if she responds to male B, since A is outside her response range. Male A cannot see the flash of female Z, either because she is beyond the *dmsf* range or because she is out of site, but can find her by watching the flashing behaviour of male B. Since females may aim their light at specific males the (Lloyd, 1973) *dfrm* field may not be circular.

Fig. 4 : *Modèles « intrusion » d'interaction entre mâles.* Le mâle A peut répondre directement à la femelle X. Mais A ne peut voir la femelle Y que si elle répond au mâle B, A étant hors de sa zone de réponse. Le mâle ne peut voir les émisisons de la femelle Z soit parce qu'elle est au-delà de sa zone de perception, soit parce qu'elle est hors du site, mais il peut la détecter en observant les émissions du mâle B. Puisque les femelles peuvent diriger leur lumière vers un mâle donné, les champs *dfrm* peuvent ne pas être circulaires (Lloyd, 1973).

some mechanism other than chance which induces males originally out of phase with each other and flashing with different periodicities to break their ordinary rhythms and readjust them to the particular male which first responds to the female. Often observed this kind of readjustment of flashing in the field..."

Buck's description clearly indicates that males attempt to interlope, but because critical bits of information are lacking, it is not known which of the above models is most appropriate. For example, it is not clear whether the males synchronized once they observed a male interacting with a female or if they synchronized once they were drawn in close enough that synchrony was possible. R. D. Alexander (1975) has observed in *P. pyralis* the kind of synchrony we observed in *P. concisus*, suggesting that synchrony need not involve females flashes.

In *P. concisus* synchrony commonly occurs among closely spaced males that are not interacting with females. Buck's description does suggest that males can detect males that have found females without being synchronous with them. This means that the initial stages of interloping do not require synchrony. The synchrony he observed may have the principal advantage of maintaining the species-specific rhythm in the final stages of interloping. It seems unlikely that interloping males need to compute delay at this stage; one of their own kind has already determined that. It is possible that synchrony allows the female to determine the rhythm of each approaching male, which means that model 1 applies. But Buck (pers. comm.) has shown that females respond to a variety of flash rhythms, implying that the synchrony may not function in preserving the rhythm. The second interloping model is a possible alternative. As a test, a number of artificial lights, each approximating the light of a single male could be varied and flashed either synchronously or asynchronously.

ENHANCEMENT

6. *The Response Enhancement Model.*—This model utilizes the notion of a super-normal stimulus. Synchrony would be selected in both males if by flashing synchronously they collectively generate a greater stimulus and thence a greater female response than they would by flashing asynchronously. According to Buck and Buck (ms) enhancement is achieved by two separate but mutually reinforcing mechanisms: augmentation of peak flash intensity and intermittency of signal. According to Buck and Buck: "Augmentation of flash intensity by synchronization can be evaluated conservatively as follows: For ten males with interflash periods averaging 1000 milliseconds and flash duration 100 msec, enhancement by random flash coincidences during 1000 successive 100 msec intervals averages 1.6 reinforcement units ... compared with 10 units for actual synchronization. Hence the mean increase in peak light intensity due to synchronization would be of the order of 6-fold. The further signal enhancement via intermittency ... cannot be evaluated without data on latency, refractory period, etc., for the firefly eye. However, the finding that rate of rise of light intensity is more important than absolute intensity in eliciting response ... supports the assumption that flash synchronization will increase conspicuousness of a tree display over and above the augmentation of light intensity."

Case, Hanson, Polunin, and Barnes (1972) provide some indirect evidence of enhancement. They found that *Pteroptyx* males could be attracted to bright electric lights flashing in tune with the fireflies. Alexander and Moore (1958) propose a similar enhancement effect of synchrony in *Magicicada*. In *Pteroptyx* (Lloyd 1973b) showed that both males and females tend to orient preferentially to groups of males displaying the highest light intensity, indicating a response-enhancement might be feasible in a massive aggregation as well. But no response-enhancement produced by synchrony has been established. It would be difficult to test in any event, because if females were more strongly attracted to a group of synchronizing males than to a group of non-synchronizing males, they could be responding to the species-specific rhythm in one case and failing to respond to a confused rhythm on the other.

DENSITY EFFECTS

Under model 3 we discussed the effect of density on noise levels. We now consider interaction distances which are affected by density and how synchrony might affect such distances under various models.

a) *Dfsm* is not expected to be much altered by density, at least within the range of naturally attained densities (*Fig. 5A*). But *dfrm* is expected to decline as density increases, for two reasons : (i) *Voluntary dfrm* reduction : In the presence of a large number of males, where mating has a high probability of occuring, females can afford to respond only to very nearby males or otherwise be more selective. Greater selectivity results in a reduced risk of predation and perhaps a savings in energy which can be reallocated to some other feature under strong selection, such as egg production. (ii) *Involuntary dfrm reduction:* A further decrement in *dfrm* may be due to difficulties females have in detecting species-typical flash patterns. Such difficulties would be expected to be most pronounced when signal parameters other than the flash itself, such as flash repetition rate or pattern, were involved and when there was some considerable cost attached to making the wrong choice. Under models 1 and 6, synchrony tends to allow a higher *dfrm.*

b) *Dmsf* is expected to decline only minimally as density increases. If males eyes are refractory to a flash which immediately follows another flash, *dmsf* could decrease markedly. But the existence of some very rapid flash repetition rates in some species suggests that refractoriness may not be important. But *dmdf* (hence also *dmrf*) is expected to decrease markedly due to the increased noise-to-signal ratio (*Fig. 5B*). Under models 2 and 3 we expect synchrony to have an increasingly marked effect on *dmdf* as density increases.

c) Models 4 and 5 suggest mechanisms by which *dmrf* could increase as density increases and even to exceed *dmsf* (*Fig. 5C*). According to these models, males begin to interact with females over increasingly larger distances through conspecific cuing.

CONCLUSIONS

We believe that all of the above models are testable at least in theory. Technical problems may make testing some of them quite difficult. The reasonably firm conclusions which one can draw from the research on firefly flashing and synchrony to date are these : (1) Flashing is the means by which pairs are formed and synchronous flashing only occurs under conditions of close proximity between males. It is *only* under such conditions that signal interference would operate, and under which males can perceive one another and interact. Close spacing may be achieved through active congregation of males (*Pteroptyx*) or it may be a secondary consequence of high density (*Photinus*).

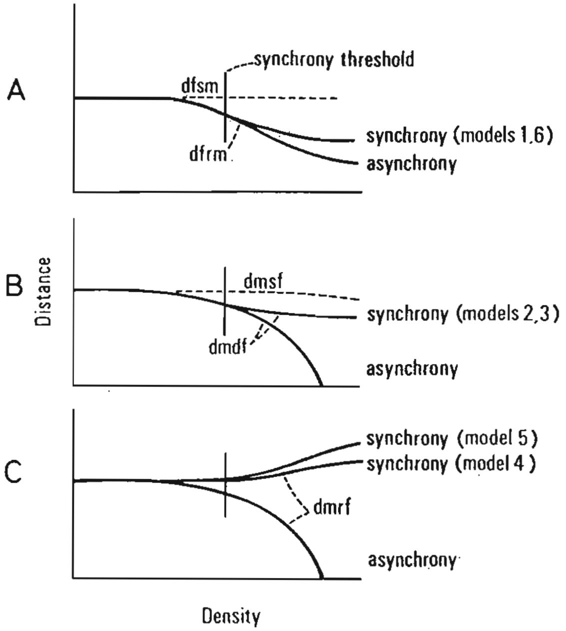

Fig. 5 : *Hypothetical effects of density and synchrony on interaction distances.* The synchrony threshold is the density at which synchrony is physiologically possible.
A) *dfrm* drops because of two interacting factors : (i) females can afford to be more choosy when males are abundant, hence may voluntarily reduce their responsiveness ; (ii) females may become confused by numerous male flashes and may be less able to perceive species-typical flashing rates. Synchrony models 1 and 6 would tend to remove the latter component of *dfrm* reduction.
B) *dmdf* is expected to go to zero when the noise of male flashes completely obscures the occasional male flashes. Under synchrony models 2 and 3 the noise levels are reduced sufficiently to measurably improve *dmdf*.
C) Under models 4 and 5 *dmrf* might actually increase with density as males begin to use the flashes of other males.

Fig. 5 : *Effets hypothétiques de la densité et du synchronisme sur les distances d'interaction.* Le seuil de synchronisme est celui où la densité rend possible physiologiquement le synchronisme.
A) *dfrm* diminue en raison de deux facteurs agissant en interaction : (i) les femelles peuvent se permettre d'être plus sélectives lorsque les mâles sont abondants, ce qui peut les amener à réduire volontairement leur réactivité ; (ii) les femelles peuvent être perturbées par les nombreuses émissions des mâles et peuvent être moins aptes à percevoir les rythmes caractéristiques de leur espèce. Les modèles 1 et 6 tendraient à supprimer cette dernière composante de la réduction de la *dfrm*.
B) *dmdf* est supposé tendre vers zéro lorsque le « bruit » des émissions des mâles brouille complètement les émissions occasionnelles des mâles. Selon les modèles 2 et 3 les niveaux de « bruit » sont suffisamment réduits pour améliorer de manière mesurable la valeur de *dmdf*.
C) Selon les modèles 4 et 5, la *dmrf* peut s'accroître en fait avec la densité puisque les mâles commencent à utiliser les émissions des autres mâles.

Active aggregation and synchrony are tenuously connected phenomena. The existence of sexual aggregation among non-synchronous insects (Alexander, 1975) and the tight aggregations among non-synchronous Jamaican fireflies indicates that synchronous flashing evolves after aggregations become advantageous for other reasons. Buck and Buck (1966) showed that Thai fireflies observed in a darkroom show a definite attraction to each other's light even before synchronization begins. Of course synchrony among the members of an aggregation may, through signal enhancement, further promote aggregation.

If aggregated males have a higher reproductive success than non-aggregated males, one arrives at the seeming paradox that males can compete and cooperate at the same time. We can imagine 10 males in a field all competing for the available females. If a cluster of three males

Table II : *Some conditions promoting synchrony. Conditions 1 through 4 are more or less essential for synchrony to occur and relate primarily to physiological capacities to synchronize. Conditions 5 and 6 relate principally to factors which make it useful to reduce the noise-to-signal ratio in male-female or male-male communicative interactions.*

1. Signals consist of brief flashes of uniform length.
2. Repetition rate of flashing very regular and not grouped into doublets, triplets, etc.
3. Repetition rate of flashing not too fast (less than two flashes/sec. ?) and not too slow (more than one flash/six seconds ?).
4. Individuals sufficiently aggregated to permit synchrony (i) to occur in the first place and (ii) to be beneficial.
5. Repetition rate in male flashes constitute an important species-specific parameter (i.e., one by which females distinguish between species).
6. Delay between male-flash and female answer an important species-specific parameter (one by which males distinguish their own females).
7. Females with tendency to respond only to strongest male signal.

Tableau II : *Conditions amenant au synchronisme. Les conditions de 1 à 4 sont plus ou moins essentielles au synchronisme et concernent principalement les capacités physiologiques à ce synchronisme. Les conditions 5 et 6 ont trait principalement à des facteurs qui le rendent utile pour réduire le rapport signal-bruit dans les communications ♂-♀ ou ♂-♂.*

1. Signaux constant ou émissions brèves et de durée uniforme.
2. Taux de répétition des émissions très régulier et non groupé par 2-3, etc.
3. Taux de répétition pas trop rapide (inf. à 2/seconde) et pas trop lent (supérieur à 1 toute les 6 secondes).
4. Individus suffisamment rassemblés pour permettre au synchronisme d'abord de reproduire, puis d'avoir une action favorable.
5. Taux de répétition des émissions des mâles consistant un paramètre important et caractéristique de l'espèce (permettant par exemple aux ♀♀ de distinguer les espèces).
6. Délai entre l'émission du mâle et la réponse femelle constituant un paramètre important spécifique de l'espèce (un de ceux permettant aux mâles de distinguer leurs ♀♀).
7. Femelles ayant tendance à ne répondre qu'au plus fort signalement des ♂.

attracts nine females, thereby increasing their respective RS's, the males have cooperated to achieve their higher RS. Nevertheless, they continue to compete among one another for females so attracted. Clearly the continuance of such aggregations requires that the benefits of the aggregations (in terms of number of matings) exceed the costs (in terms of reduced RS due to competition among males).

Table II arranges the factors which favor the evolution of synchrony into two major categories :

a) the physical properties which make synchrony physiologically possible and.

b) the physical properties of the signal code which makes synchrony advantageous to the participating individuals.

Acknowledgements : We are greatly indebted to John Buck, James Lloyd, and Richard Alexander for their criticisms of earlier versions of this manuscript. Although we have not followed all of their suggestions, the paper has evolved to a higher state as a result of their careful reading of it.

SUMMARY

A case of mass synchronization in a New World firefly is described. Under high densities male *Photinus concisus* Lloyd synchronize their flashes. They differ from New Guinea fireflies in failing to form sedentary and semi-permanent aggregations. Several models are given to explain the advantages of synchrony.

REFERENCES

Alexander R.D., 1975. Natural selection and specialized chorusing behaviour in acoustial insects. In : *Insects, Science and Society. Academic Press, Inc.*, edit., New York, pp. 35-77.

Alexander R.D., and T.E. More., 1958. Studies on the acoustical behaviour of seventeen-year cicadas (Homoptera ; Cicadididae : *Magicicada*). *Ohio J. Sci., 58,* 107-27.

Baldacini N.E., V. Fiaschi and F. Papi, 1969. Rhythmic synchronous flashing in a Bosnian firefly. *Monitore Zool. Ital. (N. S.), 3,* 239-245.

Buck J.B., 1935. Synchronous flashing of fireflies experimentally induced. *Science, 81,* 339-340.

Buck J.B., 1937a. Studies on the firefly. II. The signal system and color vision in *Photinus pyralis. Physiol. Zool., 10,* 412-419.

Buck J.B., 1937b. Flashing of fiireflies in Jamaica. *Nature, 139,* 801.

Buck J.B., 1938. Synchronous rhythmic flashing of fireflies. *Q. Rev. Biol., 13,* 301-314.

Buck J.B., and E. Buck, 1966. Biology of synchronous flashing of fireflies. *Nature (London), 211,* 562-564.

Buck J.B., and E. Buck, 1968. Mechanism of rhythmic synchronous flashing of fireflies. *Science, 159,* 1319-1327.

Case J.F., F.H. Hanson, I. Polunin, and A.T. Barnes, 1972. Mechanisms and adaptive significance of aggregation in synchronous flashing fireflies. *Am. Zoologist, 12,* 683.

Hansen F.F., J.F. Case, E. Buck, and J. Buck, 1971. Synchrony and flash entrainment in a New Guinea firefly. *Science, 174,* 161-164.

Kiester A.R., and M. Slatkin, 1974. A strategy of movement and resource utilization. *Theory Pop. Biol., 6,* 1-20.

Lloyd J.E., 1966. Studies on the flash communication system in *Photinus* fireflies. *Misc. Publ. Univ. Mich. Mus. Zool., 130,* 1-95.

Lloyd J.E., 1968. A new *Photinus* firefly, with notes on mating behaviour and a possible case of character displacement (Coleoptera : Lampyridae). *Coleop. Bull., 22,* 1-10.

Lloyd J.E., 1969a. Flashes, behaviour and additional species of Nearctic *Photinus* fireflies (Coleoptera : Lampyridae). *Coleop. Bull., 23,* 29-40.

Lloyd J.E., 1969b. Flashes of *Photuris* fireflies : their value and use in recognizing species. *Florida Entomol., 52,* 29-35.

Lloyd J.E., 1973a. Fireflies of Melanesia : Bioluminescence, mating behaviour, and synchronous flashing (Coleoptera : Lampyridae). *Environm. Entomol., 2,* 991-1008.

Lloyd J.E., 1973b. Model for the mating protocol of synchronously flashing fireflies. *Nature, 245,* 268-270.

Lloyd J.E., 1973c. Firefly parasites and predators. *Coleopterists Bull., 27,* 91-106.

Mast S.O., 1912. Behaviour of fireflies (*Photinus pyralis*) with special reference to the problem of orientation. *J. Anim. Ecol., 2,* 256-272.

Rau P., 1932. Rhythmic periodicity and synchronous flashing in the firefly, *Photinus pyralis,* with notes on *Photuris pennsylvanicus. Ecology, 13,* 7-11.

Richmond C.A., 1930. Fireflies flashing in unison. *Science, 71,* 537-538.

Trivers R.L., 1972. Parental investment and sexual selection. In B. Campbell (ed.). Sexual Selection and the Descent of Man : 1871-1971. Chicago : Aldine. 379 pp.