TOWARD A FUNCTIONAL INTERPRETATION OF SYNCHRONOUS FLASHING BY FIREFLIES

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In typical roving fireflies of the Western Hemisphere neither males nor females are gregarious. Rhythmically flashing males fly individual patrols over low vegetation in which females are perched. If a female answers the signal of a male the two fireflies may begin a courtship involving a series of alternating, timed flashes (McDermott 1910–1917, 1914; Mast 1912; Buck 1937a; Lloyd 1966, 1971).

In certain species of the tropical Far East the fireflies gather in trees by thousands, and the males flash in rhythmic synchrony. Since mating occurs in such trees it has been assumed that the communal display is some sort of sexual adaptation, but none of the published studies has provided an integrated explanation for the congregating, for the use of trees for assembly, and for the flash synchronization. In this paper we present such an explanation, based, insofar as possible, on strict selectionist considerations.

MASS SYNCHRONOUS FLASHING

Over the past 300 yr mass synchronous flashing of fireflies has been reported from many tropical regions within the great arc stretching from the Philippines and New Guinea through Malaysia, Indonesia, and Thailand to Ceylon and eastern India (Buck 1938; Buck and Buck 1968). The classical displays, as seen along the banks of the Chao Phraya River below Bangkok, comprise myriads of fireflies perched on the leaves of mangrove trees, flashing in unison “...hour after hour, night after night, for weeks or even months” (Smith 1935, p. 151). Morrison (1927, 1929) and Smith discovered that the synchronously flashing fireflies are males. Haneda (1941) found that females are also present in the trees, though they take no part in the synchrony, and that mating pairs are common. Many males and females remain in assembly trees by day (Haneda 1941, 1966; Buck and Buck 1966; Bassot and Polunin 1967). Presumably the display of the following evening is begun by these fireflies rather than by newly assembling specimens. In Malaysia certain individual display trees are said to be used by the natives as nocturnal marks in river navigation (Watson 1928) and we heard a similar story from rivermen south of Bangkok. Ivan Polunin studied synchronized fireflies in a particular tree near Singapore during 5 successive yr (personal communication). These indications, plus collection records for several species and areas, argue that although there may be some seasonal fluctuation in population density many firefly tree congregations are essentially permanent. Since individual adult fireflies usually do not live more than a month, at least in captivity, the tropical mass displays are presumably maintained by recruitment from populations that breed throughout the year.

In some roving fireflies the entire luminous dialogue can be observed directly, and unequivocal conclusions may be drawn about function (e.g., Buck 1937a; Lloyd 1966). In synchronizing species, on the contrary, the difficulties in observing individual fireflies

continuously during their approach flight to the display tree, and in sorting out "display" from "response" flashing among the crowded in-tree fireflies have thus far thwarted attempts to put together a coherent picture of courtship and mating behavior. Consequently both Lloyd (1973b, 1973c) and we (Buck and Buck 1966, 1976) have bolstered our particular views of what is going on in firefly swarms with observations and data from more than one synchronizing species and from nonsynchronizing species of America and Europe as well as the Far East. In spite of this tacit assumption that "synchronous flashing" is a monolithic behavior it has become increasingly clear that displays may differ significantly from species to species and area to area (Ballantyne and McLean 1970; Lloyd 1973b). To caution against facile generalization, a range of reported behaviors, some not clearly compatible with hypotheses developed in this paper, is described in Appendix I. More specifically the reader should keep in mind that Lloyd's model, based primarily on several fireflies of the New Guinean highlands, and our formulation, derived from one species from Thailand and Malaysia and two from the lowlands of Karkar Island and New Britain (see below), may refer to basically different behaviors and may in any case invoke irrelevant or erroneous species data.

We base our courtship model primarily on the Thai variety of *Pteroptyx malacca* because the males normally display while perched and because they maintain their individual positions for long periods. In this species several types of in-tree luminescence have been identified besides the monotonous and apparently unmodulated 2/s display flashing rhythm of the perched males. Males typically emit a high frequency flicker (12/s) when flying within or close to the tree but also occasionally synchronize with in-tree males while in flight. Flickering is also a common response to mechanical disturbance (except sexual: luminescence typically either ceases during copulation or is reduced to a dull glow). Perched females emit irregularly timed, long-duration glows that are dimmer than the male's emission. Occasionally fireflies flashing in the species rhythm (hence presumably males) were seen joining the swarm from a distance. No intersexual signaling or responses were recognized, nor was anything interpretable as individual-to-individual communication noted between in-tree and out-of-tree fireflies. Admittedly the overpowering beat of the male rhythm makes it both visually and psychologically difficult to focus on possible events during the interflash "dark" periods.

In *Pteroptyx cibellata* (New Britain) and *Luciola pupilla* (Karkar Island) in-tree behavior is still more difficult to decipher because many (most?) of the visible males are in constant slow flight as they emit their 1/s display flashes (Appendix I). In these species also the males may flicker (5-15/s) when alighting or taking off (see also Lloyd 1968, 1973b), or when disturbed mechanically, or, occasionally, during hovering flight. Sporadic glows among the massed flashes of the rhythmic male display were traced to perched females and long glows or close-timed series of long, dim flashes are emitted by females joining, traversing, or leaving the swarm. We saw one instance interpreted as an attraction of a flying (glowing) female to a hovering (flashing) male and two instances of a flickering male landing on a female's leaf. We observed sparse two-way traffic of glowing females between tree and ground. We saw nothing recognizable as interindividual communication. In a laboratory test a female of *P. cibellata* was found able to flash spontaneously and rhythmically, though not in the male cadence. This behavior contrasts with that of females of many roving species that normally flash only in response to stimulation.

**PHYSIOLOGY OF SYNCHRONIZATION**

Laboratory work on both roving and gregarious species of firefly has demonstrated volleys of action potentials in the ventral cord and in peripheral lantern nerves,
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associated 1:1 with spontaneous flashing, and in two roving species the flash-control "pacemaker" has been localized to the brain (Case and Buck 1963; Bagnoli et al. 1976). In several synchronizing species it has been shown that the synchronization is sufficiently precise to exclude the possibility that the flashes in any one mass episode are responses to flashes of a leader or leaders in the same episode (Buck and Buck 1968; J. Buck, E. Buck, J. F. Case, and F. E. Hanson, unpublished manuscript).

Experiments in which lowland New British Pteroptyx cribellata males were entrained to a rhythmically flashed electric light showed that each stimulus received by the eyes resets the animal's flash pacemaker to the start of its cycle (Hanson et al. 1971). During entrainment to an artificial signal each of the firefly's flashes is a response to visual input one cycle previous, and normal synchrony is presumably also maintained by a cycle-by-cycle succession of mutual resettings among males within eyeshot of each other. Similar results have been obtained with the Malayan Pteroptyx malaccae (J. F. Case and F. E. Hanson, personal communication). These laboratory data, plus the observations that Pteroptyx males synchronize when brought together in groups (Buck and Buck 1968) and that flashing synchronously with neighbors seems to be practically their only luminescent activity during life (e.g., Smith 1935), lead to the important conclusion that flash synchronization is reflex and obligatory whenever males are sufficiently close to one another. Although complex adjustments of phase and rhythm are involved in reaching and maintaining synchrony the process does not require communication or elective response in any usual sense but occurs automatically.

In synchronizing fireflies the precise phase shifting of the pacemaker's endogenous rhythm in response to visual input is not a trivial or casual mechanism. Ability to synchronize occurs in relatively few firefly species. Further, though congregation leads to mass synchrony in such species, congregation in itself need not induce flash synchronization. We have seen sparkling tree swarms of the American genus Photuris and of the Jamaican Photinus pallens (Buck 1937b) which were as large as Southeast Asian displays but in which the crowded fireflies showed no trace of synchronous flashing. In Pteroptyx cribellata and Luciola pupilla the strength of the compulsion to synchronize was dramatically illustrated by instances of males in spider webs keeping time with swarm neighbors and by a laboratory observation that a male dying in preserving fluid maintained synchrony with a perched group in a nearby jar (J. Buck, E. Buck, and F. E. Hanson, unpublished observation).

It has often been suggested that one function of mass male courtship congregations is to increase the reach of the advertising signal (e.g., Alexander 1975; Wilson 1975; Otte 1977). This objective is realized to some extent in the unsynchronized mass choruses of acoustic insects such as Magicicada (Alexander and Moore 1958), but it may not be appreciated how much the signal-to-noise ratio is improved by precise synchronization. Enhancement is achieved via two separate but mutually reinforcing mechanisms, augmentation of peak flash intensity and intermittency of signal (Buck and Buck 1966). (A third consequence, emphasis of species-specific signal rhythm [Lloyd 1973c] will be discussed later.) The degree of intensity augmentation reasonably obtainable by flash synchronization can be illustrated as follows: for 10 males with flashing periods averaging 1,000 ms and flash durations 100 ms, enhancement by random flash coincidences during 1,000 successive 100 ms intervals averages 1.6 reinforcement units (computed from replications among 1,000 random digits taken 10 at a time) compared with 10 units for actual synchronization. Hence the mean increase in peak flash intensity due to synchronization would be of the order of sixfold, assuming signal enhancement to the eye via either rise in rate of photon capture by single ommatidia, increase in number of ommatidia stimulated, or a combination of these physiological effects. The further enhancement via intermittency, though very familiar and well documented for human
perception, cannot be evaluated without data for latency and refractory period for the firefly eye. However, the laboratory finding that rate of rise of light intensity is more important than absolute intensity in eliciting response by females of roving species (Papi [1969] in the Italian Luciola lusitanica; J. F. Case and J. Buck [unpublished observation] in the American Photinus greeni) is consistent with the assumption that flash synchronization will increase the conspicuousness of a tree display over and above its augmentation of light intensity.

THEORIES OF THE FUNCTION OF SYNCHRONOUS FLASHING

In view of the occurrence of nuptial swarms in a wide variety of insects (“which typically gather in concentrated masses over prominent landmarks…”; Wilson 1975, p. 57) and of the universal sexual significance of luminescence in roving fireflies, it is not surprising that almost all explanations proposed for mass synchronous flashing relate to reproduction. The data already presented indicate that firefly displays have no periodic reproductive or developmental significance like the migrational or seasonal swarms in better known gregarious and social insects. Haneda (1941, p. 362), who discovered the mating in display trees, proposed that “…synchronous flashing is a behavior pattern by which males invite females to a group.” He did not suggest any advantage in the behavior. Wynne-Edwards (1962), in contrast, regarded the congregational synchrony as a ritual display designed to limit population numbers rather than to promote reproduction. Both this general explanation and its specific application to fireflies have been strongly criticized (e.g., Williams 1966; Lloyd 1971).

The first suggestion providing a rationale for both the flash synchronization and the mass assembly is the anthropopsychic hypothesis we devised after witnessing Pteroptyx malaccaae displays in the mangrove-Nypa swamps of Sarawak and Thailand (Buck and Buck 1966). What struck us most forcibly, on the basis of previous experience with roving fireflies, was that this impenetrable terrain would make pair courtship via alternating line-of-sight exchange of signals virtually impossible. In roving fireflies it may require dozens of alternated signals, involving nearly continuous communication and accurately timed responses, to guide the male to the female: if more than two or three consecutive signals are missed the courtship breaks off. We therefore proposed that a concentration of males in a tree, forming a luminous mass large enough and bright enough to be visible for considerable distances in all directions, might serve as a beacon for females who would fly to the tree, mate, and then fly away to disperse their eggs. We considered the flash synchronization a refinement for enhancing the drawing power of the display (see Physiology of Synchronization).

In our “beacon” hypothesis we visualized the display as ideally a steady-state community in which a constant number of males, stabilized by a balance of in-flying recruits and old fireflies dying off, is reacting with a constant flux of females, stabilized by a balance of those joining the tree congregation and those leaving, after mating, to lay their eggs in the surrounding habitat. There is no direct evidence of a flow of females through the trees but mass samples collected over only a few minutes contained a preponderance of males of 60%–74% in Pteroptyx cribellata and Luciola pupilla of New Britain (Haneda 1966; J. Buck, E. Buck, and F. E. Hanson, unpublished observation) and 70% in P. malaccaae of Thailand (Buck and Buck 1968).

We originally proposed that swampland fireflies “…have evolved indiscriminate centralized mating instead of the system of individual courtships which is… the more usual plan…” (Buck and Buck 1966, p. 563) because we could detect no individual-to-individual communication in the tree displays and because pair formation in Jamaican Photinus pallens congregations clearly involves a large element of chance (Buck 1937b).
It was implicit in the beacon hypothesis that each male participating in the tree display would have more chance of finding a mate than if he were solitary but we did not attempt to spell out the reproductive benefit. Doubtless, in the wisdom of a decade ago, we would not have recognized any problem in the statement that synchronous flashing is an adaptation for benefiting the population or species as a whole.

Contemporaneously with our paper the seminal book of Williams (1966) reexamined many supposed examples of group-adaptive behavior in the austere light of Darwinian natural selection at the individual level. Williams pointed out numerous and often subtle conceptual pitfalls in confusing mass behavior with mass benefit and benefit with evolved function and concluded that, except where real or "misplaced" kinship is clearly involved, essentially all instances of apparent cooperative behavior are (p. 203) "...the statistical effect of individual adjustment." In this vein Lloyd published two important papers which not only exposed the deficiencies of our beacon hypothesis, particularly its neglect of individual behavior, its susceptibility to nonsynchronizing mutant "cheaters" and its postulate of indiscriminate mating, but provided many additional data (Lloyd 1973b) and a detailed Darwinian blueprint of courting among mass synchronizing fireflies (Lloyd 1973c). Since Lloyd's model was the first to apply evolutionary principles to both the formation and the functioning of the mass tree display we shall use it as a framework not only for analyzing its own merits but also for interpreting the considerable body of additional data now available.

**THE LLOYD MODEL**

In spite of extensive field study Lloyd was no more successful than we in deciphering a consistent or complete picture of in-tree behavior in any synchronizing species. He did, however, make a major contribution by emphasizing the theoretical requirements that "...the benefit of synchronizing [must] accrue to the individual male that is behaving in this manner..." and that this benefit must include the enhancing of "...his own reproduction as he competes with conspecific males..." (Lloyd 1973c, p. 269). In attempting to reconcile mass synchronous flashing with the requirements of natural selection theory, he constructed a six-step hypothetical mating protocol based on a wide variety of display, competition, and chase interactions among American and exotic species of firefly and information from nuptial systems in other insects.

In Lloyd's scheme the male's flashing rhythm plays an essential role, being the species-specific instrument of attraction of both sexes to the tree and a cue by which males and females recognize males and orient within the tree. Males are presumed to recognize the female luminescence also. The fundamend of the model is that small scale flash synchronization is used by the individual male in competition with conspecific males. Postulated competitive uses include preservation and accentuation of the species-specific flashing rhythm and enhancement of emission intensity of a male's "locus" in the tree (region where two or more synchronized males are close together). Such flash reinforcement is viewed as competitively advantageous in influencing incoming females to land near small "clusters" of synchronized males, and, during close in-cluster competition, in favoring one locus over dimmer competing loci (Lloyd 1973c). Lloyd also suggests that one male in a synchronized group might usurp the place of another in courtship, though it appears to us that displacement must be subordinate to whatever is the primary employment of synchrony in courtship. Lloyd concludes that mass synchronous flashing "...is probably of little reproductive significance..." and "...may be merely the gross consequence of individual males synchronizing with their neighbors as they compete in small clusters for females on an extremely localized level...." (Lloyd 1973b, p. 991).
Lloyd’s exposition of the Darwinian requirements of firefly courtship led us to reexamine our own data in relation to individual behavior. We had studied carefully the distribution of rhythmically flashing, perched *Pteroptyx malaccae* fireflies among the leaves of a number of display trees in Thailand and Sarawak and concluded that these crowded males occur not more than one to a leaf, mostly on the upper surfaces, and distributed rather uniformly through the foliage at a minimum spacing of 5–10 cm. The important point is not that the males are so close to one another but that they are no closer. Whatever the nature of the long-range attraction that brings males to the tree, it does not crowd them together, several to a leaf.

The impression of spacing or territoriality in the local distribution of males in the mass tree congregation dovetails nicely with findings in two sets of experiments with the Thai *P. malaccae* done for other purposes. The first dealt with the initiation and build up of synchronization within groups of 50 males liberated in a darkened room. These experiments showed that the insects were strongly attracted to one another during a preliminary flickering-in-flight stage (and, incidentally, in the absence of females). This stage may correspond to the approach flights of *P. malaccae* males to display trees since males flying outside the tree often flicker (12/s) rather than flash in the 560 ms species rhythm. When the flickering animals alighted and began to settle down to flash rhythmically, preliminary to group synchronization, they no longer showed the strong tendency to be attracted to each other’s light and in fact rarely established themselves closer together than 10–15 cm (Buck and Buck 1968).

In the second set of experiments pairs of males were confined in a glass-fronted chamber 75 cm wide, 32 cm high, and 2 cm deep. The confined space prevented flight, forced the fireflies to walk, and let each be closely followed with individual photo-meters. These animals sometimes synchronized together for hundreds of cycles while walking on the vertical glass surface. If, however, they happened to converge to within a centimeter or so, one male invariably attacked the other and drove him off, with much flickering by both (J. Buck, J. M. Bassot, and E. Buck, in preparation). These experiments suggest that there is indeed a distance-dependent reversal in the attractive effect of light. Males are first mutually attracted, then perch in a relatively stable mutual spacing. At still shorter distances apart they repel each other aggressively. The mechanism of the effect is unknown, but the possibility that input light intensity may become limiting is suggested by the laboratory finding (in roving species) that response is inhibited if the eye is stimulated too intensely (Case and Buck 1963; Magni 1967; Case and Trinkle 1968; Bagnoli et al. 1976). Similarly, when males were attracted from a distance toward a string of rhythmically flashing synchronized lamps in which each individual lamp was considerably brighter than a single firefly, the fireflies veered off when they came close to the lure (*Luciola pupilla* on Karkar Island: J. Buck, E. Buck, and F. E. Hanson, in preparation).

Lloyd never used the word “lek,” but his postulated small clusters of males displaying competitively for the attention of females certainly define a system involving sexual selection by the female rather than by the male as implied in our beacon hypothesis. In any case, several of our other mentors have suggested lek analogies (see also Alexander 1975) which, together with our evidence for aggressive territoriality, have led to a reinterpretation of many of our observations and experiments on the hypothesis that the firefly tree display is a huge lek. We propose that incoming males establish themselves individually on separate leaves or equivalent mutually spaced territories which they defend against encroachment by other males and on which they display by flashing in the species-specific rhythm. We did not detect local clustering in any well populated tree. Nonetheless Lloyd’s “cluster” is still a convenient term to denote a transitory group of
neighbor males near enough to one another to display simultaneously to the same female.

Several in-lek behaviors can be reasonably proposed. As Lloyd suggests, the male may choose his landing site primarily on the basis of being close to other males. Lloyd assumed that in-tree males can recognize incoming females but did not specify that incoming males orient to in-tree females. In all synchronizing species known to us the flash of the male consists of one or more very brief (50 ms), sharp spikes, whereas the female's flash, besides being dimmer because of her smaller lantern, has a much longer duration and much slower rise and fall of light intensity (see figures in Buck and Buck [1968] and Lloyd [1973b]). Females also often emit long, dim glows, and in the Melanesian fireflies *L. pupilla* and *Pteroptyx cribellata* the female's light is green, whereas the male's is yellow (discovered by Haneda [1941, 1966]; emission maxima 553 and 562 nm, courtesy of T. A. Hopkins). Potentially, therefore, the male has available one or more sexual identification cues, assuming visual discrimination similar to man's, and it seems quite reasonable to suppose that an approaching male modifies his landing so as to be close to a female if one is in sight and that the luminescence of the female aids sex recognition and orientation by the male during the competitive display stage of courtship. It may be one of the dividends of flash synchronization by the male that the resulting long dark intervals (90% of the entire pacemaker period in some species) would make the weaker, longer-duration, out-of-phase luminescence of the female more easily recognizable. One of our reviewers suggested that luminescence during the dark interval might in fact be a female identification cue.

Though individual in-tree perched males of *P. malaccae* were observed to maintain their positions and flashing rhythm for substantial periods they did occasionally shift location, with flickering, as they might be expected to do if not approached by a female within a certain period or if driven away by another male. Transit flickering is beautifully shown as long strings of light "beads" in Polunin's full tree photograph from near Singapore (Zahl 1971) and in some of our time exposures from near Kuching (see also photograph of males indoors in Buck and Buck [1976]). Bouts of fixed-position flickering can sometimes also be seen in a display tree, and it is tempting to speculate that these tantalizing signals behind the synchronic facade are connected with male combats.

We have not been able to follow the behavior of the female upon entering the swarm, but, since she should be able to identify conspecific males by their flashing rhythm and probably also by flash kinetics (and emission color, in Melanesia), she could choose to land near males, perhaps on the basis of locus intensity, as Lloyd proposed.

**THE FLASH SYNCHRONIZATION PARADOX**

Our revised view of what is going on in a synchronized tree display preserves the basic descriptive features of the Lloyd model of in-tree courtship, individual male display, and competition for selection by the female. It appears to offer certain supportive improvements, including evidence of male territoriality and aggression, a more straightforward protocol, and possibly a more definite place for the luminescence of the flickering male. It differs from the Lloyd model in the role assigned to flash synchronization.

Lloyd interprets the Darwinian imperative to mean that flashing synchronously with a conspecific neighbor must aid the individual male in competition with that neighbor. It is not at all apparent that his specific examples of such aid (emphasis of species-specific recognition rhythm, locus enhancement, interloping) meet this criterion (see below), but in any case we argue that synchrony cannot be more than a proximate cause
of individual reproductive enhancement. The reason is that flash synchronization is, by definition, a group behavior. It takes at least two to synchronize, and neither can gain from the behavior unilaterally. One male cannot be a better synchronizer than another with whom he is mutually entrained. The female has no way to choose between males simply on the basis that they are flashing in coincidence with each other.

The physiological work on the flash-control pacemaker makes the competitive impartiality of synchrony particularly clear. Because the entrainment mechanism in firefly A is reset by flashes of B, C, and so on automatically, firefly A cannot avoid flashing synchronously with the others, nor they with him. This equivalency is illustrated in the long serial laboratory recordings from synchronized pairs that we made with J. M. Bassot, already referred to in relation to aggression. These separate, concurrent records from two mutually entrained males show that the phase relationships are reciprocal, with first one individual, then the other, assuming a slight lead for one or a few cycles. There is no dominant-subordinate relationship by which either animal can maintain a fixed lead or lag with respect to the other, thus possibly enabling the female to distinguish between the two. Nor is the situation changed if the scenario is cast in terms of sexual selection by the male rather than by the female. Nor does it make any difference in principle that the synchronization is automatic. Even if a particular male could choose whether or not to try to synchronize with a neighbor, for whatever benefit, he would be dependent on the participation of the other individual and could not modify the mutual signal to his own advantage. This is not to say that flash synchronization is useless—only that it cannot in itself benefit one participating firefly to the reproductive disadvantage of another.

The fact that flash synchronization is a joint or group behavior leads directly to a paradox. Since flash synchronization is clearly a genetically perpetuated behavior it must, as Lloyd rightly argues, be capable of improving the reproductive fitness of the individual male. Yet flash synchronization is just as clearly a joint behavior, theoretically unable to benefit one member of the group preferentially.

**PROPOSED ROLE OF MALE FLASH SYNCHRONIZATION IN SEXUAL SELECTION BY THE FEMALE**

Setting aside, for the moment, the paradoxical implications of flash synchronization in firefly courtship, we take up the questions of what male behavior is being used in competition, if synchronization of flashes is not, and how synchrony is functioning if it is not serving competitively. Our view is that flash synchrony functions not in direct competition but in making direct competition possible. In support, we first identify a behavior that could be used directly by the individual male in competitive display and then argue that this behavior has to be synchronized with comparable behavior in other males in order to be effective.

The behavior we are suggesting for use in male competition is modulation of flash intensity. By this we mean control of the effective emission of the individual male, not that of a communal locus. There are several indications that males do brighten their individual flashing in situations that might involve or lead to competitive display. For example, in several groups of captive fireflies containing initially asynchronous or poorly synchronized males, we observed that the flashes of the individual males brightened as synchrony developed (*Luciola pupilla* and *Pteroptyx cribellata*, lowland Melanesia). Similarly, Malayan *Pteroptyx malaccae* males exposed to lamps that flashed in their species-specific rhythm brightened their flashing dramatically as they were drawn out of the tree (Case et al. 1972). Another pretty example was seen in the field when a single *L. pupilla* male flying to a display tree with which he was out of phase,
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brightened his flashes very perceptibly as he phase shifted into synchrony with the tree (J. Buck, E. Buck, and F. E. Hanson, unpublished observation).

Though there are some questions about the physics and physiology of photic competition (see Appendix II A), flash intensity has the major advantage of being individually controllable. Within limits, each male can improve his chances individually by increasing the intrinsic brightness of his flash. He may also be able to enhance his signal by moving closer to the female, although such position shifting could be limited by attack by neighbors or by a possible physiological requirement to maintain male spacing (Appendix IIA). Finally, it seems quite possible that twisting of the male's abdomen during flashing, observed by Case et al. 1972, and strikingly shown in one of Polunin's photographs (Zahl 1971), might be used to aim the light organ at a nearby female and so further enhance the male's signal (see, however, Appendix IIB).

Though we have no direct evidence of how males display competitively in the presence of females or of how females select mates, there is a compelling reason for favoring male flash intensity as the criterion used by the female in sexual selection, namely, that it could provide a physiological explanation of why the males' flashes have to be synchronized. This possible mechanism is the fall in sensitivity that receptor-response systems often exhibit immediately after stimulation. For example, after the male of P. cribellata has been stimulated artificially, the firefly is not affected by any additional signals intruded during the first half of the 1,000 ms cycle (J. Buck, E. Buck, J. F. Case, and F. E. Hanson, in preparation). Similarly, in the roving firefly Photinus greeni the female cannot be restimulated for several hundred milliseconds after receiving the male's signal (Buck and Buck 1972). If the Pteroptyx female likewise becomes refractory immediately after seeing one flash, two or more flashes would have to be perceived nearly simultaneously in order for her to be able to compare their intensities. Such refractoriness could thus provide a physical basis for Lloyd's surmise that females may "...not select males unless they are flashing in unison with neighbors..." (Lloyd 1973c, p. 269).

RESOLUTION OF THE SYNCHRONY PARADOX

From the above discussion it appears that flash intensity is a promising vehicle for male-male competition and also might provide an explanation for the involvement of male flash synchronization in sexual selection by the female. We nevertheless have not yet resolved the paradox that a group behavior would thereby be assigned an essential role in individual reproduction. According to current evolutionary thinking, such a group-selective benefit could only be considered if it involved either kin selection or reciprocal altruism.

We discount kin selection because of the a priori unlikelihood that the thousands of fireflies in a tree population are genetically close. However, indications that congregating might involve some inbreeding are sufficient to justify putting the evidence on record (Appendix III).

In our scenario each male in a synchronizing cluster is maintaining his own competitive eligibility and simultaneously and inadvertently helping maintain the eligibility of his neighbors. Since eligibility to compete is directly connected with eventual reproductive fitness, each synchronizing male is promoting to some degree the reproduction of his neighbors. In fact if the female monitors the displays for some time before choosing and if a particular male becomes a member of several clusters successively as females mate and depart, the postulated male behavior appears to fit closely the major conditions specified by Trivers (1971) as favorable for reciprocal altruism, namely, (a) many altruistic interactions per lifetime, (b) repeated interactions
with the same small set of individuals, and (c) "pairs of altruists ... exposed 'symmetrically' to altruistic situations" (p. 37). However, the tradeoff in the firefly cluster is too even. Statistically the total reproductive benefit gained by any one male is exactly balanced by the total benefit dispensed by him. This makes it impossible to fulfill the basic formal requirement of reciprocal altruism that the benefit to the recipient exceed the cost to the donor—that is, that the overall transaction (after reciprocation) actually provide net advantage to the donor rather than being truly altruistic.

For the third time, therefore, we return to the synchrony paradox. We are dealing with genetic perpetuation of a behavior which appears to be intimately concerned with courtship and which depends on an evolved, complex, highly organized, neural oscillator specialized for automatic mutual stimulation. We observe that synchronous flashing is almost the only activity engaged in by the male firefly during his entire adult lifetime. Yet the behavior is unequivocally a joint or group activity and so apparently cannot qualify for natural selection as a promoter of individual reproduction. This paradox exists quite independently of our explanation of why flash synchronization is necessary. If however, our conjecture that the response of the female is inhibited during a substantial part of the male's interflash period were correct, a very important consequence would follow: the courtship would have built-in protection against mutant cheaters that did not participate in the synchrony. If the courting female were able to perceive only those flashes that arrived almost simultaneously, she could not react to signals that were out of phase. We propose, therefore, as a working hypothesis, that synchronous flashing can persist as a reproductively essential group behavior because it is thus protected. Selection against cheating, like kin selection, would thus constitute a special case of group selection rather than an exception to the Darwinian stricture against group adaptation. The ultimate benefit to the female from being able to select synchronizing males will be discussed later.

**ADAPTIVE IMPLICATIONS OF MASS CONGREGATION**

Lloyd's belief that mass synchronous flashing may be incidental to local courtship is perfectly reasonable insofar as the physiology of synchronization is concerned. Given a mosaic of close-spaced local clusters, amalgamation of the males' flashing into a single synchronized display would be not only possible but virtually mandatory on the basis of the resettable flash pacemaker. However, given the observed mutual photic attraction in both sexes and the consequent mass assembly, the resettable pacemaker would also bring about mass synchrony automatically and to unlimited extent wherever males were sufficiently close to one another. This would be true irrespective of whether subsequent matings were indiscriminate or resulted from sexual selection by the male or involved courting within clusters of males displaying to individual females. Moreover, since flash synchronization is a joint behavior (which therefore cannot be individually selective), there can be no qualitative distinction between local and mass synchrony. Consequently, attention now focuses on the occurrence of mass congregation and on the possibility that flash synchronization has a mass as well as local significance.

The facts that the feeding stage of the Lampyridae is the subterranean or aquatic larva and that mass displays occur in a large variety of trees (Millard 1905; Buck and Buck 1966; Bassot and Polunin 1967) pretty well exclude foraging or bonanza exploitation (Alexander 1974) as reasons for firefly assembly. The only other supposed major inducer of animal congregation (aside from sex) is predation, against which flocking or schooling is thought to protect participants either by "saturating" predators or by sheltering members that seek the interior of the group (Williams 1966; Alexander 1975; Wilson 1975). Fireflies in general appear to be relatively free from flying enemies, with
only a few ambiguous reports of bird and bat attack and many examples of avoidance reported (Lloyd 1973a). In the one report involving a synchronizing species, from the Malay Peninsula near Singapore, it was observed that when clouds of Pteroptys malaccae males were drawn out of their display tree by bright electric lights tuned to the species flash frequency, “intense bat predation [began] immediately” (Case et al. 1972, p. 683). It was concluded from this experiment that “...a major factor in selecting for aggregative synchronous flashing is predator pressure tending to favor reduction in flight time...” (Case et al., p. 683). The generality of this interesting observation is in some doubt, however, since bats have not been observed to attack Oriental firefly species under normal conditions. In any event the firefly situation seems not really analogous to protective schooling or flocking since the swarm is stationary and permanent, and it is physical screening by the tree that provides shelter, not congregation per se. Also, protection might be only a consequence of assembly for some other purpose since it appears that a more efficient way for the individual firefly to reduce flying time would be to move to the nearest tree rather than risk additional exposure in traveling to a communal refuge, on the average more distant.

In our opinion, indications that synchronous flashing may be adaptive at the congregation level come from two considerations. The first concerns the recruitment of individuals into swarms. If males and females were attracted to tree displays from no farther than they can see flashes of individual in-tree fireflies, it might be possible to argue that the function of mutual flash synchronization by males is limited to local courtship. In experiments on Karkar Island with Frank Hanson we collected groups of Luciola pupilla fireflies from a display tree, moved them various distances across a lawn from the tree, and released them. Both males and females flew immediately and directly back to the tree from distances of at least 25 m. Individuals believed to be males of P. malaccae and Pteroptys cribellata have also occasionally been seen flying to a display swarm from comparable distances. However, the greatest distance which we are reasonably sure involved individual-to-individual response in P. malaccae was less than 2 m indoors (Buck and Buck 1968). An increased male signal reach due to congregational synchrony seems therefore probable, whether the effect is attributed to increased total luminescence (Buck and Buck 1966), increased visual field, or reinforcement of the male flashing rhythm (Lloyd 1973c).

The second indication that synchronous flashing may be adaptive at the population level as well as in local courtship stems from the perpetuation of mass congregation, that is, from the inherent compulsion of fireflies of synchronizing species to join large conspecific congregations. In typical roving firefly species the mature larvae are distributed widely over suitable habitats. If larvae of synchronizing species are similarly distributed, the occurrence of extraordinary quasi-permanent concentrations of winged adults in particular trees, with essentially no fireflies in the surround (Appendix III), should be very unlikely. We devised a simple model which indicates that it might be of the order of 10 times as efficient, in terms of distance traveled, for males to seek females individually (or vice versa) through a population distributed at random over a habitat than it would be for both sexes to journey to a central point for mating and then for the females to fly back to disperse their eggs (Appendix IV). There is, thus, no obvious theoretical reproductive gain to individual males from gregariousness. The fact that mass congregation is nonetheless strikingly developed in these fireflies thus suggests that it may be group adaptive.

Whether courtship involves males searching for females or females inspecting males, it is clearly advantageous to have an excess of the opposite sex available. If the overall population sex ratio is 1:1, however, it is not apparent that an equal increase in the numbers of both sexes is advantageous. How, for example, does it profit a male to join in
a display that attracts one additional competitor for each additional female? How is the female benefited by a convocation system that attracts one female competitor for each potential mate? Why does not the female simply establish herself near where she emerges from her pupal skin in the soil and select a mate from among males attracted to her light, as do females of many roving species?

An environmental factor that might put a premium on congregation for both sexes is the presence of serious physical obstacles to sustained line-of-sight communication, a unique problem for organisms that use light signals. Male competition and female monitoring can proceed readily within a small cluster-size domain in a mass congregation, but it is difficult to believe that such domains could form from widely scattered fireflies amid dense vegetation if long-range attractions had to depend on maintained individual-to-individual photic contact as they do in many roving firefly species. Now that there is some reason to believe that courtships going on in the mass synchronized assembly could be inherently protected against nonluminous and nonsynchronous cheaters, it is no great step to modify our original hypothesis (that the tree display is an indiscriminate convocational beacon for the benefit of males) to one postulating that the display increases the numbers and spatial concentrations of both sexes to the level where individual male display and courtship competition can occur efficiently. Such concentration should result in a greater total number of matings, as compared with the same number of individuals randomly distributed over an area of heavily vegetated habitat equal to the range of the beacon. Since pair formation could be safeguarded against males that did not participate in synchrony, assembly might constitute a group-selective adaptation potentially benefiting every gregarious conspecific firefly within the reach of the tree display and putting nongregarious individuals at a disadvantage.

DISCUSSION

The new data we have presented and the interpretations we have suggested are fully consistent with the perspective of Lloyd that synchronous flashing is an adjunct to individual mating. As such, it is one of the many behaviors that contribute ultimately to the reproductive fitness of the male firefly. The ways in which this very conspicuous behavior is employed for sexual objectives are still incompletely understood, aside from its obvious role in aiding mass congregation, and all hypotheses concerning synchronous flashing in courtship have to be regarded as primarily heuristic. However, Lloyd's idea of competitive local display by the males seems sound regardless of whether his or our particular vision of sexual selection is ultimately confirmed.

We have deliberately confined ourselves to the initial selection of a prospective mate by the female and to behavior in species notable for large-scale synchrony. Our objective has been to focus on the meaning of flash synchronization. We have no evidence of how the male and female may interact once a pair has formed or of whether that association can be interrupted (e.g., by Lloyd's "interloping") or may progress to other types of precopulatory communicative exchange, as Lloyd (1973c) postulates. We have at present no reason for going beyond the most parsimonious picture of pair formation and copulation, namely, for a female established in the tree to select a particular male, transfer to his leaf, walk to him (i.e., toward his signal), and submit (see also Appendix II.B). We are fully aware of and sympathetic to the evidence from thinly synchronized and nonsynchronizing highland species that led Lloyd to postulate complex intersexual communication. However, the evidence is overwhelming in the direction of basic diversity of mating systems, even among congregational species of fireflies (Appendix I), and we have come to believe that the elucidation of the courtship problem will be

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advanced by giving up the seductive and procrustean objective of forcing all systems into the same mold.

Group-selection theory teaches that synchrony is not manipulatable to individual advantage. Important insights into swarm firefly behavior are made possible by the evidence that an evolved physiological mechanism, the resettable flash pacemaker, makes flash synchronization automatic, given sufficient male propinquity. This obligatory mutual entrainment of males argues that there can be no distinction between local and mass synchrony and is consistent with the observed independence of flash synchronization from the presence of females.

Male emission intensity as the criterion of sexual selection by the female is strongly favored by the probable existence of a physiological response in the female, temporary refractoriness after stimulation, that would exclude out-of-phase males from the competition. Modulation of flash intensity also appeals to us because it has the elegant simplicity and economy typical of evolved mechanisms. A single behavior—flashing—is controlled in two ways for separate purposes: in timing (for eligibility to compete) and in intensity (for competition itself). In response to our preliminary report (Buck and Buck 1976), Lloyd (personal communication) pointed out that male flash intensity, even if correctly identified as the selective criterion, furnishes only the proximate mechanism of the female’s requirement for male flash synchronization but not the ultimate (genetic) cause. Some reason must be supplied for the natural selection of females that only choose mates from among synchronized males. We grant that a female programmed to select as her mate the brightest available synchronously flashing male would have a higher probability of having her genome perpetuated because her sons would also tend to be brighter (and so better competitors), having had half their genes from a sexually successful male (Lloyd 1973c). But this statement of the genetic expectation applies to any perpetuated male courtship behavior that the female selects and so will not help assess the worth of our or other specific protocols until that remote day when breeding tests on fireflies are possible. Meanwhile we feel that it has been useful to concentrate on reasonable and internally consistent hypotheses that have at least some physical and physiological reality.

The precise form taken by competition and display is of less interest to us than the role of flash synchronization, but it is encouraging that the tenuous indications of in-tree behavior are consistent with some known patterns of lekking. Since there is no evidence of a dominance hierarchy in the firefly assembly, it corresponds better to the leks of the Hawaiian Drosophilidae (Spieth 1974) than to those of Plathemis dragonflies (Campanella and Wolf 1974). As far as we are aware, no previously reported insect lek involves continuous synchronized group display unless Walker’s (1969) Oecanthus congregations are considered to be a lek. The infrequent mass displays of Magicicada (Alexander and Moore 1958, 1962; Alexander 1975) could not be using sound competitively in the same way as Pteroptyx malaccae may be using light, since the cicada concert involves sinusoidal contemporaneous chorusing rather than synchrony. R. K. Colwell and L. L. Wolf have kindly called our attention to the leks of the males of certain tropical hummingbirds which occur on “traditional” grounds in dense vegetation and in which, in addition to aggressive defense of territory and visual display, long-lasting chorusing occurs (e.g., Stiles and Wolf 1979). This singing, in which calls are concerted but not synchronized, is important in the maintenance of each male’s territory and is intensified by all males in the vicinity upon the (infrequent) arrival of a female at the lek (B. Snow 1974). It is interesting, parenthetically, that some hummer leks persist from 6 mo to throughout the year (D. Snow 1968; Hilty 1975).

One consequence of the automatic nature of flash synchronization is to shift the focus
from exclusive preoccupation with rationales for employing synchrony to recognition of the importance of mass congregation per se, a behavior often considered to involve definite disadvantages (e.g., increased competition, vulnerability, and contagion: Williams 1966; Alexander 1974, 1975; Wilson 1975). Support for our suggestion that mass flash synchronization confers a population-wide sexual benefit (Buck and Buck 1966) is primarily circumstantial, although Alexander (1975, p. 71) generalized our thesis in postulating that in “male aggregations … in which mating is the sole function for both sexes, every male profits from cooperation, such as synchrony in chorus, which increases the number of females attracted to his particular group.” There is no direct evidence that assembling provides more mating encounters than those available outside the tree (or indeed that it confers advantage of any kind on either male or female). Sexual benefit from congregation might also seem improbable statistically (Appendix IV), but by introducing physical obstacles into the model habitat it is easy to render centralized mating more efficient than random search. In any case, in addition to our basic argument that total mating encounters might increase and Lloyd’s points about the advantages of enhancing the species-specific rhythm, a beacon mechanism would provide additional rationales for (1) the observed mass congregation (concentrating males and females to a level suitable for close-range courting); (2) congregating in trees (using a construct ideal for conspicuousness and spatial concentration of the population); (3) flash synchronization (augmenting the drawing power of the beacon by increasing peak flash intensity and making the light intermittent); and (4) the tendency for synchronizing species to live in areas that are densely vegetated (or were in the preagricultural past) whereas roving species tend to inhabit relatively open sites (Buck and Buck 1966). It is in fact quite possible that the nonspecific contribution of synchrony to the chances of the individual males eventually reproducing is greater than that conferred in making possible the direct competition. Perhaps, however, the most compelling argument for interpreting this group behavior as adaptive derives again from appreciation of evolutionary strategy in general: the frequent multiple consequences of a particular behavior at several levels and the exquisite reinforcement and interlocking of different behaviors. It may be more than accidental that a single, well-defined behavior—flash synchronization—is fitted for (a) long-range convocation, (b) short-range sexual display, and—if our hypothesis is correct—(c) as an essential adjunct of the competitive agent itself.

**SUMMARY**

In certain firefly species of tropical Southeast Asia the males habitually congregate in trees in huge numbers and flash in rhythmic synchrony all night, each night. Though females do not synchronize, they are attracted to the trees and mate there. Many fireflies remain in the trees by day. We believe that each display tree approximates a steady-state population in which a constant number of males, stabilized by a balance of inflying and eventual death, is interacting with a constant flux of females, stabilized by a balance of in- and out-migration. There are some very tenuous indications that different tree populations may be partially isolated and somewhat inbred.

The mass-display fireflies are unique in possessing a neural mechanism that automatically synchronizes the rhythmic flashing of conspecific males. Mass congregation and mass synchrony are therefore inseparable.

All evidence agrees in indicating that the mass synchronized assemblies are exclusively reproductive. In the Thai *Pteroptyx malacae* and the Melanesian *Pteroptyx cribellata* and *Luciola pupilla* we believe that courtship and mating involve two successive photic interactions. Distant males and females are being attracted indisci-
minately into the tree by the massed rhythmic luminescence of the in-tree males. The
range and species-specificity of this attraction are enhanced by the flash synchroniza-
tion. Simultaneously males established individually in the tree and flashing rhythmically
in small, defended territories compete for in-tree females. In extension of Lloyd's
analysis, we postulate mutual recognition via one or more sexual differences in light
emission and surmise that the female probably does most of the short-range moving
connected with pair formation. We postulate that the female selects her mate on the
basis of the intensity of his signal relative to those of other males visible to her
simultaneously. As in Lloyd's model the selection must depend on a genetic predilection
of females for males that are flashing synchronously. Poststimulus refractoriness is
suggested as the mechanism for the predilection. The synchronized tree congregation
thus performs a long-range attraction of both males and females to the tree and
simultaneously operates as a huge permanent lek. In the various in-tree interactions,
flash synchronization is thought to improve mating opportunity for all participants and
to exclude possible conspecific cheaters. The orthodox view that large-scale synchrony
must be only the incidental or statistical consequence of a small-scale adaptive synchrony
is questioned on the following bases:
1. From natural selection theory, flash synchronization per se, being a group behav-
ior, cannot serve as the competitive agent for promoting the reproductive fitness of an
individual participating male, no matter how small the synchronizing group.
2. Flash synchronization is, for physiological reasons, obligatory between two or
more close-together males. Mass synchrony depends on mass congregation.
3. Because most fireflies court by continuous line-of-sight photic contact, environ-
mental obstacles such as about in the jungly vegetation of Southeast Asia could be a
major obstacle to dialogue-type communication. Conversely, the formation by males of
a large, concentrated communal light beacon, visible through vegetation for long
distances in all directions, might attract more females per unit time than a given male
would meet in solo search through a population dispersed in dense vegetation.
4. Such a congregation, it is argued, would benefit all participating males, penalize
none, and be safeguarded against nonflashing or nonsynchronizing cheaters by the
female's requirement for flash coincidence during comparison of male flash intensities.
Mass congregation could thus, we suggest, be a group adaptation, made possible by
unique physiological and ecological circumstances. The observed evolutionary perpetu-
ation of the behavior is made possible by the fact that flashing—the act that, when
synchronized, permits nonspecific sexual gain at two levels (increased mate accessibility
for both sexes and eligibility for individual competition between males)—can also
be modulated to serve as the competitive instrument between conspecific males vying
for selection by females. Any synchronizing male in the congregation who mates will
therefore transmit the genetic basis for the flash synchronization as well as that
controlling competitive use of flash intensity, and the female will gain by having selected
a competitive mate.

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APPENDIX I

TYPES OF MASS SYNCHRONOUS FLASHING

As illustrated in Buck and Buck (1968) and Lloyd (1973b), the light emissions which are synchronized by the males vary from simple single flashes to multiple flickers and differ in period over a 10-fold range.

Trees on the Malay Peninsula are populated by a species which is indistinguishable from the Thai Pteroptyx malaccae by present taxonomic criteria and which emits the same two-peaked flash but differs in several behavioral aspects and in having an interflash period of about 850 ms (at 28°) instead of 560 ms. In the same Malaysian areas, and sometimes in the same trees, occurs also a slightly smaller species, Pteroptyx tener, with a single-peaked flash and 300-ms period. A second species of Thailand (Pteroptyx valida), found in small numbers in P. malaccae trees, emits a volley of about 15 very sharp spikes (v > 30/s) and apparently does not synchronize (Buck and Buck 1968).

Even more different from P. malaccae are the single-flashing Pteroptyx cribellata and Luciola pupilla of lowland New Guinea, Karkar Island, and New Britain, with periods of about 1,000 ms. In these species many of the males synchronize in hovering flight among the tree branches rather than while motionless on a leaf, and the displays are not confined to trees along watercourses. This hovering display mode poses difficulties for present hypotheses of in-tree courtship, since it seems unlikely that sustained competition could be maintained among the synchronized males that are drifting about in constantly changing configurations. In these species it therefore seems necessary to postulate that courting is carried on by that fraction of the displaying population that is perched and that this stage is either preceded by or interrupted by periods in which some of the males shift position.

Mass synchrony in P. cribellata and L. pupilla breaks down and reestablishes itself spontaneously every 100-200 flashing cycles. Wavelike mass flashing is often seen as a transient stage in resynchronization. A similar progression from essentially complete disorganization, with few individuals flashing, through waveforming to full synchrony is also seen in display trees of these and other species that have been disturbed mechanically or are recovering from inhibition caused by strong artificial light.

An additional New Guinean species, phenotypically very like the lowland P. cribellata but with an interflash period of 5,000 ms (18°), is found in the Eastern Highlands, and still another, which emits a high-frequency flicker instead of a single flash, inhabits the Central Highlands (Lloyd 1973b). Cinema records from this species (by T. A. Hopkins, analyzed by K. Friedman) suggest that group synchrony is triggered by the first individual to flash in each episode and propagates as a wave. A similar triggered or follow-the-leader flash coordination was observed in a rice paddy firefly in Bali by J. F. Case (personal communication). Perhaps the strangest behavior of all is in an unidentified species of West New Guinea in which both males and females are reported to participate in the synchronous flashing and in which the swarm may move from tree to tree (Haneda 1966).

Trees simultaneously harboring significant numbers of two or more firefly species (Buck and Buck [1966] in Sarawak; Case et al. [1972] in peninsular Malaysia; Lloyd [1973b] in New Guinea) pose a problem. In many of the crowded trees we observed for
miles along the tidal reaches of the Samarahan River in Sarawak the numbers of *P. malaccae* and *P. tener* were so nearly equal that regular rhythm was hardly ever seen, and then only very locally and transiently. Though individuals from the surround could presumably be attracted by the cumulative light intensity of such trees, it is difficult to see how competitive comparisons of individual signals, or dialogue, could go on amid the apparent chaos, particularly any interchange involving several successive cycles. Furthermore, such assemblies violate the expectation that the male’s flashing rhythm would exclude other species. Hence, unless mixed tree communities are regarded as nonadaptive accidents they raise difficulties for the view that the species-specific male flashing rhythm is a prime element in courtship. However in a Malayan tree harboring both *P. malaccae* and *P. tener*, Case et al. (1972) showed that either species could be induced to brighten its flashing by exposure to external lamps driven in the species-specific rhythm.

An interesting puzzle is posed by a jarful of males of *L. pupilla* from Karkar Island that was observed to synchronize with a similar group of captive males of *P. cribellata* from New Britain. Since *P. cribellata* occurs in at least two localities also inhabited by *L. pupilla*, it seems possible that these species of different genera but essentially identical period (1,000 ms) could congregate and synchronize together.

It is important to know that mass synchronous flashing is universal neither in fireflies of Southeast Asia nor in species of particular genera nor in fireflies of a particular (present) habitat type. Of 22 Melanesian species of *Pteroptyx* and *Luciola* discussed by Lloyd (1973b) only six showed some degree of synchronization, while others in the same area behaved more like rovers, with one-to-one signaling and chase behavior. We have studied the lowland New Guinean *Luciola obsOLEtA* (Lloyd 1972), which Lloyd (1973b) mentions as closely similar to the rover-like highland species, and on that basis we are convinced that courting in those forms involves quite different systems from that in mass synchronizers like *P. malaccae*, which Lloyd unfortunately has not seen.

The frequent association of synchrony with densely vegetated habitats may be significant in terms of the evolutionary origin of the behavior but since synchronous and roving types sometimes occur together today and since, as Buck and Buck (1966) point out, mangrove swamp areas in tropical South America and Africa have not been studied, the ecological correlation is by no means secure.

**APPENDIX II**

**Questions and Caveats about Our Hypotheses of Firefly Synchrony**

A. *Light intensity as a competitive instrument.*—If intrinsic flash intensity were the only criterion in female sexual selection it would appear to put a premium on early encounter and one would expect to find displaying males confined to a shell on the periphery of the tree (which has not been remarked upon by any observer). An even greater difficulty is that intrinsic flash intensity would be expected to be of minor importance compared with emitter-receiver distance. For two males respectively one and two feet from a female, the more distant would have to flash four times as brightly as the closer in order to be competitive (inverse square effect). A third pause-giving consideration is the laboratory evidence, for the female of the American roving species *Photinus greeni*, that the female responds uniformly over a $10^4$ male signal intensity range (J. F. Case and J. Buck, unpublished data). Granted that the *P. greeni* response is a triggered or all-or-none behavior, not one requiring intensity discrimination, its wide intensity response range raises a question about the postulated in-lek competition.

The observed spacing of the males in the display trees, if maintained during courtship, might reduce the importance of the distance factor in emission intensity. One possible reason for maintained spacing is the presumed desirability of preserving the visual discreteness of the flashes being compared. It is not known whether the firefly compound eye can process two or more separate images simultaneously, but on a priori
grounds it would certainly appear desirable that the simultaneous flashes of several males not be imaged at the same point in the retina.

**B. Dual-purpose behaviors.**—Lloyd assumes that the synchronized rhythmic flashing of the male serves both to attract males and females from a distance and in close-range competition between males. In a somewhat similar way we have suggested that the "aiming" of the male's light organ by abdominal torsion, a known response to artificial male flashing rhythm outside the tree (Case et al. 1972), and suggested by Lloyd to be a response of in-tree males to out-of-tree females joining the swarm, might be used normally in enhancing the male competitive signal in close range display to in-tree females. Such speculative assignments of one behavior to both long-range and short-range signaling, which functions could hardly be carried on simultaneously with optimal efficiency, imply uses at different times or by different individuals. For example, one might assume that newly recruited males in the tree swarm serve primarily in displaying for long-distance attraction, whereas the older males are occupied primarily in short-range courtship and mating or vice versa. Such an assumption would be reasonable both in view of the probability that the males in the tree at any instant span a wide range in age and sexual maturity and in view of the known male age hierarchies in many mammalian and bird leks. However, any division of labor would invite cheating by subordinates, as George Williams has pointed out to us, and could not be entertained seriously without direct evidence.

**APPENDIX III**

**Population Aspects of Mass Congregation**

Considering the highly speculative bases of both the Lloyd and the lek models, the possibility of kin selection merits examination as a conventional mechanism for reproductive benefit from mass congregation. We have played down this possibility because of the inherent unlikelihood of close genetic relationship among the thousands of individuals in a typical firefly display tree in the apparent absence of selective mating, or development, or of any social differentiation. None of the conditions for kin selection listed in Eberhard's (1975) review appears to apply. There are, however, a few provocative indications that tree displays may represent partially isolated populations.

In spite of Smith's (1935) dramatic description of an unbroken line of river bank firefly trees (Thailand) and somewhat similar reports from West New Guinea (Haneda 1966) and Malaya (J. F. Case, personal communication), we are convinced of a well-defined tendency for each synchronizing tree (or occasionally a group of close-spaced display trees) to occur in relative isolation. Even in the nearly virginal conditions prevailing for many miles along tidal reaches of the Samarahan River (Sarawak) there were many mangroves which were of the same kind as those in which firefly swarms occurred, and similarly situated, but which were completely free of the insects (Buck and Buck 1966). The implication that a tree display depletes a considerable surrounding area of fireflies is supported by such statements as "The fireflies congregate in trees... which are usually somewhat isolated"; (Bassot and Polunin [1967, p. 19]; Malaya) and "The formation of high densities in some trees while adjacent ones are vacant or nearly so is a common occurrence" (Lloyd [1973c, p. 269]; New Guinea)—and is implied in the existence of the navigational trees in Malaysia already referred to.

Our original observations led us to speculate that "Such assemblies might be expected to build up competitively, leading eventually to one or a few large swarms that had outdrawn nearby smaller centers because of higher mean light emission." (Buck and Buck 1966, p. 562). The physiology of firefly transfer from one group to another would actually be rather mysterious since, if integrated light intensity were truly the only factor involved, the inverse square relation argues that an individual in a small swarm would receive a stronger signal from his fewer, but closer, neighbors than from the larger but distant group. Nonetheless, in artificial-lure experiments of J. F. Case and his associates (personal communication) it was found that small congregations, established
originally around synchronized electric lights at some distance from the supply tree, dwindled away over a night or two, once the pilot lights were gone. An even more convincing instance of population transfer was provided by a lucky field observation, by the same group, of a pair of firefly trees just at sunset. While the larger tree was still sunlit, fireflies were migrating from it to a smaller tree, already in shadow. After nightfall, however, the traffic was from the smaller tree to the larger.

Since population spread via larval movement in or on the ground would be extremely slow, the isolation of a firefly display tree could be considerable if females, after mating, laid their eggs no farther away from the tree, or less far, than the reach of the communal light. The tree would then be a vortex to which each generation’s progeny largely returned. The facts (or assumptions) that male migration is always centripetal and that females mate only in the tree also appear to insure a higher degree of inbreeding than if populations from different trees intermingled freely and individual fireflies migrated at random.

The tenuous indications of population isolation do not justify proposing any specific kin selection or population evolution mechanism for firefly congregations. Williams (1966, p. 111) discussed a suggestion of Wright (1945) to the effect that “…group selection would be especially effective in a species that was divided up into many small populations that were almost but not quite isolated from each other.” Williams pointed out the many genetic and ecological obstacles to the actual existence of species having the necessary balance of population size, degree of isolation, amount of migration between populations, and mutation rate. We have no evidence that synchronizing firefly species meet quantitatively any of the criteria set forth by Wright and by Williams, nor do we assume that they do, but Wright’s suggestion should be kept in mind for future investigation in view of the indications of possible tree population inbreeding.

APPENDIX IV

MODEL FOR COMPARATIVE ENERGETIC COSTS OF ROVING VERSUS CENTRALIZED MATING

We constructed a model for sexual interactions in a population in which (a) males and females are 50:50, (b) each mobile partner at once sees and proceeds to the nearest member of the opposite (sedentary) sex, and (c) each individual mates once. Males and females were distributed over a 10 × 10 grid as follows: squares to the number of the first digit in a table of random numbers were counted off from left to right along the top line and “M” was put in the square reached with the last number. Then, proceeding farther along the top line and continuing in the second line if necessary, the second random number was counted out and “F” put in its last square. The third random number was then counted out consecutively and another “M” entered. Continuing in this way, males and females were distributed alternately over the 100 squares of the model habitat. At the end of the first coverage the counting returned to the top line of the grid and traversed it a second time. Four such randomized passes over the grid, recorded successively in the four quadrants of each square (fig. A1), distributed 43 males and 43 females, and resulted in one square containing four fireflies, four with three, 19 with two, 32 with one, and 44 with none. (Quadrants with two letters correspond to the occurrence, in the random number table, of two zeros in succession.)

Males were scored according to the length of the minimal rectilinear path to the nearest female, with the score being increased by an equivalent amount for each other male equally near to the particular female and by double the minimal amount for each competitor closer to the female than the male being rated. The mean corrected rectilinear travel distance necessary for each of the 43 males to reach his closest female neighbor was 1.46 grid units. The mean rectilinear distance of the 43 males from one of the center four squares of the grid (the analogue of the tree) was 4.2 units. Hence, other things being equal, it is three times as costly, energetically, for a male to visit a concentration of females (or for a female to visit a concentration of males) as for him to
search for an individual mate among fireflies distributed randomly over the habitat surface. Correspondingly, for females to congregate for centralized mating, then disperse again randomly to disseminate eggs over the habitat, should be six times as demanding as compared with a sessile role in roving courtship followed by in situ egg laying. Hence the overall species cost of centralized reproduction under the most stringent conditions might be of the order of 10 times that of pair courting.

If the maximum reach of the light of the tree were more than the postulated eight rectilinear units (mean travel distance four units, fig. A1), the differential in favor of roving courtship would be higher. On the other hand, any departure from the conditions specified initially, such as more males searching at any one time than there are receptive females available or a male spending extra time in unproductive searching (both of which situations often occur in roving species), will reduce the differential favoring courtship by individual pair signaling. However, a preponderance of males in the tree in relation to females of passage would also reduce the benefit of centralized mating to the individual male. In sum it seems unlikely that such distributional differences could, by themselves, make mating in tree assemblies the favored scenario.

**LITERATURE CITED**


### FIG. A1.—Random distributions of 43 males and 43 females over 10 × 10 grid
SYNCHRONOUS FLASHING BY FIREFLIES


