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Exactly fifty years ago John Buck wrote a review of synchronously flashing fireflies for *The Quarterly Review of Biology* (Vol. 13:301–314, 1938). Since that time we have learned much about the biochemistry and physiology of firefly luminescence. The firefly lantern has even become a tool for the assay of the major energy compound of cells, ATP. The study of flash communication in many firefly species has revealed that timing relations between the flashes provide the necessary information in this system for sexual and species selection. Nowhere is the ability to control the timing of flashes more strongly exhibited than in the synchronously flashing fireflies of Southeast Asia. These fireflies provide the ultimate test of our biochemical, physiological and behavioral theories of firefly flash communication.

SYNCHRONOUS RHYTHMIC FLASHING OF FIREFLIES. II.

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ABSTRACT

Synchronized flashing by males of some firefly species involves a capacity for visually coordinated, rhythmically coincident, inter-individual behavior that is apparently unique in the animal kingdom except for a few other arthropods and for man. This paper reviews (1) diverse communicative interactions that have evolved from elementary photic signals, (2) physiological mechanisms of synchronism, and (3) theories about its biological meaning.' Work of the past 20 years shows that flash synchrony is widespread geographically and taxonomically, appears in an astonishing range of spectacular display types, utilizes several neural flash-control mechanisms and is pervasively but enigmatically involved in courtship. No proposed function for synchrony has been fully established but theory and physiology concur in indicating that synchrony aids male orientation toward the female, female recognition of male flashing, or both. Increased mate choice for the female is one likely ultimate benefit.

INTRODUCTION

OVER THE PAST four hundred years many anecdotal accounts of synchronous flashing of myriads of fireflies in trees in Southeast Asia have been scattered through travel books. Early in this century sightings of synchrony among flying fireflies in American meadows began to appear. No reasonable explanation of the behavior was offered: in fact a strong aura of incredulity or even mysticism pervaded the subject.

Fifty years ago, when I published the first review of the behavior (Buck, 1938), Indochina

was weeks away, few biologists had seen Oriental tree swarms and "the" firefly was an odd insect that one remembered catching as a child. The fast film, laboratory oscillosope and image-intensifier that would eventually confirm and dissect synchrony were, like the jet airplane and the neodarwinian revolution, still in the future. It was not surprising, therefore, that hardly anything could be said about either mechanism or meaning of this remarkable communal behavior.

Today the phenomenon has been photographed, charted and videotaped, shown to occur in several modes and in many species, assigned a variety of functions and modeled from a substantial information base about oscillatory cells and neural networks. Though no less memorable a spectacle, the behavior has graduated from enigma to general significance in the fields of coordination physiology, group communication and evolutionary biology. At the same time its mysteries have multiplied. Each step of physiological elucidation has revealed new black boxes and each behavioral insight has left major puzzles yet unsolved.

A Sampling of Synchronies

A few interesting accounts that have come to light since the 60-odd references in previous surveys (Buck, 1938; Buck and Buck, 1968, 1978; Case, 1984) will give the subject's flavor. Pride of place in antiquity passes from Kaempfer's (1727:78–79) description of synchronized flashing at the classic locality, the banks of the Chao Phraya (Meinam) River in Thailand, to Hakluyt's (1589:151) account of what was probably the same phenomenon, as seen by Sir Francis Drake's 1577 expedition: ". . . our General . . . sayled to a certaine little Island to the Southwards of Celebes, . . . throughly growen with wood of a large and high growth. . . . Among these trees night by night, through the whole land, did shew themselves an infinite swarme of fiery wormes flying in the ayre, whose bodies beeing no bigger than our common English flies, make such a shew of light, as if every twigge or tree had been a burning candle."

More than three centuries later Porter (1934, 1978:123–126) observed a very different behavior in far southwestern Indiana in which, from the ends of a long row of tall riverbank trees, synchronized flashes ". . . began mov-

ing toward each other, met at the middle, crossed and traveled to the ends, as when two pebbles are dropped simultaneously into the ends of a long, narrow tank of water. . . ."

In 1961 Adamson (p. 29) described a still different type of display, the first from Africa: "It is then too that one sees the great belt of light, some ten feet wide, formed by thousands upon thousands of fireflies whose green phosphorescence bridges the shoulder-high grass. The fluorescent band composed of these tiny organisms lights up and goes out with a precision that is perfectly synchronized, and one is left wondering what means of communication they possess which enables them to coordinate their shining as though controlled by a mechanical device."

A generation later, a flurry of full-dress bioluminescence expeditions had obtained photometric, cinematographic and electrophysiological measurements from congregational displays in Thailand, New Britain, New Guinea and Malaysia, confirming the reality of mass synchrony and uncovering a variety of types (Buck and Buck, 1966, 1968; Bassot and Polunin, 1967; Hanson, Case, Buck and Buck, 1971; Lloyd, 1973a,b; Hanson, 1978, 1982; Buck, Buck, Case, and Hanson, 1981; Buck, Buck, Hanson, Case, Mets and Atta, 1981; Case, 1980, 1984). Contemporaneously, Otte and Smiley (1977) photographed group wave synchrony of flying fireflies in central Texas, Ohba (1984) recorded two frequencies of synchrony in a Japanese species and Cicero (1983) described spectacular and enigmatic bouts of chain-flashing, tightening into synchronized strings, by fireflies on the ground in, of all places, the Arizona desert. Thus, work of the past 20 years has shown that "synchrony" is a complex of behaviors.

Defining Synchrony

In the present context synchronization is only of interest if rhythmic. Isolated simultaneous events usually signify merely that several individuals with equal reaction times have responded to the same stimulus, as in the wheeling of flocks of birds (Potts, 1984) or schools of fish. The apparently perfectly coinciding flashes of groups of fireflies excited by explosions (Ruedemann, 1937) or piano music (Eskelund, 1947:147) have implications in regard to effects of sudden change in at-

mospheric pressure or oxygen tension on flash-generation but not to the main foci of research on flash synchronization — the physiological control of the mutual entrainment and the significance of the behavior.

Natural rhythmic group synchrony must be defined arbitrarily since the flashing is never in perfect unison. Even a sinusoidal time distribution of flashes will catch the eye as a probably non-chance phenomenon and if there is total extinction between peaks few will doubt that the behavior reflects a specific entrainment mechanism. In practice, firefly "synchrony" refers to coordinated rhythmic group flashing, a definition covering serial responses to rhythmic photic driving (led or triggered synchrony), sequential individual-to-individual excitation (wave synchrony) and other types of mutual flashing discussed below.

Rhythmic communal synchronization occurs in body movements and sound production of a few insects and other arthropods (see Buck, 1938; Buck and Buck, 1968, 1978). It is also typical of many human activities — e.g., dancing, the spontaneous rhythmic applause clapping by Russian opera, ballet and circus audiences and, notably, music. Even conducted orchestral music involves a large element of mutual cueing between performers. I well remember the memorial concert for the conductor Hans Kindler, which the National Symphony Orchestra played before an empty podium. Analysis of concerted rhythmic behaviors thus has wide application.

In 1938 it appeared that a sharp distinction could be drawn between the flash synchronization of tropical Asian fireflies and that of North American forms. The Oriental displays often featured vast numbers perched in trees, flashing in perfect coincidence ". . . hour after hour, night after night, for weeks or even months . . ." (Smith, 1935:151), whereas American reports emphasized rarity and transience, often with the flashing spreading through a dispersed flying population as a wave. It still appears that flashing rarely shows even small scale rhythmic synchrony in New World firefly species in which males search on the wing for individual sedentary females and conduct flash dialogs with them ("rovers") but both the behavioral distinction and the geographical dichotomy have blurred with additional study.

Better classification of display types is now possible from study of responses of individuals to experimental flashes of electric light (see below) but even the physiological distinctions that have emerged must be considered provisional in view of the surprising diversity in firefly flashing and of instances in which one mechanism of flash coordination may simulate another.

Role of Female

In species in which the female normally responds to each flash of the male after a fixed delay, excellent synchrony among females can often be induced by beaming a flashlight over the habitat, but this behavior does not persist independently. In spite of occasional allusions to female participation (Hess, 1920) natural flash synchrony in dialog fireflies seems a behavior of males exclusively.

Little is known about involvement of females in mass synchrony in Southeast Asia. Direct observation is difficult, even in species like *Pteroptyx malaccae* in which the fireflies are mostly perched on leaves, because of the dense population, overwhelming beat of the male flashing, and "the problem of focusing on . . . small insects at a somewhat uncertain point in space during an instant of illumination in otherwise total darkness" (Case, 1980:613). Often, also, there are individuals of other firefly species in the trees. Females of *Pt. malaccae, tener* and *cribellata* apparently do not participate in either synchrony or dialog and their flashes are described as dimmer, longer and more irregularly timed than the male's (Haneda, 1966; Bassot and Polunin, 1967; Buck and Buck, 1968; Lloyd, 1973b; Buck and Buck, 1978; Case, 1980). In the only female investigated physiologically (*Pt. cribellata* of New Britain), individuals can flash spontaneously in a loose rhythm and synchronize with a laboratory photic driver, albeit much less precisely than the male, but have a free run (spontaneous) period 50 per cent longer than the male's and hence should not be able to entrain with males (Buck, Buck, Case and Hanson, 1981). Haneda (1966) found that *Pt. cribellata* females caged separately from males did not synchronize but in an unidentified species of western New Guinea he reported males and females synchronizing together in a tree.

PHYSIOLOGY OF MALE-MALE
PHOTIC INTERACTION

Synchronized flashing in firefly congregations implies that each participant is responding to visual input from others. There is a large literature demonstrating that single male and female fireflies of both synchronizing and nonsynchronizing species respond to flashes from other fireflies and to light signals from artificial sources, and that both spontaneous and responsive flashing are under nervous control.

Photic interactions between fireflies are typically all-or-none rather than graded. Hence, although response can be inhibited photically under laboratory conditions (e.g., Case and Buck, 1963; Case and Trinkle, 1968; Brunelli, Magni, and Pellegrino, 1977), both males and females normally respond to any of a wide range of suprathreshold stimulus flash intensities, as might be anticipated in animals that signal in nature over widely variable distances and relative light-organ orientations. Similarly, though modulation of flash intensity or frequency has been described in a few species (e.g., Lloyd, 1972, 1973c; Carlson and Copeland, 1978), firefly flashes ordinarily have fairly uniform intensities, durations and delays, and spontaneous flashing (usually by males) is in a fixed, characteristic rhythm.

Typical male-female dialogs tend to be quite stereotyped in emission timing — so much so that flashing characteristics have come to be accepted as an important, and sometimes essential, part of taxonomic descriptions (e.g., Barber, 1951; McDermott and Buck, 1959; Lloyd, 1966, 1969a, 1973b; Ballantyne, 1987). Recently a new type of response, male-male dialog, has been recognized. As detailed below, this has made possible the deciphering of several flash synchronization mechanisms.

One untoward corollary of the narrow species-specificity of some flashing behaviors is that mistaken or uncertain species identifications can cause confusion and error. Two instances are relevant here. The first is that the male of the Thai race of "*Pteroptyx malaccae*" has a flashing period of 560 ms (Buck and Buck, 1968) whereas the Malay form of the thus far taxonomically indistinguishable *Pt. malaccae* studied by Case and his colleagues has a flashing period of about 900 ms (Hanson, 1978). Since I suspect that these fireflies will eventually be found to be distinct species, I have had

to distinguish Thai and Malaysian races. The second taxonomic debacle is that in a recent careful restudy of part of the genus *Pteroptyx* (Ballantyne, 1987), the much-used "*Pteroptyx cribellata*" from New Britain has been renamed *Pt. effulgens*. In this paper I have retained *cribellata* because so many cited data and references involve this name.

Phase-Advance Synchronization

In some early reports synchrony was attributed to communal response to a particular leader. There is no evidence, however, of hierarchical distinction among fireflies. Blair (1915) and Richmond (1930) postulated that all individuals flash rhythmically with nearly the same period, due to alternate discharge and recovery of a battery-like mechanism and that each insect flashes immediately if stimulated near the time at which he would normally flash. The leader would thus be merely the firefly that happened to flash first after the last concerted flash. This hypothetical but prescient explanation is consistent with recent data from several species, most clearly in the common American *Photinus pyralis*, a form not usually observed to synchronize.

During courting, the solitary *Photinus pyralis* male flies along slowly, flashing about every 6 s (23°), and the sedentary female answers each of his signals after a 2-s delay (latency) (McDermott, 1911; Mast, 1912). The roving male responds to the female if, and only if, her answering flash occurs during the "early window," 1.5 to 2.5 s after his flash (Buck, 1937b; Case, 1984). Responses involve orientation and approach, but not giving a flashed answer. In addition, when two males are less than a meter apart and A flashes during B's "late window," 3.5 s or more after B's flash, B may flash immediately (0.4 s) (Buck, 1938; Case, 1984; Buck, Buck, Case and Hanson, unpub.). A's stimulus flash and B's response are thus closely clumped in time in comparison with the 6-s species interflash interval — i.e., A has caused B to synchronize with him.

After a *Photinus pyralis* male-male interaction, the participants continue on their respective courses and are usually out of range of each other within a cycle or two. There is no indication that B's flash is other than an automatic or reflex response (I shall call it "triggered") or that either male attracts the other. Males

are also triggered readily by artificial flashes imposed during the late window.

Phase-Advance Entrainment Model

Male A's flash not only triggers B's flash but resets (phase-shifts) the rhythm of B's spontaneous flashing so that he continues to flash close to the time of A's flashes even when A flies out of visual range. A previously unpublished working hypothesis to explain this phase-shifting of the flashing rhythm (Fig. 1) posits the following: (1) During rhythmic spontaneous flashing the flash-control pacemaker in the brain cycles between a basal level of excitation and a fully excited flash-triggering level (cycle a). (2) Each time excitation reaches the triggering level a neural message is sent to the light organ in the abdomen, evoking a flash after a motor delay of about 0.2 s (arrows). At the same time excitation returns quickly to baseline (cycle is reset endogenously). (3) When a photic stimulus (SIG) occurs during the male's normal late sensitivity window (LW) it raises excitation at once to the triggering level, initiating a flash and resetting the

pacemaker. If stimulation is rhythmic and the driver's flashes fall during the late windows of successive firefly cycles, each is reset and rhythmic synchrony with the driver ensues, and if the rhythm is faster the firefly responds with correspondingly shortened cycles (b-d). Since this type of resetting causes triggered individuals to flash earlier than normal, it will be called "phase-advance synchronization."

Spread of Synchrony in Rover Congregations

Flash synchronization occurs in the field within small groups of *Photinus pyralis* males that are courting the same female, and has been induced experimentally (Buck, 1935). Originally, Buck proposed that the synchronized flashing of a group of males around Female X would, because of its enhanced intensity, stimulate answers from distant Female Y who would thereby attract her own synchronized cluster of males, in phase with the original group, and so on. The discovery of male late-window triggering provides a mechanism for this "attraction."
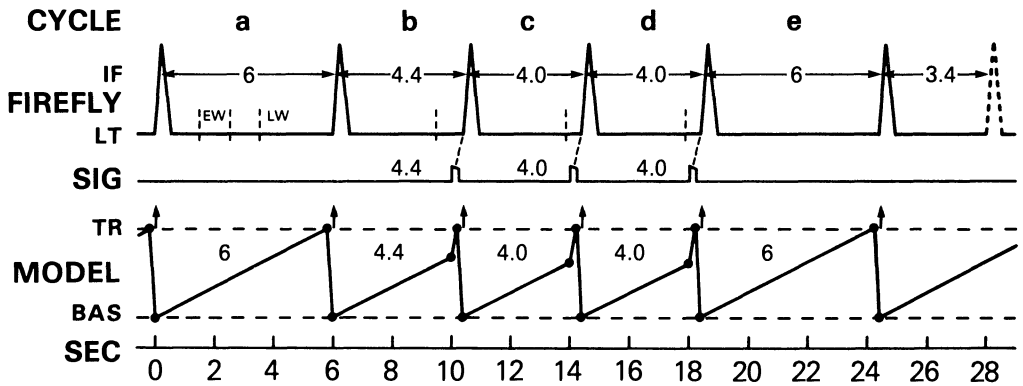
Though Male B is not attracted to Male A

FIG. 1.   FLASHING OF *PHOTINUS PYRALIS* MALE IN
RELATION TO PACEMAKER RESETTING MODEL

Upper trace shows light emission (LT) in 6 successive flashes. First cycle (a) has the normal spontaneous 6 s interflash (IF) duration. Next cycle (b) shortened to 4.4 s by external flash signal (SIG) 0.4 s earlier, during the late sensitivity window (LW). Cycles c and d have also been reset by successive signals at 4 s intervals, and shortened cycles would continue if the rhythmic driving continued. Cycle e reverts to the natural 6 s period after cessation of driving. The phantom flash 3.4 s later indicates the phasing of the flashing rhythm had there been no resetting. The model trace indicates the postulated cycling of flash-pacemaker excitation between flash-triggering level (TR) and basal level (BAS). When excitation reaches TR, either normally (cycles a and e) or after having been abruptly raised to TR (reset) by a photic signal (cycles b-d), a neural message is sent from brain to abdominal light organ, exciting a flash. The 0.4 s total resetting delay in this species is made up of 0.2 s for the photic triggering and 0.2 s of motor conduction and excitation delay.

when triggered by A (nor A to B), if A is in dialog with a female at the time he triggers B, B is thereby put in proper phase to recognize (orient toward) A's female when she responds to A, and to court her independently. Synchrony will continue between A and B (and any other males near enough to be triggered by either A or B) as the males converge on the female. Since the triggering is a short-range response, such synchrony will not spread except in dense populations. There, mass synchrony should occur spontaneously, and whether or not responding females are present. In congregations too large for an individual flash to be seen throughout, it would be expected that the concerted flashing rhythm would occur as waves radiating out from one or more foci as sequential excitation spreads centripetally.

"Wave," "chain" or "sweeping" synchrony features in many field accounts of known or probable rover species (e.g., in *Photinus consanguineus*: Hess, 1920; *Luciola mingrelica*: Baldaccini, Fiaschi and Papi, 1970; *P. concisus*: Otte and Smiley, 1977). It has also been reported in unidentified fireflies (Porter, 1978; several citations in Buck, 1938). In *P. pyralis*, the individuals in any one male-male interaction of course flash in a particular sequence, but video study of pairs and small groups shows that in different episodes, because of the variability of the male's flashing rhythm, flashes may coincide or the original follower may do the triggering (Buck, Buck, Case and Hanson, unpub.).

Prevalence of Phase-Advance Synchrony

Courting codes dependent on a fixed response delay of the female have been found in many fireflies (e.g., Lloyd, 1966) but rarely has any but very localized synchrony been reported. In *Photinus pyralis* transient synchrony in a dense congregation was seen once in 10 years by Rau, 1932 (see also R. Alexander, 1975). In my long experience with that species the phenomenon has been patchy and ephemeral. Even in large populations dispersed over open terrain it is at best a transitory behavior among a few to a few dozen flying neighbor males that flash in good register for a few cycles before gradually dispersing and being replaced by one or more local clusters elsewhere. Miller (1935) gave a very similar

description of "constellations" in the Jamaican *P. synchronans*. The synchrony of *P. concisus,* as observed by Otte and Smiley (1977), who saw it in only two seasons of four, and by Elisabeth Buck and myself (unpub.), agrees closely with that in *P. pyralis* and in *Luciola mingrelica* (Baldaccini, Fiaschi, and Papi, 1970). In Hess's (1920) description of hundreds of fireflies filling a small valley, the synchrony spread as an augmenting wave and was triggerable artificially. Episodes could be hastened by 20 per cent.

Phase-Delay Synchronization

When males of *Pteroptyx cribellata* of New Britain are exposed to rhythmic flashes of electric light they flash in coincidence with them if the imposed "driving" rhythm is the same as that of their spontaneous flashing (Fig. 2a, 3d cycle); they appear to flash later than the corresponding signal when the driving period is shorter (2b, dotted lines); and they lead the signal when the driving period is longer (2c, dotted lines). In other words, at faster driving frequencies the firefly's interflash is shortened, and at slower driving frequencies it is lengthened (Hanson, Case, Buck and Buck, 1971: Buck, Buck, Case and Hanson, 1981).

Entrainment Model

When *Photinus pyralis* males entrain to rhythmic signals they flash after each signal, a behavior consistent with direct serial triggering and driveability at higher-than-normal rate (Fig. 1, b–d). The same explanation could apply to the apparent phase lag of *Pteroptyx cribellata* entrained at a frequency higher than normal (Fig. 2b) but it fails to account for the synchrony at slower-than-normal driving, in which the animals appear to flash ahead of the corresponding signals (Fig. 2c).

From evidence that the male's flash periodicity accurately mirrors the cycling of the flash pacemaker in the brain (Buck, Buck, Hanson, Case, Mets and Atta, 1981; Buck, Buck, Case and Hanson, 1981) it was deduced that in *Pteroptyx cribellata* a photic signal resets excitatory state not to the triggering level, as in *Photinus pyralis*, but to the basal level. If excitation is set back to the baseline rather than forward, the cycle, instead of being terminated prematurely, is restarted and runs for its full normal duration before reaching the triggering level

and exciting a flash. When reset by signals de-livered at the normal species rhythm (ca. 1 Hz) the two rhythms come into synchrony in the following cycle (Fig. 2a).

To explain apparent cycle shortening (en-trainment to faster-than-normal rhythm) it was postulated that a signal seen near the end of the flashing cycle, after the pacemaker has ini-tiated a normal endogenous flash-exciting neu-ral message, and that message is on its way down the cord to the light organ, can reset the timing cycle as usual, but cannot prevent the already "committed" flash from occurring also (Fig. 2b). The neural delay necessary to allow observed cycle-shortenings — of the order of 200 ms — has been confirmed directly by elec-trophysiological measurements (Buck, Buck, Case and Hanson, 1981).

When the driving period is longer than the animal's the firefly flashes in advance of each contemporary signal (Fig. 2c). This seeming anticipation is an artifact. Because of the full-cycle resetting, response is really being made to the signal of the *preceding* cycle (dashed lines) not the concurrent (closest) signal (dotted lines).

In *Pteroptyx cribellata*, in contrast to *Photinus pyralis*, there is apparently no late window. The pacemaker can be reset by a signal introduced anywhere in the interflash interval, the true response flash appearing always one full cycle later (dashed lines, Fig. 2). Though the pho-tic response of *Pt. cribellata* enables the male to duplicate a wide range of flashing rhythms it is not apparent where in nature this ability would be useful. Rather, the entrainment mechanism seems adapted to maximize the chances that one male's flash will reset another male's flashing cycle and bring about con-specific synchrony.
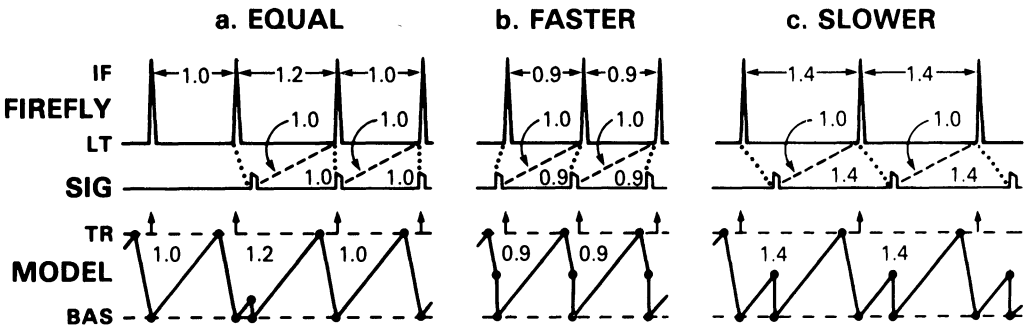

FIG. 2.   FLASHING OF *PTEROPTYX CRIBELLATA* MALE IN PACEMAKER RESETTING MODEL
    Diagram modified from that in Buck, Buck, Case, and Hanson, 1981. LT = light; IF = interflash duration. (a) Rhythmic driving at the 1-s species rhythm. First, one cycle of spontaneous flashing. The first signal flash (SIG) occurs 0.2 s after the firefly's second flash, lengthening the interflash to 1.2 s. After that the firefly duplicates the driving rhythm and flashes in synchrony with each successive signal as long as rhythmic driving continues. The pacemaker model represents each flash (small vertical arrow) as occurring 0.2 s after pacemaker excitatory state has reached its triggering level and then fallen sponta-neously back to basal level, restarting the cycle of rising excitatory state. When an external photic signal is seen, excitation is abruptly reduced again to baseline.
    (b) Rhythmic photic driving at faster-than-normal rhythm (0.9 s period). Two successive cycles of steady-state driving are shown, with the firefly duplicating the rhythm and flashing 0.1 s after each signal. In the corresponding pacemaker model excitation is reset immediately to baseline by each signal, shorten-ing the triggering-to-triggering interval (and interflash) to 0.9 s.
    (c) Rhythmic driving at slower-than-normal rhythm (1.4 s). Two cycles from steady-state entrainment are shown, with the firefly duplicating the driving period. The pacemaker (bottom trace) is shown as being reset by each external flash (SIG), 0.4 s after the preceding flash, lengthening the interflash to 1.4 s.
    In the three driving sequences note that although the male rhythm changes markedly, and the firefly sometimes flashes later than the nearest-in-time signal (b, dotted lines connecting signal symbol and rise of flash) and sometimes earlier (c), the delay between signal and true response (dashed lines connect-ing signal and subsequent flash) remains a constant 1 s.

Establishment of Concerted Flashing in Habitual Synchronizers

According to Buck and Buck (1968) the male of the Thai race of *Pteroptyx malaccae* flashes in a 12 Hz twinkle or flicker while flying to, around, and through the tree but, once at rest, he usually soon shifts to flashing at about 560 ms intervals. Flickering males flying indoors (in the absence of females) were attracted to each other, even colliding, but once at rest on a wall and flashing rhythmically at 560 ms they rarely established themselves closer together than 10 to 15 cm. Centers of synchrony built up slowly, two individuals often flashing independently for up to half a minute (ca. 50 cycles) before the flashes coincided. At this point their rhythms locked together and continued in synchrony thereafter. Synchronized groups of up to a dozen, formed thus, spanned distances of up to 1 m.

Swarm assembly and synchronization in some species do not require perching. In *Pteroptyx cribellata* and *Luciola pupilla*, normal tree synchrony involves a population in constant, slow, hovering flight. In these and some other species, males flying outside the tree may synchronize with those within.

The involvement of male-male aggression in the assembly of *Pteroptyx malaccae* is moot. In another laboratory experiment, walking synchronizing males darted at one another, with much flickering, if they converged to within a centimeter (Buck and Buck, 1978, observations with J. M. Bassot). We suggested that there is a distance-dependent reversal in the attractive effect of light. Males are first mutually attracted, then perch in relatively stable spacing, then, at still shorter distances, repel each other aggressively. We further suggested that incoming males establish themselves on separate leaves which they defend against encroachment by other males and on which they display by flashing in the species-specific rhythm (see also Lloyd, 1973a). Neither suggestion has been confirmed.

It was reported long ago that specific firefly trees were used for river navigation (Watson, 1928:17), implying a population that is quasi-permanent rather than new each evening. In some species, fireflies of both sexes have been found in trees by day (Haneda, 1941, 1966; Buck and Buck, 1966; Bassot and Polunin, 1967) but in other species they are apparently absent (Haneda, 1966).

From observations on the Malaysian *Pteroptyx malaccae*, Case (1984:214) reported that "While aggregations are stable over many nights, the aggregation is built up each day, before flashing is well established, from individuals remaining from the previous night or by a large-scale fly-in of largely non-flashing males from nearby shelters around dusk. . . . As the evening's display starts, the first few individuals seen are in synchrony, and synchrony is maintained virtually continuously, even in flight. Sex ratios in the aggregation are dominantly male early in the evening but even out with the arrival of recruits as the evening progresses. At least in *Pt. tener*, synchrony wanes after midnight, and departures from the display trees are common as dawn approaches (Kumar, 1979; J. Case, unpub., 1983)."

Wave Flashing in Habitual Synchronizers

In roving species with short-latency, phase-advance male-male entrainment, where individual males trigger others within eyeshot, spread of luminescence as a wave would be expected. Phase-shifting has not been investigated in the wave synchronies reported in certain tropical Asian species such as a Balinese rice-paddy firefly seen by J. F. Case and a high-land New Guinean flickerer (Buck and Buck, 1968:468), and Haneda's (1966) West Irian form.

Unexpectedly, wave synchrony can also occur in species with phase-delay synchronization when local groups drift out of register because of slight individual variations in flashing period. Haneda (1966) reported wave spread between groups of *Pteroptyx cribellata* fireflies in top, middle and bottom of a large tree. R. Alexander (1935) observed waves sweeping from tree to tree in Thailand as in Porter's (1978) Ohio River display. Buck and Buck (1968:1321) described an ephemeral "local swirling or wavelike effect" in *Pt. malaccae* and noted (1978:486) that "Mass synchrony in *Pt. cribellata* and *Luciola pupilla* breaks down and re-establishes itself spontaneously every 100–200 flashing cycles." Wavelike mass flashing is often seen as a transient stage in such resynchronization and in tree populations recovering from external mechanical or photic disturbance.

The possibility of human visual illusion needs to be kept in mind also, since Case and his colleagues were unable to confirm instru-

mentally their visual impression that ". . . synchronized community flash maxima move rapidly as a concerted front, or wave, from a source to distant parts of the aggregation" (Case, 1984:213). In videotapes recorded at three widely separated points in a large display they found slight asynchrony between local groups, but no sweeping spread.

Phase-Delay Synchrony in Rovers

Photinus macdermotti, *P. greeni* and *P. consanguineus* are closely related American roving fireflies in which the male emits rhythmically a *pair* of advertising flashes rather than a single flash as in *P. pyralis*. In none of these species has group synchrony been observed in the field (the "*P. consanguineus*" display of Hess, 1920, involved a singly flashing species) but observations on interactions between individual captive males strongly implicate phase-delay resetting.

In *Photinus macdermotti* the male's paired flashes are 2 s apart and are usually repeated rather irregularly at intervals approximating four seconds. The female responds 1.2 s after the second of the male's paired flashes. Lloyd (1979, 1981a,b) and Carlson and Copeland (1985, 1988), working with different populations of this species, observed that one male sometimes emitted a single flash coinciding with the second of another, nearby, male, and sometimes flashed shortly after the female's response to the other male. Calling the first type of response "synchronous" and the second type "delayed," Carlson and Copeland postulated that the synchronous flash was a response to the first flash of the other male's pair and the delayed flash a response to the second. From numerous measurements they showed that both responses had a 2-s latency. Since 2 s is the normal male intra-pair interval, the responses correspond to the type of full-cycle setback (phase-delay) synchronization previously known only from *Pteroptyx cribellata* rather than the immediate phase-advance resetting characteristic of rovers such as *Photinus pyralis* and *P. concisus*. Other responses in *P. macdermotti* will be considered later in the Functions section.

Further Physiological Aspects of Synchrony

Comparison of Phase-Advance and Phase-Delay Resetting

Phase-delay synchrony tends to be more regular than phase-advance synchrony. Pho-

tometric recordings of the Thai *Pteroptyx malaccae* showed flash registration during synchrony so precise that the flashing of several males together was sometimes indistinguishable from that of a single animal (Buck and Buck, 1968). In contrast, cinema films of *Photinus concisus* (Otte and Smiley, 1977) and video measurements on *P. pyralis* (Case, 1984) showed spreads of more than a second between individual flashes in a given synchronic episode. In the Thai *Pt. malaccae*, standard deviations for electronically recorded flashing rhythms of individual males were sometimes as low as 2.5 for a 560 ms mean period, indicating that 95 per cent of the periods fell between 555 and 565 ms. The *Pt. malaccae* male is 10 times as regular as the typical *P. pyralis* male, to judge from stopwatch records from free-flying males of the latter species (Buck, 1937b). In fact the *Pt. malaccae* flashing rhythm is often considerably more regular than traditonal "clockwork" rhythms such as human heartbeat during sleep and the calling of the whipporwill (Buck and Buck, 1968).

The lower flash coherence in phase-advance synchronic episodes can probably be attributed to the physiological delay (latency) in male-male triggering (up to 0.5 s in different species) whereas phase-delay flashing in a particular episode does not depend on resetting in that episode. In both types of entrainment, flash registration in a given cycle is also influenced by the pacemaker period preceding the flash of that cycle. If the flashing rhythm is variable enough, a male that flashes earlier than another in the nth episode may flash in unison with him in the (n + 1)th or even flash later. Whether flash pacemakers of species with phase-delay synchrony are intrinsically more regular than those of phase-advance species is uncertain because of the difficulties in separating the variability of the pacemaker from the variability of the brain-to-lantern motor conduction pathway (Buck, Buck, Hanson, Case, Mets and Atta, 1981) and because the periods of typical free-flying rover males are likely to be more influenced by environmental conditions than those of the typically perching males in East Asian trees.

Period-Matching and Phase-Shifting

In the *Pteroptyx cribellata* phase-delay synchrony the animal is able to phase-shift its flashing by major increments (i.e., to produce

interflash periods much longer than normal) without altering its intrinsic pacemaker period. The apparent shortened interflash cycles (Fig. 2b) are also achieved without change in duration of the pacemaker's endogenous period. This type of resetting makes the male unable to flash in exact unison with any but the normal species rhythm.

When a *Pteroptyx cribellata* male that is being driven rhythmically is switched suddenly from one frequency to another, it may only take a cycle or two for full, 1:1 phase-lock to be attained (Fig. 3A). Subsequently he maintains a rhythmic steady-state synchrony which is in unison with the driver if the driver's period equals the firefly's but which is otherwise permanently out of phase by some fixed amount that may be several hundred milliseconds (Buck, Buck, Case and Hanson, 1981). Steady-

state signal-to-response interval is always the same, regardless of driving frequency.

Three other tropical Asian species, *Pteroptyx tener*, *Pt. malaccae* and *Luciola pupilla*, are much slower at entraining and can synchronize only over a narrow range of frequencies. However, these species can eventually establish stable *zero-phase* synchrony with rhythms different from their normal spontaneous periods. Though they may at first be up to 100 ms out of phase with a driving signal, gradually, over many cycles, they alter their flashing period until they are flashing in coincidence with each driver signal (Fig. 3B; Hanson, 1978, 1982; Case, 1984).

If the high precision of synchrony in the Thai *Pteroptyx malaccae* applies also in the Malaysian race of *Pt. malaccae*, in *Pt. tener* and in *Luciola pupilla*, it strongly indicates that these
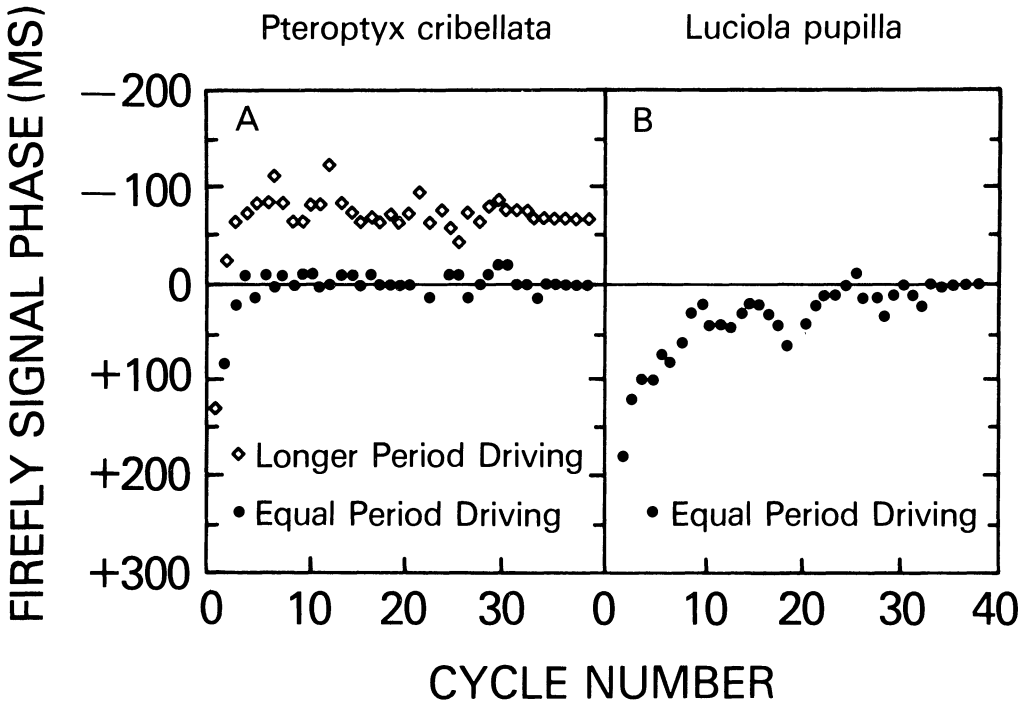

FIG. 3.   RATE OF ENTRAINMENT TO RHYTHMIC DRIVING

Left hand panel shows durations of 40 successive response cycles of two *Pteroptyx cribellata* males, the upper series showing lengthened periods in response to a driver cycle longer than the normal firefly period and the lower showing exactly synchronous responses to equal-period driving. In both instances the firefly reached synchrony in the third cycle of driving and maintained its flashing period constant thereafter. Right panel shows that it required nearly 25 driving cycles for the *Pt. malaccae* male to match the driver period. *Pt. cribellata* data from Buck, Buck, Case and Hanson (1981); *Pt. malaccae* data from Hanson (1978).

species use a phase-delay resetting mechanism. If so, the long delay in reaching phase-lock suggests that these species have a very limited phase-shifting capacity per cycle. A plausible explanation for this limitation is that excitation, rather than being reset completely down to the basal level in one step, as in *Pt. cribellata* (Fig. 2), is reduced only slightly in each successive cycle, making synchronization a lengthy, stepwise process. It is unclear whether this ability both to shorten and lengthen the endogenous flashing period, together with their very limited capacity for resetting, sets these species apart as exhibiting a third major mechanism of flash synchronization.

Phase-delay synchrony occurs also in some tree crickets (Walker, 1969) and in man (Dunlap, 1910) but has not been found in any other animal. Man, however, has the additional and unique ability to act in unison with an indefinitely large and almost infinitely graded range of rhythms.

Maintenance of Steady-State Synchrony

Presumably whatever mechanism operates to bring males into synchrony would keep them in phase in a mass congregation by means of continued minor resettings whenever small fluctuations in flashing period caused departures from optimal entrainment (Otte and Smiley, 1977; Case, 1984). Buck and Buck (1968) observed immediate breakdown of entrainment, and agitated twinkling, in *Pteroptyx malaccae* individuals shielded from the main swarm; they viewed this as evidence of need for continuous visual feedback and monitoring by each individual.

Two Entrainment Periods

Ohba (1984) recorded flying males of the dialog species *Luciola cruciata* synchronizing at both 2-s and 4-s periods. This report raises the interesting possibility that the Japanese species resembles the American *Photinus macdermotti* in which some populations have a 2-s period when patrolling and an alternating 2-4-2-4-2- emission sequence when courting (Lloyd, 1969b; Carlson, Copeland, Raderman and Bulloch, 1976). *P. macdermotti* does not synchronize in large congregations.

Possibly related laboratory behaviors have been seen in *Pteroptyx cribellata*, in that the male

may respond only to every other exogenous stimulus when these are presented at twice the frequency to which he gives 1:1 responses (Buck, Buck, Case and Hanson, 1981; Case, 1984), and he may skip flashes while flashing spontaneously, while still maintaining his endogenous timing rhythm (Buck, Buck, Hanson, Case, Mets and Atta, 1981). If, as concluded from the latter experiments, the pacemaker can continue to run at its normal rhythm even when the animal does not flash, the potential exists of synchronizing at multiples of the basic frequency.

Parallels with Circadian Oscillators

In analysing firefly pacemakers, Hanson (1978, 1982) called attention to parallels between rhythm and entrainment in firefly flashing and in the Van der Pol oscillator formalisms used by Aschoff (1965) and Wever (1965)
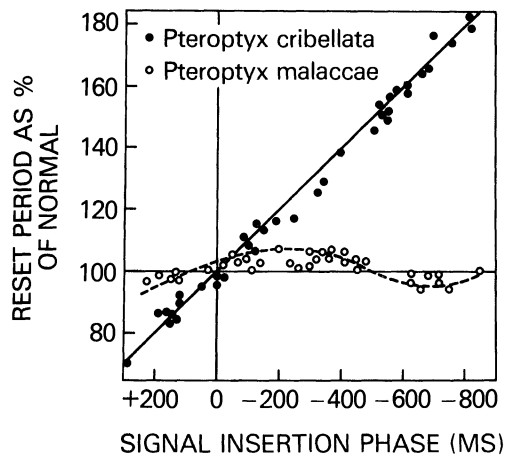

FIG. 4.   PHASE-RESPONSE DIAGRAMS FOR RESPONSES OF *PTEROPTYX CRIBELLATA* AND *PT. MALACCAE* TO PHOTIC SIGNALS

Abscissa shows time of presentation of external signal flash (+ = before firefly flash; −, after). Ordinate indicates consequent shortening or lengthening of reset cycle. *Pt. cribellata* flash timing is reset in direct proportion to firefly-signal phasing over the entire cycle, whether stimuli are single isolated flashes at random times or presented rhythmically. *Pt. malaccae* has only slight ability to reset its flashing according to signal input phase and can duplicate only signal periods very close to its spontaneous period. *Pt. cribellata* (free run period 1 s) data from Buck, Buck, Case and Hanson (1981); *Pt. malaccae* (Malayan subspecies; free run period 0.8 s) data from Hanson (1978).

in describing circadian clocks. Pendular oscillators (constant period; only small phase-shifts possible) and relaxation oscillators (variable period; entrainment possible in single period) are the two extremes of a continuum of oscillator behaviors. The *Pteroptyx cribellata* phase-response curve approaches the ideal relaxation oscillator, while those of *Luciola pupilla* and *Pt. malaccae* are closer to the pendulum (Fig. 4). Hanson also found that the frequency of group synchrony in *Pt. tener* was slightly higher than the flashing frequency of isolated males, a condition consistent with excitation in a group of interacting oscillators (Pavlides, 1973).

Whether analogs of the physicomathematical continuum exist among nervous systems of actual synchronizing firefly species is uncertain. F. E. Hanson and I attempted to entrain *Photinus pyralis* males to rhythmically flashed strings of small electric lights simulating a synchronized cluster of males courting a female, but without the usual female reply flash. In small-scale field trials we found that fireflies sometimes led the pilot lights for several cycles (Buck and Buck, 1968, and recent video recordings). Though hard to maintain empirically, the behavior invites further investigation because of the importance of knowing whether phase-advance and phase-delay entrainments are distinct and mutually exclusive mechanisms, or both can occur in one species or perhaps even intergrade.

Though the rhythm of the male's evening flashing period persists in constant darkness in some species (Plate, 1916) [not in others] and can be phase-shifted (Buck, 1937a), the firefly circadian oscillator has not been studied directly. In the cockroach, the oscillator is located in the lobular region of the brain (Sokolove, 1975). In *Luciola lusitanica* the pacemaker controlling rhythmic flashing has also been localized to the lobula (Bagnoli, Brunelli, Magni and Musameci, 1976). There is thus some suggestion that the neural controls for the circadian rhythm and for the flashing rhythm may both be in the same region of the brain, close to the eye.

Any connection between circa-second ("ultradian") and circadian rhythms would have appeared very implausible were it not for the fact that in *Drosophila* both the 24-hour rhythm of imaginal emergence from the puparium and the 1-minute repetition period of the male

vibratory "love song" are controlled by the same gene (e.g., Rosbash and Hall, 1985). There is no known reason for the two firefly oscillators to be either genetically or anatomically associated, or even to share design features, but these possibilities suggest interesting questions for future research.

Even the most advanced analysis of the firefly flash-control center (Bagnoli, Brunelli, Magni and Musameci, 1976) is far from the neural network level, let alone identified cells, but enough progress has been made in invertebrates with oversize neurones, particularly molluscs and crustacea, to provide numerous plausible models for a flash-control pacemaker. At the single-cell level it suffices to call attention to the phase-response curve for electrical resettability of a rhythmic "bursting" neuron of *Aplysia* (Perkel, Schulman, Bullock, Moore and Segundo, 1964; Pinsker, 1977), which resembles the whole body response of *Pteroptyx cribellata*. At the network level a wealth of relevant models have been described (e.g., Selverston, 1985; Prosser, 1986).

Some additional flash-control physiology is discussed later in connection with specific theories of the function of flash synchrony.

FUNCTIONS OF SYNCHRONY

Before considering specific theories of function for synchronous flashing it will be helpful to discuss a few initial considerations, such as the role of synchrony in courting, and the significance of mass versus local synchrony.

In most fireflies, flashing functions solely and unequivocally in bringing the sexes together for mating and light signals are the only communicative mode prior to contact. Synchronization of flashing can therefore be assumed to be involved in courting. From the neodarwinian viewpoint the very existence of inherent synchrony is evidence that males that synchronize have better mating prospects than males that do not, and that the behavior has been naturally selected. It is, parenthetically, an interesting footnote on the first 350 years of interest in synchronizing fireflies that no one speculated about the biological meaning of the displays. Only within the past 25 years has the question of function been addressed seriously.

In all synchronizing rovers in which the mode of male-female communication is established, the male is the advertising member and

the female the answering. In roving fireflies, though there is an almost endless variety of courtship protocols, the number of females responding at any one moment is typically much smaller than the number of advertising males. It is generally assumed that the true firefly sex ratio in nature is 1:1, but that females have a shorter life span and also leave the courting population as soon as mated. The usual male preponderance in synchronizer trees is consistent with the Buck and Buck (1966) surmise that both males and females are constantly entering the tree but only (mated) females leave. Ivan Polunin (pers. commun.) has compared females coming to trees just after dark with those on the ground, finding the former markedly younger (as judged by stage of egg maturity). In any case the usual courting scenario involves many flying males competing for a few females, often sedentary, which fact implies an advantage to the female by virtue of enhanced mate choice.

Since there are many different manifestations of synchrony and many courtship protocols it seems likely that synchrony functions differently in different species in relation to the three major reproductive problems faced by all males and females: (1) identifying a conspecific individual of the opposite sex, (2) reaching that individual or being reached by it, and (3) selecting (or being selected by) that individual for copulation. A priori, it might be that synchrony is involved in any or all of these stages. The main criteria for judging function models are (1) compatability with observed behavior, (2) compliance with Darwinian principles, and (3) physiological plausibility.

Flash synchronization appears to occur automatically or reflexly, depending on propinquity. Statements such as "one male timing his call to overlap precisely with that of another" or "two males adjust their calls initially to achieve synchrony" are unwarranted if meant literally. Synchrony differs also from other inherent abilities such as flight in not being a potentially competitive behavior. All males need to fly during courtship, and, since they may not fly equally well, some may gain by outflying others in approaching a potential mate. In contrast, flash synchronization in itself cannot promote the reproductive success of an individual male because one participant

cannot be a better synchronizer than another (Buck and Buck, 1978, 1980). Reproductive benefit may thus be presumed to derive not from synchronized flashing used as a tool for improving individual mating prospects but in making possible some other behavior with competitive potential.

An important question about synchrony is whether mass or population-wide concerted flashing is significant in itself or ". . . is 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:991). In spite of the initial implausibility of Lloyd's view to one who has seen the vast and stunning displays of the tropical Orient, it is a valid and parsimonious possibility, given a gregarious species, and is consistent also with the build-up of mass synchrony by means of entrainment spread between individual males.

To argue that mass synchrony per se is a selected behavior would require evidence that it, or congregation per se, has some overriding function. The question has been discussed by Buck and Buck (1978), Case (1980) and Otte (1980) but the only formal hypothesis is the "beacon" theory (Buck and Buck, 1966 — see below). Further implications of congregation will be discussed after consideration of the various function models.

Functional Mass Synchrony? The "Beacon" Model

In their study of tree fireflies along swamp rivers in Malaysia and Thailand, Buck and Buck (1966, 1968) established that males exclusively participate in the synchronized flashing, that there are females in the trees, though fewer, that mating occurs in the trees, and that fireflies fly in both directions between display trees and surrounding jungle. Arguing from experience with roving dialog species, and noting that tropical vegetation should pose extraordinary difficulties for pair-courting animals that have to maintain line-of-sight contact, Buck and Buck suggested that synchronized displays serve as nightly beacons for females who fly in, mate, then fly back to dry land to lay their eggs. Synchrony was thought to enhance the attractiveness of display trees by emphasizing the intermittency of the light and augmenting flash intensity. (It was estimated

by Buck and Buck, 1978, that the increase in unit areal intensity could be up to six-fold.) They contrasted this system of "indiscriminate mating" with pair dialog in roving fireflies. It was implicit in the scenario that more courting opportunities per male would be available by means of mass synchrony than by means of pair-courting.

With the advent of born-again Darwinism it was not surprising that the simple-minded beacon theory came under attack. Lloyd (1973a,b) criticized the group-selection implicit in Buck and Buck's view that mass synchrony has been selected because it provides increased mating opportunity to all participating males. He emphasized instead the selective necessity that the behavior promote the reproductive prospects of the individual. Otte and Smiley (1977) concurred, and Otte (1980:587) decried also the neglect of "interspecific reproductive interactions in molding synchrony," and the confusion of function with effect.

Lloyd also argued that if females were attracted generally to the tree, rather than to specific male "loci," large-scale synchrony would not persist because cheaters—aberrant males that did not flash (thus saving energy)—would have an advantage in obtaining females. J. F. Case (pers. commun.) believes, on the contrary, that because synchronization has proven selective value there would have to be an equilibrium in favor of maintaining the display. If cheaters came to dominate, the whole system would fail.

Buck and Buck's assumption of indiscriminate mating was based on (1) the occurrence of immediate copulation between walking males and the first female encountered on linear palm tendrils in nonsynchronous tree swarms of *Photinus pallens* (Buck, 1937c); (2) the fact that, in many rovers, copulation occurs as soon as the male reaches the female, with no sign of selection by the female (e.g., Mast, 1912; Buck, 1937b; Lloyd, 1966; Papi, 1969); and (3) the apparent gregariousness of males of mass-synchronizing species. Nonetheless, until it is found that such males mate indiscriminately, Lloyd's view that mass synchrony is secondary to local courting appears secure.

Lloyd also criticized, on the basis that cooperative altruism cannot benefit non-kin, the suggestion of Case, Hanson, Polunin and Barnes (1972) that advertising from trees is adaptive because it reduces predation by bats, and the contention of Wynne-Edwards (1962) that mass synchrony is a ritual display limiting population size.

Local Synchrony as the Focus for Selection

Lloyd (1973a,b) was the first to apply neo-darwinian principles to the function of flash synchronization. His several models for tree synchronizers, and the models of Otte and Smiley (1977) and Otte (1980) for *Photinus* fireflies, conform to the requirement (Lloyd 1973a:269) that ". . . the benefit of synchronizing [must] accrue to the individual male that is behaving in this manner . . ." by ultimately enhancing ". . . his own reproduction as he competes with conspecific males." The principal model scenarios are discussed below. Each (1) refers to local courting, with mass synchrony being incidental; (2) implies that male flash synchrony is necessary for mating; and (3) implies iterative use of synchrony.

1. Rhythm Preservation Model

Thesis: Synchrony preserves the male's species-specific flashing rhythm, which identifies males to females (and, secondarily, attracts males and females to a tree). This hypothesis is based on the supposition that conspecific males and females can use the flashing rhythm for identification (orientation) and approach. Proposed benefits of synchrony, in addition to the a priori protection against cheaters, are that it would make it easier for the female to distinguish rhythm than if males were randomly phased (Lloyd, 1973a) and would aid females in distinguishing between conspecifics and fireflies of other species (Otte, 1980). For the rhythm cue to operate, males or females or both would need to be programmed to orient to rhythm and females would need to respond more to synchronizing males than to nonsynchronizers (Otte and Smiley, 1977). In my opinion, rhythm could not be a criterion for female choice unless she could rank the rhythms of individual males on some quantitative basis such as long-term flashing regularity. Physiologically, this seems dubious.

The species-specific signal of the *Photinus greeni* male is a flash pair (Lloyd, 1969b; Buck and Buck, 1972). The female responds at a fixed interval after the second flash of this phrase. The fact that the male then orients to-

ward her shows that he has a sensory timing circuit tuned to her latency. In this species the female, who rarely flashes spontaneously, can be sufficiently excited by long-continued photic driving that she emits paired flashes at the male's timing (Buck and Case, 1986), suggesting that male flash-timing circuits are present also in the female, though normally quiescent.

The opposite situation — female timing circuits in the male — is suggested by two bits of evidence. First, males of *Photinus pyralis* (who normally never respond by flashing except when triggered) have been induced, by being made to fly in circles, to answer photic signals with a 2-s delay, as the female of that species does normally (Buck, unpub.). Second, Lloyd (1969b) reported that a *P. greeni* male, after having seen a two-flashed phrase of electric light and the female's response to it, was able to supply the second flash of the next stimulus phrase, thus synchronizing with the driver. This response suggests that the male can integrate the timing of his own rhythm and that of the female.

If common neural circuits do exist in the two sexes, ability to recognize rhythm seems credible. There is no direct evidence of female response to rhythm, as distinct from other aspects of male flashing, in either habitual synchronizers or dialog species. Males of roving dialog species typically flash rhythmically, but are often highly irregular while flying around obstacles or walking. Females do not need to be stimulated rhythmically and remain responsive for long periods without photic input.

2. Signal Identification Model

Thesis: Synchrony lets males distinguish between a female's flash and a flash of another male. Since the female's luminescence often differs from the male's in intensity, duration or contour (or, occasionally, in color: Haneda, 1966; Buck and Buck, 1978), sexual emission differences might act as recognition cues for the male. Synchronized rhythmic flashing by males would create a dark interflash interval during which a male, if programmed to respond to such a cue, could more easily distinguish the flash of the female from flashes of other males (Maurer, 1968; Buck and Buck, 1976, 1978; Otte and Smiley, 1977; Otte, 1980). Such discrimination would be especially valuable if females were scarce (Otte, 1980).

Though it seems plausible that fireflies could recognize each other's flashes by means of qualitative or quantitative emission differences, extensive use of artificial stimulation has shown that in most species both sexes tolerate wide variations in flash intensity, duration and color. This model does, however, differ from some of the others in being relatively easy to test. This model appears vulnerable to non-flashing cheaters.

3. Recognition of Female Delay

Thesis: Male synchrony makes it easier for males to detect the female response delay. In species in which the female responds to the male's signal after a fixed delay (latency) (e.g., *Photinus pyralis*, *P. greeni*) males flashing synchronously should be able to distinguish the female's answer from out-of-phase flashes of conspecific males or of other species (Otte and Smiley, 1977). Otte (1980) emphasized the importance of such noise reduction by synchrony in the Rhythm, Signal Identification and Female Delay models.

Otte and Smiley equated the benefit of synchrony in latency courting with better identification of female responses (i.e., better dialog). I would modify the emphasis to suggest that the benefit would lie in keeping the female responsive in a crowd: If there were many males, flashing at random times, and a female answered each, no male would receive properly timed answers. The ultimate result of synchrony should thus be more matings, though whether this means more opportunity for males to find the (scarce) females, or more mate choice for the female, depends on unknown competition and selection factors.

4. Enhanced Intensity Model

Thesis: Brighter male flashes improve his mating prospects. Since male fireflies can modulate their light emission, direct male-male competition by means of flash intensity is a possibility, on paper at least. The benefit for the male would be possible selection by the female. Flash intensity might also play roles in other signal recognition factors such as rhythm, flash duration, etc. (cf. Lloyd, 1973a) and in mass assembly (see Congregation, below). There is also a large literature showing *inhibitory* effects of light flashes on various firefly behaviors.

Buck and Buck (1978) analysed the competition-via-flash-intensity problem exhaustively, citing examples of flash brightening under conditions suggestive of competition but also adducing a number of serious caveats, including (1) the aiming of the male's flash at particular females by means of abdominal torsion (postulated by Lloyd) and the altering of male-female distance (inverse square law), would have large effects on perceived emission intensity and would have to be factored in with emission control; (2) females of dialog species normally are equally responsive over an enormous intensity range (10^4 in *Photinus greeni*, Case and Buck, unpub.; Case, 1984); and (3) in some species the male has been said to dim his flashes progressively as he approaches the female (Carlson and Copeland, 1978).

In common with the post-stimulatory fall in sensitivity that neural receptor-response systems typically undergo, the reset *Pteroptyx cribellata* male is not affected by additional signals intruded during the first half of his 1-s flashing cycle (Buck, Buck, Case, and Hanson, 1981). Similar results were obtained with *Photinus greeni* (Buck and Buck, 1972; Buck and Case, 1986) and *Luciola lusitanica* (Brunelli and Magni, 1984). From this evidence, Buck and Buck (1978:479) argued that "If the *Pteroptyx* female . . . becomes refractory immediately after seeing one flash, two or more flashes would have to be perceived nearly simultaneously for her to be able to compare their intensities." On this basis they contrived an intensity-based courting model that requires synchrony, provides for male-male competition, and protects against cheaters. It assumes male territoriality and lek-like grouping of males around females (as well as photometric discrimination by the female). Neither assumption has been confirmed.

5. Interloping Model

Thesis: By getting into synchrony with Male A, who is in dialog with a female, Male B might take over A's potential mate. Copulation competition has been observed when several males have reached the same female (e.g., Maurer, 1968; Case, 1980, 1984) but the only clear instances of intrusion early in courtship are in *Photinus pyralis*, in which additional males often join, flashing synchronously with the original male,

and court in parallel (Buck, 1935), and in the *P. macdermotti* phase-delay rivalry discussed on p. 273. Lloyd (1981a:100) defined "interloping" as ". . . quickly getting into place [between the primary male and his female] during the dark interflash period. . . ." Otte and Smiley (1977) and Otte (1980) pictured interloping as allowing courting Male B, who is synchronized with courting Male A, to gain access to A's female in addition to his own.

There are thus three scenarios for "outsider" males intruding on courtship. In the light of male-male responses, I consider triggering interactions to be accidental rather than aggressive. Lloyd postulates overt competition. Otte gives the interloper a choice between the female with whom he was already engaged and the one found by the male with whom he has become synchronized. In my opinion, competition with conspecifics is not a selection requirement for synchrony; only advantage over nonsynchronizers is required. Lloyd's view of interloping, though quite tenable by analogy with behavioral feats of certain other insects, adds the complication of having to explain how synchrony permits the male to "get into place" ahead of the original male. It also appears that such behavior would lead to a gregarious species.

Necessary questions about interloping are how the interloper becomes synchronized, what is achieved thereby and what are the selected behaviors. I propose to consider the simplest version, in which Male A is courting and Male B is not, at the time synchrony begins.

In phase-advance triggering, Male B's flashing cycle is accidentally reset by A's flash, putting him in phase with A. If A is courting at the time, B may begin independent dialog with A's female. This only requires B to orient toward the female's flash, and immediately gives B a chance to court, which he previously lacked. His reproductive prospects are thus enhanced by his interloping. Also, with two or more suitors the female has a greater chance of being mated than with one (or, in species with active sexual selection by the female, greater choice among potential mates). Presumably these would be the main selective advantages of interloping. Mutual synchrony also confers a proximate benefit for each male in

the cluster (vs. nonsynchronizers) in giving opportunity for reorientation toward the female's flash at each response episode.

Being triggered into synchrony with A does not carry with it any *initial* advantage over A in the subsequent race toward the female. In this competition B starts on equal footing with A and any other males in a synchronized cluster focused on a particular female. Further competition must involve other behavior models that are synchrony-independent — in particular, accuracy of orientation and speed of flight. Lloyd's less parsimonious scenario appears to require B also to be able to perceive the gestalt of A's courtship and be able immediately to get closer to A's female than A has progressed himself, i.e., to have abilities not possessed by A and not related to the accident of B's having been photically triggered initially.

The "synchronized" and "delayed" male-male responses of the pair-flashing *Photinus macdermotti* discussed earlier (p. 273) seem not overtly competitive but Lloyd (1979) described variants that would be forms of interloping. In one such response the interloping male "injected" a single flash between the paired flashes of another male. Lloyd interpreted this behavior as an attempt to disrupt the other's courting and steal his female. Lloyd (1981b,c) also regarded single flashes by Male B that overlapped the female's response to Male A (my paraphrase) as female-simulating or "transvestite" mimicry of a predatory *Photuris* female's mimicry of the *P. macdermotti* female, with the objective of disrupting dialog.

Carlson and Copeland (1988) saw the above responses only rarely in their population of *Photinus macdermotti*. They demonstrated that both the injection and transvestite response latencies fell within the variability limits of the basic 2-s "synchronized" and "delayed" responses. Finding that after 2-s male-male interactions some female responses were aimed at the "rival" male rather than toward the primary courter, they opted for jamming avoidance (noise reduction) as the function of male-male triggering in *P. macdermotti* (see Models 1–3). The interactions would thus fall under the rubric of behaviors that operate to give the male a *chance to compete* for another male's female rather than being in themselves actively competitive.

Photinus macdermotti phase-delay (?) resetting, occurring in a species that does not exhibit group synchronous flashing, suggests that male-male interactions need not be rhythmic in order to function. Each episode has the possibility of an effect, and it may be that the regularity of mass synchrony as it usually occurs means only that the particular males flash rhythmically, hence trigger rhythmically.

6. Conspecific Cueing Model

Thesis: Male gets information about inaccessible female by watching dialog behavior of a male with whom he is synchronized. In *Photinus pyralis*, neither the triggered nor the triggering male appears to pay any attention to the other's behavior, but this is not necessarily true in other species or with other male-male entrainment paradigms. Otte and Smiley (1977) and Otte (1980) proposed that when Male B synchronizes with courting Male A, B may be able to locate A's female, who is out of range or otherwise inaccessible to B, using changes in A's behavior. B's behavior would thus be a sort of interloping.

The principal evidence cited by Otte in support of conspecific cueing was the observation that additional males of *Photinus pyralis* may join a male-female pair in dialog (Buck, 1935). The discovery of automatic male-male triggering, however, removes the necessity for Buck's assumed ". . . mechanism . . . which induces males originally out of phase with each other . . . to break their ordinary rhythms and readjust them to that of the particular male which first responds to the female" (Buck, 1935:340). It also vitiates the similar suggestion of Buck and Buck (1972:201) that "the male [of *P. greeni*] recognizes not only the female's response delay interval but its relation to the preceding stimulus flashes."

Male B's ability to locate a visible female by timing the latency of her response to Male A is understandable if A and B are synchronized. It is less clear that B could find an initially invisible female through changes in A's behavior, even were he in synchrony with A at the time A began dialog. If, for example, A belonged to a species in which the male aims his lantern at the female, and B noted the direction in which A aimed, he might "deduce" from that the location of the female and ori-

ent toward her (or perhaps interlope to his advantage as in the Lloyd model); but that is assuming a lot in behavioral capability. It cannot be excluded that males might be cued by complex, even nonluminous behavior — for example, by convergence of flight paths — but to attribute to B what amounts to comprehension of the gestalt of A's courtship goes well beyond what have been established as possible behaviors in fireflies.

7. Synchrony Requirement Model

Thesis: Female will not respond if suitors' flashes are not in unison. Lloyd's (1973a) offhand speculation that females may select males that are synchronizing because synchrony has become an identification cue for sexual selection by the female begs the question and was not elaborated. I think, nevertheless, that it merits elevation to formal model status because it comes close to providing a direct, rather than proximate, rationale for genetic fixation of flash synchronization — namely, the provision of multiple potential mates — and because recent experiments appear to give support.

Buck and Buck's (1978) surmise that the female's postresponse refractory period would make synchronized input necessary (see also Intensity Model, p. 279) is applicable to any proposed function of synchronized flashes. Hence, it provides a physical basis for Lloyd's speculation. It has now been demonstrated directly that the responses of the *Photinus greeni* and *P. pyralis* females to flashes from two males are strongly inhibited unless they are closely phased (Case, 1984; see his text for the visual physiology). Case remarked ". . . if the second male flashes immediately on seeing the flash of the first, the female probably sees the pair as a single flash and replies. Thereafter, so long as they remain synchronized, the . . . males enjoy the profits of increased detectability as they seek the female" (p. 205). Case's discovery also implements Otte's (1980) surmise that "If males are under sustained selection [by the female] to synchronize, then [male] physiological responses should in time be molded by selection to ensure synchronization" (p. 587).

Pteroptyx females have not been studied, but the *Pt. malaccae* male shows an analogous inability to synchronize with any but closely phased signals (Case, 1984; present Fig. 4) Hence, by extrapolation from the indications

of shared circuitry in male and female (see Rhythm Model), it may be that the *Pt. malaccae* female, like the females of *Photinus pyralis* and *P. greeni*, has a physiological requirement for synchronized input.

Since the *Pteroptyx cribellata* male does not have a close-phase requirement for synchrony (Fig. 4), Case's (1984:215) suggestion that "the neurobiological basis for synchrony [may be] latent in fireflies generally" may be overly optimistic. If predilection for synchronized input is wide-spread among synchronizing fireflies, however, it might obviate or simplify several of the other models. For example, it would (1) explain the female's preference for synchronized males implicit in the Rhythm and Intensity Models, (2) safeguard the Signal Identification Model against cheaters, (3) supply a more basic mechanism for keeping the female responsive (in the Delay Model), (4) undercut the Intensity Model by making synchrony per se, not flash intensity, the entity detected by the female, and (5) supply an additional benefit of interloping, namely, keeping the female responsive when several males are courting (out-of-phase flashes would inhibit her response and all males would lose). Regardless of rationale, female insistence on male synchrony might also provide blanket exclusion of other species. In view of its putative importance, female refractoriness in synchronizing species urgently merits investigation.

8. Congregation in Relation to Synchrony

Given inherent rhythmic flashing and close-range male-male triggering, synchrony must occur whenever males are sufficiently near one another. Given an advantage to males that flash synchronously over those that do not, or an opportunity to join conspecifics in small-scale courting, or a female requirement that flashes from more than one male be synchronized, genetic fixation of triggering would be explained. Given triggering and a crowded mosaic of many locally courting synchronizing clusters, mass synchrony should be inevitable.

In view of the above considerations, pronouncements such as "Mass congregation and mass synchrony are . . . inseparable" (Buck and Buck, 1978:484), "Congregation and synchrony are causally connected, with the former often making the latter advantageous" (Otte, 1980:590) and ". . . synchrony is a natural con-

sequence of crowding" (Case, 1984:215) seem justified. The origin of congregation has likewise been explained: ". . . congregation evolved when a number of males acting in concert attracted a greater per-male quota of females than solitary males and . . . the noise problem created by the crowd of males was alleviated through synchrony" (Otte, 1980:590) and "The physiological drive in the evolution of synchronous flashing is . . . adaptation to the spatial discrimination problem while permitting dense aggregations of fireflies" (Case, 1984: 217). This cannot be the whole story, however, since enormous swarms of *Photinus pallens* and of various species of *Photuris* normally congregate in trees and flash all night without any synchrony (Buck and Buck, 1978).

In *Photinus pyralis*, and probably in other dialog species, mating often, perhaps usually, occurs after solitary male courting without synchrony. Males remain together only if a female is mutually visible, and congregation rarely progresses beyond isolated local clusters. Furthermore, the energetic cost of centralized mating has been estimated geometrically to be more than three times that of pair courting for both male and female (hence about ten times overall: Buck and Buck, 1978, Appendix IV). Why, then, are areas around *Pteroptyx* congregations depleted of fireflies and the population crowded together in trees? If synchronous tree congregations represent amalgamated local courting clusters (Lloyd, 1973a), it is not apparent that the amalgamation should change either the male/female ratio (the crux of models providing more females per male) or affect selection factors making local courting the essential activity going on in swarm trees. Why, then, are swarm species gregarious?

Ivan Polunin (pers. commun.) has found firefly swarms (*Pteroptyx malaccae, tener,* and *valida*) in more than 40 species of trees, though the riparian "firefly mangrove" *Sonneratia caseolaris* is heavily favored in Johore. He leans toward the beacon assembly hypothesis. He has seen bat predation and also believes that fireflies may feed on nectaries. He finds a very strong negative correlation between firefly swarms and the presence of a large predatory red ant, *Oecophylla smaragdina*, fireflies almost never assembling in trees that harbor these ants.

Buck and Buck (1966, 1968) considered that no conventional inducer of insect swarming, such as feeding bonanzas, shelter, protection from predators or kin selection, is a likely overall cause of firefly assembly.

A parsimonious evolutionary view is that ancestral congregational fireflies gathered because of nonspecific photopositivity and that trees became foci for assembly simply because they are prominent. Photopositivity may have made possible the fixation of the [steady] light emission when it arose originally in the primordial firefly stock (Buck, 1978) and should continue to have value in animals dependent on photic signaling.

Though nonspecific photic attraction does not seem to exist in *Photinus pyralis* (a species that courts very early in the evening when the surroundings are quite light), courting by means of photic attraction to steady luminescence exists today (*Lampyris, Lamprodes, Phengodes*). Photopositivity is also clearly the attractant in *P. pallens* and probably in swarming photurids. In both, individuals of both sexes are conspicuously attracted to continuous artificial light from house windows, instrument pilot lamps and patches of lighted herbage. In fact in *P. pallens* artificial, self-maintaining foci for convocation can be established by illuminating the shrubbery temporarily (Buck, 1937c).

Case and colleagues induced assembly centers for *Pteroptyx malaccae* around arrays of lights flashed in the species' rhythm and they observed natural populations transfer from dim trees to bright ones (details in Buck and Buck, 1978:489, and Case, 1984:214). In certain other species, both males and females are attracted to trees from 25 m, much farther than the 2-m apparent reach of individual male-male communication; photic attraction does have limits, however, since individuals in swarm trees are not crowded together, several to a leaf, but spaced apart (Buck and Buck, 1968, 1978).

Unfortunately, it is not known whether *Pteroptyx* species are attracted to steady light, individually or collectively, so the relative potencies of flash intensity and flashing rhythm in mass assembly are unknown. Laboratory observations of *Pt. malaccae* showed mutual attraction when males were flickering but not when synchronized (Buck and Buck, 1968). The occurrence of trees containing substantial numbers of a second or even third species

(Buck and Buck, 1966, 1978; Kumar, 1979; Case, 1984; I. Polunin, pers. commun.) suggests that rhythm is not sufficient to effect complete species separation (see Rhythm Model).

In sum, phototaxis may be a factor in mass assembly, with trees serving as nonspecific foci. In terrain with many obstacles to line-of-sight communication, the original beacon rationale might apply as a proximate factor in congregation, supplementing R. Alexander's (1975) postulate 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" (p. 710). There is no evidence that a larger number, or indeed any, females *are* attracted, and it is far from clear that small-scale courting might proceed more efficiently in a mass assembly mosaic than in separate small clusters. Badly needed data include: a statistically robust measure of the active sex ratio in swarm trees, the average number of clustered males per female (if discrete clusters exist), and the rate of mating by males in clusters versus solo males.

Overview of Functions and Modeling

The above models propose that benefit to the synchronously flashing male could come from (1) enabling him to recognize the female's flash as the aiming point for orientation and approach (Signal Identification; Delay; basic Interloping; Conspecific Cueing); or (2) giving him modes of competition with other conspecific males (Intensity; Lloydian Interloping). The female is viewed as benefitting from (1) facilitated male signal recognition (Rhythm) and (2) increasing the number of males from which to choose a mate (Synchrony Requirement). A female requirement for synchronized input would also act synergistically in several of the other models.

Insight into the operation and plausibility of several models has been improved by suggestive physiological findings, including the existence of synchronization by at least two modes of automatic photic triggering, the possibility that male and female share certain flash-timing circuits, and the potential of the female's post-response refractory period to explain why males synchronize their flashing.

Most effects ascribed to synchrony are prox-imate and only the Required Synchrony Model translates directly into individual mating benefit (increased mate choice for the female). Most models provide the male only *opportunity* to orient or display to the female. In *Photinus pyralis*, and presumably in other rovers with courtship coded for female response delay, competition after formation of clusters of synchronized courting males seems to consist simply of a race to the female, with immediate copulation. In most other systems the implication of synchrony in either competition or selection is obscure. In many of the models synchrony seems merely to decrease the photic noise from out-of-phase flashing of conspecific males. Major uncertainties exist about the ability of the male to utilize multiple photic inputs competitively.

The role of congregation is unclear. Whether or not there is a preponderance of males in the population, males might encounter more females, or find females more readily, if they flashed synchronously in small clusters. Mass congregations are most parsimoniously interpreted, both functionally and mechanistically, as secondary mosaics of such clusters but it is unclear that mass synchrony would be better than local for either male or female. Gregariousness of tree synchronizers suggests that general photopositivity (not demonstrated) and physical obstructions in the environment might play a role in the formation of mass congregations. If photic attraction should occur independently of courtship or before interactions between individual males and females begin, congregation per se would have a proximate functional role in courtship. In this connection Kumar's (1979) observation of preliminary late afternoon assembly of non-flashing males of *Pteroptyx tener* is of much interest.

Modeling is seriously handicapped by major observational lacunae. No synchrony-related behavior has been identified that could serve as the basis for sexual selection, rhythm and synchrony per se being unselectable and flash intensity probably unselectable. Though both males and females of tree synchronizers fly into the trees, it is not known whether females are sedentary in close-range courting or move to the male as in a lek, or indeed, whether there is *any* female-to-male pre-contact interaction. In triggering rovers like *Photinus pyralis*,

synchrony is involved only early in courtship, before male competition begins and before the start of sexual selection by the female (if it occurs).

More bionomic, behavioral and physiological information is needed, not only to flesh out and test the various models, but to avoid the pitfalls in the common working assumptions that what one firefly does or may do, another can or may do, and that some basic protocol for synchrony, applicable at least to most synchronizing species, underlies the apparently disparate behaviors.

A striking example of discrepancy between fact and theory is the totally unexpected nature of male-female postcontact photic behavior in *Pteroptyx tener* and *malaccae*. In these species, contrary to all current theories of what ought to or might happen when the sexes meet, direct observation and video recording under deep red light showed that the male mounts the female, curls the end of his abdomen over her head and flashes directly into her eyes, while maintaining synchrony with the main swarm (Case, 1980, 1984). Whether this behavior signifies male effort to release female mating behavior or competitive swamping of her visual system (Case's suggestions), or is a "genital pocket display" (Lloyd, 1981,a:118, for *Pt. valida*), it is clear that the already confused role of male light emission in courting in *Pteroptyx*, if not in all mass synchronizers, needs restudying. Case (1980) also described complex and lengthy leg and body movements in both sexes, emphasizing how much remains to be discovered.

Further evidence that even apparently reasonable explanations of seemingly straightforward courting behavior may not be valid has been obtained recently. In the dialog species *Photinus concisus*, the male, contrary to expectations, cannot identify the female reliably from her response latency because that interval is the same as the male-male interaction delay (Buck, Hanson and Buck, unpub.). Thus, the very species studied by Otte and Smiley (1977) appears not to fulfill their Delay Recognition Model's requirement (see also Papi, 1969, for *Luciola lusitanica*). Hence, one general lesson is that there is no substitute for adequate direct field and laboratory study prior to theorizing.

In sum, there clearly would not be so many models if any one of them was robust, and indeed none has been shown convincingly to apply in even one firefly species. However, none has been falsified and it seems highly likely that at least the main avenues of the natural selection of synchronous flashing have been correctly identified and stand ready for informed investigation. It may even be that physiology and inspired selectionism have already joined felicitously to suggest one major function of synchrony—increasing the female's choice of potential mates, effected by a built-in requirement for synchronized input. In any case this and other heuristic intersections of laboratory and field work demonstrate the essential roles of both physiology and theory in defining biological function (Jamieson, 1986).

DIVERSITY AMONG SYNCHRONIZING FIREFLIES

One of the difficulties in arriving at firm, generalizable conclusions about either mechanism or biological function of synchronized flashing is the diversity of behaviors in different species even from the same genus and habitat (Buck and Buck, 1978, Appendix 1). The male flash differs widely in period (0.5 – 5 s) and in contour (single flashes in *Pteroptyx cribellata* and *Luciola pupilla*; double flashes in *Pt. malaccae* and *Pt. tener*; a 30 Hz flicker in *Pt. valida* and a highland New Guinea species; Buck and Buck, 1968, 1978; Lloyd, 1973a,b; Hanson, 1978). Similarly, the high precision of synchrony in the Thai *Pt. malaccae* contrasts with the very loose coordination in *Pt. valida*, a species that occurs in the same area, and sometimes in the same tree (Buck and Buck, 1968; Case, 1984); and the wide entrainment limits of *Pt. cribellata* (Buck, Buck, Case and Hanson, 1981) differs greatly from the very limited ranges of *Pt. malaccae* and *L. pupilla* (Figs. 3, 4; Buck, Buck, Hanson and Case, 1972; Hanson, 1978, 1982.)

The stereotype of sedentary fireflies perched on the leaves of riparian trees (e.g., the Thai *Pteroptyx malaccae*), must now be amended to include a variety of other behaviors, such as those of *Pt. cribellata* and *Luciola pupilla*, species that synchronize in flight among the branches of forest trees in New Britain; the spectacular unidentified highland New Guinean species that flies high in the air in swarms of 40 or more, giving long-sustained twinkles about every 5 s, each paroxysm apparently be-

ing triggered by the first to flash (unpublished frame-by-frame study by K. Friedman of a T. A. Hopkins film); the mysterious African belt display (Adamson, 1961); and the enigmatic *Photinus knulli* (Cicero, 1983). In addition, just as the apparently exact (phase-delayed?) synchrony in Africa upsets a supposed distinction between Oriental and Occidental displays, wave (sweeping) mass-flashing (apparently involving phase-advance and phase-delay synchronization in different species) has now been observed in several tropical Asian species, and the phase-delay resetting discovered in *Pt. cribellata* may occur also in rovers.

The documented geographical range of synchrony has been enlarged to include Kenya, Japan, Texas and Arizona. Yugoslavia is the first European venue (Mikšić and Mikšić, 1965; Baldaccini, Fiaschi and Papi, 1970). My mail has brought eyewitness or vicarious accounts of sightings in Vietnam, Mexico and Queensland. The early presumed association of synchrony with particular species of trees has been dispelled. Seemingly the only secure generalizations are that Far Eastern synchronizing species are truly gregarious and do not initiate courtship by means of individual-to-individual dialog.

SUMMARY

During the 50 years since synchronized flashing among fireflies was first reviewed the phenomenon has emerged as a pervasive behavioral complex fully rivalling animal behaviors in which odor or sound, rather than light, is the primary communicative modality. It illustrates the richness and variety of responsive repertories that can derive from the relatively simple insect nervous system and, in spite of its strict limitation to courtship, presents a protean functional and evolutionary puzzle even without consideration of the many other facets of reproductive ecology that interact with the programming of light emission and signaling.

Though an ability of two organisms to "keep time" with each other is apparently limited to arthropods and man (Buck, 1938; Buck and Buck, 1968) physiological work on flash-synchronization has broadened understanding of the neural production and control of rhythm and entrainment in general. It has long been known that human beings have a "sense of rhythm" and orchestrate by reference to cues in the preceding, rather than contemporaneous cycle (Dunlap, 1910), but it has not been recognized generally that both the maintenance of a natural spontaneous rhythm and entrainment to foreign rhythms might be referable to very simple oscillatory cells or networks. On the other hand, in spite of the existence of resettable neurons in many molluscs and crustacea (and presumably in all higher animals), and their known ability to interact by means of both excitatory and inhibitory synaptic connections in coordinating a wide variety of rhythmic activities, it remains a mystery that no mammal besides man can perform any sort of whole-body group rhythmic activity that is truly synchronized.

From behavioral and evolutionary viewpoints, firefly synchrony illustrates the wealth of variations that can be played upon the simple theme of communication by means of light signals. In spite of questions raised about the physiological plausibility of this or that theory it is fair to say that no proposed explanation of the biological significance of flash-synchronization has been eliminated. Similarly, in spite of the breadth and ingenuity with which selectionist considerations have been applied to the behavior, an unequivocal rationale for its evolution is still elusive.

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