BIOLOGY OF SYNCHRONOUS FLASHING OF FIREFLIES

By DR. JOHN BUCK and ELISABETH BUCK
Laboratory of Physical Biology, National Institutes of Health, Bethesda, Maryland

REPORTS of synchronous rhythmic flashing by fireflies in South-East Asia have been appearing for more than two hundred years. Smith's[1] description of displays along the Chao Phraya (Meinam) River south of Bangkok will serve to introduce the phenomenon: "Imagine a tree thirty-five to forty feet high thickly covered with small ovate leaves, apparently with a firefly on every leaf and all the fireflies flashing in perfect unison at the rate of about three times in two seconds, the tree being in complete darkness between the flashes . . . Imagine a tenth of a mile of river front with an unbroken line of *Sonneratia* trees with fireflies on every leaf flashing in unison, the insects on the trees at the ends of the line acting in perfect unison with those between. Then, if one's imagination is sufficiently vivid, he may form some conception of this amazing spectacle." The flashing, Smith continues, is confined to male fireflies and ". . . occurs hour after hour, night after night, for weeks or even months . . .".

This behaviour is strikingly different from that of most fireflies in other parts of the world: in fact, such large-scale, long-lasting, concerted rhythmic activity is seemingly unique in the animal kingdom. For this reason the phenomenon has been a perennial source of interest tinged with scepticism[2]. Yet the many accounts have not led to a consensus about certain important observational details of the synchrony, or to satisfying explanations of either the physiological mechanism of the mass flashing or of its biological significance.

On the basis of a recent visit to Thailand[3] and Borneo[4] we have reported elsewhere[5] some photographic and photometric measurements on a Thai species of firefly indicating that the synchrony of flashing varies less than 16 msec in a cycle of 560 msec, and have described observations on the build-up of synchrony under laboratory conditions which shed some light on the physiology of this firefly's "sense of rhythm". In this article we shall consider some more speculative aspects of Oriental concerted flashing related to its distribution and possible function. Two general premises are involved. First, the whole behaviour pattern, since it represents the product of countless millenia of evolutionary selection, must have a definite and important function in the life of the participating firefly species. Secondly, Oriental mass synchronism is a complex of behaviours (congregation *per se*, congregation in trees, choice of trees near water, flashing, synchrony) which may or may not be functionally related and which probably have quite different relative importances.

Riverbank Firefly Congregations

Morrison[6,7] and Smith claimed that the male Thai fireflies fly out from the adjoining jungle each evening ". . . for the purpose of engaging in this nightly display"[1]. This statement implies that the trees are populated anew each evening, an idea which we believe to be incorrect. Not only were riverbank trees near Bangkok full of fireflies in early evening, but we also found many of the insects present in mid-morning in a tree which we had studied the previous evening. Fireflies have also been seen by day in trees harbouring synchronizing swarms in New Britain[8] and in non-synchronous trees in Jamaica[9]. In Sarawak we found the tree inhabitants still flashing at midnight and at 6 p.m., as did Haneda[8] in New Britain. Resident fireflies thus account for at least part of the successive evening congregations. Fireflies were indeed seen flying to communal trees in both Thailand and Sarawak, but at the same time some were also seen flying away. The possible significance of these flights will be discussed later.

Practically nothing is known about the longevity of fireflies in Nature, but even at carefully controlled humidities and temperatures captive adults of most species die in a few days. This suggests that congregations that maintain themselves for weeks or months must be replenished constantly. Because a West African firefly species has been found to breed throughout the year[10], and the adults of several species in Jamaica[11] and in New Britain[12] are active in every month, tropical firefly trees could presumably be maintained for long periods, perhaps indefinitely, by recruits from a population in a more or less steady state of reproduction[13].

So far as it is known, all adult fireflies come from pupae in the soil—the pupae come, in turn, from larvae that live on or in the soil, or in water. Haneda found mating pairs and larvae on the ground in the Botanical Garden at Rabaul near silk-cotton trees in which fireflies were flashing synchronously. However, the mangroves bordering the swamp rivers of Thailand and Borneo stand in mud that is scoured by tidal currents so swift that it seems impossible that larvae, even if aquatic, could survive on the riverbank. Thus the swarms of fireflies in the trees must migrate from the interior swamp.

Good firefly trees were not common along the Chao Phraya River, but even in Sarawak, where the terrain is much closer to virgin swamp and firefly trees were more abundant, there were many mangroves of the same kind as those in which firefly swarms occurred, and similarly situated, which were completely free of the insects. The observed distribution of the firefly population therefore requires more than random flight from hinterland to the edge of a river. When watching male Thai fireflies in a darkroom we discovered that there is a period, before the flying specimens alight and synchronism begins to build up, when they are definitely attracted to each others' light[5]. This positive phototaxis suggests that male fireflies arriving at the fringe of riverbank trees would be attracted by flashing congregations there, or, if no previous swarm existed, might themselves form a nucleus by mutual photic attraction. Such assemblies might be expected to build up competitively, leading eventually to one or a few large swarms that had outdrawn nearby smaller centres because of higher mean light emission. Many potential display areas may therefore exist for each that develops to a spectacular level. The corollary that a good display tree would take some time to establish agrees with other indications that the assemblages are not renewed nightly.

The fact that flashing behaviour changes (from rapid twinkling to a steady tempo of two per second) after the male fireflies alight[5] is not a peculiarity of the particular Thai species or of the perching habit. Flash patterns in resting fireflies are usually quite different from those in flight[14]. What is unusual in tree fireflies is the maintenance of steady spontaneous flashing while perched—almost all roving fireflies flash irregularly, if at all, while at rest.

In sum, riparian firefly trees may be viewed as quasi-permanent assemblies, formed by way of photic attraction and maintained by recruitment.

Congregation Trees

An association of fireflies in South-East Asia with "certain", "favourite" or "particular" trees, especially mangroves, is widely recognized. In New Guinea the so-called "firefly mangrove" is *Sonneratia caseolaris* (which includes the former *S. obovata*, *S. acida* and *S. lanceolata*)[15]. The trees are well known to the natives and are said to be used in nocturnal navigation[16]. *Sonneratia* is also the "exclusive" firefly mangrove in Thailand, according to Morrison and to Smith (but see later). In Malaysia, although *Sonneratia* is common, the genus *Avicennia* must be considered an important firefly perch as its Malay name, "api-api", is also a name for firefly[17].

In Sarawak we found riverbank fireflies congregated in *Scyphiphora hydrophyllacea* and *Lumnitzera* sp. (near Kampong Senari), *Sonneratia alba* (Paya Paloh and Bako Park), *Avicennia marina* (Bako Park) and *Sonneratia caseolaris* (Paya Paloh)[18]. It was not uncommon to find *Sonneratia* and *Avicennia* trees growing side by side, each harbouring fireflies. Flashing was also seen in trees identified by our guides as mango and sago. Around Bangkok most assemblies were in *Sonneratia*, but one of our best displays in terms of population density and completeness of synchrony was in a small thorn bush (*Acanthus ilicifolius*). Synchrony was also seen in *Ziziphus mauritiana* and in another, unidentified, tree. The only instance of perch selection in either Thailand or Borneo was a negative one involving the ubiquitous nypa (nipa) palm (*Nypa fruticans*) on which it was rare to find even a single firefly.

Numerous other trees have been mentioned as firefly perches (see particularly Millard[19]), but even our own very limited experience is sufficient to show that there can be no causal relation between synchronous flashing, or even congregation, and particular kinds of trees. Nevertheless, the evidence confirms an essential involvement of trees in firefly behaviour. There has been no previous attempt to analyse this association aside from Morrison's vague suggestion that there may be ". . . something in the sap . . . which attracts the animals". This particular possibility seems very unlikely in view of the variety of acceptable trees and the very long duration of the displays, but in any event our samples of branches from firefly trees did not give any indication that the insects were being attracted by flowers or fruit. Fireflies in a Jamaican swarm have been seen possibly drinking from palm fruit scars, but the same species also congregates on acacia[9]. Furthermore, it is generally believed that most fireflies do not feed during adult life. On the whole, therefore, the evidence is very strong that trees are not an objective in themselves but are involved incidentally to some other firefly activity.

Aggregation and Mating

Since it is firmly established that male and female of most, if not all, roving-type fireflies are brought together for mating by individual-to-individual photic signalling, it is natural to enquire whether the flashing congregations in trees have any sexual significance. Both Morrison and Smith specifically denied this possibility but their stand was based on the misapprehension that female fireflies are always wingless and thus would be unable to reach the trees. The fact is that females of the riverbank species we studied in Thailand and Borneo are present in the trees, and in large numbers. The same situation was found in firefly trees in New Britain by Haneda. The females do not participate in synchronous flashing with the males, but this perhaps re-inforces the suspicion that they are in the trees for another purpose.

In the Jamaican trees large numbers of coupling pairs were found and the suggestion was made that the aggregating behaviour serves to promote mating[9]. Haneda similarly felt that the synchronous flashing of the New Britain male fireflies calls the females. In Thailand we unfortunately concentrated so hard on observing and recording the various kinds of flashes in the trees[5] that it was not until we had returned to the United States that we realized the significance of possible non-luminous activity (most fireflies cease flashing while mating). We did find a coupling pair on the gunwhale of our canoe after we had beaten the foliage with our insect nets in making a mass collection, and we observed that such beatings always flushed out many more animals than we would have expected from the density of flashing. Thus mating presumably does occur in the firefly trees of Thailand as in Jamaica and New Britain.

One further tenuous indication of mating habits comes from eye size. It is fairly well established that in firefly genera in which a roving male seeks a sessile female the eyes of the male are much larger than those of the female; but if the female takes a mobile part in the courtship the eyes are more nearly equal in size. In all the species of riverbank fireflies we have examined the eyes of the males and females are about equal. This finding is compatible with the idea that females as well as males are attracted to the congregations. Nets placed around a small firefly tree might give evidence of the postulated two-way (but not necessarily luminous) traffic and might make it possible to ascertain whether incoming females are primarily virgin and departing females mated[20].

Possible Rationale of Mass Mating

If fireflies do convene at the water's edge for mating, the utility of trees as fixed and dry sites for assembly is obvious, particularly since the insects do not mate on the wing. The assembly trees would presumably be selected by chance, and mangroves, being common, would be used often. However, it is not obvious why the riverbank should be chosen for assembly in the first place or why the fireflies in question should have evolved indiscriminate centralized mating instead of the system of individual courtships, which is not only the more usual plan among fireflies but would appear to be more efficient in terms of dispersal of the species.

In most species of roving firefly, males in an already widely distributed population search on the wing for stationary females. Recognition and homing depend on the pair being able to see each other nearly continuously in order to distinguish the signal code of their own species from those of other species patrolling the same terrain. Our experience with American, Caribbean and upland Malayan[21] forms indicates, as might be expected, that roving fireflies are found primarily on open ground, such as meadows, forest glades, road clearings, savannah and jungle trails.

There could scarcely be imagined a terrain less favourable for line-of-sight recognition than the flat, tangled, mangrove-nypa swamps of South-East Asia in their virgin state. A firefly tree on a watercourse, however, might provide a sufficiently bright and large beacon, perhaps enhanced by reflexions, to attract fireflies that wander out into the clear over the water, and might provide enough opportunities for mating to compensate for the (assumed) long flights required of the mated females for egg dispersal. We propose therefore that, in tropical swampland, mass mating has evolved instead of pair courtship because sustained photic communication between individuals is impossible.

Significance of Mass Synchrony

As reported elsewhere[5], not all the firefly trees which we saw in Thailand showed concerted flashing, and the trees we studied in Sarawak, where synchrony has been seen by professional biologists[22], showed only transitorily and incompletely co-ordinated flashing. We suspect that we failed to see well-developed synchrony in Sarawak because at the time of our visit the riverbank trees were harbouring approximately equal numbers of three species of fire-

flies (all of the genus *Pteroptyx*[23]), with consequent clashing of rhythms and breakdown of entrainment. Even in Thailand, where two other species of *Pteroptyx* were together in the trees, the synchrony of the dominant males only produced its wondrous effect because the numbers of the second species were very small. In Thailand we also felt that synchrony was more complete in more densely populated trees, in line with our "laboratory" finding that the visual feedback that brings two individuals into step operates only over relatively short distances[5]. It seems likely, therefore, that a species of firefly capable of flashing synchronously may produce displays ranging from apparently perfect unison to completely random sparkling depending on such factors as population density and purity.

There is little indication that synchronization of flashing is essential for either development or maintenance of arboreal congregations of fireflies. However, if the insect eye reacts like the human eye there are two reasons why synchronous emission would be more effective than disordered flashing as a beacon for assembly. An obvious effect would be to change a relatively continuous luminescence to an alternation of light and dark. (This principle is, of course, widely used in advertising signs in order to enhance their efficiency in catching attention.) The second advantage of coincidence of flashes would be to increase greatly the brightness of the tree, making it visible at greater distances.

Geography of Firefly Tree Aggregations

However reasonable the hypothetical rationale of riverbank aggregation and synchronous flashing may appear, it would be optimistic to suppose that observations made over a few evenings have settled major questions of communal behaviour of fireflies—even for the principal Thai species which we studied. For example, the basic postulate of mating in the trees still requires confirmation, as also do the proposed flights of male and female.

First-hand accounts of mass synchronism in the Philippines, Malaysia, New Guinea, Indonesia, Thailand, Burma and tropical India outnumber those from the rest of the world by thirty to ten[2]. The Oriental displays conform in general to the kind seen in Thailand: huge, long-lasting congregations in riverbank trees, flashing in nearly exact coincidence. Most of the occidental reports involve dispersed populations in flight, active for only short periods, and flashing in waves. The distribution of Oriental-type synchrony corresponds at least roughly with that of Oriental mangrove-nypa swampland, whereas the Western reports are almost all from open terrain.

There is, therefore, reason to regard the congregation of fireflies on trees as being linked to a specific type of topography. However, there is not a single display described in the literature that does not need further critical study of behaviour and habitat in specific relation to mating. Also, many more virgin Oriental swamplands will have to be sampled, as well as comparable areas in Africa and South America, before the nuptial device apparently used by *Pteroptyx* in Thailand can be considered the principal one evolved for coping with swamp conditions[24].

[1] Smith, H. M., *Science*, **82**, 151 (1935).

[2] Buck, J. B., *Quart. Rev. Biol.*, **13**, 301 (1938).

[3] We thank the American Philosophical Society and National Geographic Society for travel grants, and Professor Kloom Vajropala and Dr. Boonsong Lekagul for help in Thailand during October 11–20, 1965.

[4] We thank Messrs. John Dunsmore, John Turner, R. B. Jagat and Peter Ashton for innumerable favours and extensive assistance in Sarawak during September 25–October 1, 1965.

[5] Buck, J., and Buck, E., *Science* (in the press).

[6] Morrison, T. F., *J. Siam. Soc., Nat. Hist.*, Suppl. **7**, 71 (1927).

[7] Morrison, T. F., *Science*, **69**, 400 (1929).

[8] Haneda, Y., in *The Luminescence of Biological Systems*, edit. by Johnson, F. H., 452 (Amer Assoc. Adv. Sci., Washington, 1955).

[9] Buck, J. B., *Nature*, **139**, 801 (1937).

[10] Kaufmann, T., *Ann. Entomol. Soc. Amer.*, **58**, 414 (1965).

[11] McDermott, F. A., and Buck, J. B., *Trans. Amer. Entomol. Soc.*, **85**, 1 (1959).

[12] Dun, G. S. (personal communication).

[13] Moonlight is known to depress firefly activity (see also Smith (ref. 1) and Buck (ref. 9)) so there may be a monthly cycle of tree population density.

[14] Seliger, H. H., Buck, J. B., Fastie, W. G., and McElroy, W. D., *Biol. Bull. (Woods Hole)*, **127**, 159 (1964).

[15] Backer, C. A., and Van Steenis, C., *Flora Malasiana*, Ser. 1, **4**, 280 (1951). Brass, L. J., *J. Arnold Arboretum*, **19**, 174 (1938). White, C. T., *J. Arnold Arboretum*, **10**, 346 (1929). Rand, A. L., and Brass, L. J., *Bull. Amer. Mus. Nat. Hist.*, **77**, 341 (1940). We thank Dr. L. J. Brass for help in explaining the nomenclature of tropical mangroves.

[16] Watson, J. G., *Mangrove Forests of the Malay Peninsula*, Malayan Forest Records No. 6 (1928).

[17] Burkhill, I. H., *A Dictionary of the Economic Products of the Malay Peninsula*, **1**, 273 (1935).

[18] Dr. B. C. Stone kindly identified the mangroves collected in Sarawak.

[19] Millard, W. S., *J. Bombay Nat. Hist. Soc.*, **16**, 520 (1905).

[20] Wynne-Edwards, V. C., in *Animal Dispersion in Relation to Social Behaviour* (1962) has discussed firefly synchronism as a type of conventionalized "epideictic" display or social aggregation aimed basically at population regulation rather than maximizing mating opportunity. If so, the firefly example would be unusual in being apparently a more or less steady-state affair rather than being confined to a breeding season. However, much more study of possible size limitation and spacing of swarms will be required before this interesting suggestion can be assessed.

[21] We thank Lord Medway for enabling us to collect at the Gombak Field Station of the University of Malaya, and Dr. John Bullock for arranging our stay at Fraser's Hill (Selangor).

[22] Anderson, J. A. R., Dunsmore, John, and Lord Medway (personal communications).

[23] We thank the late Mr. F. A. McDermott for identifying our fireflies.

[24] A species of *Colophotia* has been reported to be "the" synchronizing firefly of Thailand (Reinking, O. A., *Science*, **53**, 485; 1921) and we have also seen a large sample of *Luciola brahmina*, said to have been collected in the spring along the Chao Phraya River, and also supposed to have been flashing synchronously. Observational errors may well be involved in both reports, but the possibility of more than one synchronizing firefly species in the same area raises some very interesting questions and cautions against generalizations from limited geographical and seasonal experience.

For the convenience of readers, the following extracts are reprinted from Dr. Buck's communication "Flashing of Fireflies in Jamaica" (*Nature*, May 8, 1937, and ref. 9 above):

"DURING the past summer, the members of the Seventh Botanical Expedition of the Johns Hopkins University witnessed displays of firefly activity in the British West Indies as spectacular in their way as any reported from the Orient.

"In front of the expedition's laboratory at Chestervale, in the Blue Mountains of Jamaica, there was a thatch palm which bore below its whorl of leaves an inflorescence a metre in diameter. For about a week in June, and again a month later, this inflorescence was transformed nightly into a sphere of seething flame by the flashes of thousands of fireflies which gathered there. Later, other displays were discovered, particularly on two large acacia trees overhanging the Clyde Valley which harboured such prodigious swarms of fireflies that the nebulous glow was visible half a mile away.

"All the fireflies on these trees were of one species, *Photinus pallens*, and the females outnumbered the males in the ratio of 4 : 3. Each firefly flashed regularly about twice a second while walking along the twigs, and entirely independently of any other individual. There was no sign of synchronism or of response between any individuals or between different trees. The flashing was not inhibited by heavy rain, by lightning, or by the beam of a powerful flashlight, but did not occur on moonlight nights.

"Whatever the cause of the aggregation, it serves an important function in bringing the sexes together for mating, and many coupling pairs were observed on the palm tendrils. The mating, however, appears to be due entirely to accidental contact of the sexes during their peregrinations on the branches. The aggregation habit thus seems to take the place of the accurate systems of flashing signals which serve to bring male and female together in some species of firefly."

JOHN B. BUCK