The Luminous World of John and Elisabeth Buck[1]

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SYNOPSIS. Highlights of the research careers of John and Elisabeth Buck are presented, illustrating their importance as investigators of firefly biology including taxonomy, morphology, physiology and behavior, and as catalysts of collegial exchanges advancing progress among investigators of bioluminescence in its widest aspects over the past 50 years.

John Bonner Buck began research on fireflies while an undergraduate in the summer of 1933. He was a solitary researcher only briefly because he and Elisabeth M. Mast married after she completed her zoology A.B. at Radcliffe and he was on the Rochester Institute faculty. She thereafter become his partner in virtually all of his research on fireflies (Fig. 1). This symposium honors them for their joint research on fireflies and for their innumerable collegial interactions with workers on fireflies and many other aspects of bioluminescence. Their thoughtful and meticulous research is a model deserving emulation. Their enthusiasm, typically embedded in warm friendships, has spread widely in the research community over the last half century, and has particularly influenced these authors.

Born in Hartford, CT and relocated to Baltimore in his high school years, John Buck naturally gravitated to The Johns Hopkins University where he received sound preparation in biology, particularly cytology and physiology on the Homewood and medical campuses. His advisor was S. O. Mast, then pioneering in the physiology of behavior. While still an undergraduate, John independently undertook a summer vacation study on the flashing behavior of *Photinus pyralis*, which abounds in Baltimore every July. Working in his back yard, aided by a schoolboy neighbor, he timed flashes and measured temperature and ambient light with equipment from the departmental storeroom. All this was inspired by Professor Mast's classroom discussion of his work on photic behavior in *Photinus pyralis* (Mast, 1912). John said nothing to Mast about his summer project so it must have been a pleasant surprise to receive this solid piece of work when Mast brought his family home from summer in their Woods Hole refuge from Baltimore's fabled heat and humidity. Mast, in the Johns Hopkins biology faculty tradition of the day, was a veteran summer investigator at the Marine Biological Laboratory, and this institution was eventually to attract John and Elisabeth.

Mast took decisive action and John was immediately admitted to graduate study. In fact, John already had the remainder of his thesis in mind and carried it out the next summer when fireflies were again available. Part of his thesis was reported in his paper on periodicity and diurnal rhythm (Buck, 1937*a*). The work was both sound in design and heroic in execution because John was, himself, the 24-hour recording instrument (Fig. 2). His data plainly showed what must have been one of the earliest examples of a circadian rhythm involving bioluminescence.

In his second thesis paper (Buck, 1937*b*), having determined by stopwatch that the critical response interval for the female's reply to the male's flash is about 2 sec, he provided firefly behaviorists of coming generations evidence that a clean experiment on flash communication in the field is actually attainable. He did this by attracting patrolling males to a captive male induced to flash with properly timed pinches. This showed there was nothing unique about the female's light organ of relevance to communication between the sexes except for the timing of her reply to the patrolling male. After this bit of elegance, he ventured perhaps precariously farther. In an experiment, so far as we know never repeated, one eye of a male was painted over with black enamel. The recovered firefly did not orient to flashes from the blind side but flew sideways towards the light, keeping the good eye oriented to the flashes. Exhibiting uncharacteristic panache, John used this result to question Jacques Loeb's (1918) then popular theory of photic orientation in insects, which required paired eyes.

By then John was already looking beyond *P. pyralis*, having already taken notice of its in-flight male-male interaction flashes in which one male seeing another flash may get off a flash with minimal delay. If others are in the air nearby there may result a brief period of synchronous flashing based on resetting of the patrol flash cycles of several participating males. He offered this behavior as a model to explain the remarkable male flash synchrony of S.E. Asian fireflies that can involve them by the thousands. This was already a matter of considerable speculation (Buck, 1935). Confirming and working out the mechanism of synchronization ultimately became a major research interest for both John and Elisabeth.

John went on a NRC Fellowship to postdoctoral studies at the California Institute of Technology, where he pursued cytological interests, then to the faculty at

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FIG. 1. John and Elisabeth Buck, 1985, West Virginia.

the Rochester Institute of Technology and finally to The National Institutes of Health where he became head of the Laboratory of Physical Biology. Reflecting his own wide interests, the Laboratory included researchers on vision, photosynthesis, muscle physiology, insect respiration, and many aspects of bioluminescence.

A second vital research base for the Bucks was Woods Hole, where they still summer, and where at this writing they celebrated their 91st birthdays amidst family and friends. At the Marine Biological Laboratory, John taught in the 1940s and later directed the summer Invertebrate Zoology Course, for many years a notable attractant of future MBL investigators. The Bucks interacted with a host of scientific visitors mixed with family and their associates in summer research at the MBL. Among firefly investigators of relevance to this symposium are J-M Bassot (1967), Helen Ghiradella (1998), and Donata Oertel (Oertel *et al.*, 1975; Oertel and Case, 1976). Down almost to the present John and Elisabeth gained relief from the intensity of MBL summer life by competing in the Woods Hole Yacht Club races. These frequently chaotic events John memorialized for the local newspaper with analytical reviews under the byline, ''Old Salt,'' wherein he deftly excused low placement in the order of finishing of their Cape Cod knockabouts, Chelonia I and II, with explanations such as finding at a critical moment only laundry in the spinnaker bag.

John accomplished important work in his early career on a broad spectrum of firefly problems, especially his masterful work on light organ structure and physiology (Buck, 1948) which was certainly by far the most complete documentation at the time and still is a valuable resource. Buck's structural interests persisted throughout his career, including studies on light organ ultrastructure in synchronizers (Peterson and Buck, 1968) and on peroxisomes in photocytes (Hanna *et al.*, 1976). He made taxonomic contributions on both American and Jamaican fireflies (Buck, 1947), happily facilitated by a long collaboration with a remarkably productive amateur, Frank A. McDermott (obituary of F. A. M. with bibliography, Buck, 1968). Among other interests were important studies on the then recently discovered mechanism of discontinuous

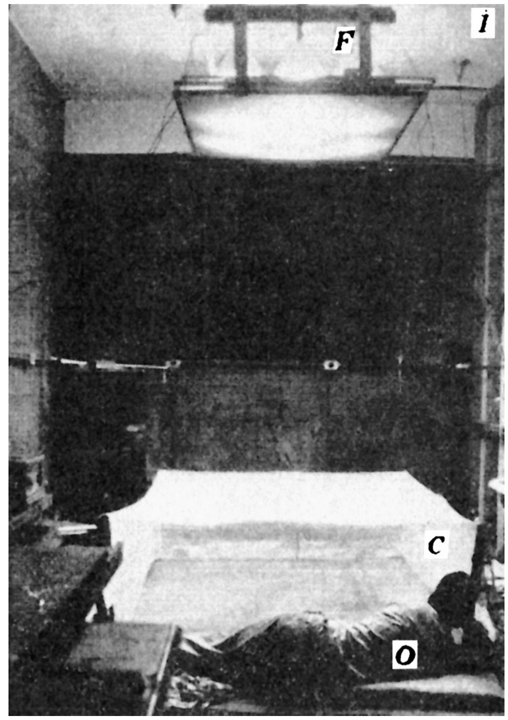

FIG. 2. Experimental arrangements as shown in Buck's doctoral thesis. Darkroom fitted for artificial day/night cycle. O. Observer (Buck) in sleeping bag, C. netting cage with free-ranging fireflies, F. Observer-controlled room lighting.

ventilation in insects for which his interest in firefly light organ tracheation was highly complementary to at least one approach to the problem of luminescence control (Buck, 1962, and antecedent papers there cited).

In his 1948 monograph John commented on physiological control of the firefly flash. Somewhat later he engaged in a broad phyletic approach to flash control (Buck, 1955). Ultimately he entered the field experimentally with a study on the pseudoflash with J. W. Hastings, soon to attain prominence in the molecular biology of bioluminescence and circadian biology (Hastings and Buck, 1956). Somewhat later Buck also influenced a related thesis by A. D. Carlson on neural effects on the pseudoflash, thereby establishing a valuable relationship with yet another important recruit to the field (Carlson, 1961).

After some earlier discussions of a mutual problem in tracheal respiration, Case's scientific interactions with the Bucks began in earnest at the MBL in 1959 in studies on the neurophysiology of the lantern (Buck and Case, 1961; Case and Buck, 1963; Buck, Case and Hanson, 1963) and leading eventually to behavioral studies. Their interactions have continued intermittently to the present (Buck and Case, 2002). Hanson joined the early firefly work in Woods Hole (Hanson, 1962) in the summer before starting graduate studies and some years later collaborated with John in studies on the alcyonarian coelenterate, *Renilla*, on American firefly dialog behavior, and on synchrony in S.E. Asian

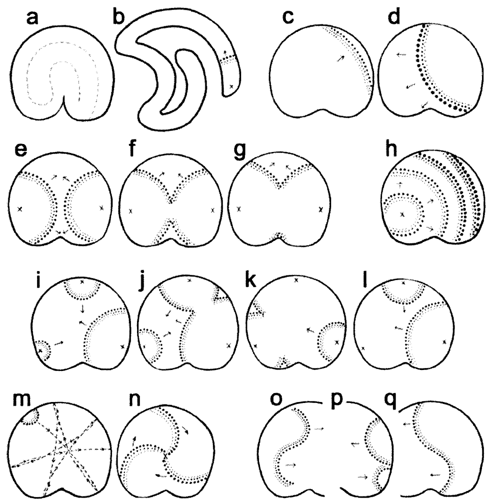

FIG. 3. Renilla luminescence experiments. From Buck's drawings. Renilla colony viewed from above, colony diameter up to 10 cm, depending on extent of inflation. (A, B) colony cut into single strip sustains luminescent wave propagation end to end, arguing for a multipath nerve net. (C, D) luminescent wave propagates to edge of colony and reflects back. (E, F, G) propagation of two simultaneous waves and their fusion. (H) multiple waves from serial excitation at one site. (I, J, K, L) more complex propagation of multiple waves. (M, N, O, P, Q) patterns of spontaneous waves resulting from ''autoexcitatory'' state.

species. The lantern neurophysiological studies of the 60s left behind several mysteries, particularly the extremely long final synaptic latency of the flash, approximately 50 to 200 ms depending on the species (Buck and Case, 1961; Case and Buck, 1963). As some participants in this symposium can testify, if only from frequent e-mail correspondence, Buck considers the current rebirth of research on lantern excitation as important new hope for progress in understanding these final stages in light emission.

John's interests in bioluminescence have not been confined to insects. He was one of the earliest to theorize about the evolution and adaptive significance of marine bioluminescence by calling attention to the possibility that bioluminescence can account for the well developed eyes of organisms inhabiting the deep seas beyond the reach of astronomical light (Buck, 1961). His chapter in Peter Herring's landmark volume, ''Bioluminescence in Action'' (Buck, 1978) remains a valuable and frequently cited work on the functions of bioluminescence across all phyla.

John briefly forsook the firefly as an experimental target on a visiting professorship with Prof. T. H. Bullock, then at UCLA. This included study of the luminescence of the sea pansy, *Renilla*, an alcyonarian soft coral. The work involved long periods in a dark aquarium room at the Kerchoff Marine Laboratory. Without low-light imaging equipment, he made minute observations of the intricate patterns of luminescence that race across the surface of this colonial organism in response to various modes of stimulation (Buck, 1973). Some of his acute visual observations are shown in Figure 3. The luminescent behavior of the colony sometimes became sufficiently dramatic to evoke in his taped notes such terms as ''boiling,'' ''pinwheel'' and ''propeller.'' His later work on *Renilla* emphasized luminescence of the individual zooids of the colony and the photomultiplier was used in recording from this system for the first time (Buck and Hanson, 1967). As they and earlier investigators realized, these remarkable patterns of luminescence reflected the underlying activity of the colonial nerve net system that was not to be directly identified until technological progress permitted electrophysiological demonstration of a neural network devoted to luminescence (Anderson and Case, 1975). His fascination with *Renilla* luminescence behavior can be understood by viewing more recent low-light video of *Renilla* excitation at http://lifesci.ucsb.edu/~biolum.

Throughout their careers John and Elisabeth were interested in both laboratory and field studies on fireflies. John first visited Jamaica with a Johns Hopkins expedition in 1936. He was impressed by the remarkable displays of thousands of *Photinus pallens* (Buck, 1937) and described several new species (Buck, 1947). Later they were involved in several Johns Hopkins expeditions to Jamaica in the company of William D. McElroy and Howard Seliger. Jamaica's ample firefly species list prompted important behavioral and taxonomic work as well as the first photoelectrically measured emission spectra from fireflies (Seliger *et al.*, 1964*a*). These expeditions were amusingly documented in ''Notes from the Underground,'' a not-so-scientific report on the realities of scientific expeditions (Buck, 1964).

After seeing the capabilities of Seliger's portable photometer in Jamaica (Seliger *et al.*, 1964*b*), Buck and Hanson built a nominally portable photometer and chart recorder combination (Buck and Buck, 1968) that saw heavy duty in direct field recordings, thus applying a check on potential inaccuracies of purely visual observations. With this equipment they first examined the time-dependent signaling of *Photinus greeni*, a firefly conveniently to be found in their Woods Hole neighborhood (Buck and Buck, 1972). The same apparatus was to accompany them on their travels in S.E. Asia where the first field records of synchronously flashing fireflies were obtained (Buck and Buck, 1968), if one discounts Bassot and Polunin's ingenious and impromptu open lens rotation of a 35 mm camera in front of a synchronous display (Bassot and Polunin, 1967).

The Bucks' long-held interest in synchrony had been repeatedly inflamed by reports such as that from the Dutch physician Engelbert Kaempfer chronicling his voyage down river from Bangkok in 1680: '' 'The glowworms . . . represent another shew, which settle on some Trees, like a fiery cloud, with this surprising circumstance, that a whole swarm of these insects, having taken possession of one Tree, and spread themselves over its branches, sometimes hide their Light all at once, and a moment after make it appear again with the utmost regularity and exactness. . . ' '' (Buck and

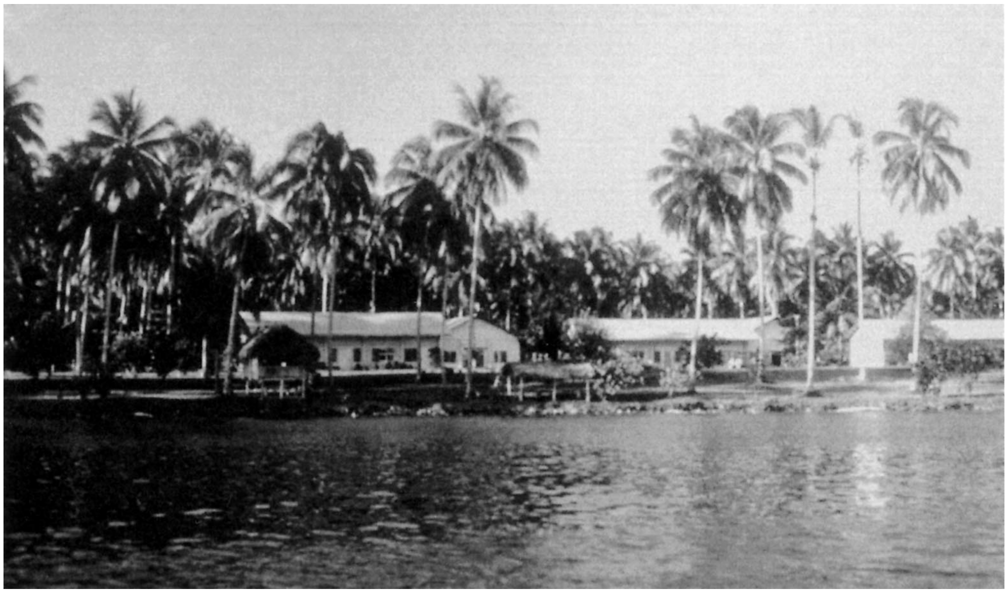

FIG. 4. Maiwara, the base camp and laboratory research site for the New Guinea expedition, near Madang, on the North Coast of Papua-New Guinea, September 1969.

Buck, 1968, p. 3). Finally succumbing to such blandishments, in 1965 they ventured to Thailand and Borneo to observe this phenomenon with their own eyes. Their first view of it must have been a life-altering experience: ''As we drew in toward the dark shoreline, pale nebulous patches began to resolve, at a distance of 30 meters or so, into bushes or trees spangled with hundreds of tiny lights pulsing steadily in a rapid rhythm of about two per second. Each time we saw this hurrying, soundless, hypnotic, enduring performance it impressed us anew as uniquely different from any behavior we had ever seen'' (Buck and Buck, 1968, p. 3). They promptly activated the aforementioned portable photometer-chart recorder and obtained the first electronic recording of firefly synchrony.

Back home at NIH, where the mission is to promote research bearing on human health, the Buck's awareness of the importance of rhythmic neural processes to bodily functions lead them to a productive study of voluntary rhythms and synchrony in humans, a plentiful supply being available locally among the members of the Laboratory of Physical Biology. This work provided a better understanding of human abilities, to be sure, but also a deeper insight into the various types of synchrony and their mechanisms (Buck and Buck, 1968; Mets, 1975). They probably also had in mind that if the opportunity were to arise to do more experimentation on synchronous fireflies, then they would be better prepared to plan experiments and understand the results.

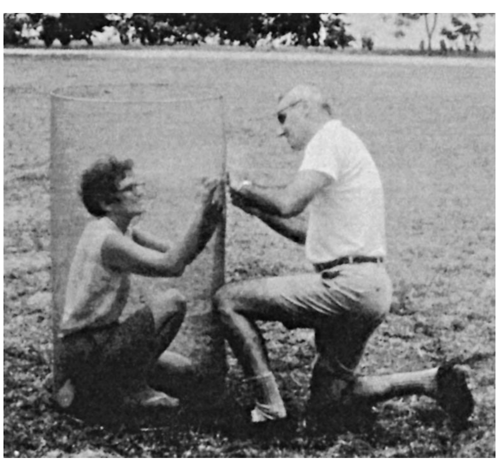

FIG. 5. Elisabeth and John Buck preparing for firefly experiments at the Maiwara, New Guinea research site.

Precisely this opportunity arose in 1969 when John, with Elisabeth in support, led the NSF Alpha Helix South East Asian Bioluminescence Expedition to Papua-New Guinea for studies on terrestrial and coastal marine bioluminescence, including synchronous flashing fireflies (Figs. 4, 5). Here some members of the group used multi-channel photometric recordings of fireflies, either synchronizing with other fireflies or with electronically driven artificial lights, the frequency and timing of which were manipulated by the experimenter. These machines spewed out data sufficient to keep the Bucks and us occupied for years modeling the process of achieving and maintaining synchrony in *Pteroptyx cribellata* (Hanson *et al.*, 1971; Buck and Buck, 1976; Buck *et al.*, 1981). Forays from the base camp by the Bucks, Hanson, Hopkins and Bassot documented firefly synchrony in the highlands, where a species with an astonishing 5 sec period was observed, and in several other parts of Papua-New Guinea and New Britain.

We two members of this expedition were inspired to further efforts on synchronous fireflies and organized a mini-expedition to Bangkok and Singapore in

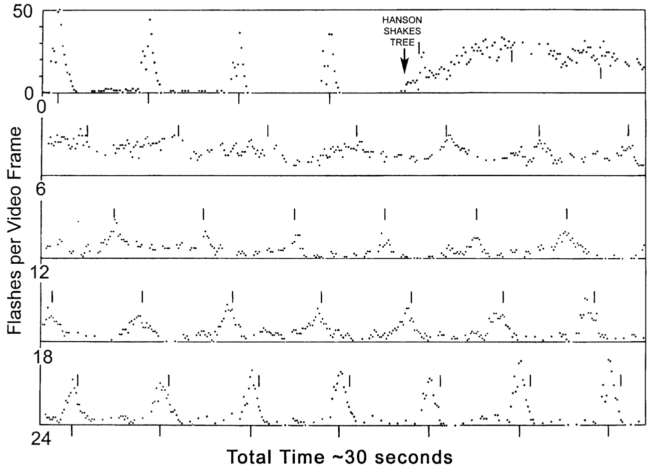

FIG. 6. Synchrony interruption and reestablishment in *Pteroptyx malaccae*. A small tree is briefly shaken interrupting the characteristic two-peaked flash, seen even from the whole tree of perhaps 100 males. A 30 sec sequence was plotted frame by frame. Flashes per frame scale on top trace. Vertical marks indicate actual and anticipated synchronous peaks based on previous peaks including the four before the shake. Last communal flash at lower right shows full reconstruction of two-peaked synchrony only a fraction of a second off the original timing. Beside the Benuit River, Johore, Malaysia, 1972.

1975 to more fully investigate the firefly on which the Bucks initiated quantitative field studies, *Pteroptyx malaccae*. Our initial question was, do these fireflies actively get into synchrony or do they randomly drift into synchrony and somehow lock in? To do this Case trained his camera equipped with a ''Starlight'' image-intensifier rifle scope on a small tree full of synchronizing *P. malaccae* while Hanson gave the tree a brief shake to interrupt synchrony (Fig. 6). Thus satisfied that attaining synchrony was indeed an active process, as the Bucks had proposed, the expedition participants, including James Parmentier and A. T. Barnes with the indispensable collaboration of Prof. Ivan Polunin, Singapore's resident expert on fireflies and most other living things on the Malay Peninsula, set to work. Once again the data spewed forth, this time into more portable tape decks, and, to everyone's surprise, showed this species to synchronize in a totally different manner than the two New Guinea species above (Hanson, 1978, 1982). Thus the synchrony modeling effort begun by the Bucks grew into a fascinating example of comparative behavioral physiology showing that the same observed behavior—flash synchrony—is achieved and maintained in three different ways by three different species (*Pteroptyx cribellata*, *P. malaccae*, and *Luciola pupilla*). Since the explications of synchrony in the Papua-New Guinea and Asian species, the Bucks have followed with much interest the more recent reports of synchrony in the United States *Photinus concisus* in Texas (Otte and Smiley, 1977), *Photinus knulli* in Arizona (Cicero, 1983), and *Photinus carolinus* in Tennessee (Copeland and Moiseff, 1995). The first of these elicited a trip to the area by the Bucks; once again they recorded electronically in the field and brought back specimens for lab study (Buck *et al.*, 1982). These versions of synchrony are quite different from those in the exotic species, again underscoring the diversity in synchronic behaviors in fireflies. Furthermore, the unpublished observations by the Alpha Helix group in Papua-New Guinea indicate that even more bizarre types of synchrony await investigation; perhaps, and we hope, we have only scratched the surface.

To end on a personal note, and speaking we are sure for many others involved in this symposium, the authors acknowledge with gratitude the stimulation provided to us by the Bucks during their quest for knowledge of their luminous world. It has been a rare privilege to be both their scientific associates and personal friends.

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REFERENCES

Anderson, P. A. V. and James F. Case. 1975. Electrical activity associated with luminescence and other colonial behavior in the pennatulid *Renilla kollikeri*. Biol. Bull. 149:80–95.

Bassot, J-M. and I. V. Polunin. 1967. Synchronously flashing fireflies in the Malay Peninsula. Sci. Reports of the Yokosuka City Museum 13:18–20.

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

Buck, J. B., 1937*a*. Studies on the firefly. I. The effect of light and other agents on flashing in *Photinus pyrolis*, with special reference to periodicity, and diurnal rhythm. Physiol. Zoology. 10: 45–58.

Buck, J. B., 1937*b*. Studies on the firefly. II. The signal system and color vision in *Photinus pyrolis*. Physiol. Zool. 10:412–419.

Buck, J. B. 1947. Studies on the firefly, IV: Ten new lampyrids from Jamaica. Proc. U.S. National Museum 97:59–79.

Buck, J. 1948. The anatomy and physiology of the light organ in fireflies. Ann. N.Y. Acad Sci 49:397–482.

Buck, J. 1955. Some reflections on the control of bioluminescence. *In* F. H. Johnson (ed.), *The luminescence of biological systems*, pp. 323–333. Amer. Association for the Advancement of Science, Washington.

Buck, J. 1961. Speculations on the interrelations and evolution of photic organs. *In* W. D. McElroy and B. Glass (eds.), *Light and life*, pp. 754–770. Johns Hopkins University Press.

Buck, J. 1962. Some physical aspects of insect respiration. Ann. Rev. Entomology 7:27–56.

Buck, J. 1964. The march of science Jamaican style. The Johns Hopkins Magazine, April pp. 4–8.

Buck, J. B. 1968. Frank Alexander McDermott (1885–1966). Entomological News 79:49–54.

Buck, J. 1973. Bioluminescent behavior in *Renilla*. I. Colonial responses. Biol. Bull. 144:19–42.

Buck, J. B. 1978. Functions and evolutions of bioluminescence. *In* Peter J. Herring (ed.), *Bioluminescence in action,* pp. 419–460. Academic Press, New York.

Buck, J. and E. Buck. 1968. Mechanisms of rhythmic synchronous flashing of fireflies. Science 159:1319–1327.

Buck, J. and E. Buck. 1972. Photic Signaling in the firefly *Photinus greeni*. Biol. Bull. 142:195–205.

Buck, J. and E. Buck. 1976. Synchronous fireflies. Sci. Am. 234: 74–85.

Buck, J., E. Buck, J. F. Case, and F. E. Hanson. 1981. Control of flashing in fireflies. V. Pacemaker synchronization in *Pteroptyx cribellata*. J. Comp. Physiol. 144:287–298.

Buck, J., and J. F. Case. 1961. Control of flashing in fireflies. I. The lantern as a neuroeffector organ. Biol. Bull. 121:234–256.

Buck, J. and J. Case. 2002. Physiological links in firefly flash code evolution. J. Ins. Behavior 15:51–68.

Buck, J., J. F. Case, and F. E. Hanson. 1963. Control of flashing in fireflies. III. Peripheral excitation. Biol. Bull. 125:251–269.

Buck, J. and F. E. Hanson. 1967. Zooid response in *Renilla*. Biol. Bull. 133:459.

Buck, J., F. E. Hanson, E. Buck, and J. F. Case. 1982. Mechanism and function of synchronous flashing in the firefly *Photinus concisus*. Biol. Bull. 163:398.

Carlson, A. D. 1961. Effects of neural activity on the firefly pseudoflash. Biol. Bull. 121:265–276.

Case, J. F., and J. Buck. 1963. Control of flashing in fireflies. II. Role of central nervous system. Biol. Bull. 125:234–250.

Cicero, J. M. 1983. Lek assembly and flash synchrony in the Arizona firefly *Photinus knulli* Green. The Coleopterists Bulletin 37: 318–342.

Copeland, J. and A. Moiseff. 1995. The occurrence of synchrony in the North American firefly *Photinus carolinus*. J. Insect Behavior 8:381–393.

Ghiradella, H. 1998. The anatomy of light production: The fine structure of the firefly lantern. *In* F. W. Harrison and M. Locke (eds.), *Microscopic anatomy of invertebrates*, Vol. 11A, *Insects*, pp. 633–381. Wiley-Liss, New York.

Hanna, C. H., T. A. Hopkins, and J. Buck. 1976. Peroxisomes of the firefly lantern. J. Ultrastr. Res. 57:150–162.

Hanson, F. E., Jr. 1962. Observations on the gross innervation of the firefly light organ. J. Ins. Physiol. 8:105–111.

Hanson, F. E. 1978. Comparative studies of firefly pacemakers. Federation Proc. 37:2158–2165.

Hanson, F. E. 1982. Pacemaker control of rhythmic flashing of fireflies. *In* D. Carpenter (ed.), *Cellular pacemakers*, Vol. 2, pp. 81–99. John Wiley & Sons, New York.

Hanson, F. E., J. F. Case, E. Buck, and J. Buck. 1971. Synchrony and flash entrainment in a New Guinea firefly. Science 174:161–164.

Hastings, J. W. and J. Buck. 1956. The firefly pseudoflash in relation to photogenic control. Biol. Bull. 111:101–113.

Loeb, J. 1918. Forced movements, tropisms, and animal conduct. Lippincott, Philadelphia.

Mast, S. O. 1912. Behavior of fire-flies (*Photinus pyralis*)? with special reference to the problem of orientation. J. Animal Behavior 2:256–272.

Mets, L. J. 1975. A general method for distinguishing the fundamental timer for a biological rhythm from cyclic processes which it times. Biophys. J. 15:177A.

Oertel, D., K. A. Linberg, and J. F. Case. 1975. Ultrastructure of the larval firefly light organ as related to control of light emission. Cell. Tiss. Res. 164:22–44.

Oertel, D. and J. F. Case. 1976. Neural excitation of the larval firefly photocyte: Slow depolarization possibly mediated by a cyclic nucleotide. J. Exp. Biol. 65:213–227.

Otte, D. and J. Smiley. 1977. Synchrony in Texas fireflies with a consideration of male interaction models. Biol. Behav. 2:143–158.

Peterson, M. K. and J. Buck. 1968. Light organ fine structure in certain Asiatic fireflies. Biol. Bull. 135:335–348.

Seliger, H. H., J. B. Buck, W. G. Fastie, and W. D. McElroy. 1964*a*. The spectral distribution of firefly light. J. Gen. Physiol. 48:95–104.

Seliger, H. H., J. B. Buck, W. G. Fastie and W. D. McElroy. 1964*b*. Flash patterns in Jamaican fireflies. Biol. Bull. 127:159–172.