FLASHES OF *PHOTURIS* FIREFLIES: THEIR VALUE AND USE IN RECOGNIZING SPECIES[1]

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ABSTRACT

Mating flashes provide excellent clues for recognizing biological species of fireflies. Since *Photuris* species also flash in contexts in which species-specificity would appear to be irrelevant, mating flashes must be distinguished; since the parameters of mating flashes that do *not* encode species information may vary considerably, these signals must be critically analyzed. The use of mating flashes for species recognition has spatial and temporal limitations.

The mating flashes of fireflies have been found to be valuable aids in taxonomy. In his classic study of *Photuris* Barber (1951) relied upon these flashes for species recognition and discovered the presence of several morphologically cryptic species. More recently, through studies of flashing behavior, I have found several cryptic species in *Photuris*, *Photinus*, and *Pyractomena* (Lloyd 1966a, 1966b, 1966c, unpublished). Mating flashes are of special significance in taxonomy since they have been found to be of importance in reproductive isolation (Lloyd 1966c). However, since many species flash in contexts other than mating, contexts in which species-specificity would appear to be irrelevant, the taxonomist must recognize mating behavior and mating signals. Furthermore, the flash parameters that encode species information differ among fireflies and the taxonomic significance of variation observed among signals cannot be appraised until the elements that are communicatively significant have been determined.

This paper presents some recent observations on the behavior of nearctic *Photuris* that have a bearing on the use and value of flashes in species recognition. I will discuss why it is difficult to recognize mating signals, why it is difficult to determine the elements that encode species information, and some limitations in the use of mating signals for recognizing species. Since several of the *Photuris* species discussed in this paper have not been named, code letters are used. A description of the relatively simple behavior and signals of *Photinus* will introduce the general elements of firefly mating conduct, and a survey of their behavioral characteristics pertinent to signal analyses will provide a standard of comparison for *Photuris*.

Photinus Fireflies

In most *Photinus* species males fly about their habitat emitting a signal (flash pattern) that is constant and simple in form, and repeated at fairly regular and short intervals (Lloyd 1966c). *Photinus* females almost never fly and flash; they remain on the ground or vegetation and flash in answer to the flash pattern of their own males. Males fly and walk to answering

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females, and after a few flash exchanges reach them and copulate with them. Males and females seldom flash except during sexual communication or when captured by predators or held captive in spider webs or puddles of water.

Analyses of *Photinus* signals are easily conducted. Experimental determination of critical signal parameters can be made in the field with free insects and in the laboratory with captive ones. Several factors contribute to this: waveforms of the flashes are simple and can be approximated with incandescent bulbs; captive females will answer simulated and actual male flash patterns; free males will approach simulated female flashes and the response flashes of captive females; and most species are terrestrial rather than arboreal. Signal discrimination tests can be performed on free males (Mast 1912, Buck 1937, Lloyd 1966c) as well as on captive males in mazes (M. Maurer unpublished), and arenas (Lloyd unpublished). Information-carrying elements have been experimentally determined in the signals of several species (Buck 1937, Buck and Buck 1965, Lloyd 1966c). Flash length, flash rate and number in multipulse flash patterns, and time delay of female response flashes have been found significant in various species.

Photuris Fireflies

The mating flashes and behavior of *Photuris* are difficult to recognize and analyse for several reasons: 1) It is difficult to recognize their mating signals because (a) flashes are emitted in other contexts and (b) the signals emitted by flying males may be altered or changed completely during the course of evening mating activity or under different ecological conditions. 2) It is difficult to identify and experimentally determine the elements of *Photuris* mating signals that convey species information because (a) the signals are structurally complex, (b) *captive* females of many species will not respond to male or artificial flash pattern stimulation, and (c) mating activity takes place in ecological situations where direct observation and experimentation are difficult.

OTHER CONTEXTS: *Photuris* females of several species mimic the flash responses of females of other species (Fig. 1A, B, C), attract their males and devour them; females of a species in the *Photuris versicolor* complex mimic the signals of at least two other species, each of which has a different signal (Lloyd, 1965, and in prep). Prey species belong to the genera *Photuris*, *Photinus* and *Pyractomena*. The flashes predaceous females emit in response to the flashes of the males they attract are not necessarily the same as their mating flashes. With inadequate observation *Photuris* females can be incorrectly associated with males of other species or with the mating signals of females of other species.

Recent observations indicate that *Photuris* females and males use their luminescence for illumination (Lloyd 1968). Both sexes emit characteristic flash sequences when landing (Fig. D, E), flash intermittently while walking about on the ground, and females commonly flash immediately before taking flight. These flashes apparently function in illuminating the substrate and surrounding vegetation. Such flashes would have adaptive value since there are a variety of hazards when flying near the ground or landing (e.g. spider webs, wet vegetation, water puddles). It is doubtful that these flashes have any sexual significance since other individuals are not attracted to fireflies flashing in this manner, and observations thus far have not revealed characteristic species differences.

Photuris fireflies flash when grasped, handled, knocked to the ground, or confined. Very little stimulation is required to induce this flashing. It has been suggested that flashing intimidates predators. Harvey (1952) cites several anecdotal references but considers "the idea of the lantern of the fire-fly as a means of defense or warning signal . . . very dubious" with "the possibility of attraction just as probable." The flashes of confined *Photuris* may be homologous with those emitted when walking, perhaps functioning in illumination, or with those emitted when grasped.

SIGNAL CHANGES IN FLYING MALES: By direct observation and by marking, releasing, and recapturing I have found that males of *Photuris* "A" have three different flash patterns. During the first 20 minutes of activity each evening they emit a long flash (ca 0.4 sec) at 4 second intervals (Fig. 1 F). Later they emit short flashes of about 0.15 seconds in duration (Fig. 1 C). The transition between the long and short flashes may be gradual with several flashes of intermediate length emitted. The flight of males producing these flashes is slow and hovering. The third signal, 2-5 flashes of the same form as the short flash (Fig. 1 G), is emitted at any time during the activity period whenever males are flying rapidly over coarse vegetation or marsh grass. Males are attracted to an artificial light that is flashed immediately after their single, short flash. When a light is flashed after the 2-5 pulse signal, males change to the single, short flash as they approach. This illustrates that pulse-number variation is intraspecific and of no taxonomic significance except as it aids or complicates field identification. The adaptive significance of such signal variation may be related to ecology—e.g. a long flash at high ambient light intensities and a multipulsed signal and fast flight over bushes, coarse vegetation, or expansive sites might enhance a male's chances of being seen by a female. However, a species could employ different signals in a specific sequence for mate recognition, or each different signal could have a specific function in attraction and mating such as the calling and courtship songs of crickets (Alexander 1961). In any event, without adequate observation, this species might have been described as 3 or more species although in fact it is one of the 4-6 north Florida species collectively known as *Photuris lloydi* McDermott.

Barber (1951) suspected that males of *P. lucicrescens* Barber emit both a short flash and a long, crescendo flash, and that *P. tremulans* Barber emits both a short flash and a long pulsating flash. K. Smalley (personal communication) has observed a species in Kansas that emits a single short flash early in the evening and a long crescendo flash later. She observed mating following exchanges of short flashes.

STRUCTURALLY COMPLEX SIGNALS: Males of some species incorporate subtle or rapid intensity modulations in their mating signals and it is often impossible for the human eye to detect these elements. For example, the flicker of one species (Fig. 1 H) and the two flashes of another (Fig. 1 I) can be resolved only at low temperatures or when the insects are flying rapidly. Electronic recording systems are essential for analysis, and sometimes for positive field identification. Several species have "crescendo" flashes in which intensity builds up slowly to a maximum and then decreases rapidly. Crescendo flashes are extremely difficult to analyze elec-

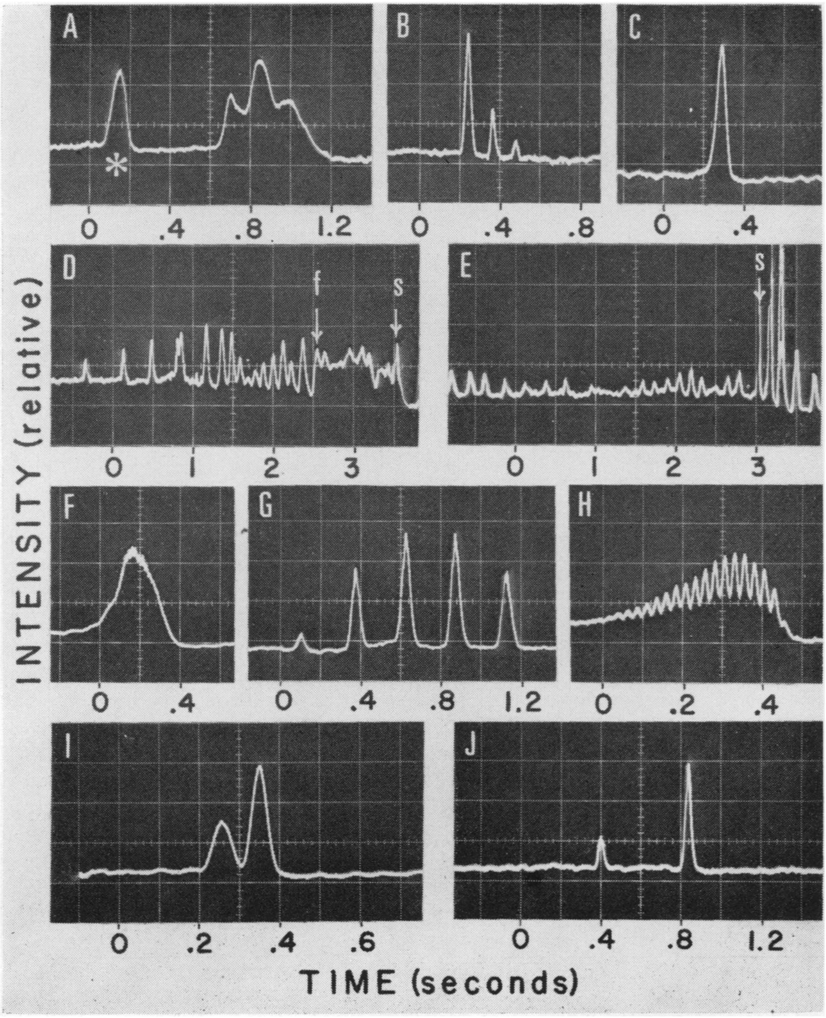

Fig. 1. Ocillograms of firefly flashes. All flashes were recorded in the field. Flashes are detected by a photo-multiplier tube, transduced to a frequency modulated audio signal that varies proportionally (9-12 kc) with light intensity, and recorded on magnetic tape (7.5 ips). For analysis, recorded tones are transduced to a variable dc voltage that is then fed into a storage oscilloscope with a calibrated time base. Changes in baseline result from different background light intensities during panning (e.g. B, G), from a feedback control in the recording system (e.g. A, C, H), and from sustained emission of light by the firefly (e.g. D at point f). The recording system was designed and built by Alton Electronics, Gainesville, Florida. A. Flash response of an aggressive mimic female (*Photuris versicolor* complex), *=artificial flash (75°). B. Flash pattern of aggressive mimic's own males (79°). C. Late-evening flash of *Photuris* "A" male (78°). Aggressive mimics answer this flash, attract and devour *Photuris* "A" males. D. Landing flashes of *Photuris* "A" female, (78°). f, fusion of flashes at an altitude of 5-10 inches. s, flash emitted immedi-

tronically; commonly, such a flash will range from an intensity too dim to be recorded to one that overdrives the electronic recording system.

The relative intensities of discrete pulses may also encode species information. In the flash patterns of *Photuris* "Q", the first pulse is obviously less intense than the second, and in all recordings this relationship exists (Fig. 1 J). There is also a consistent intensity relationship among the pulses in the flash pattern of a Florida species in the *P. versicolor* complex (Fig. 1 B).

The functional units of male signals of most species are obvious because of their structural organization. If the functional unit is a single flash, or flicker, it is repeated at intervals of at least 2 seconds in duration. If this unit consists of several flashes, then the interval between units is longer, but the intervals between flashes of the unit are usually less than 1 second in duration. The phrasing of the male signals of some *Photuris* species give no clear indication of functional units. For example; the male mating signal of *P. congener* LeConte is a continuous series of single, short flashes at less than 1 second intervals. Although the female response is not known, aggressive mimics (females of species in the *P. versicolor* complex) attract *P. congener* males by flashing an erratic, rapid flicker. The signal that stimulates *P. congener* females may be a single flash and its length the species-specific element, but the critical parameter could be the flash rate established by a short series of single flashes; the communicative unit advancing in time along a continuous series of pulses.

The flashes of *P. brunnipennis floridana* Barber males are like those of *P. congener* males but this species appears to have yet another signal system. When several males of *floridana* are placed in a small container they flash in synchrony. Single males, when placed in a circular arena (diameter 20 inches), flash synchronously with and walk rapidly toward an artificial blinker that is flashing at intervals similar to their own. The presence of a mechanism for synchrony and the behavior of captive males with respect to artificial stimulation suggests that courtship in this species involves male and female synchronization. Such a signal system is not known for any firefly, and although in some Asian species huge aggregations synchronize (Buck and Buck 1968) this has not been seen in Florida.

Captive females not responsive: Female response flashes are an integral part of the species-specific codes and it is essential to determine the delay and pulse characteristics of these flashes. When confined in glass

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ately upon landing when female's light is no longer directed at the ground. E. Landing flashes of *Photuris* "A" male (73°). s, first flash emitted upon landing. F. Early-evening flash of *Photuris* "A" male (71°). The noise ("grass") at the peak of the flash resulted from an overload alarm and indicates that his portion of the recording is not an accurate representation of the actual flash. G. Roving flash pattern of *Photuris* "A" male (74°). Intensity differences among pulses are not characteristic of this species' flash pattern; presumably they result from the flight angle of the firefly with respect to the recorder. Flashes 2-5 distorted at peak. H. Cryptic flash pattern of *Photuris* "D" male (about 76°). I. Cryptic flash pattern of *Photuris* "HS" male (61.5°). J. Flash pattern of *Photuris* "Q" male (61.5°). Intensity difference between pulses is characteristic and noted in all recordings.

cages *Photuris* females flash erratically and will not answer male or artificial flash patterns. When not confined, they leave. This behavior precludes experimental techniques, such as discrimination tests, that have been useful in determining the critical parameters of *Photinus* signals. Buschman (1966) was able to elicit flash responses from caged females of *Photuris divisa* LeConte.

Mating in inaccessible places: Many *Photuris* species are arboreal and fly and flash at the tips of branches high in trees. Presumably mating takes place there. It is nearly impossible to mark and recapture males of an arboreal species to determine if they emit more than one kind of mating signal; to locate and observe free, virgin females; or to conduct discrimination tests. Males of some treetop species can be attracted to the ground with simulated female flashes, but negative results may arise from male discrimination on the basis of female (i.e. decoy) location.

Limitations In Taxonomic Use Of Mating Signals

As guides for the recognition of species, mating signals have limitations. They cannot be presumed to vary between species that never come into contact geographically, seasonally, or diurnally. For example: *Photuris* "HS", a species observed in central New York State, has a distinctive flash pattern (Fig. 1 I). The *Photuris* I observed in Kentucky emitting the same signal may or may not belong to the same species. In another case, *Photuris* with slow flickers (7-11 per sec) have been observed in Florida, Michigan, and Maryland. There are slight differences in flicker frequency, morphology and ecology among the populations observed. The significance of the observed differences, and similarities, cannot be known without extensive field observations in the areas separating these localities.

Since some fireflies have 2-year life cycles (Hess 1920) those seen on consecutive years are potentially or actually different species in spite of behavioral identity. It is likely that some species have more than one brood each year for adults of a Florida species in the *P. versicolor* complex reared from eggs deposited in late April emerged in late September (Minnick and Lloyd unpublished). Since adults of these broods will compete in different photic environments it is conceivable that their signals might differ.

Concluding Statement

In early June a marsh in southern Michigan sparkles with a confusing array of seemingly random firefly flashes. At least 12 species in 3 genera are present, but an accurate count is now impossible. There are undoubtedly species that are morphologically cryptic, and perhaps species that are photically so; some that change their flashes during the course of an evening, some that flash while landing or ovipositing, some that are active early but are still flashing when a late-flying sibling begins activity, some that are attracting males of another species which they will devour, and some that flash at such long intervals that their flight paths cannot be followed without an ultra-miniature telemetry system. In another habitat a lone, flashing firefly may be seen, but the simplicity of beginning a behavior analysis here is illusory. At most one can obtain only an uncertain one-half of the mating code and another dead specimen. The study of *Photuris* species must begin with large populations in spite of the apparent confusion and known complexities. Mating flashes must be recognized, mating codes analysed, and distributions and life cycles understood.

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