MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 130

Studies on the Flash Communication System in Photinus Fireflies

BY

JAMES E. LLOYD

Museum of Zoology, University of Michigan

ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
NOVEMBER 25, 1966

MISCELLANEOUS PUBLICATIONS
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Ou hito ni akari wo misuru hotaru kana
The firefly
Gives light
To its pursuer

Oemaru (In: Blythe, 1952)

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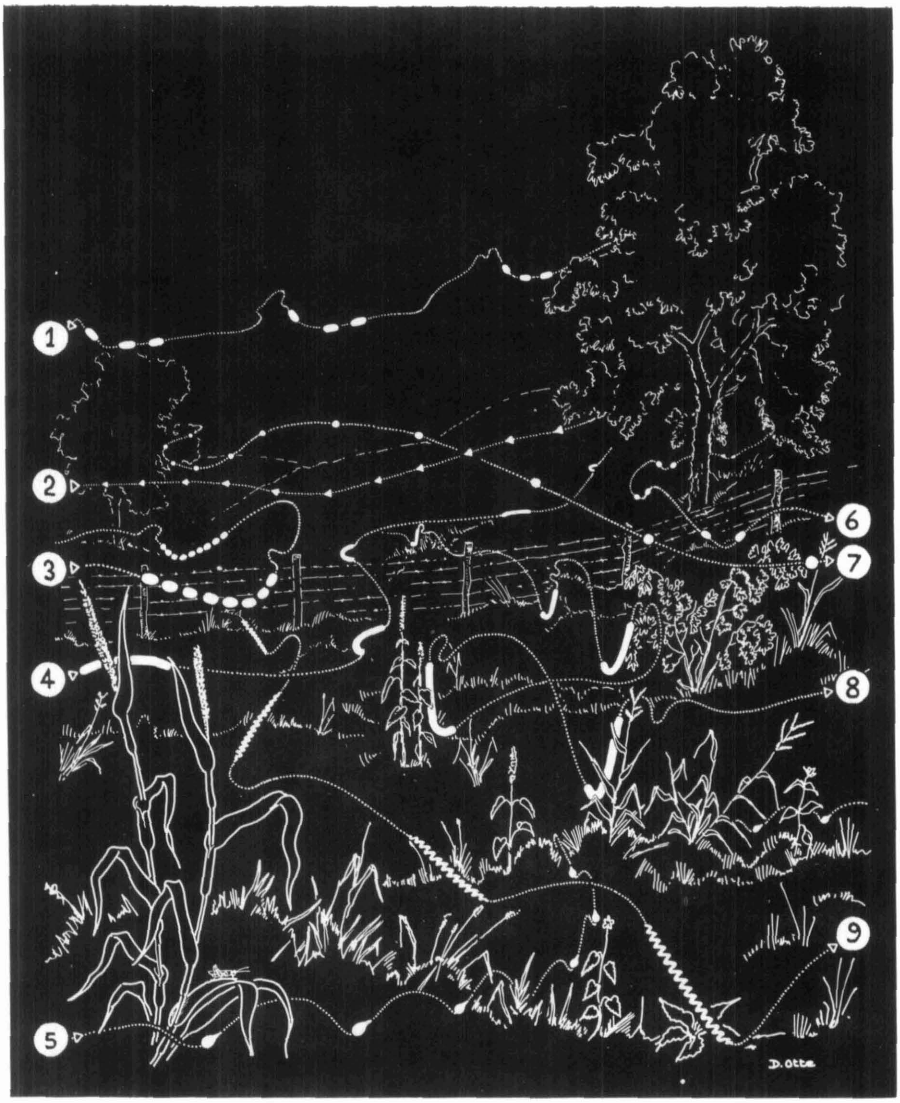


FRONTISPIECE

Flashes and flight paths of males of several different species as they would appear in a time-lapse photograph. Arrows indicate direction of flight. The species illustrated are not all sympatric. (1) *P. consimilis* (slow pulse), (2) *P. brimleyi,* (3) *P. consimilis* (fast pulse) and *P. carolinus,* (4) *P. collustrans,* (5) *P. marginellus,* (6) *P. consanguineus,* (7) *P. ignitus,* (8) *P. pyralis,* and (9) *P. granulatus.*

STUDIES ON THE FLASH COMMUNICATION SYSTEM IN *PHOTINUS* FIREFLIES*

THE FIRST indication of human awareness of the function of light production in fireflies is found in a legend from India of cobras attracting fire flies to glowing stones (Harvey, 1957). The function of flashing as a mating adaptation was established early in the twentieth century largely through the studies of McDermott (1911–1917). During this period the flashes of males of several species and the response flashes of females of a few species were described, and the role of species-specific flash signals in reproductive isolation was demonstrated. In 1951, Barber, through observations of male flash-patterns, recognized several cryptic species in the genus *Photuris*.

Although numerous recent studies have dealt with the physiology and biochemistry of firefly luminescence, only five have been concerned with the communicative function (Schwalb, 1961; Kaufmann, 1965; Lloyd, 1964*a*, 1965*a*, 1965*b*). There have been no studies or theoretical discussions considering the general biological and physical factors governing the functioning and evolution of communication in fireflies.

In spite of a voluminous literature on North American fireflies, the signals of most described species are unknown. The presumed functioning in reproductive isolation of the various parameters of the flash signal system, such as color and flash rate, is mentioned frequently in textbooks, not because the significance of these parameters has been demonstrated, but because variations among some species have been observed.

The purpose of this study is to establish a foundation of general knowledge on firefly mating behavior; such general information should pinpoint species best suited for studies on the role of flash signals in reproductive isolation. The approach is a comparative study of mating behavior in several closely related species. The genus *Photinus* was selected because of: (1) a relatively large number of species in eastern North America, (2) terrestrial rather than arboreal habits, and (3) apparent simplicity of function of the flashing in adults.

METHODS, MATERIALS, AND EQUIPMENT

Throughout this study the fine revision of the genus *Photinus* by Green (1956) was used for the identification of species. Localities for study were

* Extracted from a thesis presented to the Graduate School at Cornell University for the degree of Doctor of Philosophy, January, 1965.

selected from those listed under each species in the revision, and collectors of some specimens were contacted to obtain more precise locality information (Fig. 1).

Distribution maps are based on data given in the revision; on specimens borrowed from the collections of The Carnegie Museum, Pennsylvania State University, Oklahoma State University, New York State Museum, California Academy of Sciences, United States National Museum, Chicago Natural History Museum, Kansas State University, Illinois Natural History Survey, University of Missouri, Guelph University (Guelph, Ontario, Canada), Entomological Research Institute (Ottawa, Ontario, Canada), Buffalo Museum of Science; on specimens seen in the Florida State Collection, The United States National Museum, Cornell University, and The University of Michigan Museum of Zoology; on specimens sent to me by various individuals; and on specimens collected during this investigation. Landforms are those of Raisz (1957).

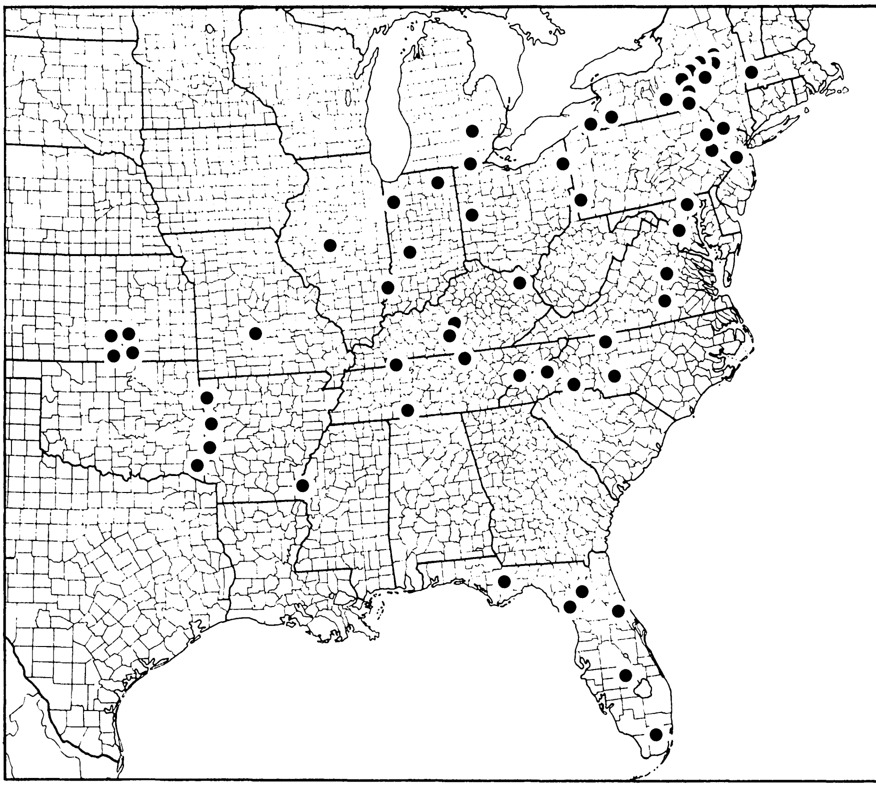


FIG. 1. Localities visited during this investigation

Each specimen from demes studied has been labeled "Behavior Voucher Specimen." These have been deposited in the collections at Cornell University, United States National Museum, University of Florida, University of Michigan Museum of Zoology, Florida State Collection, California Academy of Sciences, and the Museum of Comparative Zoology at Harvard University. Specimens collected only for distribution records have also been distributed among the above collections.

It is possible, indeed likely, that determinations of some specimens will be found to be incorrect upon additional studies on the behavior of species in this genus. This situation exists because of the limited numbers of demes studied and the possibility that I observed fireflies belonging to undescribed members of pairs of cryptic species and associated their behavior with the sibling's name. Behavior Voucher Specimens thus serve in the capacity of "behavior types."

The following terminology is used in describing light emission. A *glow* is a steady emission of light; the term by itself does not indicate intensity level. A *flash-pattern* or *phrase* is that unit of light emission of the male which stimulates the female *response flash* and is repeated at somewhat regular time intervals by advertising males. A *pulse* is a single emission of light of short duration. Flash-patterns of some species are composed of a single pulse; those of other species, two or more pulses. In some species, pulses appear to twinkle as though barely perceptible *amplitude modulations* are present.

The amount of time spent studying a particular deme varied, depending upon the number of individuals present, the complexity of the flashed signals, and the difficulties encountered in locating responsive females. For each deme the following data were recorded: (1) time of day active and ambient light intensity at beginning of activity, (2) ambient temperatures, (3) male flash-pattern and pulse length, (4) male flash-pattern intervals, (5) location of females, (6) female response delay time, (7) female flash-response and pulse length.

Time active and ambient light intensity: Periods of flashing are given in reference to sunset time. Sunset times were calculated for the various sites and dates of observations by means of the Air Almanac (U.S. Naval Observatory). Ambient light intensities, measured with a Bunsen photometer, are given in footcandles. Because of the great variability in intensities at a given time in an area, several readings were made at various places, and at various angles near flying, flashing males, and an average value recorded. Readings of both time and light intensity were made when the first flying flash was seen, unless otherwise noted. Difficulty was encountered in calibrating the photometer, and the absolute values given may be in considerable error; however, they are useful for species comparisons.

Temperature: Temperatures are given in degrees Fahrenheit. Temperatures associated with specific male flash-pattern intervals were taken at the approximate mean height of male flight paths. Temperatures associated with female response-flashes were taken one foot above the ground.

Male flash-pattern and pulse length: Pulse intervals in flash-patterns of species with multipulsed male phrases were measured with a stopwatch. Measurements are given in seconds from the beginning of the first pulse to the beginning of the next. Pulse lengths were estimated by comparing them with flashes of known lengths produced by the MF (monostable flasher, see description below).

Male flash-pattern interval: Time intervals between flash-patterns of advertising males were measured with a stopwatch. Measurements are given in seconds from the beginning of the first pulse of one phrase to the beginning of the first pulse of the next phrase.

Location of females: Females were difficult to locate; most were found by flashing a flashlight in a manner simulating the male flash-pattern and watching for female flash responses. Some females were found by the flashes they were emitting in answer to male fireflies, others by the dim glow emitted by their lanterns (females of some species glow during the evening period of mating activity). Beating with a net just before a species became active in the evening sometimes produced females, but these could seldom be induced to flash.

Female response delay time: Female response delays were recorded with the PT (photocell transducer, see description below) connected to a portable tape recorder, using the MF as the stimulus. Females to be recorded were placed in glass cages. They would climb the glass and expose their light organs in positions easily accessible to the PT photocell probe. The MF bulb was placed slightly above them and from 15–30 cm. away. Stimulus flashes similar in length and pulse composition to the previously observed male flash-patterns were presented to the females. Stimulus flashes were recorded through direct pickup of the MF bulb by one of the PT photocells. Females with long time delays were also timed with a stopwatch. Female delay times were measured from the beginning of the last pulse of the stimulus flash-pattern to the beginning of the response flash. This convention was followed because (a) females of some species are known to time from the beginning rather than the end of stimulus pulses (Fig. 2C) and (b) more precision can be obtained with a stopwatch if the beginning rather than the end of the flash is taken as the "mark."

Female flash length: Female flash lengths given are from tape recordings made with the PT using the MF as the stimulus.

Notes were taken on the general physical and biological characteristics of the habitats, male flight paths, and male approaches to responsive females.

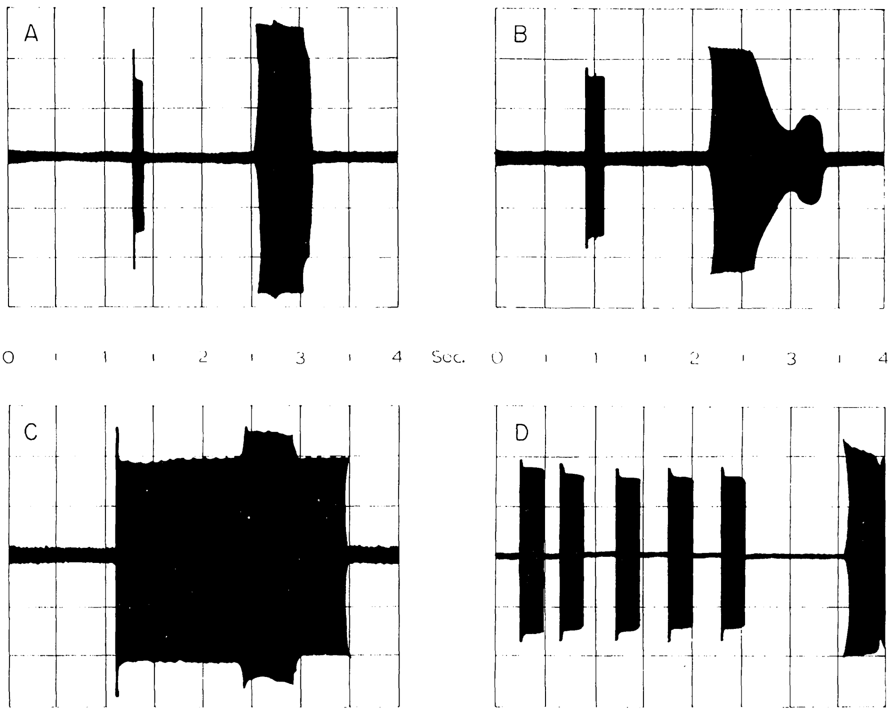


FIG. 2. Drawings from oscilloscope traces showing responses of a single female of *Photinus australis* to different kinds of electronic flashes. Initial low intensity pulses are electronic flashes; high intensity pulses following them are female responses. Note consistent time delay in all four responses: (A) normal short stimulus; (B) slightly longer stimulus (note intensity increase at end of female flash); (C) female interrupts long stimulus indicating that she times from the beginning of the stimulus flash; (D) female answers last pulse of a series (responses to early flashes must have been inhibited by subsequent flashes).

In all species (except as noted) males were attracted to the MF or flashlight. When attracting males, I held the tip of the penlight against the ground so that bright direct rays from the bulb could not be seen. As approaching males drew near, the tip of the flashlight was pushed farther into the ground so that the light was less bright. Living specimens of several species were sent to The Johns Hopkins University for spectrum analysis (Biggley, *et al.* in prep.).

Recording technique and equipment description: The MF was designed and built to my specifications by the Eli Scientific Company of Freeville, New York, specifically for this investigation. The following operational description was provided with the equipment,

The monostable flasher . . . is little more than a flashlight bulb and electric switch. Its purpose is to emit a flash of previously determined duration. . . .

Its name comes from the title of the switching circuit enabling it to perform this function. This circuit consists of a pair of transistors connected so that until things are disturbed, one transistor is turned hard [on] and the other hard [off]. When the user presses a push button this equilibrium is disturbed. The circuit, unable to avoid extremes, abruptly reverses transistor states, the [on] transistor going [off] and the [off] transistor going [on]. But a capacitor in the circuit, charged by this transition, loses its charge through a calibrated leak—the duration control—and after a certain very reproducible time, the circuit reverts again abruptly, to its resting condition. This behavior led to the term monostable; one stable state and another which is stable only for a little while.

Another pair of transistors acts as intermediary between the monostable, which requires very little current, and the lamp which requires a substantial current. They are connected so that in the resting condition they are turned off. In the short term [on] condition they supply operating current to the lamp, producing the flash.

The following operational description of the PT was provided with the equipment by the Eli Scientific Company who designed and built it to my specifications. "The transducer assembly consists of a pair of photocells on short flexible cables connected to a small aluminum box, on which are the controls and a microphone.

The microphone is connected to a tape recorder to make a complete record of the transduced data, supplemented with verbal notes.

The two photocells are connected to separate input circuits, which feed a common output circuit. The input circuits operate in the following way:

A small cadmium sulphide cell is biased with an adjustable voltage. When the cell is dark, very little current flows. The slight illumination provided by the firefly [at distances up to two inches] reduces the series resistance of the cell. An increased current flows, which, amplified by a pair of transistors, reverses the bias voltage applied to a semiconductor diode.

A part of the circuit is a single-transistor phase shift oscillator. It runs continuously, applying a signal to one terminal of the diode. But as long as the diode is reverse biased, very little signal passes through. Illumination of the photocell causes the diode to become forward biased, so . . . it becomes just another piece of wire. A diode used in this manner is termed a diode switch.

When the diode switch closes, the signal is applied to the input of a simple amplifier. The amplified signal is fed to a small loudspeaker, passing then into the microphone and tape recorder. The signal is loud enough to be heard by the worker so that he has a continuous check on the performance of his gear.

The second channel is the same in design except for a minor revision in the phase shift oscillator, giving a tone about one octave different from that of the other oscillator.

The controls consist of a sensitivity adjustment for each channel, an audio gain control to adjust the loudness of the output tone, and a switch for turning everything on and off. The high voltage is supplied by a 300 volt photoflash battery.

This system permitted the recording of flash lengths and time delays—it recorded accurately on the time base only. Indications of changes in flash intensity can be seen in the recorded signal, but the observed increments and decays don't necessarily represent the increments and decays of the firefly flashes.

The tape recorder used in conjunction with the PT was the Norelco Continental 100, Model No. EL3585. A calibration tone (tuning fork, 523.3 cps) was recorded on each tape, permitting a check of the tape speed when the tapes were analyzed in the laboratory.

Tape recordings were analyzed with a Tektronix Storage Oscilloscope Type 564; Type 2A61 Differential Amplifier; Type 2B67 Time Base Unit. The signal was fed directly from the speaker of the tape recorder into the oscilloscope. The sweep was triggered either by the input signal or manually; the sweep speed used depended on the length of the flash interaction being analyzed. The calibrated time base of the oscilloscope permitted time readings to be made directly from the face of the oscilloscope and to be read to one-one-hundreth of a second (Fig. 2, Pl. I).

OBSERVATIONS AND EXPERIMENTS

FLASHED SIGNALS AND ASSOCIATED BEHAVIOR

At the turn of the twentieth century some biologists insisted that adult firefly flashes functioned only in defense or in some aspect of firefly biology which was completely unknown. McDermott (1911) pointed out that if an observer took but a few minutes, the function of the flashes in sexual attraction could easily be observed. In the genus *Photinus* this is especially true. In one instance within a period of five minutes I attracted two males to my flashlight, located a female by her flashed response to my flashlight, and decoyed another male to within two meters of this female. I then oriented him with the flashlight so that his next flash could be seen by the female. Thereafter, she answered his flashes; a minute later, after five flash exchanges, they were mating. Males of all species tested are attracted to the tip of the flashlight (which they climb upon and antennate) when it is flashed in a manner roughly simulating the flashes of females in duration and delay. Females of all species tested responded to the flashlight and MF.

Typically, flashing and mating behavior of *Photinus* fireflies is as follows: At the time of evening characteristic for the species, males arise from the grass and fly and flash, most of them keeping within an ecologically well-defined area such as a lawn, forest edge, stream bed, or wet corner of a pasture. Male flight paths during moments of light emission are characteristic for the species; some species can be identified by this behavior alone (Frontispiece). Females are found on the ground and on grass stems or other low vegetation. When a male receives a flashed answer from a female after a species-characteristic interval following his own flash, he turns and flies toward her. After a few seconds he repeats his flash-pattern; if he again receives the correct flash response he continues his approach. Flight terminates a few centimeters from the female after from one to ten flash exchanges. After landing, the male usually completes the approach by walking and exchanging flashes with the female. Males mount females immediately upon contact. For complete attraction, only flash signals are necessary, and in all species tested, males were attracted to females caged in airtight glass containers. During approaches, females frequently fail to answer some of the male flashes, but when they resume answering, males continue their approaches. Males remain in the area of a previous response, emitting their flash-pattern for several minutes after females are removed.

In most species, activity lasts for about one-half hour and then decreases slowly over the next 30–40 minutes, until eventually only an occasional flash can be seen.

Accounts of Species

Studies were made on 25 of the 31 Nearctic species of *Photinus*. In addition to these, some species not observed during this investigation deserve comment. The species are treated separately. Order of presentation follows Green (1956), and his groupings within the genus are used and extended. Preceding the presentation of each group is a short introduction dealing with its identification and general characteristics.

The Genus *Photinus*

McDermott (1964) gave temperate and tropical America and the Antilles as the distribution of the genus. Green recognized 28 species occurring in America north of Mexico, including one species known from a single pair collected at Nogales, Arizona, and probably widely distributed in Mexico. Green also suspected the presence of one or more species that he could not distinguish on the basis of morphology. Three cryptic new species were found during my investigation through behavioral observations. Two of these have been described and named (Lloyd, 1966). The distribution of the genus in North America is given in Figure 3.

Green (1956) arranged the Nearctic species of the genus into two primary divisions, each characterized by a distinctive type of male genitalia.

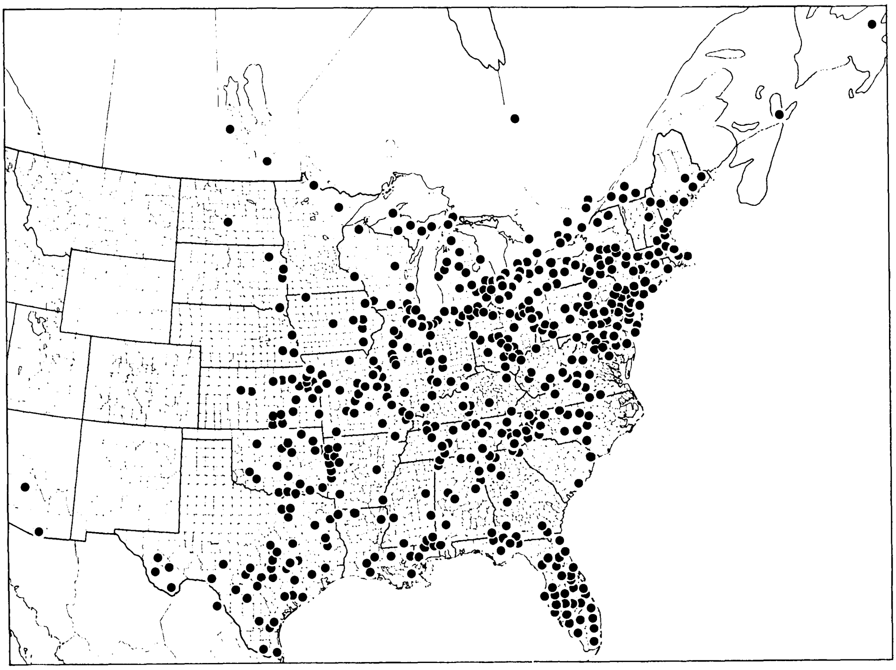


FIG. 3. Distribution of the genus *Photinus* in North America. In this and other maps each dot represents a county record (see Methods, Materials, and Equipment).

In Division II (below) the median lobe of the aedeagus has two sclerotized ventrobasal processes. These processes are absent in Division I. The genitalia in Division II define several species groups, and in Division I they identify a number of species.

Division I

Each species in this division is identified primarily by means of male genitalia, although in some species, locality and morphological characteristics other than genitalia are useful. Green recognized eight species, one of which is nonluminous.

Studies were made on four of the described luminous species. In general these diminutive species are early flying, single-flashing fireflies found along forest edges and roadside hedges, and over sheltered lawns in isolated colonies. In the Mohawk Valley of New York State this division is represented by intermediates between *P. marginellus* LeConte and *P. curtatus* Green, the males of which fly over lawns, fields, pastures, and meadows, sometimes continuously for miles in unbelievable numbers.

Species of Division I are found throughout the United States east of Kansas (Fig. 4).

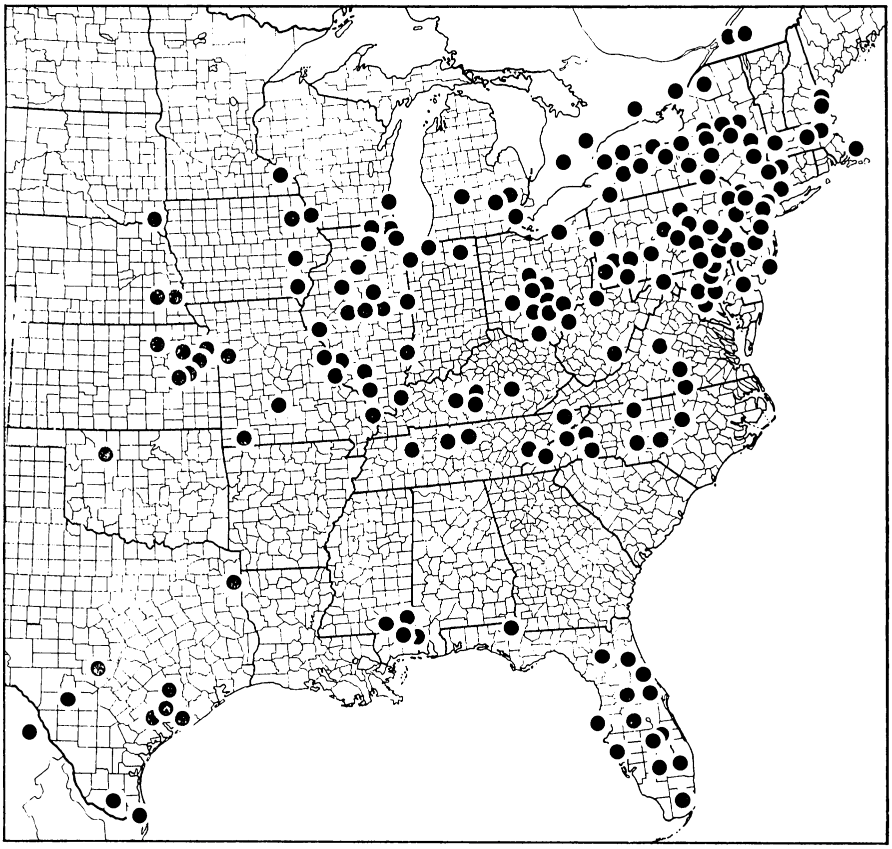


FIG. 4. Distribution of *Photinus* Division I

Photinus cooki Green (Fig. 5)

Five individuals of this nonluminous species were collected at the type locality, Crailhope, Kentucky, July 18–19, 1963, and July 6, 1964. Nothing further can be added to the observations reported by Green. This seems to be a very rare species, for it was not seen at any other locality, and there are few in collections.

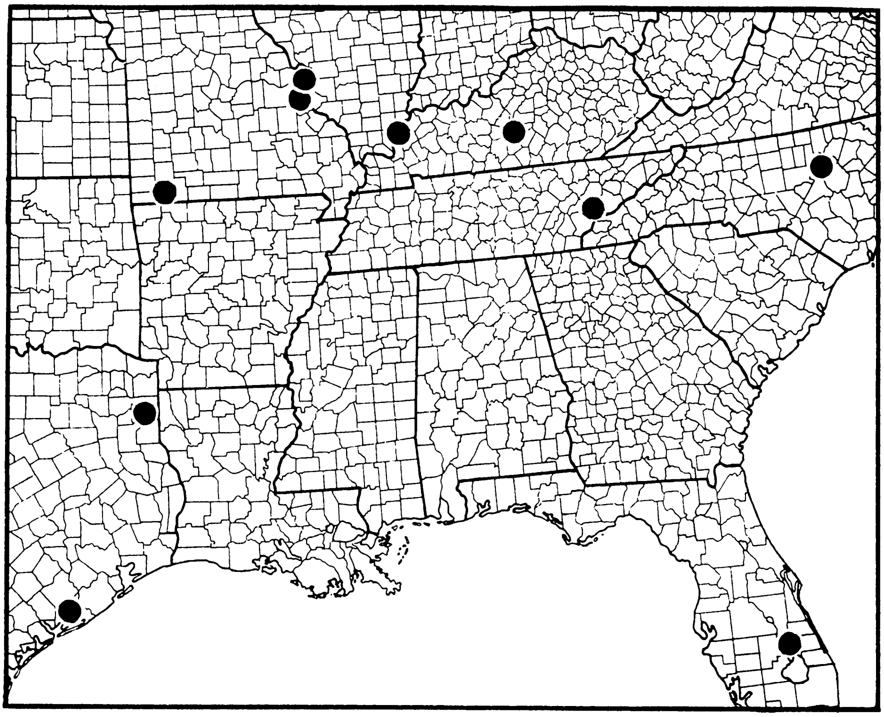


FIG. 5. Distribution of *Photinus cooki* Green

Photinus marginellus LeConte (Fig. 6)

This species was seen at several localities in Connecticut, Kentucky, Michigan, North Carolina, Pennsylvania, and Virginia. It was studied at Gatlinburg, Tennessee; Ithaca, New York; and Branchville, New Jersey. It occurred in small isolated colonies in roadside hedges and shrubs, along streams, and at sheltered edges of lawns. In Ithaca, the season of adult activity was from late June to late August.

Male flashing activity began between one and 23 minutes after sunset. Considerably less variation was noted if observations were made at the same position in the study area. For example, observations of first flying flash on five evenings at the same position in the Gatlinburg study area fell within a five-minute range. Ambient light intensity readings made at the time and position of the first flying flash on four evenings on the same deme in Ithaca averaged 0.01 fc (footcandles). Onset of male flying and flashing activity was slow, several minutes elapsed between first flash and full activity. During the first 15 minutes of activity males flew close to the ground, but flight altitudes gradually increased to several meters by full darkness. Peak flashing activity lasted approximately 30 minutes and then slowly diminished; by one hour after sunset only an occasional flash was seen.

Flight paths of males of this species consist of a series of hopping movements or arcs in the vertical plane (Frontispiece). During early evening

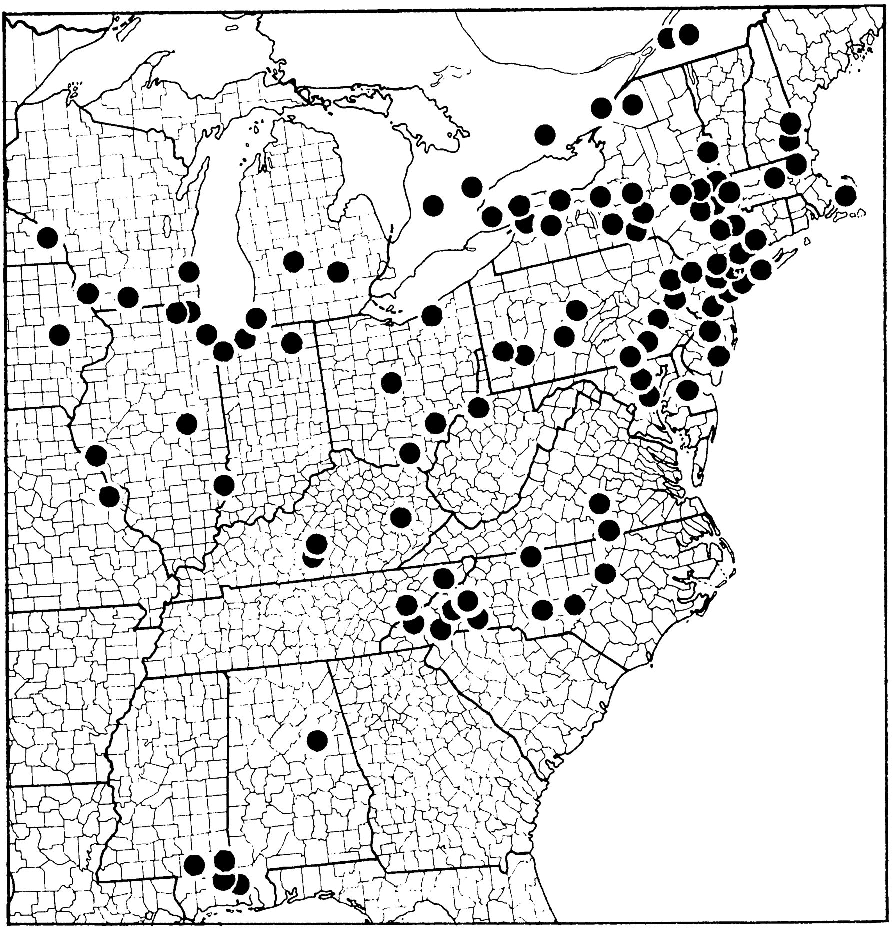


FIG. 6. Distribution of *Photinus marginellus* LeConte

activity these movements are small and are performed 15–50 cm above the ground among branches and leaves of low vegetation. The hop, or upward arc in flight, is performed after each flash; flight during this arc carries males 30–100 cm in the horizontal direction. Flashes are emitted between hops while males hover. Orientation during this flight gives the impression that the males are directing their flashes toward the tips of branches and weeds and shadowy places, and avoiding more open and lighted places. Flashes of several males were compared with the flashes of the MF (monostable flasher) and at 72° were estimated to average 0.30 second in duration. Mean flash-pattern interval at 74° was 2.9 seconds (standard deviation 0.3 sec; Table 1, Fig. 29) and, as with all species studied, varied inversely with temperature.

Several females were collected. These were found on low vegetation. They responded to flashes of males, the flashlight, and the MF with single pulsed flashes at short delay times. Some females were found that sometimes emitted doubled flash responses. The flashes of one recorded female averaged 0.21 second in duration at an average delay time of 0.38 second at 70° (Tables 3 and 5, Fig. 30). During flashes, females flexed their abdomens, usually in the direction of stimulus flashes.

Several approaches of flying males to females were observed. On one occasion over 30 minutes were required for the male to reach the female as he wandered about in a maze of ground ivy.

Photinus curtatus Green (Fig. 7)

Green named Division I specimens with a particular type of genitalia *P. curtatus.* During the first year of my investigation specimens resembling this form were collected in central New York State. Observations covering the points outlined in "Methods, Materials, and Equipment" (above) were made and the only aspect of their biology found to differ from that of *marginellus* was the number of individuals per deme, there being considerably fewer in *marginellus.* The geographic range of the *curtatus*-type genitalia overlaps that given for *marginellus*-type (compare Figs. 6 and 7).

Comparisons of the genitalia of specimens from Oneida, New York, Green's drawings for *curtatus,* and *marginellus* genitalia from specimens collected far from the area of sympatry, reveal that in specimens from Oneida nearly every degree of intermediacy between the two "pure" forms is present. In 1964, a separate study of this problem was made in central and south-central New York State (Lloyd, in press *b*). The following observations were made on *marginellus-curtatus* intermediates at Oneida, New York.

The deme studied numbered thousands of individuals. During peak activity flashing males could be seen along either bank of a stream for 100 m (meters) and extending 60 m deep on one side of the stream, covering extensive lawn, garden, and old field areas. On the other side of the stream, activity was seen across a large field for a distance of 200 m. The usual season of adult activity was from mid-June to late August. In 1965, activity continued until the first week in September.

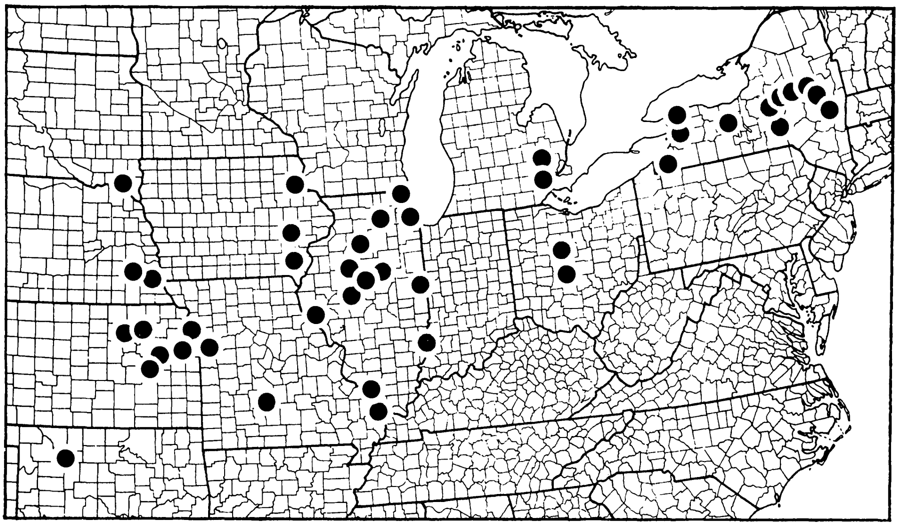


FIG. 7. Distribution of *Photinus curtatus* Green

Flashing began in the deep weeds under large trees along the stream about ten minutes before sunset at light intensities averaging 0.20 fc and moved out into unsheltered areas 7–15 minutes after sunset when light intensities in these areas had reached the same low levels.

For the first few minutes of activity males remained close to the ground, flying in the hopping manner described for *marginellus*. Later they flew higher until eventually, near the end of activity, several flew in the trees. During the last two weeks in July, the period of peak activity, many males remained active until as late as 1½ hours after sunset. Early and late season flights ended 40–50 minutes after sunset. At the end of the season several individuals began activity at the usual time, but within five or ten minutes they disappeared. Male flashes were estimated to be 0.30 seconds in duration at 66°. Mean flash-pattern interval at 73° was 2.9 seconds (s.d. 0.6 sec.; Table 1, Fig. 29).

Females were found on low vegetation. They responded to male, flashlight, and MF flashes, with single-pulsed responses at short delay times. Some females sometimes emitted double-pulsed responses. The flashes of one recorded female averaged 0.19 seconds in duration with an average delay time of 0.32 seconds at 69° (Tables 3 and 5, Fig. 30). Flashing females flexed their abdomens in the direction of the stimulus flash.

Several approaches of flying males to females were observed.

Photinus floridanus Fall (Fig. 8)

This species was seen in Highlands Hammock State Park and near the Archbold Biological Station, Highlands County, Florida; it was studied at three locations in Gainesville, Florida. At Gainesville, in the spring of 1965, activity began between April 9 and 13; flashing males were seen in Highlands County on April 10. All demes were still active on May 25, the latest date observations were made. This species was found along roadsides in hedges and bushes and at the edges of mesophytic forests, along streams, and among palmettoes on the floors of both mesophytic and hydrophytic hammocks. Demes were moderate in size, each with 50–200 males visible at peak activity; one colony seen around a large bush in a roadside ditch numbered scarcely more than 20 individuals.

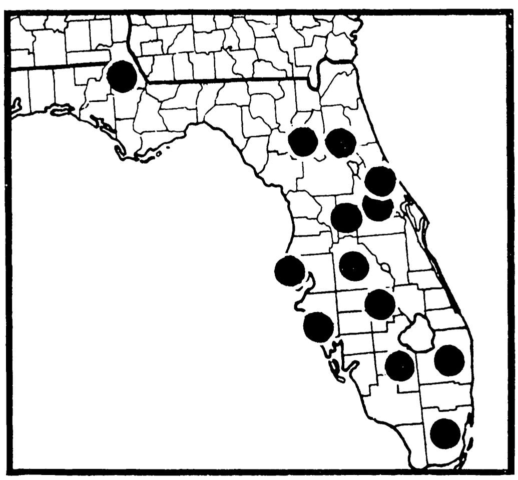


FIG. 8. Distribution of *Photinus floridanus* Fall (Florida)

Male flashing activity began between eight minutes before and ten minutes after sunset, depending upon shade conditions, and at light intensities averaging 0.03 fc. Demes occurring at forest edges commenced activity a few meters back in the forest 15 or 20 minutes before activity began at the forest edge proper. Flying males were seen as early as 36 minutes before sunset at light intensities of 0.14 fc, but these males did not flash; they landed frequently. Male flight paths were as described for *marginellus* (Frontispiece), hopping and hovering, with flashes seemingly directed at circumscribed areas in the vegetation. Flashes of several males were compared with the MF and appeared to be 0.15–0.20 seconds in duration at temperatures near 70°. Mean flash intervals at this temperature averaged 3.5 seconds (s. d. 0.29 sec; Table 1, Fig. 29).

Several females were collected. These were found on low weeds and palmetto fronds within one m of the ground. They responded to the flashes of males, the flashlight, and the MF, with single-pulsed flashes at short delay times. Occasionally some females emitted doubled pulses. This was also noted in one male. The flashes of one recorded female averaged 0.15 second in duration at an average delay time of 0.31 second at 75° (Tables 3 and 5, Fig. 30). During flashes females flexed their abdomens, usually in the direction of the stimulus flash. Three caged females and one free female were tested for this aiming.

Flashlight stimuli were presented from either the right or the left side of the females, and the direction of flexions was noted. In the results below (+) indicates the female flexed toward the stimulus flash, (−) indicates the female flexed away from the stimulus flash, and (NR) indicates no response was noted. The three negative responses of female No. 2 may be because the female aimed at reflections from the glass of the cage.

Female 1. (caged) stimuli given at five-second intervals
R + +   + + +
L   +

Female 2. (caged) stimuli given at five-second intervals
R +   + + +
L   + +   − − − +

Female 3. (caged) stimuli given at 60-second intervals
R   +   +   +   +   +   +
L + +   +   +   +   +   +

Female 4. (free) stimuli given at ten-second intervals
R +   +   + +   +
L   +   +   +   NR +

At ambient light intensities somewhat higher than those found at the start of male activity some females flexed their abdomens without flashing in response to flashlight stimulation. On several occasions flash stimuli were presented to these females. After several flexion responses which were not accompanied by flashes, they started flashing, at first feebly and then normally, with the flexions. Flashes of light presented to one female that was walking about her cage immobilized her for two to three seconds. This was repeated four to five times, after which she stopped responding.

Several approaches of flying males to females were observed. Difficulty was encountered in attracting males to flashlight flashes simulating the response of females until late in each activity period at low ambient light intensities.

Photinus sabulosus Green (Fig. 9)

P. sabulosus was seen in Broome County, New York, and Greene and

Metcalf counties, Kentucky; it was studied at Treman State Park, near Ithaca, New York, and at Slovan, Washington County, Pennsylvania. In Ithaca the season of adult activity spread from late June to late August. The number of flashing males at peak activity was probably 300–500 individuals.

Male flashing activity began about sunset and at ambient light intensities averaging 0.02 fc. Male flight behavior cannot be generalized at this time because of seemingly conflicting observations. At Ithaca, most males

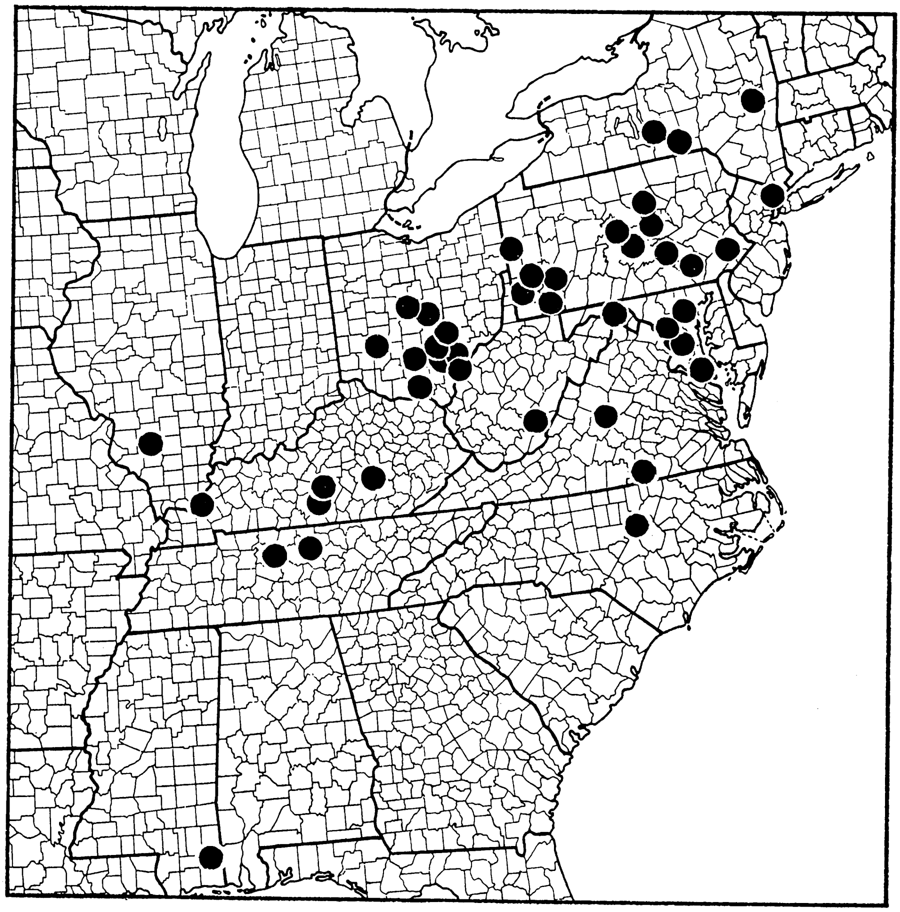


FIG. 9. Distribution of *Photinus sabulosus* Green

were active high among the leaves of trees and only a small number flew close to the ground. This was particularly noticeable after the first 15 minutes of flight. In Slovan, activity was confined to low altitudes over weeds beneath trees. Activity ended approximately 1½ hours after sunset. Flashes of males were estimated to be 0.16 second in duration at 72°. The mean flash interval at 71° was 3.8 seconds (s. d. 0.6; Table 1, Fig. 29).

Three females were found, one by her flash response to a male. The others were taken by beating in the deep grass at the Ithaca site. They responded to flashlight and MF flashes with single-pulsed flash responses at short delay times. The flashes of one Ithaca female averaged 0.15 second in duration at an average delay time of 0.38 second at 69° (Tables 3 and 5, Fig. 30). During flashes, females flexed their abdomens.

The late stages of approach of a flying male to a female were observed. Two flash exchanges were seen, and the male then landed a few inches from the female at the top of a weed 1.5 m above the ground.

Photinus acuminatus Green

This species is represented in collections by one male (holotype) taken by D. L. Wray at Pisgah Mt., North Carolina, July 14, 1939, and one female taken at Newberry, Florida, May 27, 1927.

Dr. Wray was contacted for specific information regarding the Pisgah Mt. locality, and this site was carefully searched on June 22, 1963, June 4, 1964, and July 10–11, 1964. No *acuminatus* were found in the type locality or along the highway leading to the summit of the mountain. However, *marginellus* was found at the type locality.

Division II

Green recognized four species groups in this division, primarily on the basis of male genitalia, although other characters were also used. Identification of species within these groups is based on a variety of characters such as shape of elytra, pronotal maculae, genitalic ventrobasal processes, sculpturing of pronota, and coloration of lateral elytral margins. Of the 22 described species in this division, one is nonluminous. Identification of single specimens on the basis of morphology alone is frequently impossible.

Observations were made on 18 of the described luminous species and on one species which awaits formal description. These observations have revealed behavioral affinities paralleling morphological relationships. The flash signals of the first two, *pyralis* group and *punctulatus* group, seem to be but slight modifications of the simple signals found in Division I. The signals of the *ardens* group and *consanguineus* group are much more complex.

THE *pyralis* GROUP

In some respects this group bridges the two divisions behaviorally. All species are crepuscular, as are all species of Division I and some species of other Division II groups. The species of this group, like the species of Division I, are usually found in woodland borders but in some places *pyralis* seems to be ecologically ubiquitous. Flash signals are either of the simple "flash-answer" type as in Division I and some other Division II species, or of the "flash-delay-answer" type found in other species of Division II. In two species females are long-winged and capable of flight, as in Division I; one species, *scintillans,* has brachypterous females as found in all but one species of the *punctulatus* group.

Photinus pyralis (Linnaeus) (Fig. 10)

The distribution of this species nearly matches that of the whole genus in North America. *P. pyralis* is found in a variety of habitats and usually in

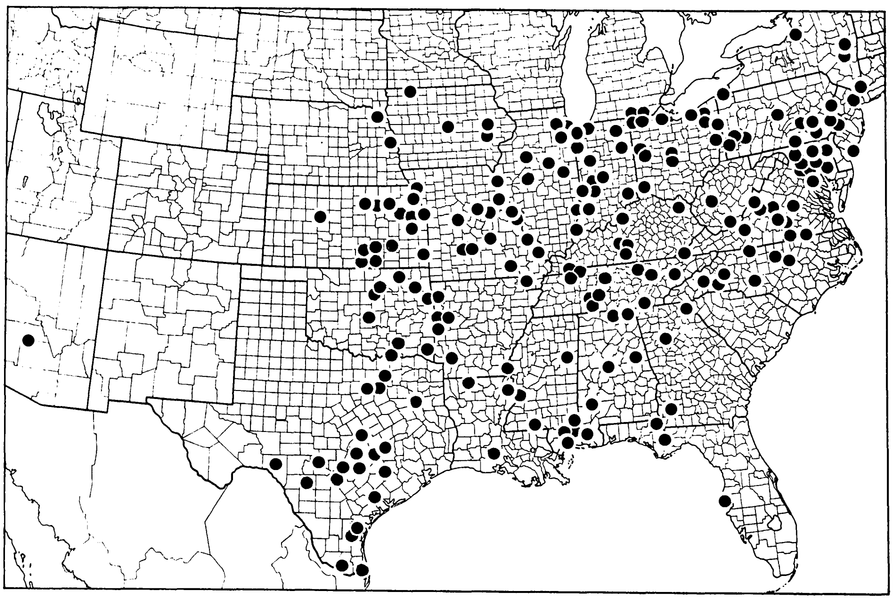


FIG. 10. Distribution of *Photinus pyralis* (Linnaeus)

great numbers. Probably for these reasons it is "The Firefly" of physiologists and biochemsits, and is the most common species collected as a commercial source of luciferin and luciferase. This species was seen in abundance in every area visited except New York, New Jersey, Connecticut, and Florida; it was studied in Lake Lure, North Carolina; Fife, Virginia; Fayetteville, Arkansas; and Slovan, Pennsylvania.

Male flashing activity began as early as 20 minutes before sunset in woods, and as late as 11 minutes after sunset on open lawns. One reading of 0.03 fc of ambient light intensity was recorded for the first flash at Slovan. During the first few minutes of activity, males flew close to the ground. Later, at lower light intensities, males flew higher, with some flying and flashing high in trees. Activity lasted 30–45 minutes, sometimes with occasional flashes for 90 minutes or more.

Flight paths of males consist of a series of hopping movements (arcs in the vertical plane, see Frontispiece). During early activity these movements are smaller than later in the evening at lower light intensities, and in this study were 0.5–2 m in length, with altitudes ranging from 0.3–1 m. The flash-pattern is a single long flash emitted between hops during a forward and then rising flight movement. The resulting flashed "gesture" resembles the letter J. Sometimes the flash begins after the horizontal part of the movement so that only the vertical gesture is illuminated. This was particularly noticeable in the Slovan deme. Orientation during flight gives the impression that males direct their flashes toward certain areas, such as bushes and small clumps of tall weeds in otherwise mowed or short grass areas. Flashes of several males were compared with the MF and measured with a stopwatch and were from 0.4 to 0.6 second in duration at temperatures from 67° to 72°. Following flashes, males hover for a few seconds. The post-flash hover period in one male after alternate flashes measured 3.2, 3.7, 3.0, 2.6, and 2.8 seconds in duration at 67°. Mean flash-pattern at 73° was 5.9 seconds. (s.d. 0.62 sec; Table 2, Fig. 29).

Several females were collected from low vegetation. They responded to male, MF, and flashlight flashes with single-pulsed flashes at moderately long time delays. The flashes of one recorded female averaged 0.50 second in duration at an average delay time of 2.80 seconds at 67° (Tables 4 and 6). During flashes, females flexed their abdomens, usually in the direction of the stimulus flashes.

Several approaches of flying males to females were observed.

Photinus australis Green (Fig. 11)

This firefly was usually found with its close relative *pyralis,* but unlike *pyralis* was nearly always confined to shaded areas and dense bushes. *P. australis* was seen at Paris Landing State Park and Davy Crocket State Park, Tennessee; Morrow Mountain State Park, North Carolina; Lieber State Park, Indiana; and Red Hills State Park, Illinois; it was studied at Torreya State Park, Florida.

Male flashing activity began 14–17 minutes before sunset in the branches of bushes along the edge of a mowed area. After 10–15 minutes, males flew just outside the foliage of the bushes. Later in the evening flight altitudes increased, and some males flashed among tree branches 2–5 m above the ground. After 30–45 minutes, activity was much reduced and sparse, and by 27 minutes after sunset only an occasional flash was seen, usually high in the trees.

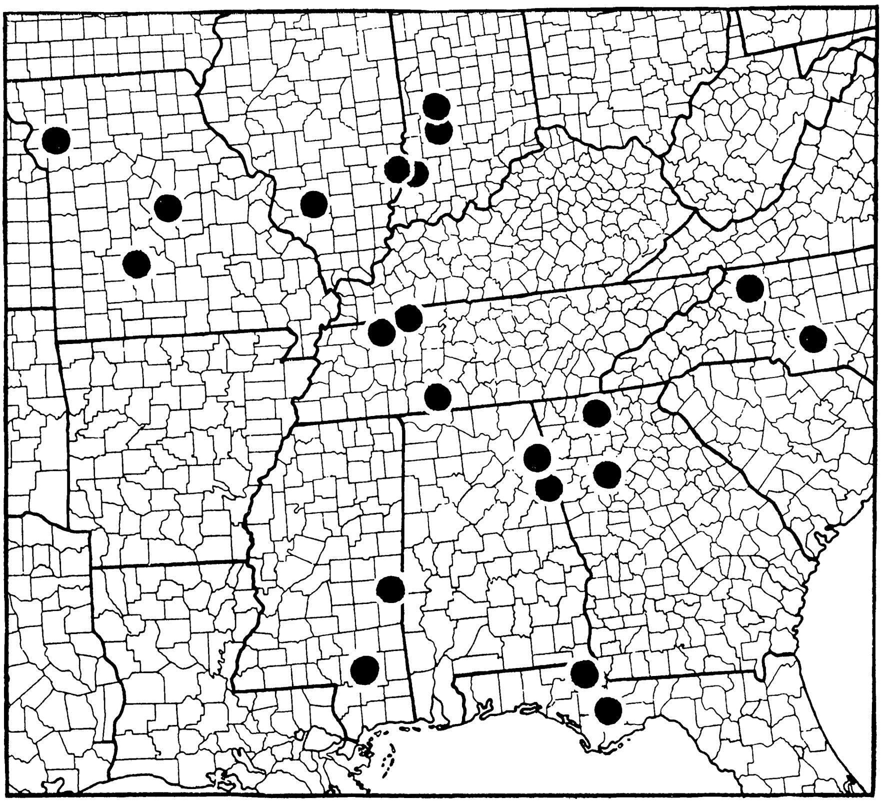


FIG. 11. Distribution of *Photinus australis* Green

Flight paths of males during early activity are similar to those described for other early-flying species. However, when *australis* is confined to restricted areas such as within bushes, the hopping and hovering flight is very slow and movements are small. The flash-pattern, a single "snappy" flash, is emitted between hops during hovering. Flashes of several males were compared with the MF and at temperatures near 80° appeared to be 0.10–0.15 second in duration. Following the emission of flashes, males remained hovering briefly before executing another hop. Mean flash-pattern interval at 77° was 3.9 seconds (s.d. 0.66; Table 2, Fig. 29).

Four females were collected. Three from Torreya Park were found on the leaves of bushes. One in Illinois was found two m above the ground in a small tree. One female from Torreya was very responsive, and 248 recordings of her flash response were made at various temperatures. Females responded to male, MF, and flashlight flashes with single-pulsed flashes at slight time delays. A sharp increase in intensity frequently occurred at the end of the flash response of one female (Fig. 2,B). Time delay durations of females varied inversely with temperature, and differences in pulse length were noticeable at recording temperature extremes. The flashes of the recorded female averaged 0.60 second in duration at an average delay time of 0.84 second at 77°, and 1.16 seconds in duration at an average delay time of 1.37 seconds at 62° (Tables 4 and 6, Fig. 30). During flashes, females flexed their abdomens, usually in the direction of the stimulus flashes.

The approach of one flying male to a female was observed.

Photinus scintillans (Say) (Fig. 12)

This species has one of the smallest ranges of Nearctic *Photinus*. Females are brachypterous, a condition otherwise found in *Photinus* only in species of the *punctulatus* group. Studies were made on *scintillans* at New Bruns-

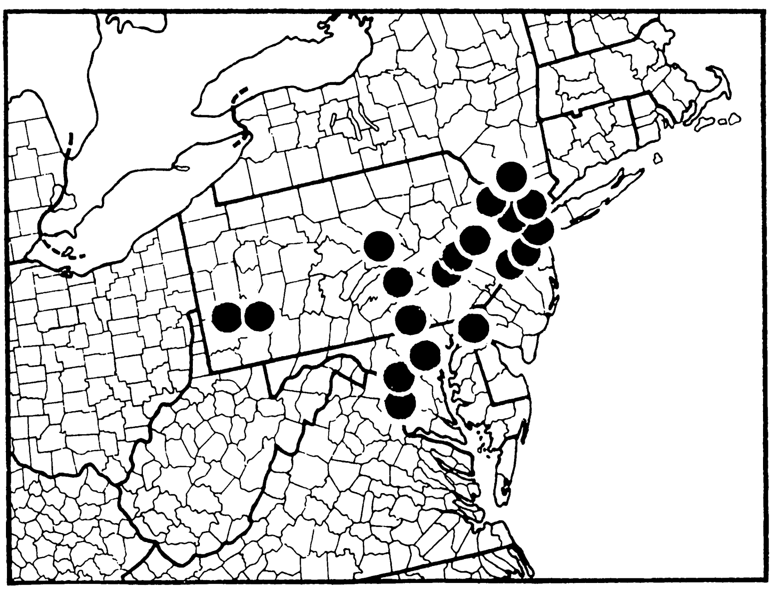


FIG. 12. Distribution of *Photinus scintillans* (Say) (New Jersey, etc.)

wick and Branchville, New Jersey; and Rock Creek Park, Silver Spring, Maryland. Ecologically and behaviorally it is similar to *marginellus*, with which it is sometimes confused. However, *scintillans* is frequently found in exceedingly large breeding populations which extend continuously along roadsides, over lawns, through woods, and across cornfields and hayfields.

Male flashing activity began at light intensities between 0.02 and 0.03 fc in large demes, and from one hour before sunset to seven minutes after sunset, depending on shade conditions. In small colonies starting time was as late as 14 minutes after sunset at light intensities of less than 0.01 fc. Activity lasted 60–90 minutes depending on deme size: large demes were active longest.

Flight paths of males are similar to those described for *marginellus*. At very high ambient light intensities the hopping movements are extremely small (10–20 cm), deliberate, and performed only a few cm above the ground and leaves of low vegetation. Males of *scintillans* also appear to direct their flashes toward certain areas while avoiding others. The male flash-pattern is a single sharp flash. One male (of thousands observed) was seen to emit a doubled flash, as was previously noted in one male of *floridanus*. The normal single flash of the males appeared to be 0.13–0.16 second in duration at temperatures of 65°–73°. Mean flash-pattern interval at 70° was 2.6 seconds (s.d. 0.50; Table 2, Fig. 29).

Several females were found on low vegetation. They responded to male, MF, and flashlight flashes with single-pulsed flashes at short time delays. The flashes of one recorded female averaged 0.18 second in duration at an average delay time of 0.42 second at 70° (Tables 4 and 6, Fig. 30). During flashes females flexed their abdomens, usually in the direction of the stimulus flashes.

Several approaches of flying males to females were observed.

THE *punctulatus* GROUP

This group is unusual in that all but one of its species (*P. umbratus*) have brachypterous females. The flash signals of all but *umbratus* are the simple flash-answer signals with short or slight female time delays. The *punctulatus* group has a more southern distribution than the other groups and is not represented in northeastern United States.

The first three species of this group form a (morphological and behavioral) subgroup within the *punctulatus* group. They are easily identified, but have largely allopatric, contiguous ranges and behave similarly. Further study is needed on this "*brimley* complex."

Photinus brimleyi Green (Fig. 13)

The break in the range of this species at the Mississippi River Valley may indicate the absence of collecting. Few specimens of *Photinus* from this area are found in collections (Fig. 3). *P. brimleyi* was seen at Queen Wilhelmina State Park and Greenwood, Arkansas; in Lewis, Stewart, Henry, and Overton counties, Tennessee; and Metcalf and Calhoun counties, Kentucky;

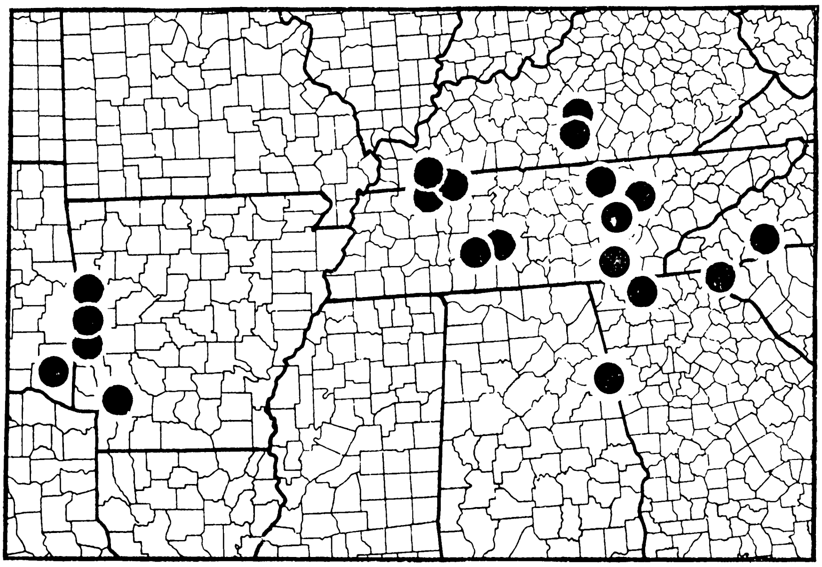


FIG. 13. Distribution of *Photinus brimleyi* Green (Tennessee, etc.)

it was studied at Idabel, Oklahoma, and Crailhope, Kentucky. It was found over lawns, fields, and meadows, in woods, and along hedgerows. Differences in body length were found in specimens from different areas. Specimens from Oklahoma averaged 7 mm; from Arkansas, 8.5; and from Tennessee and Kentucky, 11.5 mm.

Male flashing activity began 5–15 minutes after sunset (Crailhope), first in shaded places and later in the open. No observations were made on the termination of the daily activity period, but one deme in Arkansas was active when observed three hours after sunset.

Males flew straight or meandering courses 1–2 m above the ground with little or no change in altitude during flashes, and traversed 1–2 m longitudinally between flash-patterns. A peculiar hitching or jerking flight was noticed in some males. While flying rapidly they would flash, then during light emission they would stop abruptly and hover, turn off their lights, and proceed in flight. This resulted in very jagged flashes that appeared to increase in intensity during emission (Frontispiece). Other males slowed only sightly during light emission, with no spatial gestures or motions. Flashes of several males were compared with the MF and were estimated to average 0.20 second in duration at 74°. Mean flash-pattern interval at 74° was 1.2 seconds (s.d. 0.14 sec; Table 2, Fig. 29).

In Oklahoma one female was found under a low hedge next to a garage. The Oklahoma female responded to flashes of the MF and flashlight with single-pulsed flashes at a short delay time. Her flashes averaged 1.52 seconds in duration at an average delay time of 0.38 second at 76° (Tables 4 and 6, Fig. 30). During flashes she usually flexed her abdomen toward the stimulus flash when in a vertical position; when lying horizontally she rolled away from them, thus exposing her light organ in the direction of the stimulus flashes.

Photinus punctulatus LeConte (Fig. 14)

Studies were made on *punctulatus* in a large open traffic triangle near New Salem State Park, Illinois, July 25–27, 1963. This was considerably past the season of peak activity for this species. In St. Louis, Missouri, it was taken in quantity in the second and third weeks in May, 1965, as a source of luciferin and luciferase, but numbers decreased markedly by the end of the fourth week in May (Fischer, Sigma Chemical Co, personal communication). Fewer than two dozen males were seen during this study.

Males were first noted flying over the triangle 27–31 minutes after sunset. They flew and flashed 1–2 m above the ground while emitting their flash-patterns (single flashes of short duration), and covered 1–2 m longitudinally between flashes. Mean flash-pattern interval at 76° was 1.0 second (s.d. 0.15 sec; Table 2, Fig. 29).

Several females were found on the short sward on the triangle. All were found 10–20 cm above the ground at the tips of grass. They responded to male and flashlight flashes with single-pulsed flashes after short time delays. One female occasionally emitted a double-pulsed flash. The flashes of several females could be seen at distances greater than 30 m as they flashed in response to stimulus flashes of a five-cell flashlight. As noted in several other species, females also frequently flashed in response to car headlights sweeping across the area. The flashes of one female averaged 0.36 second in duration and were emitted at an average time delay of 0.32 second at 74° (Tables 4 and 6, Fig. 30). During flashes females usually flexed their abdomens or rolled in the manner described for *brimleyi*.

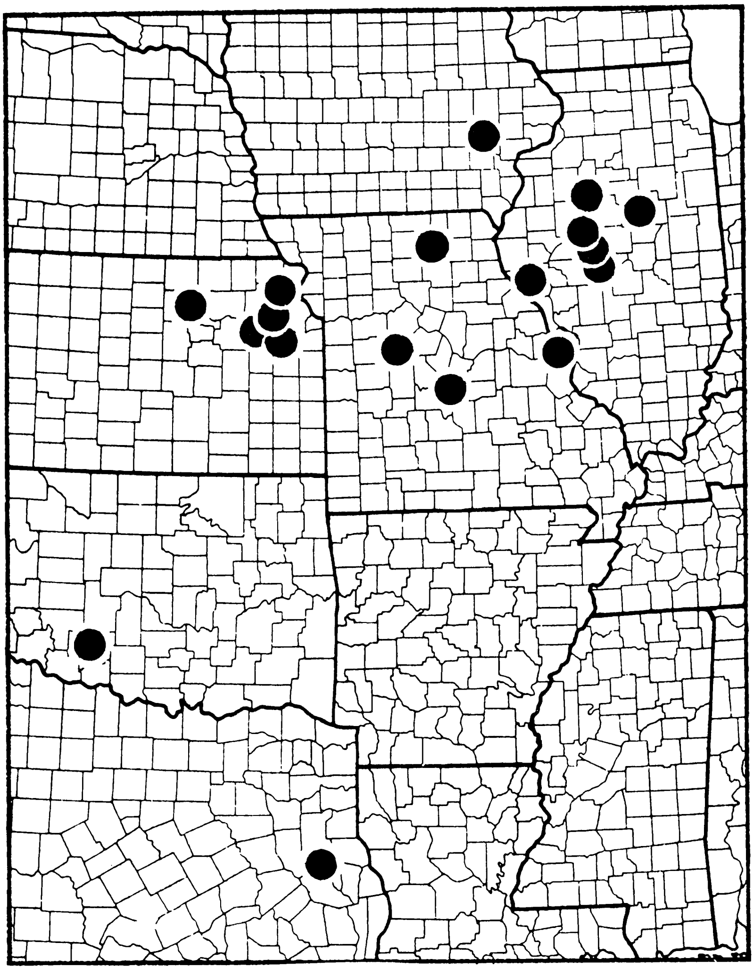


FIG. 14. Distribution of *Photinus punctulatus* LeConte (Missouri, etc.)

The approach of one flying male to a female was observed. After the first exchange, at two m, he wheeled and dropped into the grass less than ten cm from the female.

Photinus tenuicinctus Green (Fig. 15)

Studies were made on this species on Mt. Sequoia, Fayetteville, Arkansas, June 29 and 30, 1964. It was seen in abundance in Devil's Den State Park, and in the Boston Mountains along state route 23 from Cass, Arkansas, southward to the Arkansas River Valley. It was not found along the river valley nor across the river, but it was found along route 17 north of the valley. The Arkansas River thus seems to be the southern limit of its range. *P. tenuicinctus* was abundant in the forests and over shaded lawns.

Male flashing activity began 23 minutes after sunset over shaded lawns and continued for an indefinite length of time. Several individuals were seen five hours after sunset at Devil's Den Park, thousands were seen along route 23, and several were seen on Mt. Sequoia three or four hours after sunset.

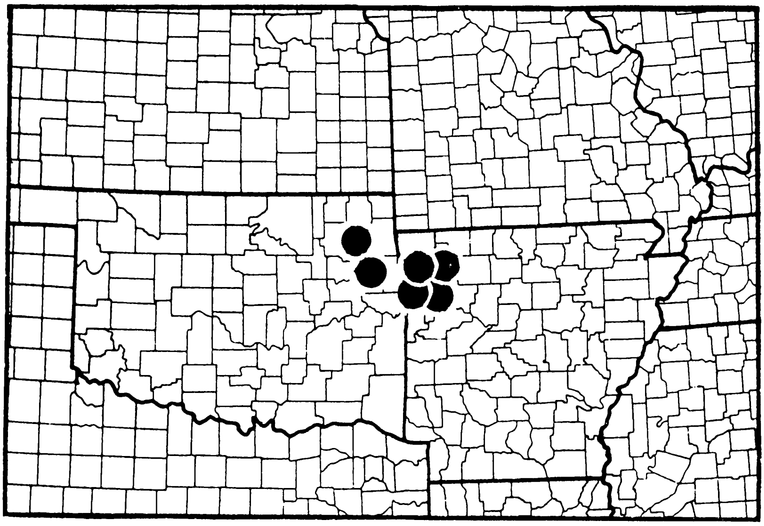


FIG. 15. Distribution of *Photinus tenuicinctus* Green (Arkansas)

Males flew 1–2 m above the ground and traversed approximately one m longitudinally between flashes. A few flew very rapidly, covering two or more m between flashes. Male flash-patterns, single sharp pulses, appeared to be 0.13–0.15 second in duration at 72°. The flashes of some males appeared to be bimodal with the second mode slightly more intense than the first. Flight was slow, and during flashes a slight vertical swinging motion was sometimes executed. Mean flash interval at 70° was 1.7 seconds (s.d. 0.23 sec; Table 2, Fig. 29).

Two females were found in short, sparse lawn grass in a grove of trees. They responded to the flashes of males, the MF, and the flashlight with single-pulsed flashes at short time delays. The average flash length of one female was 0.82 second, and her average delay time was 0.39 second at 75° (Tables 4 and 6, Fig. 30).

The approach of one male to a female was observed.

Females of this species were unknown previous to this study. A morphological description has been published (Lloyd, 1964*b*).

Photinus frosti Green

This species is known from only two male specimens. The holotype was taken April 3, 1954, in Otter Creek, Florida, and a paratype was taken at Ida, Louisiana. The Otter Creek locality was visited several times during this study and one specimen that resembled *frosti* was taken in a service station window (the source of the holotype). Thousands of *P. umbratus* LeConte, a closely related species, were seen along the roads in and around Otter Creek.

Photinus umbratus LeConte (Fig. 16)

This species was seen at Otter Creek and Enterprise, Florida; it was studied at Gainesville, Florida. At Gainesville and Enterprise, it occurred in

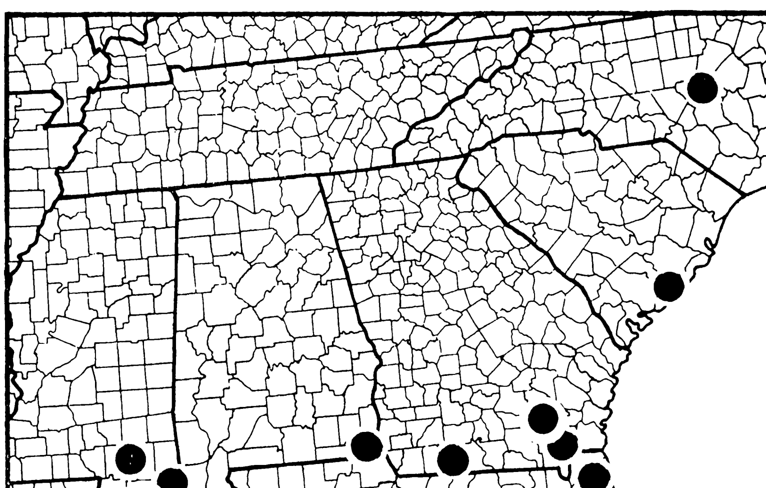


FIG. 16. Distribution of *Photinus umbratus* LeConte (Florida, etc.)

small colonies in moist mowed areas along roadways. At Otter Creek, it occurred in large numbers along roadside ditches in lush vegetation. On April 14, 1965, the first flying, flashing males were seen.

Male flashing activity began 11–18 minutes after sunset at light intensities between 0.01 and 0.02 fc. Males flashed from perches in the grass 1–2 minutes before taking flight, and at 62° they flashed from the grass but did not take flight. Activity lasted for approximately 18 minutes, and by 40 minutes after sunset only an occasional flash was seen. At the end of flying activity many males remained at the tips of grass and weeds with their lanterns glowing and sometimes flashing intermittently. Many were captured and eaten by wolf spiders at this time.

Flight paths of male *umbratus* resemble those of *pyralis* in their leisurely hops covering 1–3 m at altitudes of 0.5–1.5 m. The flash-pattern, a single long flash, is emitted during a dipping gesture. Sometimes the flashing beetles look like diminutive *pyralis,* and at other times the dip is drawn out longitudinally for 20–30 cm. At the end of the flash a hover period of 3–4 seconds is typical. Flashes of several males at temperatures of 67–72° were compared with the MF and estimated at 0.35–0.55 second duration. Mean flash-pattern interval at 72° was 6.8 seconds (s.d. 0.72 sec; Table 2, Fig. 29).

Several females were collected at the Gainesville site. These were found in the mowed grass up to one m above the ground in the tall weeds at the edge of the roadside. They were more difficult to capture than females of any other species studied. At the slightest vibration or movement they dropped from their perches to the ground below. Before capture, they responded to male, MF, and flashlight flashes with single long flashes at long delay times. After capture they seldom flashed, and none was recorded with the PT and tape recorder. Their flashes appeared to be approximately one second long. Several free females were timed with the stopwatch. Flash response delay time changed inversely with temperature from approximately 2.5 seconds at 70° to approximately 4.5 seconds at 60° (Fig. 30).

The approach of males to females was observed.

Photinus collustrans LeConte (Fig. 17)

Studies were made on this species in Gainesville, Enterprise, and Highlands Hammock State Park, Florida. In Gainesville and Enterprise it was found on lawns and other disturbed areas that had formerly been xeric hammocks. In Highlands Hammock Park a small colony was found in the mowed grass along the drive in the center of the hammock. On April 16, 1965, the first flying, flashing males were seen.

Male flashing activity began 11–26 minutes after sunset at ambient light intensities less than 0.01 fc. Females of this species usually glow dimly, when not flashing, during the time of male flying and flashing activity. Before and after the glowing period they are seldom responsive to stimulus flashes. Male flashing activity continued 15–25 minutes, depending upon deme size, and ended completely by 42 minutes after sunset.

Males flew 0.5–1.5 m above the ground. Their flight paths consist of a series of lateral arcs, each 20–50 cm long and separated from each other by 1–2 m of straight flight (Fig. 8). A slight vertical component is sometimes

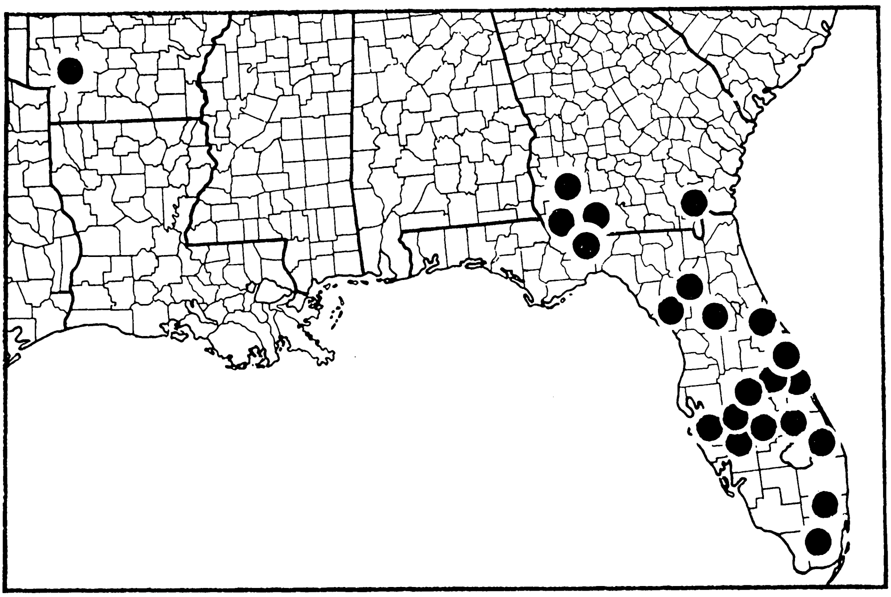


FIG. 17. Distribution of *Photinus collustrans* complex: *P. collustrans* LeConte and *P. tanytoxus* Lloyd. (Florida).

present during the entire lateral arc, or just at the very end, when they fly upward 5–10 cm and sometimes slow their flight. Some males fly slowly and others very rapidly. The flash-pattern, a single pulse, is emitted while males execute the lateral arcs. Flashes of several males were compared with the MF at temperatures between 72 and 76° and appeared to be between 0.25–0.35 second in duration at Gainesville and 0.25–0.50 at Highlands Hammock. Mean flash-pattern interval at 75° was 2.3 seconds (s.d. 0.51; Table 2, Fig. 29).

Several females were found on the ground or lying within one or two cm of the ground on the bases of grass stems. They responded to the flashes of males, the MF, and the flashlight with single-pulsed flashes at short delay times. The flashes of one recorded female averaged 0.68 second in duration and were emitted at an average time delay of 0.85 second at 65° (Tables 4 and 6, Fig. 30).

During flashes females usually rolled their abdomens away from the stimulus flashes in the manner described for other brachypterous females.

Several approaches of flying males to females were observed.

Photinus tanytoxus Lloyd (Fig. 17)

This new species, found during the investigation, is a sibling of *collustrans.* Studies were made at Gainesville and at a site 3.7 miles west of Gainesville, Florida. The Gainesville site was a turkey-oak sandhill association. The site west of Gainesville was a large pasture that probably had been a xeric hammock originally.

Male flying and flashing activity began 41–44 minutes after sunset and continued 35–70 minutes, depending on deme size. Female glowing and flashing in *tanytoxus,* as in *collustrans,* roughly correlated with male activity. Also associated with the glowing-flashing periods was an "on watch" behavior. Captive females were kept in a small box with a slice of apple. During the day they burrowed in the sand under the apple and at about the time males became active they crawled out from beneath the apple. This was noticed on several occasions; one evening note was made of the time eight females crawled out. They went "on watch" between 24 minutes before and eleven minutes after the beginning of male activity.

Males flew 0.5–2 m above the ground. Their flight paths consist of a series of arcs in the horizontal plane, each 1–2 m long and separated from each other by 2–4 m of straight flight. A slight vertical component is sometimes present during the lateral arc, or just at the end, where they fly upward slightly and sometimes slow their flight. Some fly slowly and others very rapidly. The flash-pattern, a single long pulse, is emitted while males execute the lateral arcs. Flash-patterns of several males were compared with the MF at temperatures between 67 and 77° and appeared to be 0.50–0.75 second in duration. Mean flash-pattern interval at 75° was 2.6 seconds (s.d. 0.40 sec; Table 2, Fig. 29).

Several females were found lying on the soil at the openings of tiny burrows approximately two mm in diameter. They responded to the flashes of males, the MF, and the flashlight with single-pulsed flashes at slight delay times. The flashes of one recorded female averaged 0.82 second in duration at a mean delay time of 1.04 seconds at 75° (Tables 4 and 6). During flashes females usually rolled their abdomens away from stimulus flashes in the manner described for other brachypterous females.

Several approaches of flying males to females were observed.

Photinus granulatus Fall (Fig. 18)

Studies were made on this species at Wichita, Wellington, and Winfield, Kansas. It was abundant on lawns and on the Wellington golf course, but was not found on the prairie nor in the Flint Hills east of Wichita in Greenwood County. In Wichita mating activity begins in late June, although males are seen as early as the second week in June (R. Lloyd, personal communication).

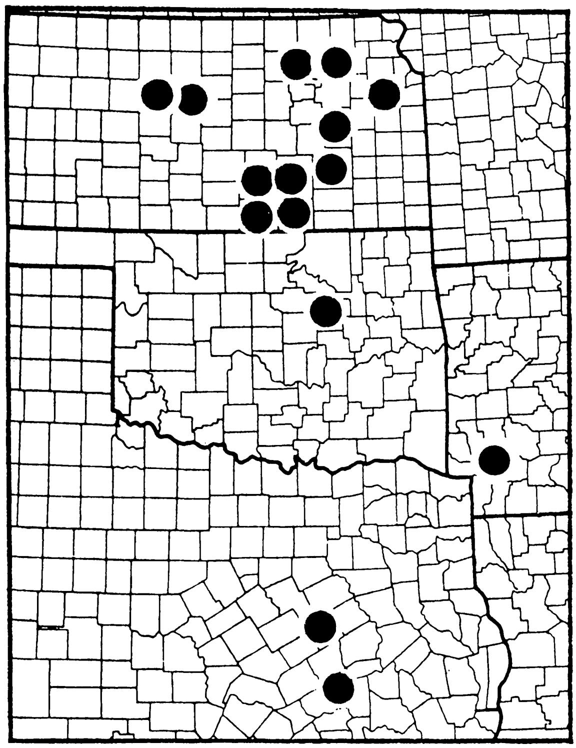


FIG. 18. Distribution of *Photinus granulatus* Fall (Oklahoma, etc.)

Male flying and flashing activity began 30–36 minutes after sunset and continued for two or more hours. Late night activity was much reduced in comparison with the first hour of flashing and frequently periods of activity alternated with periods of inactivity: several flashing males were visible at one moment and then none a moment later. Onset of flying and flashing was rapid, with only one or two minutes elapsing between the first flying flash and numerous others.

Males flew within one m of the ground, and during their single-pulsed flash-patterns they jerked rapidly from side to side. These movements made each flash appear rapidly pulsed with 5–10 amplitude modulations when viewed from the side or above; they resulted in a zigzag flight path (Frontispiece). When viewed from below the flash appeared to be bimodal. During each flash 20–60 cm were traversed in a longitudinal or slightly downward direction. An hour or so after activity began, many males flew at altitudes up to two m, and the zigzagging was much reduced. The flashes of several males were compared with the MF and appeared to be 0.20–0.22 second in duration at 75°. Mean flash-pattern interval at 72° was 1.3 seconds (s.d. 0.12 sec; Table 2, Fig. 29).

Several females were found on the lawns at the base of grass stems with their abdomens resting on the ground, their forebodies bent nearly vertical, and their legs grasping the grass stems. Females responded to the flashes of males, the MF, and the flashlight with single-pulsed flashes at slight delay times. One female was recorded. Her response flashes averaged 0.95 second in duration and were emitted at an average time delay of 0.45 second at 80° (Tables 4 and 6, Fig. 30). Between response flashes, both free and captive females glowed with a conspicuous light.

Several approaches of flying males to answering females were observed. After landing, the flashes of some males were clearly bimodal.

Photinus dimissus LeConte (Fig. 19)

This species was observed for only a few moments over a large meadow one mile west of the Arkansas border near Tom, McCurtain County, Oklahoma, July 2, 1964. Several males were seen flying and flashing 1–3 m above the tips of tall grass 2 hours and 26 minutes after sunset. The male flash, extremely bright for such a tiny insect, was similar to that of *P. brimleyi*, and appeared to twinkle as though bimodal. No jerking in flight during light emission (as found in the closely related *granulatus*) was observed. Flash intervals of 1.0, 1.0, 0.8, and 0.9 second were timed at approximately 74°.

No females were found, but judging from the very short flash-pattern intervals the female delay is probably 0.3–0.5 second in duration.

THE *consanguineus* GROUP

The flashes of this group are varied and complex. They involve multipulsed signals and long time delays: none yet studied has the simple flash-answer signal found in most of the species previously discussed.

Some of the species in this group are morphologically so similar that without notes on behavior it is difficult or impossible to distinguish one from another.

The geographic distribution of the *consanguineus* group is peculiar in that it contains four luminous species in eastern United States, but west of the Appalachians it is well represented by only a single nonluminous species, *P. indictus*. A record of a luminous member of the group from Nogales, Arizona, is presumably of a Mexican species.

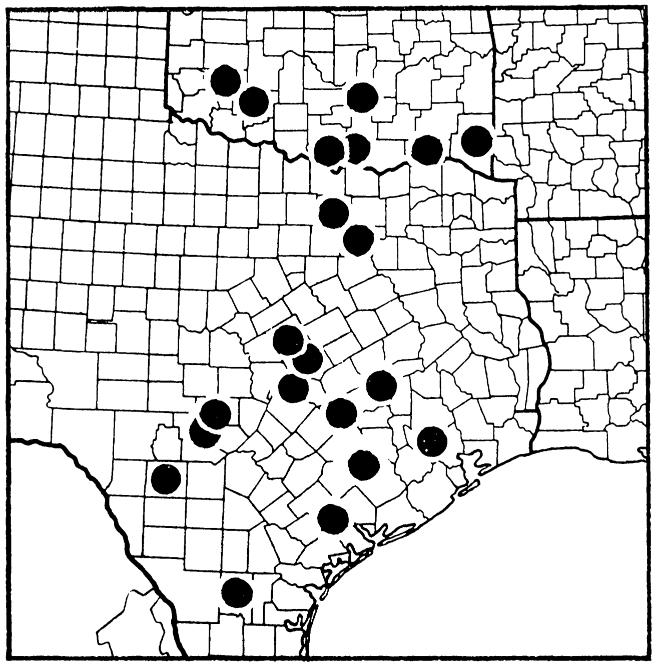


FIG. 19. Distribution of *Photinus dimissus* LeConte (Texas, etc.)

Photinus indictus (LeConte) (Fig. 20)

Several specimens of this nonluminous species were collected during the daytime by beating along roadside ditches and streams in Trumbull and Ashtabula counties, Ohio, July 31, 1963. This species was not seen at any other locality in three summers of field work, although the number of specimens in collections indicates that it is a common species.

A few individuals of this species were seen along a shallow roadside ditch in Gainesville, Florida, April 7–15, 1965. The species was not seen at any other site in over two months of field work in Florida. H. Weems (personal communication) has collected *lineellus* in numbers near Anditown, Florida. It may be a glade or marsh species.

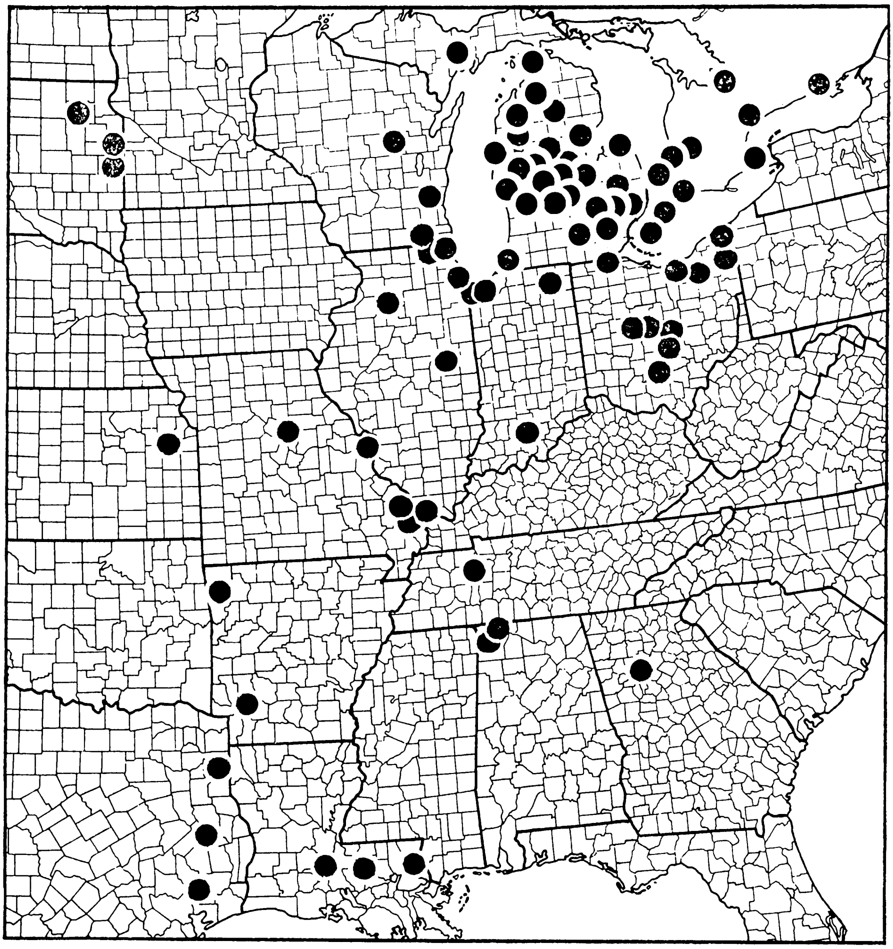


FIG. 20. Distribution of *Photinus indictus* (LeConte)

Photinus lineellus LeConte (Fig. 21)

Males emitted flash-patterns of 1–3 very short pulses at intervals of 2–3 seconds. Pulse intervals within the flash-pattern measured 0.3–0.5 second in duration at 74°.

Females were found in the wet ditch at the tips of grass 10–20 cm above the ground. Before capture they responded to two and three (but not one and four) pulse phrases of the flashlight with single-pulse flash responses, estimated to be one second in duration, at time delays of 0.5 and 0.6 second in duration.

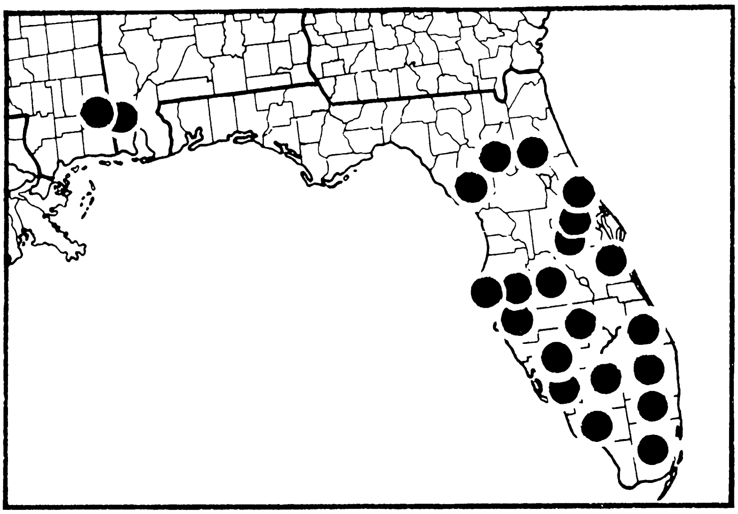


FIG. 21. Distribution of *Photinus lineellus* LeConte (Florida)

Photinus ignitus Fall (Fig. 22)

This species was seen at Red House and Ithaca, New York; it was studied at Wampsville, Oneida, and Portlandville, New York, and Fife, Virginia. It occurred in pastures, hayfields, and old fields.

In Wampsville the season of adult activity was mid-June–late July.

Male flashing activity began 39–45 minutes after sunset at light intensities considerably less than 0.01 fc, and continued for one or more hours.

Males flew in straight, level, slow flight one–two m above the ground (Fig. 8). Flashes of several males were estimated to average 0.16 second in duration at 72°. Mean flash-pattern interval at 74° was 5.1 seconds (s.d. 0.41 sec; Table 2, Fig. 29).

Several females were found in low vegetation. They responded to the flashes of males, the MF, and the flashlight with single-pulsed flashes at very long time delays. The flashes of one female averaged 0.24 second in duration and were emitted at an average delay time of 3.06 seconds at 77°. Time delay durations changed inversely with temperature (Tables 4 and 6, Fig. 30). During flashes females flexed their abdomens in the direction of stimulus flashes.

Approches of flying males to answering females were observed.

Photinus consanguineus LeConte (Fig. 23)

This species was seen at Otter Creek, Florida; it was studied at several sites in Gainesville, Florida, and at Fife, Virginia. It occurred in large

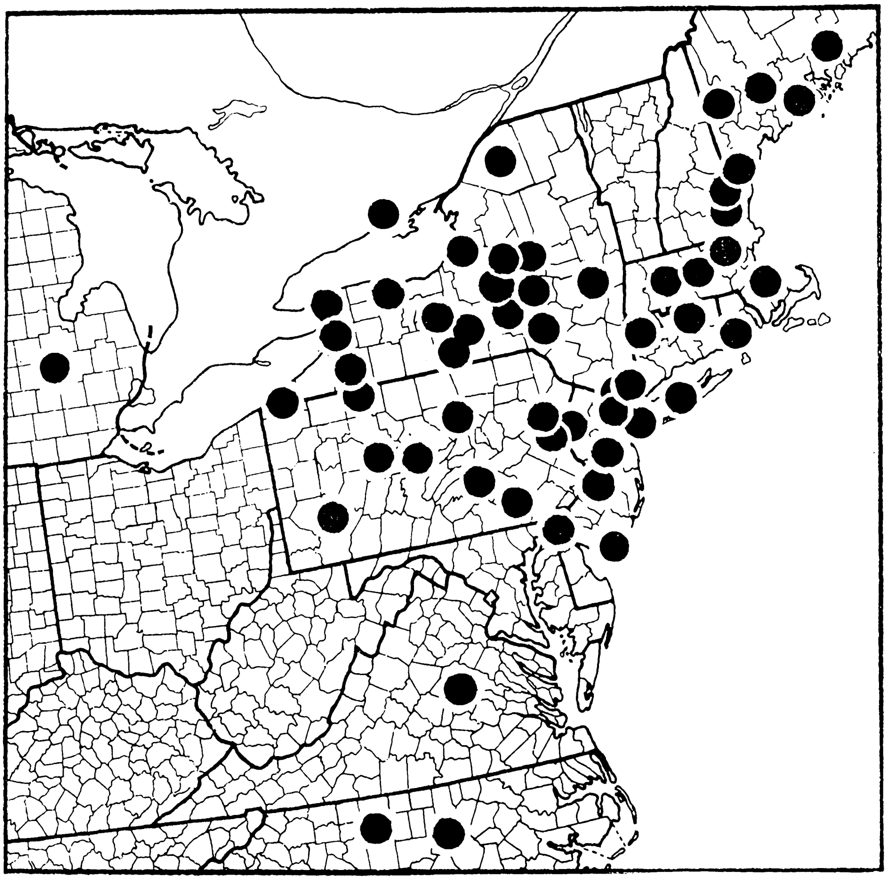


FIG. 22. Distribution of *Photinus ignitus* Fall

numbers in mesic hammocks in Florida, and in bushes and hedges at the edge of an old field in Fife. Several were seen in Gainesville on the earliest date of observations, April 7, 1965.

Male flashing activity began between ten minutes before sunset and eight minutes after sunset, depending on shade conditions. Considerably less variation was noted if observations were made at the same position in the study area. In one study area in Gainesville, on five nights of observations during two different years, activity began four–seven minutes after sunset. At another location in this same study area, on five evenings, activity began between sunset and four minutes before sunset, at ambient light intensities of about 0.01 fc. Peak flashing activity lasted 20–30 minutes, although occasional males could be seen giving their distinctive flash-patterns high in the trees well into the night.

Males flew in straight, level, slow flight 0.5–1.5 m above the ground. The flash-pattern, two quick pulses, was emitted each 0.5–2 m of flight. On the second pulse of each flash-pattern, males flew upward slightly (Frontispiece). Pulse length was estimated to be 0.20 second at 68°. The intervals of pulses within flash-patterns were 0.4–0.6 second in duration at 70–78°. Mean flash-pattern interval was 5.5 second at 73° (s.d. 0.61 sec; Table 2, Fig. 29).

Several females were collected. These were found 0.5–2 m above the ground on bushes, palmettoes, and small trees. They responded to the flashes of males, the MF, and the flashlight with single flashes at slight delay times. The flashes of one recorded female averaged 0.38 second in duration with an average time delay of 1.31 seconds at 70° (Tables 4 and 6, Fig. 30). During flashes, females usually flexed their abdomens in the direction of the stimulus flashes. After several minutes without stimulation females frequently flexed their abdomens with such force at the next stimulus that they fell from their perches.

The approach of flying males to females was observed.

Photinus macdermotti Lloyd (Fig. 23)

This new species found during this investigation is a sibling of *consanguineus*. Studies were made on *macdermotti* at two localities in Gainesville, Florida, and at Pisgah Mountain, North Carolina. It occurred in large numbers in a mesic hammock and an adjacent flatwoods in Florida, and in a hardwood forest along a stream at Pisgah Mountain. It was found in abundance in Gainesville on the earliest date of observations, April 7, 1965.

Male flashing activity began 8–12 minutes after sunset in the mesic hammock on the first few nights of observation in April, and 18–30 minutes after sunset in the open flatwoods, at ambient light intensities well below 0.01 fc. In mid-April, when a species of *Photuris* emerged in great numbers at both localities, only occasional *macdermotti* were seen, and these flew high in the trees. In May, *macdermotti* was seen frequently in both localities, but never in the earlier abundance. During May, males were first seen flying and flashing 29–35 minutes after sunset.

Males flew straight, level and very slowly one–five m above the ground. The flash-pattern, two slow pulses, was emitted each 1–2 m of flight. On the second pulse of each flash-pattern, males flew upward for distances of 5–10 cm. Pulses were estimated to be 0.16 second in duration at 71°. The intervals of pulses within flash-patterns averaged 2.8 seconds in duration at 62°, and 2.0 seconds at 73°. Mean flash-pattern interval was 6.0 seconds at 73° (s.d. 0.28 sec; Table 2, Fig. 29).

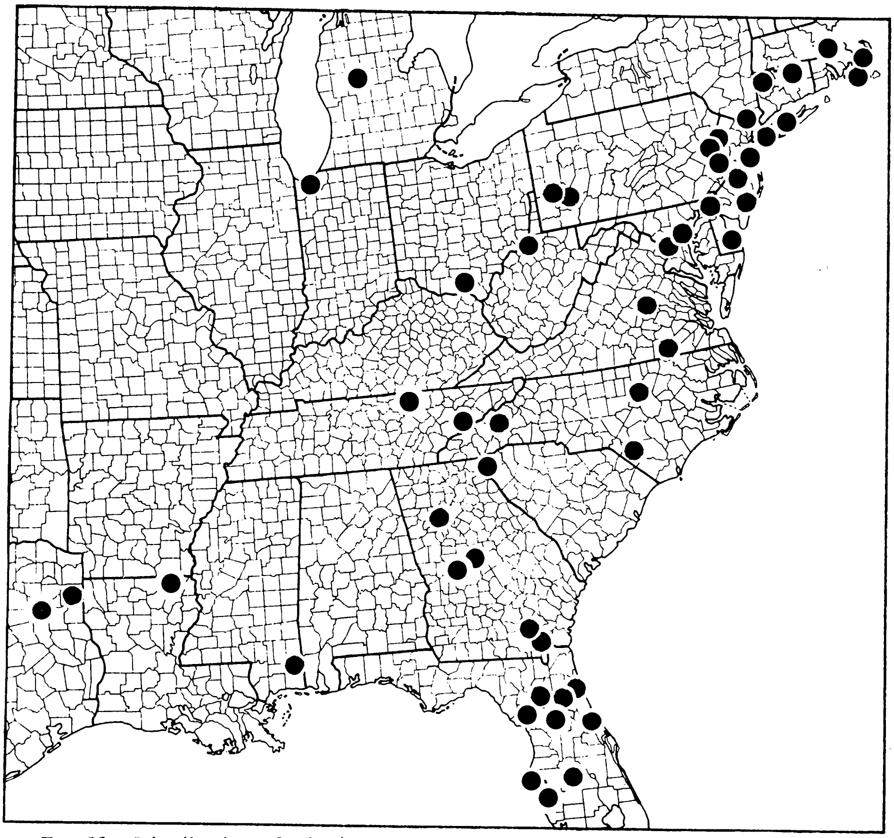


FIG. 23. Distribution of *Photinus consanguineus* complex: *P. consanguineus* LeConte and *P. macdermotti* Lloyd.

Several females were collected. These were found 0.5–1.0 m above ground on palmettoes and bushes in Florida, and 10–30 cm above the ground on roadside grass at Pisgah Mountain. They responded to flashes of males, the MF, and the flashlight with single-pulsed flash responses at slight delay times. The flashes of one recorded female averaged 0.20 second in duration and were emitted at an average time delay of 1.28 seconds at 69°. Female response delay times varied inversely with temperature (Tables 4 and 6, Fig. 30). During flashes females flexed their abdomens, usually in the direction of the stimulus flashes.

Approaches of flying males to females were observed.

THE *ardens* GROUP

As in the previous group, the signals of the *ardens* group are complex and involve multipulsed flash-patterns and time delays. Female flash responses in this group are unusual in that the pulses are frequently doubled, and these doubled pulses are typically repeated 2–4 times.

One of the described species was found to be a complex of two species that can be distinguished with certainty only on the basis of flash behavior. Until critical observations have been made at the type locality of *P. consimilis* Green, the second species cannot be formally described or named.

Photinus consimilis Green (Fast Pulse) (Fig. 24)

Observations were made on this species at two sites in Gainesville, Florida. One site was along a small stream between a mesic woods and a ten-foot bank sloping up to a sward converted from a xeric hammock. The other site was around the edge of a pond in the center of a hydric hammock. Observations were made on this species during the last week in April and the first week in May, after which few were seen.

Male flashing activity began about 46 minutes after sunset and continued for approximately one hour. Flying and flashing males were sometimes seen as late as 2¼ hours after sunset.

Males flew 1–2 m above the ground in very slow leisurely flight. The flash-pattern, 4–9 quick pulses, was emitted while moving in a horizontal or slightly downward direction. On the last few pulses of each flash-pattern, males frequently stopped moving forward and hovered (Fig. 8). Two–six m were traversed between flash-patterns and usually about one m during a single flash-pattern. Pulse length was estimated to be 0.20 second at 67°. The intervals of pulses within flash-patterns were 0.5–0.6 second in duration at 63–73°. Mean flash-pattern interval was 10.6 seconds at 66° (s.d. 1.1; Table 2, Fig. 29).

One female was taken. She was found in low vegetation about a half meter above the ground. She responded to flashlight signals of 2–8 pulses with double-pulsed responses at an average delay time of 3.2 seconds at 70° (Table 6). The doubled pulses were usually repeated 2–3 times, although sometimes this female repeated them four times. Sometimes she omitted the second pulse, but maintained her rhythm and flashed the third or fourth pulse. All time measurements were made with the stopwatch. The pulse lengths and pulse intervals for this female appeared to be similar to those for females of *ardens* recorded with the PT.

Males of this species were extremely easy to decoy.

Photinus consimilis Green (Slow Pulse) (Fig. 24)

Studies were made on this species at Gainesville, Florida. It was found in the same site as the Fast Pulse *consimilis,* at the edge of a pond in a hydric hammock. Several flashing males were seen between April 13 and May 8, 1965, although never in abundance, and no females were found.

Males were seen flying and flashing during the same time that Fast Pulse *consimilis* was active.

Males flew 2–4 m above the ground and pond in very slow and generally unidirectional flight. The flash-pattern, two or three slow pulses, was emitted during generally level flight, although on the last pulse altitude

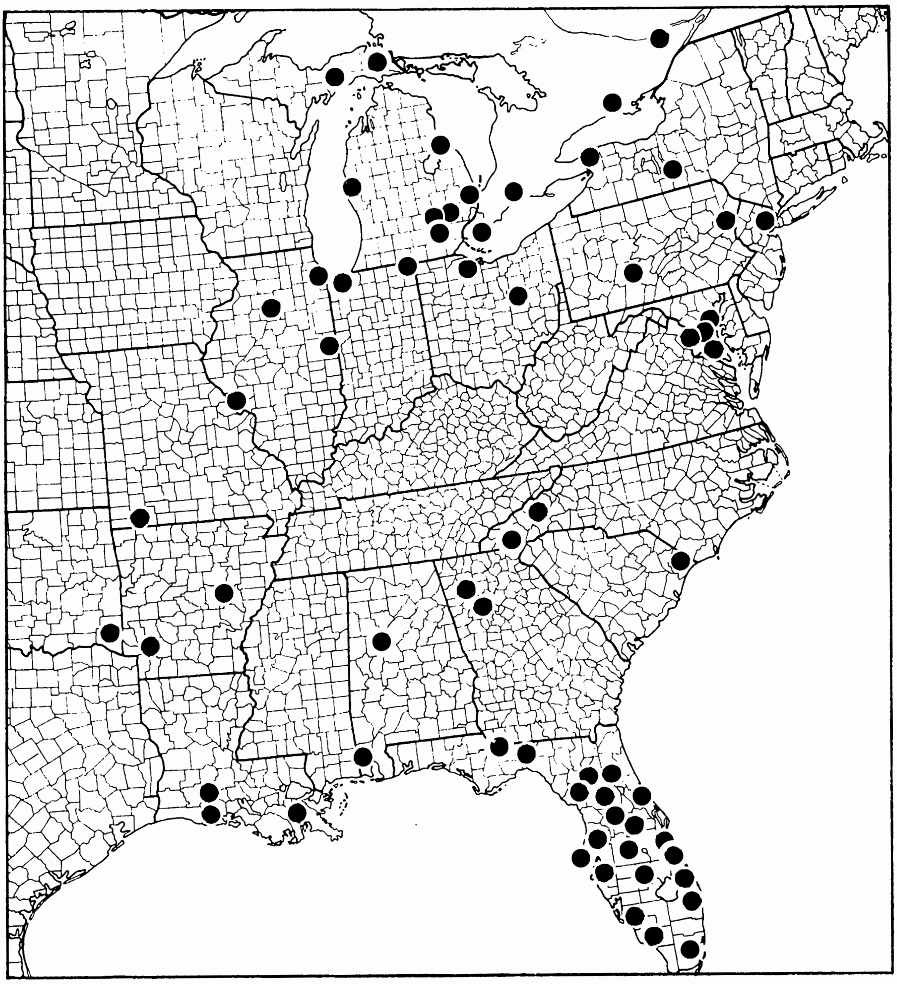


FIG. 24. Distribution of *Photinus consimilis* complex: *P. consimilis* Green, fast-pulse and slow-pulse species.

sometimes increased slightly (Frontispiece). From 0.5–1.0 m was flown during the flash-pattern and 2–6 between consecutive flash-patterns. Pulse length was estimated to be 0.40 second at 68°. Intervals of pulses within flash-patterns averaged 1.3 seconds at 72° and 1.7 seconds at 68°. Mean flash-pattern interval was 12.4 seconds at 73° (s.d. 1.06; Table 2, Fig. 29).

While searching for females by simulating the male flash with a flashlight, I received an answer from a *Photuris* female. She emitted two pulses at about a one-second interval and five seconds delay. I then mimicked her response to decoy flying males of the Slow Pulse *consimilis* species. Several were attracted to within 70 cm of the flashlight and one to its tip. Most males of most species can be attracted right to the tip of the flashlight. The poor results with this species may have occurred because the signal I flashed was not quite correct. It may also be that males of this species are especially selective because species of *Photuris* mimic their signals and prey on them (Lloyd, 1965*b*). Attempts to attract males of Slow Pulse *consimilis* by a variety of other flashes always failed.

Photinus carolinus Green (Fig. 25)

This species was seen at Pisgah Mountain, North Carolina; it was studied at Gatlinburg, Tennessee. Both sites were in hardwood forests near streams. A large population was present at Gatlinburg June 16–22, 1963. None was seen July 9, 1964.

Male flashing activity began 37–43 minutes after sunset and continued for nearly three hours. Flight paths and flash-patterns were similar to those described for *consimilis* (Fast Pulse). Pulses were approximately 0.2 second in duration and pulse interval at 64° was 0.6 second. Mean flash-pattern interval at 64° was 13.8 seconds (s.d. 1.2 sec.; Table 2, Fig. 29).

Momentary synchrony was seen in the flashes of males of this species several times. As cars passed the site, their headlights would sweep across the mountainside where most firefly activity took place. After each car passed several seconds of darkness followed, then hundreds of males would begin their flash-patterns together. This synchrony usually did not last more than a few pulses.

One responsive female was taken from short grass at the edge of a stream. Her responses to flashlight flashes of 3–8 pulses were double pulsed and averaged 6.4 seconds in time delay at 61° (Table 6). She responded to 4–9 pulsed flash-patterns regularly, but only once in several trials to a three-pulsed flash-pattern, and not at all to one- or two-pulsed patterns. Her double-pulsed responses were usually repeated two or three times (sometimes they were not repeated). All time measurements were made with a stopwatch. Pulse lengths and pulse intervals for this female appeared to be similar to those of *ardens,* and Fast Pulse *consimilis.*

Males were extremely easy to decoy, and several were attracted to the flashlight. The female was placed in a glass cage on each of several evenings of observation. She always attracted several males; as many as eight would be on her cage at one time. This suggests that some males were attracted to

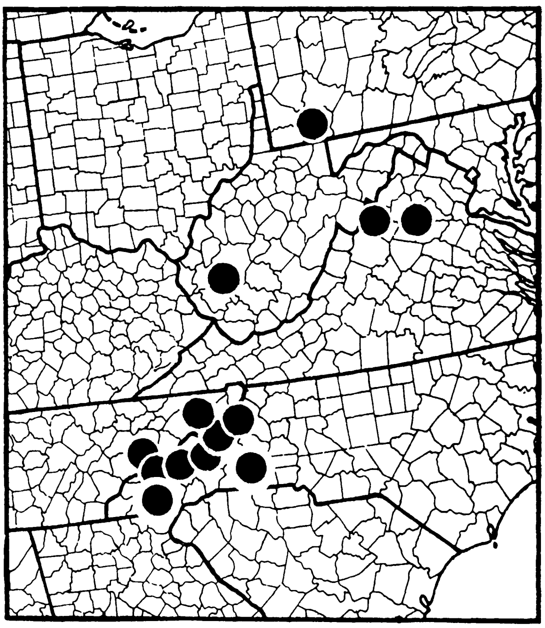


FIG. 25. Distribuiton of *Photinus carolinus* Green (North Carolina, etc.)

the flashes of the communicating pairs or perhaps to the aggregation of males. Males of this species sometimes also flashed in response to flashlight flashes, flashes of other males, and female flashes. These flashes were sporadic, frequently double pulsed, and without any particular rhythm pattern. This behavior was also noted in *ardens* and Fast-Pulse *consimilis* males.

Photinus ardens LeConte (Fig. 26)

Studies were made on this species at Raubsville, Pennsylvania, and at Portlandville, McLean, and Oneida, New York. It was found in low wet pastures that had streams flowing through or adjacent to them. In such wet situations pasturing results in humps and depressions with *Sphagnum* frequently lying over the surface of the ground beneath grass. *P. ardens* is an early summer species and is active during the first two weeks in June.

Male flashing activity began 21–34 minutes after sunset at light intensities below 0.01 fc and continued for 1–2 hours.

Males flew 1–2 m above the ground in slow flight. The flash-pattern, two or three fast pulses, was emitted while flying horizontally, slightly downward or upward. One–two m were flown between flash-patterns and usually about 0.5 m or less during the flash-patterns. Pulse length was estimated to be 0.20 second at 72°. Tape recorded flashes of one male averaged 0.34 second in duration at 62°. Intervals of pulses within flash-patterns were 0.6 to 0.7 second in duration at temperatures between 58 and 62°, and 0.5 second at 67°. Mean flash-pattern interval was 6.4 seconds at 65°. (s.d. 1.2 sec; Table 2, Fig. 29).

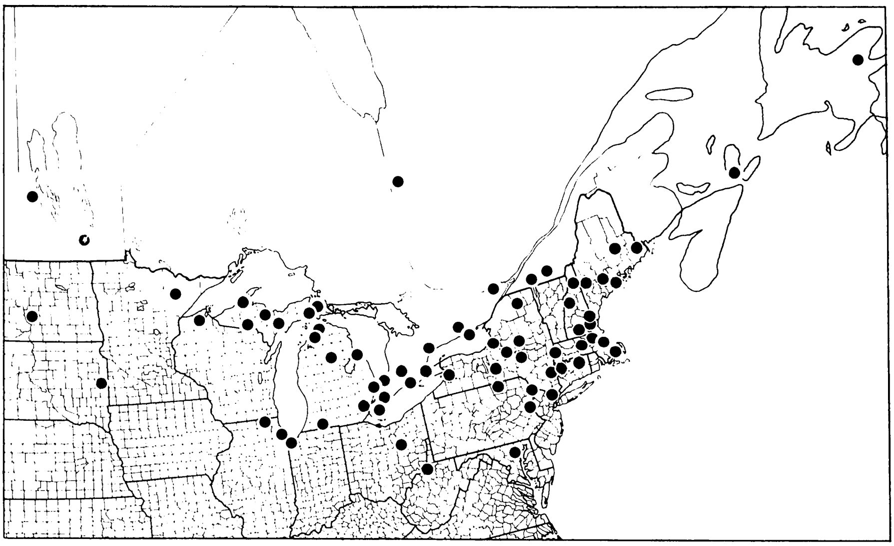


FIG. 26. Distribution of *Photinus ardens* LeConte

Several females were collected. These were found in low grass, perched 10–30 cm above the ground. They responded to the flashes of males, the MF, and the flashlight with double-pulsed responses at moderate time delays. The double-pulsed signals were frequently repeated two or three times. The flash responses of one female averaged 0.62 second in duration and were emitted at an average time delay of 1.57 seconds at 54° (Table 6). Her single pulses were 0.25 second long. These flashed responses were repeated after pauses ranging from 1.38 to 1.90 seconds in duration.

Mating behavior in this species was unusual in that mating pairs were found on the frequent evenings when the temperature was too low for flight (less than 54°). On such evenings several individuals, both males and females, flashed from the grass and females were commonly seen answering males.

THE FLASH SIGNAL SYSTEM AND REPRODUCTIVE ISOLATION

During the investigation some species pairs were noted that prompted further observation or tests on various parameters of the flash signal system thought to function in reproductive isolation. These species combinations are each treated in a separate section below. Differences and similarities in their behavior are noted, and the results of observations and experiments are presented. Equipment used in testing was described above; methods used are described below with the presentation of results.

Observations and Experiments

I. *Photinus scintillans–P. marginellus:* This combination was selected for closer study because the behavior, ecology, and signals of the two are similar, although they are sympatric. The flashes of *scintillans* appear to be shorter and sharper than those of *marginellus* (0.15 sec. versus 0.30 sec. at 70°), and also orange-yellow rather than yellow (peak 100 Å nearer red end of spectrum; Seliger *et al.,* 1964).

Six responsive *marginellus* females from Branchville, New Jersey, were placed in individual glass cages in a *scintillans* site in Silver Spring, Maryland. The cages were arranged in a cluster with about 15 cm separating them. From time to time a 0.30-second stimulus flash of the MF was presented to them as a check on their responsiveness.

During a period of about one-half hour, seven flying *scintillans* males flashed directly over the cluster at altitudes less than one meter, but none of the *marginellus* females flashed in response. The next night a similar procedure was followed, with an addition of four *scintillans* females grouped at the edge of the *marginellus* cluster. Several *scintillans* males were attracted to the *scintillans* females, but none to the *marginellus* females. The *marginellus* females did not flash in response to the flashes of *scintillans.* They did answer the one-second flashes of the occasional *Photuris lucicrescens* males that flashed near them.

Two *scintillans* females were placed in glass cages in a *P. curtatus* (probably a form of *marginellus:* see Lloyd, in press, *b*) site in Oneida, New York. Both immediately attracted males. The males were allowed to enter the cages and when they reached the females they crawled about on top of them but did not copulate.

Females of *scintillans* and *marginellus* were tested for their ability to discriminate between flashes of light that differed *only* in duration. Females to be tested were placed in glass cages. The bulb of the MF was placed slightly above them, and 20–30 cm from them. Flashes of different lengths were presented to them. The order of presentation of the two different flash lengths was adjusted during the test, according to responses to immediately preceding stimuli. The *marginellus* females were from Branchville, New Jersey, and the *scintillans* females from Silver Spring, Maryland.

Results of the tests are presented below. A plus sign (+) indicates the female answered the stimulus flash (the length of which is shown by the number at the head of the row in which the sign appears). The flash length nearest that appropriate for the tested species appears above the line. A minus sign (–) indicates the female did not flash in response to the MF flash. Int 60 indicates that 60-second time intervals separated consecutive flash stimuli in a particular test. For example: in the first test below the female was given a 0.16-second flash and she answered it. After 60 seconds she was given another 0.16-second flash, which she also answered. Sixty seconds later she was presented with a 0.34 second flash and she did not answer. Stimulus flash intervals in most tests were considerably shorter than 60 seconds. Unless otherwise indicated at least five minutes elapsed between consecutive tests on the same female.

Photinus scintillans, females

				test number
No. 1.	63°	.16	+ + + + + – –	(1)
	Int 60	.34	– – – –	
No. 1.	63°	.16	+ + + + + – + + + – + + +	(2)
	Int 15	.34	– – – – – – – –	
No. 1.	63°	.16	– + + + + + – + + + +	(3)
	Int 5	.34	– – – – – – –	
No. 1.	63°	.16	+ – + + +	(4)
	Int 5	.34	– – –	
No. 2.	62°	.15	+ + + – –	(5)
	Int 5	.34	– – – – –	
No. 2.	62°	.13	+ + + – + +	(6)
	Int 5	.20	– – – –	
No. 2.	62°	.15	+ + + + + +	(7)
	Int 5	.34	– – – –	
No. 2.	62°	.13	+ + + – – + +	(8)
	Int 5	.25	– – –	

No. 2.	62°	.13	+ + + + + +	(9)
	Int 5	.25	– – – –	
No. 3.	62°	.15	+ – + + + +	(10)
	Int 5	.34	– – – –	
No. 3.	62°	.13	+ + + +	(11)
	Int 5	.20	–	
No. 3.	62°	.15	+ + + + + +	(12)
	Int 5	.34	– – – –	
No. 3.	62°	.13	+ – – + – + +	(13)
	Int 5	.25	– – –	
No. 3.	62°	.13	+ + + – + + +	(14)
	Int 5	.25	– – –	
No. 3.	62°	.13	+ + + + + +	(15)
	Int 5	.25	– – – –	
No. 4.	62°	.13	+ + – + + + –	(16)
	Int 5	.25	– – –	
No. 4.	62°	.13	+ + + + – + +	(17)
	Int 5	.25	– – –	
No. 4.	62°	.13	+ + + + + +	(18)
	Int 5	.25	– – + –	
No. 4.	62°	.13	+ + + + + – +	(19)
	Int 5	.25	– – –	
No. 4.	62°	.13	+ + + – + +	(20)
	Int 5	.25	– – – –	
No. 5.	62°	.13	+ + + + + +	(21)
	Int 5	.25	– – – –	
No. 5.	62°	.13	+ + + + +	(22)
	Int 5	.25	– – – – –	
No. 5.	62°	.13	+ + + + + +	(23)
	Int 5	.25	– – – –	
No. 5.	62°	.13	+ + – – – +	(24)
	Int 5	.25	– – – –	
No. 5.	62°	.13	+ + + +	(25)
	Int 5	.25	– – – – – –	

Photinus marginellus, females

No. 1. 68° .34 + − + + + + (26)
Int 15 .15 − − − −

No. 1. 68° .34 + + + + − + (27)
Int 15 .15 − −

No. 1. 68° .34 + + + + − − + + + − + + + +
Int 15 .15 − − − − − − −
\+ − + + (28)
− −

No. 1. 68° .20 + + + + − − − + − (29)
Int 15 .16 − − −

No. 1. 68° .25 + + + + − + − (30)
Int 15 .20 − + − + − +

No. 2. 68° .34 + − − + + + (31)
Int 15 .15 − − − −

No. 2. 68° .34 + + − − − + (32)
Int 15 .15 − −

No. 2. 68° .34 + + − + + + + + + − + − +
Int 15 .15 − − − − − − −
\+ + + (33)
− −

No. 3. 68° .34 + + + + + + (34)
Int 15 .15 − − − −

No. 3. 68° .34 + + − − − + (35)
Int 15 .15 − −

No. 3. 68° .34 + + − + − + − − + − + + +
Int 15 .15 − − − − − − − − −
\+ + + + (36)

In these tests females of both *marginellus* and *scintillans* demonstrated, by their selective responses, their ability to discriminate on the basis of pulse length. In *scintillans* only one inappropriate pulse length was answered (test 18). *P. scintillans* females occasionally did not respond to the pulse length characteristic of males of their species. This was also noted in actual male-female interactions (see above). In *marginellus* no inappropriate pulse lengths were answered in tests in which the two stimulus pulse lengths differed appreciably, although in one test (30) the females did not seem to discriminate a pulse length difference of 0.05 second. *P. marginellus* females also failed to respond to some flash stimuli of appropriate length. Chi-squares for the responses of *scintillans* females 1–5 are significant at the 0.5 per cent level (H_0 = no difference in responses to the two pulse lengths). Chi-square for *marginellus* female No. 1 is significant at the 0.5 per cent level, and for females 2 and 3, at the 2.5 per cent level.

II. *Photinus sabulosus–P. marginellus:* These two closely related species are sympatric throughout the range of *sabulosus.* They were found together in the same site in Ithaca, New York. Although they were active during the same period of the evening, *marginellus* confined its activity to the ground level, and *sabulosus* males generally flew higher, usually in the branches of the trees. A difference was also noted in the male flash length: in *sabulosus* it was about 0.16 second and in *marginellus* about 0.30 second at temperatures near 70°.

Tests identical to those described above were performed on *marginellus* females collected at this site. No *sabulosus* females could be found at the time of testing.

Photinus marginellus, females			test number
No. 1.	63°	.34 + + + + +	(37)
	Int 5	.16 – – – – –	
No. 1.	63°	.34 + + + + + +	(38)
	Int 5	.16 – – – –	
No. 2.	63°	.34 + + – + + +	(39)
	Int 5	.16 – – – –	
No. 2.	63°	.34 + + + – – +	(40)
	Int 5	.16 – – – –	
No. 3.	63°	.34 – + + + + +	(41)
	Int 5	.16 – – – –	
No. 3.	63°	.34 + + + + + +	(42)
	Int 5	.16 – – – –	
No. 4.	68°	.25 + + + + +	(43)
	Int 5	.16 – – – – – –	
No. 4.	68°	.25 – + + + + + + + +	(44)
	Int 5	.14 – – – –	
No. 4.	68°	.25 + + + + + + +	(45)
	Int 5	.14 – – – –	
No. 5.	68°	.25 + + + + +	(46)
	Int 5	.16 – – – – – –	

No. 5.	68°	.25	+ − + − − − − − +	(47)
	Int 5	.14	− − − −	
No. 5.	68°	.25	+ + + + + + +	(48)
	Int 5	.14	− − − −	
No. 6.	68°	.25	+ + + + +	(49)
	Int 5	.16	− − − + − −	
No. 6.	68°	.25	− + + − − + +	(50)
	Int 5	.14	− − − −	
No. 6.	68°	.25	+ + + + + − − + +	(51)
	Int 5	.14	− − − −	
No. 7.	68°	.25	+ + + + +	(52)
	Int 5	.16	− − + − − −	
No. 7.	68°	.25	− + + − + + +	(53)
	Int 5	.14	− − − −	
No. 7.	68°	.25	+ + + + + + + + +	(54)
	Int 5	.14	− − − −	

In these tests females of *marginellus* from the Ithaca site demonstrated, by their selective responses, their ability to discriminate on the basis of pulse length. In two tests, females responded once to inappropriate flash lengths. Females sometimes failed to respond to the pulse characteristic for males of their species. Chi-squares for the responses of all females except female No. 2 are significant (H_0 = no difference in responses to the two pulse lengths): female 1, 2.5 per cent; 2, 25 per cent; 3, 5 per cent; 4, 0.5 per cent; 5, 5 per cent; 6, 5 per cent; 7, 2.5 per cent.

III. *Photinus collustrans–P. tanytoxus:* These sympatric sibling species differ in time of evening activity, female time delay, and male flash length. Flash length for males of *collustrans* appeared to be 0.25–0.35 second, and for *tanytoxus* 0.50–0.60 second, at temperatures near 70°. Female delay in *collustrans* was about 0.8 second and in *tanytoxus* 1.0–1.4 seconds at 75°.

On numerous occasions females of each species were placed in glass cages in sites of the sibling. No attractions took place. In fact, most females did not flash in response to males of the other species. At times outside of the normal period of activity, females would not usually flash in response to the MF even when flashes of males of their own species were simulated. During the normal activity period they would occasionally respond to MF flashes of lengths inappropriate for the species. Females of *P. collustrans* placed in *tanytoxus* sites would occasionally flash, while females of *tanytoxus* in *collustrans* sites would not. In four observed cases females of *collustrans* responded only once, and when the males of *tanytoxus* circled and flashed again the females did not continue to respond.

One *tanytoxus* female was tested for pulse length discrimination. The procedure was similar to that described above, except that flashes of several different lengths were presented to the female. Observe the change in notation.

Photinus tanytoxus, female — test number

No. 1.	75°	(+)	.56	.56	.60	.60	.32		.62		.64		.68
		(−)						.32		.25		.31	

	.56	.62			.50		.53	.56	.55	(55)
.38			1.09	.75		.50				

No. 1. 75°. Summary of pulse length discrimination.

accept			.32			.50	.53	.55	.56	.56	.56	.56	.59	.60	.60	62
reject	.25	.31	.32	.38	.38	.50										

.62	.64	.68		
			.75	1.09

IV. *Photinus consanguineus–P. macdermotti:* Males of these two sibling species were seen flying in the same site at the same time. Male pulse length and female delay are similar, but there is a noticeable difference in pulse rate within the male flash-pattern. The flash-pattern of each species consists of two pulses, which occur at intervals of about 0.5 second in *consanguineus* and 2.0 seconds in *macdermotti,* at temperatures near 70°.

While recording female flashes of both species, the flash-pattern of the sibling was frequently presented. None of the more than ten females tested in this manner, in over 100 trials, responded to an inappropriate flash-pattern.

Females of each species were placed in sites of populations of the sibling. None attracted males nor flashed in response to the flash-pattern of sibling males.

Females of both species were tested for pulse interval (pulse rate) discrimination. Tests were recorded with the PT and tape recorder. Tapes were later analyzed with an oscilloscope. The notation has already been introduced. PL indicates the pulse length used during the test.

Photinus macdermotti, females — test number

No. 1. 62°

Int ca. 8	(+)	2.34	2.26	2.37	2.38	2.38	2.37	2.42				
PL 0.16	(−)								1.67	1.67		
	2.21	3.21			2.15	2.26	2.21			2.92		
			3.12	3.20				1.66	1.67			
		2.07	2.12									(56)
	3.05											

No. 1. 62°. Summary of pulse interval discrimination.

accept					2.07	2.12	2.15	2.21	2.24	2.26	2.26	2.31
reject	1.66	1.67	1.67	1.67								
	2.37	2.37	2.38	2.38	2.42	2.92				3.21		
							3.05	3.12	3.20			

No. 2. 68°

Int ca. 8	(+)	2.05	2.18	1.87	1.93		2.14		2.15		
PL 0.18	(−)					1.49		3.18		1.69	
	2.29	2.29	2.37	2.06			2.11	2.00		1.92	
					3.20	2.16			1.46		
	1.98		2.19	2.16		1.90	1.86		2.12		
		2.70			1.82			1.42		3.00	
	2.47		2.07		1.98	2.08	2.00		2.07	2.13	
		1.95		2.86				1.74			
		2.13	2.14		2.20		2.06		2.58		
	2.89			2.45		1.11		2.96		2.48	
	2.05		2.18	2.04	2.06						(57)
		1.47									

No. 2. 68°. Summary of pulse interval discrimination.

accept									1.86	1.87	1.90	1.92	1.93
reject	1.11	1.42	1.46	1.47	1.49	1.69	1.74	1.82					
	1.98	1.98	2.00	2.00	2.04	2.05	2.06	2.06	2.06	2.07	2.07	2.08	2.11
	2.12	2.13	2.13	2.14	2.14	2.15	2.16	2.18	2.18	2.19	2.20	2.29	2.29
							2.16						
	2.37		2.47		2.58								
		2.45		2.48		2.70	2.86	2.89	2.96	3.00	3.18	3.20	

No. 3. 69°

Int ca. 8	(+)	2.21	2.27			1.98	2.06	(58)
PL 0.18	(−)			.45	.42			

Photinus consanguineus, female

No. 1. 70°

Int ca. 5	(+)	.42	.50	.50				.48		.43	.48		
PL 0.21	(−)				.29	.25	.56		.57			.43	.59

(+)		.39		.41		.43	.38			.38	.54	.47	(59)
(−)	.57		.33		.38			.36	.52				

No. 1. 70°. Summary of pulse interval discrimination.

accept					.38	.38	.39	.41	.42	.43	.47	.48	.48	.50	.50		.54
reject	.25	.29	.33	.36	.38					.43						.52	
	.56	.57	.57	.59													

In these tests females of both *macdermotti* and *consanguineus* demonstrated, by their selective responses, their ability to discriminate on the basis of pulse interval.

V. *Photinus australis–P. sabulosus:* These species are sympatric in only a small portion of their ranges. Ecology and time of activity were found to be similar, although *sabulosus* may frequent tree tops or the canopy. Flash-patterns of both are single flashes—*australis* about 0.13 second in duration at 80°, *sabulosus* about 0.16 second at temperatures near 70°. Female delay time in *australis* at 64° was about 1.2 seconds and in *sabulosus* about 0.4 second at 70°.

Free *australis* males in Liberty County, Florida, (outside area of range overlap) were tested to see if the *australis* female time delay was necessary to attract them. When flying males flashed near the flashlight, they were given a response flash simulating those of their females in duration and delay. After receiving this response they turned in flight and flew toward the flashlight for a few cms and flashed again. Following this flash, and the next three or four, the flashlight was flashed to simulate delay time in the responses of *sabulosus* females (0.3–0.4 sec.). Five males were tested in this manner. After the second flash exchange all continued to hover and flash at the normal flash-pattern interval for three or four more flashes, and then flew off.

VI. *Photinus floridanus–P. collustrans:* Males of these two species frequently came within signalling distance of females of the other species. Both were active during the same time period each evening, and they were often found in contiguous sites. Flash length of *floridanus* was 0.15 second, and for *collustrans* about 0.25 second at temperatures near 75°. Female time delay in *floridanus* was about 0.3 second and in *collustrans* about 0.8 second at 75°. The *collustrans* flash-pattern was emitted while males flew short horizontal arcs. The flash in *floridanus* was emitted during stationary or hovering flight, or during a slight upward movement. Females of *collustrans* (and *tanytoxus*) glow brightly during the evening period of activity, and their flashes are superimposed upon these glows. Females of *P. floridanus* rarely glow between flashes, and then only feebly.

Several females of *floridanus* were placed in a *collustrans* site in glass cages. Some of them flashed in response to the flashes of *collustrans* males. A few males flew to within 50 cm of the cages and flashed again. Some males received responses to the second flashes and some did not, but in all cases they flew off after their second flash. This experiment gave similar results on three different evenings with more than ten different females of *floridanus*.

Spatial gestures: All females tape-recorded during this investigation were stimulated to flash with a stationary source of light. It was not necessary to move the stimulus light through spatial figures, even though various characteristic movements were found in male flight paths during flashing. When, during lengthy recording sessions, the light was moved to a new position, females that had stopped answering would sometimes begin again.

The following test was conducted to demonstrate the significance of the illuminated horizontal arc *per se* of *collustrans* males in stimulating female responses. Eight *collustrans* females were placed in glass cages and arranged in a wide arc with about 15 cm separating adjacent cages. Stimulus flashes 0.25 second in duration were presented to them in either of two ways: from a stationary point in space one m above the cages, or during a movement 20–30 cm in length one m above the cages. These moving flashes (gestures) were made as identical as possible; the light was held in the hand and moved in an arc. An interval of 30 seconds was maintained between consecutive flashes.

Two females were not responsive, and one female responded to all stimuli. Chi-square for the five remaining females is not significant (H_0 = no difference in responses to the two stimuli) at the 50 per cent level.

Continuous glow background: Both *collustrans* and *tanytoxus* were tested for the importance, in attracting males, of the steady illumination emitted by the female light organ beween flashes. The MF bulb housing was equipped with a small flashlight bulb and battery. The bulb was fastened in the chamber of the housing used in tape recording to contain the PT photocell probe for direct pickup of the MF flashes. The glow from the bulb was transmitted up the lucite rod and appeared as a faint flow upon which flashes of the MF bulb were superimposed. From 10–15 males of *tanytoxus* and two of *collustrans* were attracted to the decoy both with and without the continuous glow.

Male flash lengths: Females of *floridanus* and *collustrans* were tested for their ability to discriminate between flashes that differed only in duration. The procedure and notation used are described above.

Photinus floridanus, females — test number

No. 1. 71° .13 + + + + + − + +
Int 5 .35 − − − − − − − −
− + + (61)
− − − −

No. 2. 74° .16 + + + + + + + + + (62)
Int 20 .34 − − − − − −

No. 2. 68° .16 + + − − − − (63)
Int 20 .30 + + − + − −

No. 2. 67° .16 + − + + + + + + + (64)
Int 20 .27 − − − + − − − −

No. 2. 67° .20 + + − + + − + + +
Int 20 .34 − − − − − + −
+ − + + + (65)
+ − −

No. 3. 74° .16 + + − + + + − (66)
Int 20 .25 − − − + + − + −

No. 3. 68° .16 + + + + (67)
Int 20 .30 + + + + − +

No. 3. 68° .16 + + + + + +
Int 20 .34 − − − − − − + − + −
− − − (68)
−

(A period of no stimulation, two minutes in duration, separated tests 67 and 68.)

No. 3. 67° .16 + + + + + + (69)
Int 20 .34 − − − −

No. 3. 67° .16 + + + + + (70)
Int 20 .27 − − − − −

(A period of no stimulation, two minutes in duration, separated tests 69 and 70.)

No. 3. 67° .20 + + + + + − + +
Int 20 .34 − + − − − − −
− + − + − − (71)
− − −

No. 3. 69° .20 + + + + (72)
Int 5 .25 + + + +

No. 3.	69°	.25 + — — — —	(73)
	Int 5	.34 + — — — —	
No. 4.	74°	.16 + — + + + + +	(74)
	Int 20	.27 — — — — — — — —	
No. 4.	68°	.16 + + + + + +	(75)
	Int 20	.30 — — — —	
No. 4.	68°	.16 + + + + +	(76)
	Int 20	.20 — — — — —	
No. 5.	69°	.20 + + + + + + + + +	(77)
	Int 20	.25 — — — — + —	
No. 6.	65°	.16 + + + + + +	(78)
	Int 5	.34 + — — — —	
No. 7.	63°	.16 + + + — + — + — — + — — +	(79)
	Int 5	.34 + + — — + — —	
No. 8.	70°	(+) .20 .20 .20 .20 .19 .19 .19 .19 .19	
	Int 5	(—) .12 .13	
		.17	(80)
		.13 .13 .14 .15 .12	
No. 9.	75°	(+) .21 .11 .16 .10 — .10 (bimodal) .27	(81)
	Int 5	(—)	
No. 9.	75°	(+) .16 .14 .13 .13 .15 .14 .10	(82)
	Int 5	(—)	

These tests demonstrate the ability of some *floridanus* females to discriminate on the basis of pulse length. Chi-squares were significant (H_0 = no difference in responses to stimulus flashes of two different lengths) for most females (1, 5 per cent; 2, 2.5 per cent; 3, 2.5 per cent; 4, 1 per cent; 5, 10 per cent; 6, 25 per cent; 7, 50 per cent). Sometimes females failed to respond to the flash length appropriate for males of their species, and sometimes they responded to inappropriate flash lengths. Their ability to discriminate, in these tests, appeared less well developed than the abilities of females, of *marginellus* and *scintillans* as demonstrated in their tests. Test 63 is interesting because it suggests that long flashes are inhibitory: the females eventually stopped responding to all flash lengths. Female No. 3 did not discriminate in test 67, but she did on other tests. In test 72, female No. 3 did not discriminate between flashes that differed in length by 0.05 second, but in tests 76 and 77, she detected differences of 0.04 and 0.05 second. Female No. 7 (one test only, No. 79) did not respond selectively to pulse lengths differing by 0.18 second.

Photinus collustrans, female No. 1. 72° .35 + (83)

Int 5 .13 + – –

(Identical results were obtained in two more tests, Nos. 84 and 85. All were performed within a two-minute period.)

These tests demonstrate behavior found in females of many species. They frequently respond to one flash of inappropriate length but do not continue responding to such signals. This was noted above in the section describing observations on site-exchanged-*collustrans* females.

VII. *Photinus consanguineus–P. floridanus:* These two species, sympatric in northern Florida, were active during the same period each evening and were found in contiguous sites. Pulse length in male flash-patterns was similar, 0.16–0.18 second. The flash-pattern of *consanguineus* consists of two pulses at 0.5 second intervals, and that of *floridanus* is a single pulse. Females were tested for their ability to discriminate pulse number.

Single flashes were repeatedly presented to five females of *consanguineus* throughout tape-recording sessions with them. Not one of the more than 100 such stimuli presented was answered. A special test was administered to one *consanguineus* female. Pulses in the two-pulse stimuli were delivered at about 0.5-second intervals.

Photinus consanguineus, female No. 1 — test number

73°			
Int 5	Stimulus	Response	(86)
	o o	+	
	o o	+	
	o o	+	
	o	–	
	o	–	
	o	–	
2-minute break - - - - - - - - - - - - - - -			
	o o	+	
	o o	+	
	o	–	
	o	–	
	o o	+	
	o	–	
	o	–	
	o o	–	
	o o	–	
	o o	+	
	o o	+	
	o	–	
	o	–	

Note the failure of the female to respond immediately to the correct stimulus, after two inappropriate stimuli were presented.

A special test was administered to three females of *floridanus*. In the notation below (as above) the "X" axis represents the time base. Pulse interval in the stimulus pattern was about 0.5 second. Stimulus pulses are indicated by (o), and female responses by (+). Thus the notation o + o indicates the female answered after the first stimulus pulse, and before the second pulse was presented.

Photinus floridanus, females			test number
No. 2.	67°	o + o	(87)
	Int 5	o o	
		o o	
		o o	
No. 4.	67°	o + o	(88)
	Int 5	o + o	
		o + o	
		o o	
		o o	
		o o	
		o o	
No. 4.	73°	o + o	(89)
	Int 5	o o	
		o o	
		o o	
No. 4.	73°	o + o	(90)
	Int 5	o o	
		o o	
		o o	
No. 5.	67°	o + o	(91)
	Int 5	o o	
		o o	
		o o	
No. 5.	67°	o + o	(92)
	Int 5	o o	
		o o	
		o o	

(Tests 89 and 90, and 91 and 92 were separated by periods of two minutes duration.)

These tests demonstrate the ability of *floridanus* females to discriminate on the basis of pulse number; probably when another pulse occurs immediately after their response to one pulse, their flash response to the next pulse is inhibited. Additional tests, in which single pulse stimuli are presented after inhibition, are needed to determine the duration of this inhibition.

VIII. *Photinus umbratus–P. floridanus:* These two Florida species were active during the same period each evening in contiguous sites. Flash-patterns of both species are single flashes: in *umbratus* these were 0.3–0.4 second in duration, and in *floridanus* about 0.15 second at temperatures near 70°. Female delay time in *umbratus* was about 2.2 seconds, in *floridanus* about 0.3 second at 75°.

Six *floridanus* females were placed in an *umbratus* site in glass cages. They occasionally flashed in response to the flashes of *umbratus* males. None of the males circled or approached.

IX. *Photinus umbratus–P. collustrans:* These two species from Florida were active during the same period each evening. Contiguous sites were not found, but males of each species probably flew within communicating distance of the other. Flash-patterns of both species are single pulses of similar duration: in *umbratus* the flash was estimated at 0.3–0.4 second in duration at temperatures near 70°, and in *collustrans* at 0.25–0.35 second. Female delay in *umbratus* was about 2.2 seconds; in *collustrans,* 0.5–0.6 second near 75°.

One *collustrans* female was placed in an *umbratus* site. She repeatedly flashed in response to flashes of *umbratus* males. None approached her, although one circled and flashed again.

Two males, attracted to within one m of the flashlight when it was flashed to simulate female responses in duration and delay, stopped their approach, flashed one or two more times from the same position, and flew away when the flashlight was flashed at a delay of 0.3–0.4 second.

Flashlight response flashes with the *umbratus* delay were presented to *collustrans* males. By the end of the 2–4-second delay, *collustrans* males usually had flown 2–4 m beyond the flashlight.

These tests demonstrate the ability of *umbratus* males to discriminate on the basis of female time delay, and the manner in which the delay of *umbratus* females can prevent approaches of *collustrans* males. Presumably *collustrans* males also detect differences in female delay-time and respond accordingly; this was not tested, however. It is quite likely that a *collustrans* male will have emitted the second flash-pattern before an *umbratus* responds to the first.

X. *Photinus umbratus–P. tanytoxus:* These two species from Florida were not active during the same period each evening: *umbratus,* active during early evening, finished activity except for stragglers by the time *tanytoxus* activity began. Flash-patterns of both species are single flashes: in *umbratus,* 0.3–0.4 second; in *tanytoxus,* 0.5–0.6 second in duration near 70°.

Several *tanytoxus* females in glass cages were placed in an *umbratus* site. They did not begin to glow (a rough indication of responsiveness) until very late in the *umbratus* activity period. None flashed in response to the flashes of *umbratus* males until after they (females) had begun to glow, although they occasionally responded to flashlight flashes. After they began glowing, some flashed in response to occasional *umbratus* males that flashed near them. No response was noted in the males.

XI. *Photinus punctulatus–P. curtatus (marginellus):* The ranges of these two species overlap extensively in the midwest. Signals appear similar, although male flashes in *punctulatus* seem shorter than the 0.30 second noted for *marginellus* males.

Two females (brachypterous) of *punctulatus* from New Salem, Illinois, were placed in the *curtatus-marginellus* (female not brachypterous) site at Oneida, New York. Both attracted males immediately. The males were permitted to enter the cages, and upon physical contact with the females they crawled about on them. They did not attempt to copulate.

The failure of males in this site to copulate, or attempt to copulate, with brachypterous *punctulatus* females, or brachypterous *scintillans* females when two were placed in this site, suggests a tactile or chemical discrimination on the part of males. This may also function as an isolating mechanism.

XII. *Photinus tenuicinctus–P. granulatus:* The signals of these allopatric species are similar. Both have brachypterous females, but those of *tenuicinctus* are much larger, darker, and have a much more firm integument.

A female *granulatus* was placed in a *tenuicinctus* site in an open petri dish. She immediately attracted a male. He was removed from the dish and she attracted another. They copulated immediately upon contact.

XIII. *Photinus ardens–P. consimilis:* Localities of specimens in collections indicate that *ardens* and *consimilis* overlap in range. The signals of *ardens* and the fast-pulse *consimilis* are similar in several characteristics, including female response flash, pulse length of male flash, and pulse rate in male flash-pattern. A difference was noted in pulse number in male flash-pattern, 2–3 being found in *ardens* and 4–9 in *consimilis* (fast pulse). Several *ardens* females were presented with the flash-pattern of this *consimilis*. Although the females sometimes interrupted long signals (7–9 pulses) with their own flashes, they usually flashed only after the stimulus signals. Many of their responses appeared indistinguishable from those of the one *consimilis* female observed. Usually the female delay was shorter than that observed in the fast-pulse *consimilis* female.

A test was conducted on several *consimilis* males at Gainesville, Florida, to determine the importance of the female delay in attracting *consimilis* males. About one-half of the males tested were attracted to the three double pulses of *ardens* group females when they were emitted immediately following the male flash-pattern. Those males not attracted hovered and repeated their flash-pattern two or three more times, and then continued moving across the site. Another test was given to such nonattracted males. The flash-response described above was given to eight males. Four approached and landed on, or next to, the flashlight. The other four hovered and flashed. Following the first flash they emitted after they gained altitude (presumably in preparation for flying away) the response was given at a three-second delay. All four completed their approach and landed near the flashlight.

Unfortunately these males were not from the region of the range overlap of *ardens* and *consimilis*. *P. consimilis* males from the area of overlap (if the fast-pulse species is the *consimilis* complex member that does overlap *ardens*) might respond differently to this test. It is possible that slow-pulse *consimilis* is the one which overlaps *ardens,* and the timing of the flash-pattern of this species, as noted above, is quite different from that of *ardens*.

Conclusions

Differences in the flashed signals of various species of *Photinus* can prevent interspecific attraction. Signal exchanges between a male and female of different species may be *prevented* if the female fails to be stimulated to flash respond to the flash-pattern of the male. Signal exchanges between a male and female of different species may *terminate* after her first response (1) because her response does not stimulate the male to remain in the area and flash again, (2) because her response is flashed after a long delay and after he has left the area, or (3) because she stops answering his flashes. Females discriminate on the basis of pulse length, pulse interval, and pulse number, as demonstrated by their selective responses to various kinds of artificial flash-patterns. Males discriminate on the basis of response delay time, as demonstrated by their selective responses to artificial flash responses.

DISCUSSION

The most common signal in *Photinus* is the simple "flash-answer" (male: single flash—female: short delay, single flash) signal. This was found in ten species, and in at least two others the signals were only slight modifications of it. This flash signal is the least change from a glowing signal; in many respects it is the most efficient.

Evolutionary Origin of Flashed Signals

Observations on mating behavior in luminescent species of beetles in several different genera throughout the family Lampyridae and the closely related Phengodidae have firmly established the epigamic role of their luminescence. The simplest system of attraction is found in *Phengodes,* where continuously glowing females attract nonglowing males (Barber, 1906). A refinement of this system and its associated light organs is found in *Lampyris noctiluca* and *L. knulli.* In these species, females turn on their lanterns and attract males during certain hours of the evening (Schwalb, 1961; Lloyd, in press *a*). The glow system of *Phausis reticulata* (Say) contains elements of the *Phengodes* and *Lampyris* systems and of the system of *Photinus.* In *P. reticulata,* females turn on their lanterns in response to the glow of males, but for attraction it is not necessary for males to see light emission begin (Lloyd, 1965*a*). The essential element of the flash system is found in *reticulata;* this is the lighting response of females to the light of males. Involved is a subtle modification of the trigger mechanism for female light emission. In *L. noctiluca* the trigger is some low level of ambient light intensity; in *P. reticulata* the female is triggered by a glowing member of the opposite sex (perhaps also by some low level of ambient light intensity). A circadian rhythm probably underlies the trigger mechanisms in these species (Buck, 1937*a*). Three steps in the evolution of luminescent communication systems suggested by *Phengodes, Lampyris,* and *Phausis* are: (1) females glow continuously and expose themselves at night and attract males; (2) during certain hours of darkness females expose themselves, glow, and attract males; and (3) during certain hours of darkness females expose themselves and when they see glowing males they glow and attract them.

Selective pressures in the transition through these steps are conjectural. Possibly involved was the metabolic expense of glowing at times when mates could not possibly be attracted, such as during daylight hours. Also during the hours of darkness, and in crevices in the daytime, a continuous glow might have acted as a beacon for predators. Such predator pressure may have been quite important, for on numerous occasions during this investigation glowing fireflies were seen being stalked (?) and captured by Phalangida and lycosid spiders.

The transition from step 3 to the simple "flash-answer" signal must have been more difficult than it appears at first sight. Light organs capable of producing flashes are much more complex than those that produce mere intermittent glows. "In the flash . . . the control mechanism achieves its highest development, as indicated by its ability to bring about bursts of light of very quick accretion and decay, of short duration, and with complete extinction between even closely spaced flashes." (Buck, 1948; Smith, 1963). One source of selection pressure that seems rather unlikely concerns the physical limitation of visual signals. Since such signals are limited to line-of-sight transmission, the recipient of a flash signal must be "looking at" the sender. The more rapid the female glow response to the glow of a passing male, the greater the likelihood that he would see her and that she would be mated. It seems doubtful that any advantage gained in this respect could have resulted in selection pressure sufficient to reduce response time from two or three seconds, as in *P. reticulata,* to a delay as short as the 0.30 second one found in females of some *Photinus* species, and also to produce the necessary modifications of the light organ.

A more attractive hypothesis to account for the rigorous selection necessary to produce such changes stresses the context of reproductive isolation and the formation of species-specific signals. Selection may have been strongest to produce a rapid female response, that is, a short time delay, to contrast with a longer delay found in a sympatric species. The delay has been found to be significant in isolating species (McDermott, 1914; see above). Selection may have acted to produce a shorter male flash, one with a rapid intensity increment and a decay that (1) contrasted with a longer pulse found in a sympatric species, or (2) enabled males to emit very rapid pulses at short intervals, thus producing a broken signal that would contrast with a steady emission. Pulse length is undoubtedly a factor in the reproductive isolation of some existing species (see above). The broken or flickering nature of the flash of *Pyractomena dispersa* Green was found to be necessary to stimulate female responses (Lloyd, 1964*a*). Such a flash contrasts sharply with a steady emission of the same phrase length. In the *Pyractomena linearis* complex, two morphologically similar species have been found (Lloyd, in press *a*). Their habitat and season of activity are similar if not identical, and their ranges appear to overlap. One produces a steady emission one-half second in duration and the other a four- or five-pulsed phrase of about the same length. Also, the range of the *P. linearis* complex complements the range of *P. dispersa,* whose pulsed flash is at present indistinguishable from that of the pulsed *linearis.*

One additional signal should be mentioned because it suggests another possible stage in the evolution of the flash signal system. Kaufmann (1965) found that in the mating signals of *Luciola discollis* there is no definite exchange of flashes between the sexes as found in *Photinus, Photuris,* and *Pyractomena.* Females emit a characteristically pulsed flash signal to which males are attracted. As a flashing male nears, female flashing vigor increases; phrase rate increases but pulse rate remains constant. There is *not a critical* element in the signal involving a precise *timing interplay* of stimulus and response flashes. Both male and female flashes in a *discollis*-like signal are distinctly different from their counterparts in a glow system so that two-way recognition is possible. Such a step has the advantage of providing for the simultaneous selection of a flashing-type organ in both male and female.

Figure 27 indicates the possible main steps in the evolution of flash communication from glow communication.

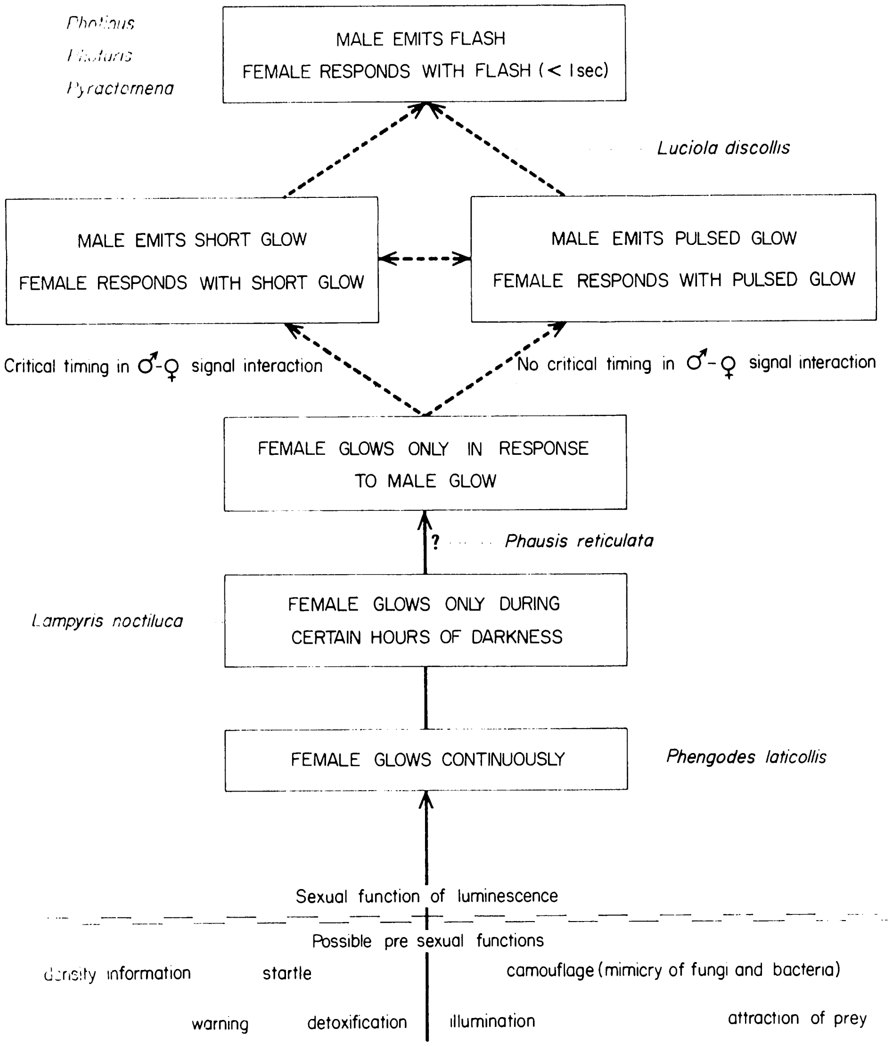


FIG. 27. Diagram of probable stages in the evolution of the *Photinus* flash-communication system.

Whatever may have been the nature of selection for the flashing light organ, the extremely short time delays now found in some *Photinus* probably represent physiological minima of the luminescent and nervous systems (Buck *et al.,* 1963; Case and Buck, 1963) and these are constantly being honed by selection as they function in reproductive isolation.

Efficiency In Flash Communication

Of the various flash signals found in *Photinus,* the flash-answer signal, under most circumstances, is the most efficient and economical. The message of males of all species in this genus, and probably other genera as well, is basically the same. It says "Here I am in time and space, a sexually mature male of species X that is ready to mate. Over." In the simple flash-answer signal, transmission is as simple and short as it can get. This signal uses the least amount of energy to complete the message. The amount of time each individual spends revealing his presence to predators is minimized. If a female can see part of the message she can see it all; the open space through which the male's advertisement reaches her will probably still exist between them to permit passage of her response. Flying males can repeat their one-pulse flash-patterns at short time intervals, thus increasing their chances of finding females without impairing signal clarity. Also, in dense aggregations of advertising males, there is less chance for confusion, and much less flash interference or "noise" than there would be with flash-patterns of several pulses or time delays of several seconds.

A situation in which the flash-answer signal is not the most efficient arises when two or more species with this signal, in identical form, are active in the same site at the same time. Under such circumstances selection should tend to intensify any differences in their biology which would increase the proportion of intraspecific matings and decrease the proportion of interspecific matings as has been pointed out by Brown and Wilson (1956) in their discussion of character displacement (Wilson, 1965). Inevitably, however, change in the flash signals which increases their efficiency in proper mate selection, but also results in signals that last for seconds rather than tenths of seconds, decreases their efficiency with respect to the characteristics listed above.

Even under the best circumstances, flash signals have one serious disadvantage: they are limited to line-of-sight transmission. Communicating individuals must (1) be "looking at" each other, and (2) be fairly close.

Adaptations that increase efficiency with respect to the first requirement are both morphological and behavioral. Males of most luminous species have large eyes, with numerous facets, that receive light from wide angles.

Female *Photinus* aim their light organs at stimulus flashes (Mast, 1912; see above). Females of *Pyractomena* have four-part light organs with a luminous area at the lateral edges of two postventral segments. While the beetle is clinging to blades of grass, luminous surfaces are exposed to either side. Females of all species studied expose themselves in open places during mating activity, and some climb up on vegetation. Males of many species fly erratic or meandering courses, and during flashes some perform aerial maneuvers such as the horizontal arcs in *collustrans* and *tanytoxus*, the dips in *pyralis* and *umbratus*, the rises in *macdermotti* and *consanguineus*, and the sudden stops in *brimleyi*. These probably function in increasing male chances of seeing female response flashes or female chances of seeing male flashes. They probably have little or no role as isolating mechanisms (see above). Males of two species of *Pyractomena* fly courses with regular, angularly displaced paths that enable them to scan large areas (Lloyd, in press *a*).

With respect to (2) immediately above, behavior that brings about and maintains aggregations of sexually mature adults increases efficiency. Habitat selection is one possible mechanism operating to promote aggregation. Fireflies of most species form dense breeding colonies that are spatially limited. Limited areas of activity narrow the distance over which sex attraction has to take place. Compact flight areas could result from male orientation during flight to specific ecological factors, such as high humidity in swampy areas. The *Photinus lineellus* colony observed in Gainesville deserves further attention in this regard. Collection dates of museum specimens indicate that the period of observation was not late in their season, yet few males were seen. Several females were collected. It was also noted that this species had been observed in abundance in the everglades. It is possible that while the early life stages of this species could develop in the roadside ditch, some important environmental cue for male orientation was absent, and during their early flights the males simply wandered away. In another case, over 50 females of *Photinus ignitus* were found on a lawn in central New York State. During three nights of observation only two males were seen. Again, absence of male orientation to the site of larval development could have been responsible. Neither males nor females have been found at this site in the three summers since. It has been noted that females seldom fly before mating. The occurrence of brachypterous or apterous firefly females in many species may indicate the ultimate in the fixation of habitat specificity. Of course the habitats involved in these cases must certainly be stable ones.

Other behavior that might function to produce and maintain breeding aggregations could employ luminescence. Kaufman (1965) found special flashes in males and females of *Luciola discollis,* an African species, that directed females ready to oviposit to sites of previously existing populations.

The extreme condition in the use of luminescence for aggregation may be represented by the synchronized flashing (chorusing?) observed in certain species of southeast Asia. Great numbers gather (?) in certain trees and flash in apparent synchrony (Buck, 1938). This behavior is so common that these trees, called firefly mangroves (*Sonneratia acida*), are preserved navigational aids (Watson, 1928).

By keeping reproductives in close proximity, not only is the efficiency of light communication increased, but the duration of the nightly mating period may be reduced, also reducing exposure to predation. The shortest daily period of mating activity yet found in a glowing firefly is that of *Lampyris knulli,* whose females glow for less than 30 minutes each evening (Lloyd, in press *a*), and the shortest period for flashing fireflies is in *Photinus collustrans,* which is active for less than 25 minutes.

Reproductive isolating mechanisms are usually divided into two groups; premating (prezygotic) and postmating (postzygotic) (Mayr, 1963; Wilson, 1965). In this investigation, study was confined to prezygotic mechanisms. These can involve differences in site or time of nuptial flight, as well as several different parameters of the signalling behavior proper. As in other animal groups, a given pair of firefly species is usually prevented from mating by more than just a single reproductive isolating mechanism, and often several mechanisms are present.

Habitat Isolation

Habitat differences are obviously important in separating breeding colonies spatially. At one location three species were found within a few meters of each other. *P. floridanus* was found just within a mesophytic woods, *P. consimilis* (fast pulse) was found in the lush grass and weeds along the edge of the woods at each side of a stream, and *P. collustrans* was active over the sward (formerly a xerophytic hammock), about three meters above the stream bank. At two other locations, demes of *ardens* were found in wet pastures, and demes of *ignitus* were in the fields across the separating highways. Near the airport at Gainesville, Florida, *tanytoxus* was active over a turkey-oak sandhill association, and a few meters down the road, at one or two m lower elevation and in a mesophytic woods, *floridanus* was active. Across the road from *floridanus,* less than five m away, was a deme of *umbratus.* At the other side of the woods, about 30 m from the *umbratus* site, was a deme of *macdermotti. Pyractomena angulata* males were frequently seen flying among the top branches of the trees in the same woods. Several other similar observations on habitat differences could be cited.

Because flash signals demand physical proximity, and because selection has favored behavior that limits the area of mating activity, the effect of habitat differences in reproductive isolation has probably been strengthened.

Another pertinent consideration is that the "noise" introduced to the signal channel by the presence of large numbers of individuals of another flashing species reduces the efficiency of the signal system, especially if the signals are at all similar in structure. It was noted above that large demes of *Photinus macdermotti* disappeared from two sites overnight when a species of *Photuris* with a similar pulse length became active in the sites. Behavior that minimizes this source of signal confusion by spatially isolating the demes will contribute to reproductive isolation. Once a species becomes established in a site, it may inhibit the colonization of the site by related species. Propagules (fertilized females) may be prevented from landing and ovipositing in an ecologically satisfactory site by the flash-patterns of resident males. Conversely, Kaufman (1965) found that in *Luciola discollis* females were attracted to sites occupied by their own species by special flashes of resident males. Inhibition could also be implemented by larval competition or predation. The swamping (e.g. signal channel saturation) of colonizers by residents is also a possibility.

On the other hand, the mobility of animals reduces the effectiveness of habitat differences. Museum collections are replete with firefly specimens taken at light traps. Such records from the Archbold Biological Station (Frost, 1964) include several specimens of *lineellus* and *consimilis*, yet I was unable to find demes of either in three visits to the station. In the extensive treatments of the genera *Photuris* (Barber, 1951), *Pyractomena* (Green, 1957), and *Photinus* (Green, 1956) records for numerous species were reported for Plumer's Island, Washington, D. C. This tiny island was a favored collecting site of Barber, who was particularly interested in fireflies. Over a number of years he found there individuals of many of the species of northeastern United States. Probably many of them were simply wandering across the island and did not come from demes situated on the island.

Temporal Isolation

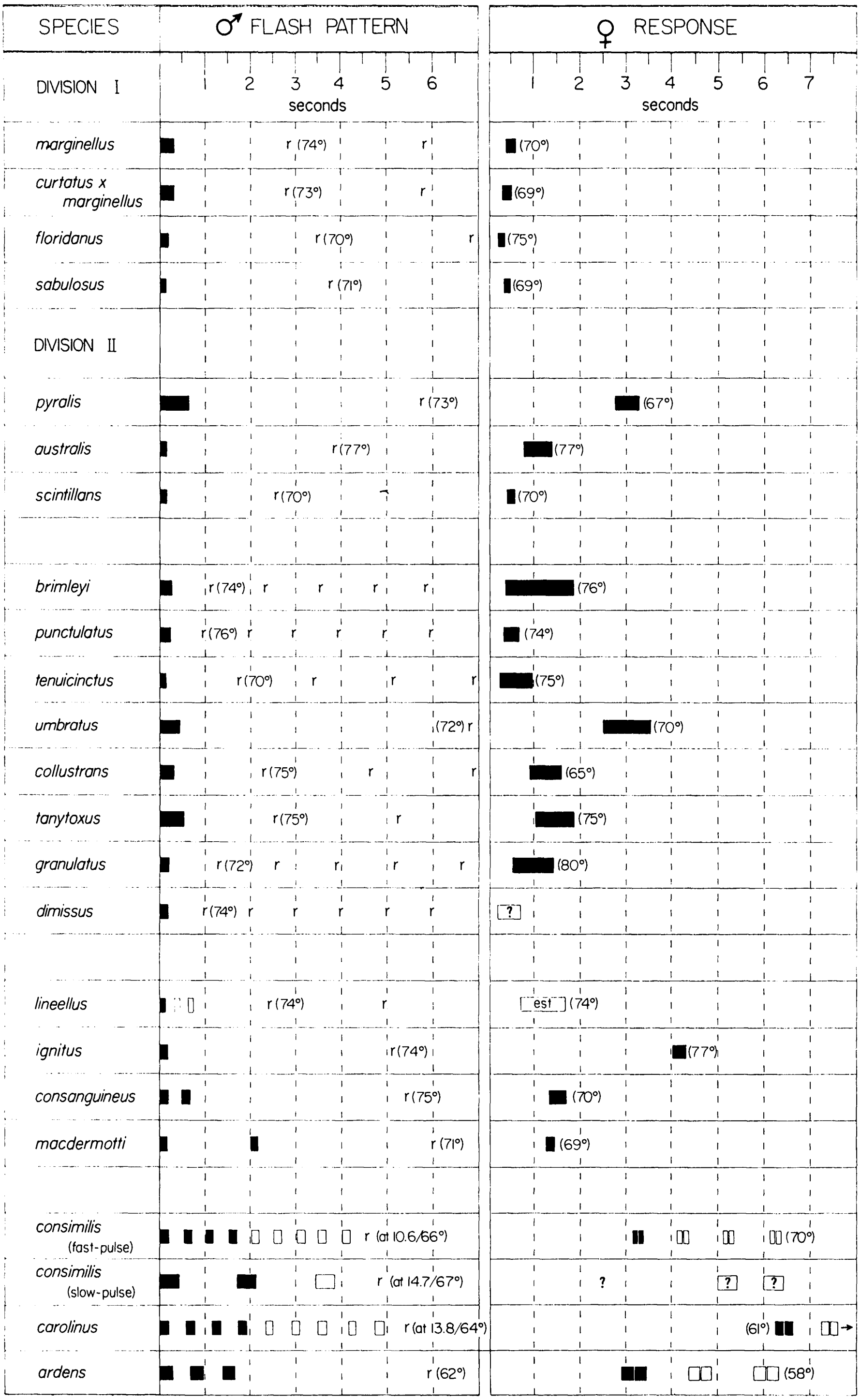
Temporal differences may isolate some species. But there is little information available on the period of seasonal activity, or time of peak activity. *Pyractomena borealis*, an upper story species (Lloyd, in press *a*), is active in Florida in the winter in the same sites that support demes of summer-breeding species. Its signal is the common flash-answer signal.

Differences in time of evening activity seem nearly to eliminate interactions between the siblings *tanytoxus* and *collustrans,* but their signals still have the potential to isolate them when the temporal mechanism fails. The evening period of activity of *ignitus* is later than that of most other sympatric species of *Photinus,* and this considerably reduces the number of flash contacts with them. *P. ignitus* also has a unique signal.

Ethological Mechanisms

Isolation of this sort is based on the production and reception of stimuli by the sex partners. Without doubt this is the most important group of isolating mechanisms operating in *Photinus.* Signal differences were found between nearly all species of *Photinus* examined. As noted above even in the cases of species that are isolated by other mechanisms, at least one signal difference was usually found. The parameters tested did not exhaust the potentialities of the flash system and experiments were not performed on such obvious variables as flash-pattern repetition rate, flash color, or female pulse length. The parameters tested were suggested by certain species pairs. No pair was found that prompted tests on female pulse length; in fact, in most species studied female pulse length was extremely variable, while female delay was highly constant within species but showed much variation among species. It is frequently possible to predict the significant communicative elements of signals on the basis of variability alone. However, some variable elements in signals may still be significant information-carrying parameters. For example, the pulse interval in the male flash-patterns of *consanguineus* and *macdermotti* is important in species recognition but there is variability in the acceptance ranges of females of both species (see above). These pulse ranges in the two species are mutually exclusive, and each is variable enough to permit signalling between a flying male in the open air, and an inactive female of his species, in spite of their body temperature (and thus signal) differences.

In addition to observations and experiments on site-exchanged females, other evidence indicates the importance of species-specific signals. Comparing signal structure with the number of sympatric species we note the following: *pyralis* has a unique signal (with the possible exception of *umbratus*) and, based on present distribution maps, its range overlaps those of all other *Photinus* with the exception of *knulli* (Mexican species, Nogales, Arizona). The signals in the *consimilis* complex are different from those of all other species but *carolinus;* these species are sympatric with all but 5 *Photinus* species. The signals of the *consanguineus* complex are unique, and so is that of *australis;* they overlap all but 7 and 8 *Photinus* species, respec-


SPECIES
♂ FLASH PATTERN
♀ RESPONSE
seconds
seconds
DIVISION I
marginellus
r (74°)
r
(70°)
curtatus x marginellus
r (73°)
r
(69°)
floridanus
r (70°)
r
(75°)
sabulosus
r (71°)
(69°)
DIVISION II
pyralis
r (73°)
(67°)
australis
r (77°)
(77°)
scintillans
r (70°)
(70°)
brimleyi
r (74°) r r r r
(76°)
punctulatus
r (76°) r r r r r
(74°)
tenuicinctus
r (70°) r r r
(75°)
umbratus
(72°) r
(70°)
collustrans
r (75°) r r
(65°)
tanytoxus
r (75°) r
(75°)
granulatus
r (72°) r r r r
(80°)
dimissus
r (74°) r r r r r
?
lineellus
r (74°) r
est (74°)
ignitus
r (74°)
(77°)
consanguineus
r (75°)
(70°)
macdermotti
r (71°)
(69°)
consimilis (fast-pulse)
r (at 10.6/66°)
(70°)
consimilis (slow-pulse)
r (at 14.7/67°)
? ? ?
carolinus
r (at 13.8/64°)
(61°)
ardens
r (62°)
(58°)

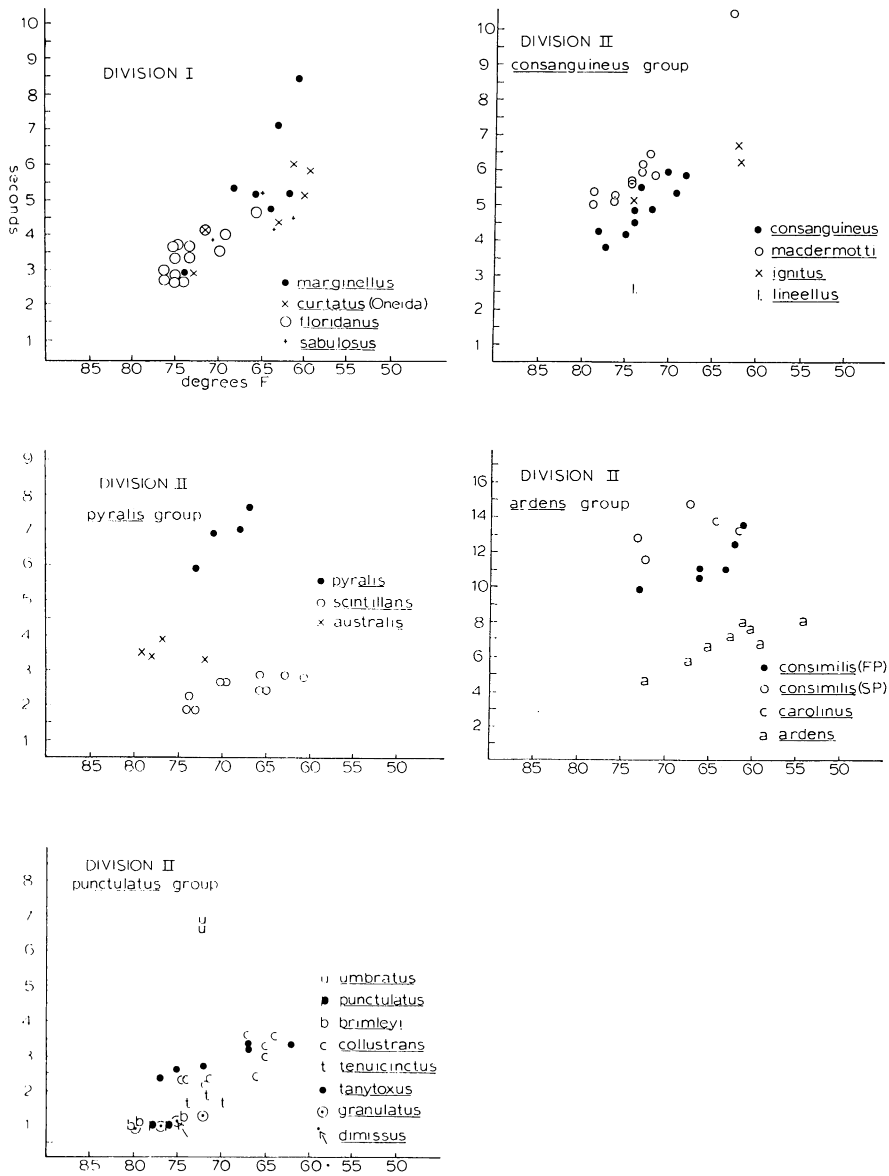


Fig. 29. Relationship of flash-pattern interval to air temperature

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Fig. 28. Flash patterns and female response flashes in *Photinus*. Time zero for female response is beginning of last pulse of male flash-pattern. Flash-pattern interval is indicated by (r). Flash-patterns are given only once; when several pulses are shown they are all part of one flash-pattern. Variable pulse numbers flash-patterns are indicated by open (versus solid) pulses.

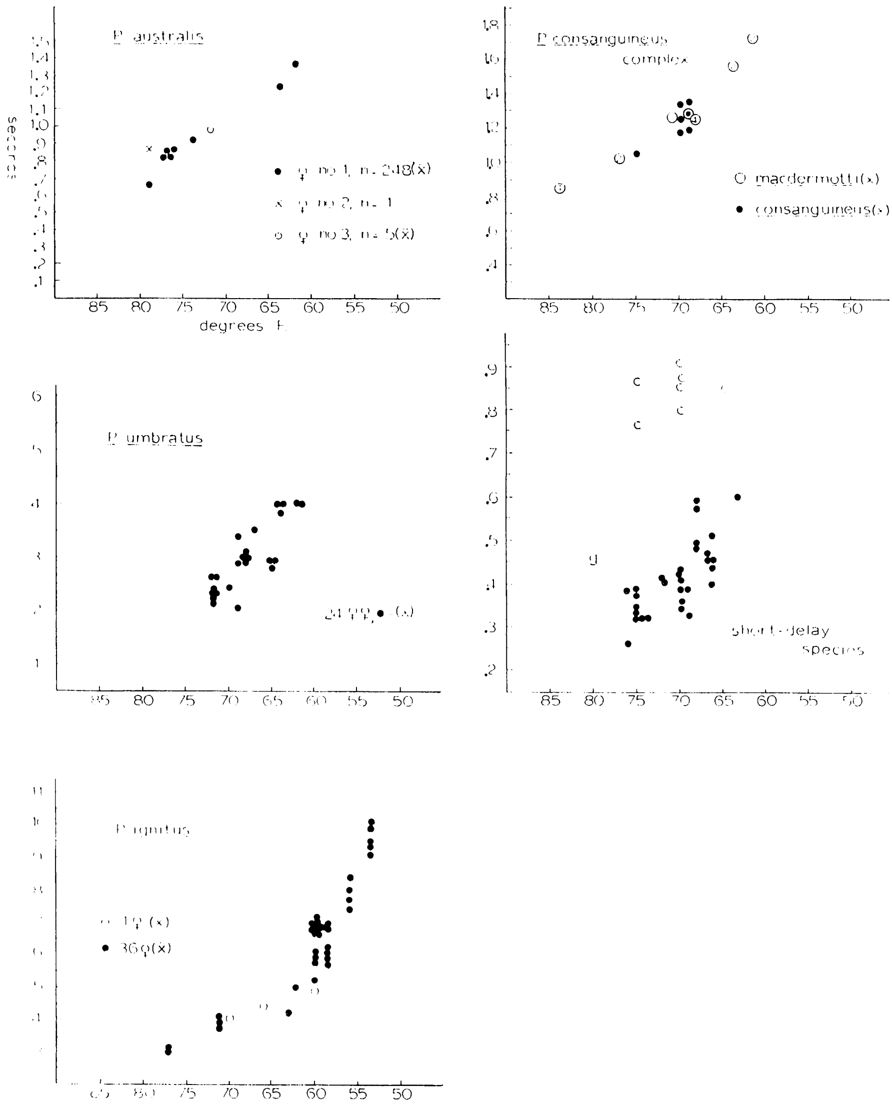

FIG. 30. Relationship of female response delay to air temperature. Numbers in circles are female identification numbers. In graph at center right (c) = *collustrans* and (g) = *granulatus*; spots indicate females of all other short-delay species recorded (see Tables).

tively. Of all luminous species pairs, about 50 per cent are allopatric. Of 36 possible pairs that display a simple flash-answer signal, 27 (75 per cent) are geographically isolated, and this does not take into consideration pulse-length differences known to be significant. The two nonluminous species, *cooki* and *indictus,* are geographically isolated from only 19 per cent of all others.

Division I species of *Photinus* illustrate strikingly the essential allopatry of species with similar signals. The four described species studied all have the simple flash-answer signal. One species in the division is nonluminous. *P. floridanus* is geographically isolated from all other luminous species of the division. *P. texanus* is separated from all but *immaculatus,* a very rare species known only from the type locality. The range given for *marginellus* overlaps that of *curtatus,* but these interbreed and probably are one species (Lloyd, in press *b*). *P. marginellus* is sympatric with *sabulosus;* signal differences have been found between them (pulse length). The locality of the single male record of *acuminatus* is within the range of *marginellus.* No *acuminatus* could be found in the type site; a *marginellus* deme was found there instead. The range of the nonluminous species, *cooki,* overlaps the ranges of all other Division I species. Assuming that all luminous species of Division I have (or had) the simple flash-answer signal, these comparisons indicate a strong selection pressure acting against similar signals in sympatric species, and perhaps point to pressure that resulted in the loss of luminescence in *cooki.*

Another peculiarity noted in the distributions of species in this division is that both *sabulosus* and *marginellus* appear to have disjunct ranges, with an isolated group of records from southern Mississippi. While this may be a collecting artifact, it is interesting that *brimleyi,* an abundant species with similar ecology and flash signal, occupies at least a portion of the area separating these populations from the major portion of their ranges.

The concordance of flash-signal pattern with morphology in some groups of *Photinus* has already been noted (see above). Alexander (1962), discussing the structure of cricket signals, pointed out that it is the significant communicative (information-carrying) element in a particular signal that will change as species multiply. Flash-patterns of the *consanguineus* group illustrate this (Fig. 28). Pulse interval is the significant element in stimulating females of *consanguineus* and *macdermotti.* The pulse intervals are different in these two species and also in the related *lineellus.* The flashes of *lineellus* also differ from those of the other two in pulse number, however, pulse number in *lineellus* is variable, which further indicates the significance of pulse interval. Another species in this group, *ignitus,* has a single pulse flash-pattern with an extremely long female delay. The fact that such a long time is needed for a complete signal exchange between sex partners suggests that this single-pulsed signal may have evolved from a multipulsed signal.

Flash-patterns in the *ardens* group are multipulsed. In fast-pulse *consimilis* and *carolinus* they are indistinguishable and consist of 4–9 rapid pulses. In slow-pulse *consimilis* and *ardens* they consist of 2–3 pulses (Fig. 28). The variable number of pulses in the signals of all species may indicate that pulse interval (pulse rate) rather than pulse number is significant. However, both pulse interval and length of flash-pattern may be important in the signals. Alexander suggested that in the signals of some crickets the minimal signal length that could carry "both the pulse rate and . . . [pulse group] length" was the significant unit.

In this discussion the origin and evolution of the signals of *Photinus* groups have been considered on a single time transect. We can only guess at the firefly species that must have interacted through the ages, at the multiplicity of environments that may have helped to shape their behavior, and at the complexities and constraints of the neurological mechanisms that directed that behavior. The simple signals we read today are products of an infinitely complicated and kaleidoscopic history.

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Tobu hotaru are to iwan no hitori kana

A firefly flitted by:
"Look!" I almost said, —
But I was alone

Taigi (In: Blythe, 1952)

TABLE 1

FLASH-PATTERN INTERVALS—*Photinus* DIVISION I

Species	Locality	Temp. (° F.)	N	Mean (Sec.)	Range (Sec.)	s.d.
marginellus	Gatlinburg	66	9	5.2	3.0	.99
	Gatlinburg	62	1	5.2	—	—
	Gatlinburg	63	4	7.1	1.5	.67
	Lake Lure	68	2	5.3	1.0	—
	Branchville	61	1	8.4	—	—
	Branchville	64	5	4.7	1.2	.53
curtatus	Oneida	59	10	5.8	1.5	.56
	Oneida	60	11	5.1	2.7	.97
	Oneida	62	26	6.0	3.9	1.2
	Oneida	63	8	4.3	2.4	.90
	Oneida	72	13	4.1	4.1	1.2
	Oneida	73	11	2.9	1.7	.65
floridanus	Gainesville	66	6	4.6	1.4	.49
	Gainesville	69	15	4.0	2.7	.84
	Gainesville	70	12	3.5	1.0	.29
	Gainesville	72	6	4.1	1.1	.37
	Gainesville	73	9	2.6	1.2	.41
	Gainesville	73	6	3.7	0.7	.29
	Gainesville	73	6	3.3	1.8	.76
	Gainesville	75	16	2.8	1.7	.40
	Gainesville	75	15	2.8	1.6	.62
	Gainesville	75	20	3.6	2.5	.89
	Gainesville	75	3	2.6	0.7	.39
	Gainesville	75	8	3.3	1.2	.41
	Gainesville	76	7	2.7	0.8	.27
	Gainesville	77	14	3.0	2.0	.56
sabulosus	Ithaca	62	5	4.5	1.2	.52
	Ithaca	63	3	4.1	1.0	.52
	Ithaca	65	22	5.2	3.1	.86
	Ithaca	71	12	3.8	2.0	.61

TABLE 2

FLASH-PATTERN INTERVALS—*Photinus* DIVISION II

Sp.cies	Locality	Temp. (° F)	N	Mean (Sec.)	Range (Sec.)	s.d.
pyralis	Lake Lure	68	3	7.0	1.2	.65
	Lake Lure	67	5	7.6	1.5	.62
	Fife	69	3	7.1	.5	.25
	Fayetteville	73	10	5.9	2.2	.62
australis	Red Hills	72	7	3.3	1.3	.50
	Torreya	77	17	3.9	2.3	.66
	Torreya	78	21	3.4	2.7	.71
	Torreya	79	13	3.5	1.6	.60
scintillans	Silver Springs	60	11	3.1	2.4	.71
	Branchville	61	5	2.4	1.4	.52
	Branchville	61	5	2.8	1.6	.61
	Branchville	63	13	2.9	1.8	.49
	Silver Springs	66	39	2.9	2.8	.71
	Silver Springs	70	13	2.6	1.8	.50
	Silver Springs	70	11	2.6	2.6	.79
	Branchville	73	10	1.8	1.0	.28
	Silver Springs	74	11	2.2	1.2	.42
brimleyi	Idabel	74	13	1.2	0.4	.14
	Crailhope	79	5	1.1	0.3	.14
	Crailhope	80	12	1.0	0.6	.18
punctulatus	New Salem	76	10	1.0	0.5	.15
	New Salem	78	7	1.0	0.1	.04
tenuicinctus	Fayetteville	74	12	1.7	0.4	.12
	Fayetteville	70	15	1.7	0.8	.23
	Fayetteville	72	11	1.9	0.4	.16
umbratus	Gainesville	72	10	6.7	2.3	.76
	Gainesville	72	5	6.8	1.6	.72
collustrans	Gainesville	64	9	3.6	1.2	.55
	Gainesville	65	11	3.3	2.0	.66
	Gainesville	65	7	3.0	0.8	.31
	Gainesville	66	6	2.4	0.8	.31
	Gainesville	67	2	3.6	1.2	.47
	Gainesville	71	3	2.3	0.2	.10
	Gainesville	72	10	2.2	0.6	.21
	Gainesville	74	11	2.3	1.1	.39
	Gainesville	75	14	2.3	1.0	.51
tanytoxus	Gainesville	62	14	3.3	1.5	.42
	Gainesville	67	10	3.2	1.4	.42
	Gainesville	67	30	3.3	1.8	.58
	Gainesville	72	18	2.7	1.7	.47
	Gainesville	75	16	2.6	1.1	.40
	3.7 miles west of Gainesville	77	11	2.4	1.2	.40
granulatus	Wichita	72	12	1.3	0.4	.12
	Wellington	75	9	1.1	0.4	.14

TABLE 2 (Continued)

Species	Locality	Temp. (° F)	N	Mean (Sec.)	Range (Sec.)	s.d.
	Wichita	77	14	0.9	0.6	.15
	Wellington	80	18	0.9	0.1	.05
ignitus	Fife	62	2	5.5	1.0	.71
	Wampsville	74	14	5.1	2.6	.72
	Wampsville	62	10	6.7	1.4	.41
consanguineus	Fife	69	4	5.3	0.6	.28
	Gainesville	68	10	5.8	2.8	1.01
	Gainesville	70	12	5.9	1.9	.51
	Gainesville	72	8	4.9	1.5	.49
	Gainesville	73	12	5.5	1.8	.61
	Gainesville	74	10	4.8	2.0	.89
	Gainesville	74	4	4.5	1.4	.62
	Gainesvlile	75	3	4.1	0.2	.12
	Gainesville	77	8	3.8	0.6	.19
	Gainesville	78	6	4.2	1.8	.62
	Gainesville	78	10	4.2	1.6	.68
macdermotti	Mt. Pisgah	62	5	10.4	2.6	1.0
	Gainesville	71	5	5.8	0.7	.25
	Gainesville	72	9	6.4	1.4	.60
	Gainesville	73	5	5.9	0.9	.33
	Gainesville	73	3	6.1	0.2	.12
	Gainesville	74	5	5.7	1.0	.45
	Gainesville	74	7	5.6	1.0	.36
	Gainesville	76	5	5.1	0.7	.31
	Gainesville	76	1	5.2	—	—
	Gainesville	78	1	5.3	—	—
	Gainesville	78	1	5.0	—	—
consimilis	Gainesville	61	3	13.4	1.0	.58
(Fast Pulse)	Gainesville	62	7	12.3	3.0	1.30
	Gainesville	63	7	10.9	3.0	1.00
	Gainesville	66	10	10.6	3.8	1.10
	Gainesville	66	1	11.0	3.9	—
	Gainesville	73	4	9.8	1.4	.66
consimilis	Gainesville	67	1	14.7	—	—
(Slow Pulse)	Gainesville	72	2	11.5	1.0	—
	Gainesville	73	3	12.4	1.06	—
carolinus	Gatlinburg	61	1	13.2	—	—
	Gatlinburg	64	5	13.8	3.0	1.2
ardens	Oneida	54	3	7.9	1.5	.75
	Oneida	59	13	6.6	1.8	.67
	Oneida	60	6	7.4	2.5	.83
	Oneida	61	9	7.8	4.2	1.20
	Oneida	62	15	7.0	2.9	.88
	Oneida	65	11	6.4	4.2	1.2
	Oneida	67	7	5.6	2.7	.95
	Oneida	72	6	4.4	1.2	.48

TABLE 3

FEMALE RESPONSE FLASH LENGTHS—*Photinus* DIVISION I

Species	Locality	Female No.	Temp. (° F)	Mean (Sec.)	Recorded Values (Sec.)
marginellus	Gatlinburg	1	63	.31	.35 .36 .28 .28 .28
	Gatlinburg	2	67	.21	.17 .17 .27 .22 .23 .22 .20
	Branchville	3	70	.21	.22 .19 .21 .20
	Branchville	4	70	.34	.34
	Branchville	5	70	.46	.46
	Ithaca	6	66	.34	.34 .32 .36
	Ithaca	7	66	.37	.37
	Ithaca	8	66	.20	.20
curtatus	Oneida	1	69	.19	.14 .15 .23 .27 .14 .16 .15 .24 .20 .19 .19 .22 .21 .18 .17
	Oneida	2	76	.29	.26 .21 .28 .25 .27 .32 .38 .36 .double pulses = .65 .54 .50
floridanus	Gainesville	1	75	.15	.15 .12 .16 .17 .17
	Gianesville	2	70	.18	.18 .18 .16 .16 .18 .17 .17 .16 .22 .20 .20 .22 .22 .20 .13 .17
	Gainesville	3	70	.18	.18 .14 .15 .16 .19 .26
	Gainesville	4	68	.27	.32 .28 .27 .23
	Gainesville	5	68	.25	.26 .23 .23 .27
	Gainesville	6	68	.18	.18
sabulosus	Ithaca	1	69	.15	.12 .10 .14 .10 .24 .17
	Ithaca	2	66	.24	.24

TABLE 4

FEMALE RESPONSE FLASH LENGTHS—*Photinus* DIVISION II

Species	Locality	Female No.	Temp. (° F)	Mean (sec.)	Recorded Values (sec.)
pyralis	Lake Lure	1	67	.54	.79 .78 .51 .42 .40 .50 .51 .49 .48 .68 .41 .52
	Lake Lure	2	67	.67	.68 .67 .61 .73
australis	Torreya	1	62	1.16	1.17 .80 .72 .76 1.11 1.21 1.18 1.06 1.00 1.07 1.20 1.27 1.09 1.19 1.30 1.15 1.40
					1.28 1.55 1.29 1.20 1.35 1.28 1.32 1.12 1.25 1.00 1.41 .92 1.08 1.21 1.23 1.21 1.11
					1.15 1.11 1.12 1.18 1.23 1.08 1.09 1.11 1.15
	Torreya	1	74	.54	.45 .33 .54 .53 .47 .53 .54 .67 .75 .74 .72 .69 .43 .73 .65 .68 .71
					.50 .57 .52 .65 .40 .65 .52 .57 .61 .31 .50 .34 .37 .84 .71 .62 .40
					.53 .88 .68 .61 .65 .46 .47 .39 .48 .71 .61 .42 .48 .48 .58 .88 .78
					.80 .74 .77 .55 .62 .57 .55 .73 .64 .74 .67 .62 .57 .44 .40 .74 .64
	Torreya	1	75	.58	.67 .69 .72 .59 .60 .42 .35
	Torreya	1	76	.52	.56 .56 .49 .51 .50 .74 .55 .60 .43 .33 .40
	Torreya	1	77	.62	.52 .53 .44 .52 .74 .66 .76 .41 .26 .31 .22 .61 .67 .78 .27 .39 .29
					.45 .42 .29 .24 .26 .54 .72 .71 .62 .67 .39 .29 .34 .31 .47 .65 .63
					.72 .76 .95 .86 .86 .83 .76 .84 .83 .77 .68 .70 .82 .82 .92 .77 .80
					.70 .77 .74 .89 .69 .61 .57 .65 .58 .46 .55 .66 .56 .56 .54 .87 .77
					.64 .60 .69 .67 .66 .60 .69 .62 .52 .47 .56 .65 .55 .74 .62 .59 .59
					.77 .64 .47 .57 .64 .68 .74 .73 .73 .80 .78 .86 .73 .56 .62 .56 .56
					.61 .62 .60 .53 .76 .76 .48 .62 .62 .60 .52 .66 .69 .84 .76 .68 .65
					.67 .72 .65 .54 .52
scintillans	New Brunswick	1	69	.30	.31 .28
	Silver Springs	2	72	.16	.13 .16 .16 .17 .16 .15 .14 .16 .18
	Silver Springs	3	70	.19	.18 .16 .15 .14 .25 .18 .16 .28
	Silver Springs	2	70	.18	.23 .17 .19 .19 .18 .20 .16 .15 .19 .18 .18 .18 .18 .18 .18 .20 .18
					.20 .19 .20 .16 .17 .19 .19 .18 .19 .19 .17
brimleyi	Idabel	1	75	2.08	.68 .56 2.75 3.35 3.00
	Idabel	1	76	1.52	2.25 1.69 1.74 1.50 1.35 1.79 1.30 1.62 1.48 2.40 .75 .32
punctulatus	New Salem	1	74	.36	.41 .53 .66 .44 .32 .39 .27 .27 .24 .24 .26 .35 .42 .35 .41 .40 .29
					.24
	New Salem	2	74	.24	.36 .28 .24 .19 .16 .20 .18 .18 .16 .21 .20 .17 .21 .13 .20 .22 .28
					.27 .21 .26 .27 .26 .29 .26 .23 .22 .25 .25 .25 .27 .32 .29 .30 .27
					.23 .24 .26 .28 .27
	New Salem	3	74	.30	.28 .31
	New Salem	4	74	.42	.42
tenuicinctus	Fayetteville	1	75	.82	.66 .68 1.16 .68 1.12 .66 .88 .73 1.06 1.07 .71 .67 .62 .76
collustrans	Gainesville	1	65	.68	.83 .88 .77 .62 .31 .48 .90
	Gainesville	2	75	.66	.48 .85
	Gainesville	3	75	.56	.56

(Continued)

Species	Locality	Female No.	Temp. (° F)	Mean (sec.)	Recorded Values (sec.)
tanytoxus	Gainesville	1	75	.83	.89 .72 .84 .76 1.13 .73 .76
	Gainesville	2	75	.87	.96 .78
	Gainesville	3	75	1.15	1.15
	Gainesville	4	75	.82	.95 .91 .98 .86 .86 1.12 .60 .84 1.12 .73 .88 .48 .72 .46 .75 .75 .99
	Gainesville	5	75	.76	.88 .75 .65
	Gainesville	6	75	.62	.62
	Gainesville	7	74	.93	1.12 .86 .73
	Gainesville	7	76	.94	.68 .85 .83 .82 1.03 .94 1.41
	Gainesville	8	76	.86	.76 .96
	Gainesville	9	76	1.47	1.13 .88 2.41
	Gainesville	10	76	1.15	1.23 1.21 1.19 .88 1.23
granulatus	Wellington	1	80	.95	1.34 .92 .61 .52 .56 .92 .99 .49 1.14 .91 .76 .96 .91 1.60 1.35 1.33 .81
					.91 1.01
ignitus	Oneida	22	77	.24	.26 .22 .23 .24 .20 .23 .33 .29 .20 .25 .25 .18
consanguineus	Fife	1	69	.32	.49 .43 .34 .14 .44 .36 .22 .35 .34 .22 .14 .32 .22 .30 .20 .20 .19
					.19 .36
	Fife	2	69	.27	.25 .34 .30 .19
	Gainesville	3	75	.17	.18 .20 .13 .11 .20
	Gainesville	3	70	.25	.22 .26 .27 .28 .24
	Gainesville	3	69	.26	.20 .32 .28 .30 .28 .24 .23
	Gainesville	4	70	.49	.53 .58 .52 .61 .60 .63 .58 1.03 .46 .42 .52 .42 .60 .65 .52 .31 .26
					.26 .27 .22 .28
	Gainesville	5	70	.38	.52 .64 .32 .25 .32 .26 .35 .36 .39 .41 .39 .33
macdermotti	Gainesville	1	69	.20	.28 .30 .28 .26 .27 .26 .24 .27 .28 .21 .18 .22 .22 .20 .21 .22 .20
					.19 .23 .15 .16 .17 .18 .25 .19 .19 .22 .22 .20 .20 .17 .15 .20 .20
					.18 .20 .18 .19 .18 .18 .18 .18 .19 .18 .19 .17 .17 .18 .23 .19 .19
					.18 .18 .19 .19 .19 .19 .19 .16 .28 .30 .28 .26 .27 .26 .24 .27 .28
					.21 .18 .22 .22 .20 .21 .22 .20 .19 .23 .15 .16 .17 .18 .25 .19 .19
					.22 .22 .20 .20 .20 .17 .15 .20 .20 .18 .18 .19 .18 .18 .18 .18 .19
					.18 .19 .17 .17 .18 .23 .19 .19 .18 .18 .19 .19 .19 .19 .19 .16
	Mt. Pisgah	2	77	.45	.64 .72 .61 .48 .41 .36 .51 .52 .57 .60 .49 .35 .49 .31 .36 .51 .33
					.36 .25 .34 .52 .47 .31 .33 .31
	Mt. Pisgah	2	62	.44	.49 .51 .52 .30 .54 .31 .40 .45 .50 .25 .25 .38 .57 .39 .47 .46
	Gainesville	3	71	.17	.17 .24 .20 .22 .17 .25 .20 .15 .16 .14 .28 .17 .17 .14 .16 .13
	Gainesville	4	71	.16	.09 .36 .14 .14 .15 .12 .13 .
	Gainesville	4	68	.27	.27 .22 .26 .23 .23 .20 .22 .19 .24 .23 .30 .30 .30 .27 .32 .31 .34
					.34 .32 .32 .32 .32 .31 .30 .28 .33 .30 .27 .23 .20 .26 .25 .26 .26
					.24

TABLE 5

FEMALE RESPONSE DELAY TIME—*Photinus* DIVISION I

Species	Locality	Temp. (° F)	Female No.	Mean (Sec)	Recorded Values (Sec)
marginellus	Gatlinburg	63	1	.60	.57 .62 .62 .60 .60
	Gatlinburg	67	2	.45	.39 .44 .44 .47 .43 .48 .47
	Branchville	70	3	.38	.39 .37 .38 .37
	Branchville	70	4	.35	.35
	Branchville	70	5	.34	.34
	Branchville	66	6	.43	.41 .49 .38
	Branchville	66	7	.51	.51
	Branchville	66	8	.40	.40
curtatus	Oneida	69	1	.32	.31 .32 .37 .35 .30 .29 .27 .32 .30 .31 .36 .37 .32 .34 .32 double pulse = .40
	Oneida	76	2	.26	.27 .24 .25 .26 .26 .28 .26 .25 .25 .26
floridanus	Gainesville	75	1	.31	.35 .33 .32 .31 .31 .30 .30 .31 .32 .31 .31 .26 .32
	Gainesville	70	2	.36	.33 .34 .37 .34 .36 .36 .36 .38 .35 .36 .36 .36 .37 .36 .36 .39
	Gainesville	70	3	.41	.42 .40 .40 .39 .38
	Gainesville	68	4	.48	.46 .50
	Gainesville	68	5	.59	.58 .54 .68 .56
	Gainesville	68	6	.57	.60 .53 .62 .55 .58 .53
sabulosus	Ithaca	69	1	.38	.38 .39 .39 .35 .37
	Ithaca	66	2	.46	.46

TABLE 6

Female Response Delay Time—*Photinus* Division II

Species	Locality	Temp. (° F)	Female No.	Mean (Sec.)	Recorded Values (Sec.)
pyralis	Lake Lure	67	1	2.80	2.78 2.80 2.91 2.94 2.72 2.78 2.68
	Lake Lure	67	2	3.00	3.02 3.01 3.00 3.05 3.01 2.96 3.01
	Slovan	67	3	3.1	2.8 2.8 3.4 (stopwatch)
	Slovan	67	4	3.2	3.2 3.2 (stopwatch
	Slovan	67	5	3.4	3.4 3.4 (stopwatch
	Slovan	67	6	2.9	2.8 3.0 3.0 (stopwatch
	Slovan	67	7	3.5	3.6 3.6 3.5 (stopwatch
australis	Torreya	77	1	.84	.86 .85 .82 .84 .84 .85 .82 .84 .84 .86 .83 .85 .83 .84 .82 .81 .83
					.81 .83 .84 .82 .82 .81 .84 .86 .81 .83 .81 .86 .84 .81 .82 .82 .80
					.87 .87 .87 .87 .83 .85 .84
	Torreya	64	1	1.23	1.28 1.30 1.23 1.27 1.28 1.28 1.27 1.27 1.19 1.24 1.22 1.22 1.17 1.23 1.23 1.20 1.27
					1.17 1.12 1.16 1.22 1.17 1.29 1.21 1.22 1.26 1.24 1.21 1.21 1.29 1.22
	Torreya	62	1	1.37	1.44 1.37 1.40 1.35 1.40 1.34 1.34 1.34 1.34 1.33 1.35 1.35 1.40 1.33 1.30 1.35 1.38
					1.37 1.40 1.39 1.32 1.33 1.33 1.38 1.34 1.30 1.38 1.34 1.33 1.30 1.35 1.30 1.41 1.40
					1.36 1.35 1.32 1.28
	Torreya	76	1	.87	.89 .90 .90 .87 .85 .86 .85 .86 .88 .87 .88
	Torreya	74	1	.91	.87 .93 .92 .91 .89 .95 .90 .91 .92 .90
	Torreya	77	1	.82	.85 .89 .86 .81 .80 .82 .80 .81 .79 .81 .75 .79 .83 .81 .81 .82 .85
					.81 .79 .85 .78 .80 .85 .85 .84 .82 .82 .86
	Torreya	79	1		.7 (stopwatch)
	Torreya	79	2		.9 (stopwatch)
	Torreya	72	3	1.0	1.0 (stopwatch)
	Torreya	77	1	.82	.83 .82 .74 .82 .75 .89 .81 .79 .75 .74 .74 .77 .77 .73 .78 .78 .77
					.78 .80 .77 .81 .84 .73 .77 .79 .77 .79 .75 .74 .74 .82 .81 .81 .83
					.78 .81 .82 .80 .78 .78 .80 .78 .78 .78 .76 .78 .79 .79 .81 .80 .81
					.84 .81 .80 .83 .84 .86 .84 .86 .87 .86 .87 .86 .85 1.05 .91 .88 .85
					.88 .90 .90 .91 .85 .86 .88 .88 .86 .90 .89 .85
scintillans	New Brunswick	69	1	.49	.48 .49
	Silver Springs	72	2	.41	.37 .45 .43 .40 .42 .39 .35 .41 .41 .40
	Silver Springs	70	3	.41	.40 .43 .42 .39 .41 .41 .38 .39
	Silver Springs	70	2	.42	.41 .41 .41 .41 .42 .42 .42 .41 .41 .41 .42 .43 .41 .40 .43 .41 .40
					.42 .44 .44 .42 .43 .44 .45 .43 .44

TABLE 6 (Continued)

Species	Locality	Temp. (° F)	Female No.	Mean (Sec.)	Recorded Values (Sec.)
brimleyi	Idabel	75	1	.37	.38 .36 .36 .29 .39 .40 .37 .37 .30 .37 .38 .40 .44 .35
	Idabel	76	1	.38	.29 .32 .41 .39 .38 .39 .38 .39 .36 .37 .34 .38 .38 .36
punctulatus	New Salem	74	1	.32	.34 .37 .30 .29 .33 .30 .36 .34 .33 .32 .33 .29 .28 .28 .31 .32 .32
					.33 .36 .36 .33 .34 .32 .32 .33 .34 .33 .31 .31 .34 .34
	New Salem	75	2	.32	.28 .29 .29 .31 .32 .32 .32 .29 .32 .31 .31 .29 .29 .32 .29 .29 .30
					.32 .32 .32 .32 .33 .33 .33 .34 .34 .35 .35 .34 .31 .31 .32 .32 .31
					.34 .33 .36 .35 .34
	New Salem	75	3	.33	.34 .31
	New Salem	75	4	.34	.34
tenuicinctus	Fayetteville	75	1	.39	.37 .31 .38 .39 .36 .41 .40 .41 .39 .34 .40 .36 .39 .40 .36 .43
collustrans	Gainesville	65	1	.85	.71 .84 .72 .83 .98 .94 .95
	Gainesville	75	1	.76	.87 .79 .62
	Gainesville	75	2	.87	.89 .84
	Gainesville	70	3	.80	.80
	Gainesville	70	4	.91	.87 .90 .97
	Gainesville	70	5	.86	.90 .82
	Gainesville	70	6	.87	.87
tanytoxus	3.7 miles west of Gainesville	75	1	1.05	1.05 .94 1.08 1.00 1.10 1.14
	"	75	2	1.37	1.31 1.32 1.47
	"	75	3	1.40	1.52 1.28
	"	75	4	1.04	.91 1.01 .97 .99 1.04 1.18 1.06 1.02 .97 1.01 1.11 .99 1.01 1.10 1.07 1.15 1.04
					.87 1.06 1.08 1.10
	"	75	5	.94	.92 .94 .95
	"	75	6	1.18	1.18
	"	74	7	1.14	1.22 1.08 1.08 1.18
	"	76	7	1.21	1.20 1.18 1.34 1.25 1.09 1.22
granulatus	Wellington	80	1	.45	.40 .41 .44 .50 .50 .41 .39 .41 .42 .43 .42 .42 .50 .45 .50 .53
ignitus	Oneida	77	22	3.05	3.29 3.08 3.06 3.05 3.19 3.05 3.17 2.97 2.91 2.98 2.94 2.99
	Oneida	77	23	3.10	3.19 3.05 3.09 2.98
					The following time delays of *ignitus* females were measured with a stop watch
	Fife	63	1	4.2	4.3 4.1

TABLE 6 (Continued)

Species	Locality	Temp. (° F)	Female No.	Mean (Sec.)	Recorded Values (Sec.)			
	Fife	62	2	5.0	5.0			
	Portlandville	54	3	9.1	9.1			
	Portlandville	54	4	9.3	9.3			
	Portlandville	54	5	9.5	9.5			
	Portlandville	54	7	10.0	10.0			
	Oneida	58	8	6.2	6.2	6.0	6.2	
	Oneida	58	9	5.8	5.8	5.8	5.9	
	Oneida	58	10	6.8	6.8	6.7	6.9	
	Oneida	58	11	5.7	5.7	5.7	5.8	
	Oneida	58	12	7.0	6.8	6.8	7.3	
	Oneida	56	13	8.4	8.3	8.5		
	Oneida	56	14	7.4	7.4			
	Oneida	56	15	8.0	8.0			
	Oneida	56	16	7.7	7.7			
	Oneida	71	17	3.9	3.9			
	Oneida	71	18	3.8	3.8			
	Oneida	71	19	4.0	4.0			
	Oneida	60	20	5.9	5.9			
	Oneida	60	21	5.2	5.2			
	Ithaca	66	24	4.4	4.4	4.3	4.5	4.5
	Ithaca	60	24	4.8	4.8	4.8	4.8	
	Ithaca	70	24	4.0	4.0			
	Wampsville	58	25	6.0	6.0			
	Wampsville	58	26	5.8	5.8			
	Wampsville	60	27	5.2	5.2			
	Wampsville	60	28	6.9	6.9			
	Wampsville	60	29	6.9	6.9			
	Wampsville	60	30	6.9	6.9			
	Wampsville	60	31	6.9	6.9	6.9		
	Wampsville	60	32	7.0	7.0			
	Wampsville	60	33	6.0	6.0			
	Wampsville	60	34	6.7	6.7			
	Wampsville	59	35	6.9	6.9			

TABLE 6 (Continued)

Species	Locality	Temp. (° F)	Female No.	Mean (Sec.)	Recorded Values (Sec.)
	Wampsville	60	36	6.9	6.9
	Wampsville	60	37	6.7	6.7 6.8
consanguineus	Fife	69	1	1.19	1.09 1.17 1.13 1.20 1.14 1.14 1.22 1.08 1.09 1.12 1.19 1.20 1.21 1.20 1.33 1.25 1.28
					1.32 1.32
	Fife	69	2	1.34	1.24 1.42 1.41 1.29
	Fife	75	3	1.04	.85 .96 .96 1.07 1.08 1.03 1.05 1.12 1.17
	Gainesville	70	3	1.18	1.22 1.26 1.10 1.16 1.16
	Gainesville	69	3	1.28	1.25 1.36 1.19 1.28 1.28 1.32
	Gainesville	70	4	1.24	1.01 1.22 1.22 1.27 1.33 1.15 1.24 1.24 1.26 1.34 1.25 1.25 1.25 1.16 1.22 1.28 1.31
					1.26 1.19 1.36 1.25
	Gainesville	70	5	1.31	1.34 1.22 1.22 1.24 1.38 1.23 1.35 1.34 1.32 1.28 1.38 1.38
macdermotti	Gainesville	69	1	1.28	1.28 1.18 1.22 1.29 1.23 1.17 1.15 1.34 1.21 1.24 1.24 1.33 1.20 1.25 1.21 1.40 1.25
					1.26 1.38 1.35 1.31 1.38 1.29 1.26 1.14 1.29 1.26 1.14 1.29 1.37 1.20 1.22 1.16 1.28
					1.37 1.22 1.27 1.29 1.27 1.29 1.27 1.31 1.31 1.21 1.26 1.38 1.36 1.33 1.27 1.28 1.26
					1.34 1.35 1.32 1.21 1.22 1.31 1.30 1.26 1.39 1.40 1.34 1.29 1.25 1.24 1.15 1.34
	Mt. Pisgah	77	2	1.01	1.00 .90 1.03 1.03 1.03 .94 .94 1.05 1.01 1.07 1.06 1.11 1.01 1.03 .95 .95 1.11
					.97 .97 .98 1.01 1.01 .97 1.08 1.10 1.08 1.02
	Pisgah	64	2	1.55	1.55
	Pisgah	62	2	1.71	1.59 1.56 1.70 1.82 1.77 1.75 1.77 1.71 1.76 1.72
	Gainesville	71	3	1.25	1.20 1.55 1.00 1.03 1.23 1.64 1.19 1.05 1.09 1.31 1.72 1.12 1.51 1.16 1.23 1.16 1.32
					1.07
	Gainesville	84	4	.84	.96 .93 .85 .88 .85 .68 .73
	Gainesville	68	4	1.23	1.46 1.41 1.18 1.14 1.18 1.08 1.18 1.04 1.13 1.17 1.15 1.28 1.35 1.26 1.27 1.10 1.14
					1.48 1.34 1.12 1.45 1.15 1.29 1.25 1.19 1.25 1.13 1.09 1.36 1.15 1.26 1.38
consimilis	Gainesville	70	1	3.2	5.0 4.3 3.2 2.2 2.7 2.0 3.0 3.0 3.0 2.7 3.3 2.8 3.3 3.3 3.3 4.0 2.3
Fast Pulse			(stopwatch)		2.2 3.0 2.7 2.8 2.7 4.3
carolinus	Gatlinburg	61	1	6.4	8.0 10.0 9.1 6.0 5.6 5.6 6.3 6.0 4.5 4.0 8.2 8.2 8.8 8.0 8.2
			(stopwatch)		
ardens	Oneida	54	1 (pt)	1.57	1.60 1.72 1.40
			(stopwatch)		
	Oneida	58	2	2.0	1.5 2.0 2.0 2.0 2.3 2.0
	Oneida	58	3	2.3	1.3 2.0 2.9 2.9
	Oneida	58	4	1.9	2.0 1.8

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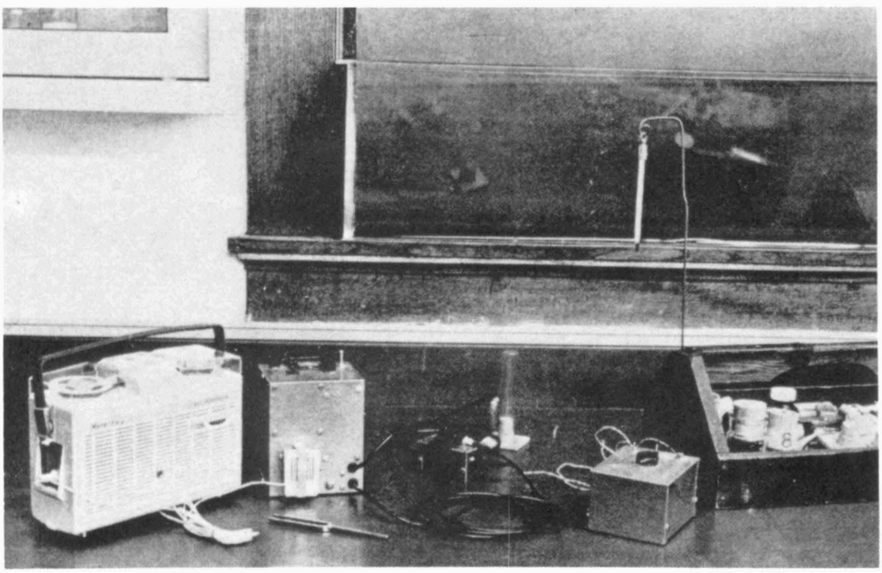
PLATE I

Apparatus for recording female flashes. Metal box at right is the monostable flasher (MF). Small metal box in the center is the MF bulb housing; immediately behind is the glass cage in which females are placed. Metal box at left is the photocell transducer; its photocells are at the ends of the black cables.



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