


The firefly gives light to its pursuer. Oemaru 



Fireflyer Companion & Letter



↔ Vol. 1, Number 3, pages 33-52, Summer 1997 ↔

Fireflies At Risk - Update

Fireflyer. firefly + er. n. abbrv. for firefly chaser. A person who thinks a lot about lightningbugs

FIREFLIES USA — 30/6/97: Ah, dear Fireflyers, there is good news tonight. Though it is only the tiniest beginning, the first evidence available on the effects of mosquito spraying on adult fireflies is good. Of course this is only one study and involves only one firefly species; of course it is from only one place in the country, and it involves only one insecticide; and, for the sake of total objectivity, of course we must keep in mind that it is only by one research facility, which is under contract to an administrative unit that is perhaps not without some interest in the outcome; but, nevertheless, it is a beginning, and it is grounds for a single byte of ecological optimism in a(n) sometimes (increasingly) dismal world. Turn to the paper by P. G. Hester (page 45) for a report of this study, and to the paper by Clay Scherer for an outline and discussion of the insecticide used in the study (page 50). In the next *FC* issue I will outline a study that you can make next summer on the effects of spraying in your neighborhood on the fireflies that live there. *fd*

Signaling With Glows, Flashes & Pheromones

What's in a name? that which we call a rose
By any other name would smell as sweet.
(Romeo and Juliet, Shakespeare)

Dear Fireflyers, Firefly communication is one behavior of wild animals — of animals in nature — that is incredibly accessible and easy to study. With a penlight and notebook, after a spring and summer of evenings in the field, a careful observer can hope to: (1) learn to distinguish several species by the flashing patterns emitted by flying males; (2) learn the flash codes of a few species by imitating (with a penlight) the flashing patterns of flying males and seeking and noting the response flashes of waiting females; (3) attract flying, signaling males to the penlight by flashing answers to males like those flashed by their females; (4) find and observe the predaceous fireflies (*Photuris* females) that mimic the females of other species, attract males, and eat them; (5) observe the aerial attacks of *Photuris* females on targets that are made to flash and "fly" like fireflies; and (6) find *Photuris* species that use two (or more) distinctive flash patterns during their searches for mates.

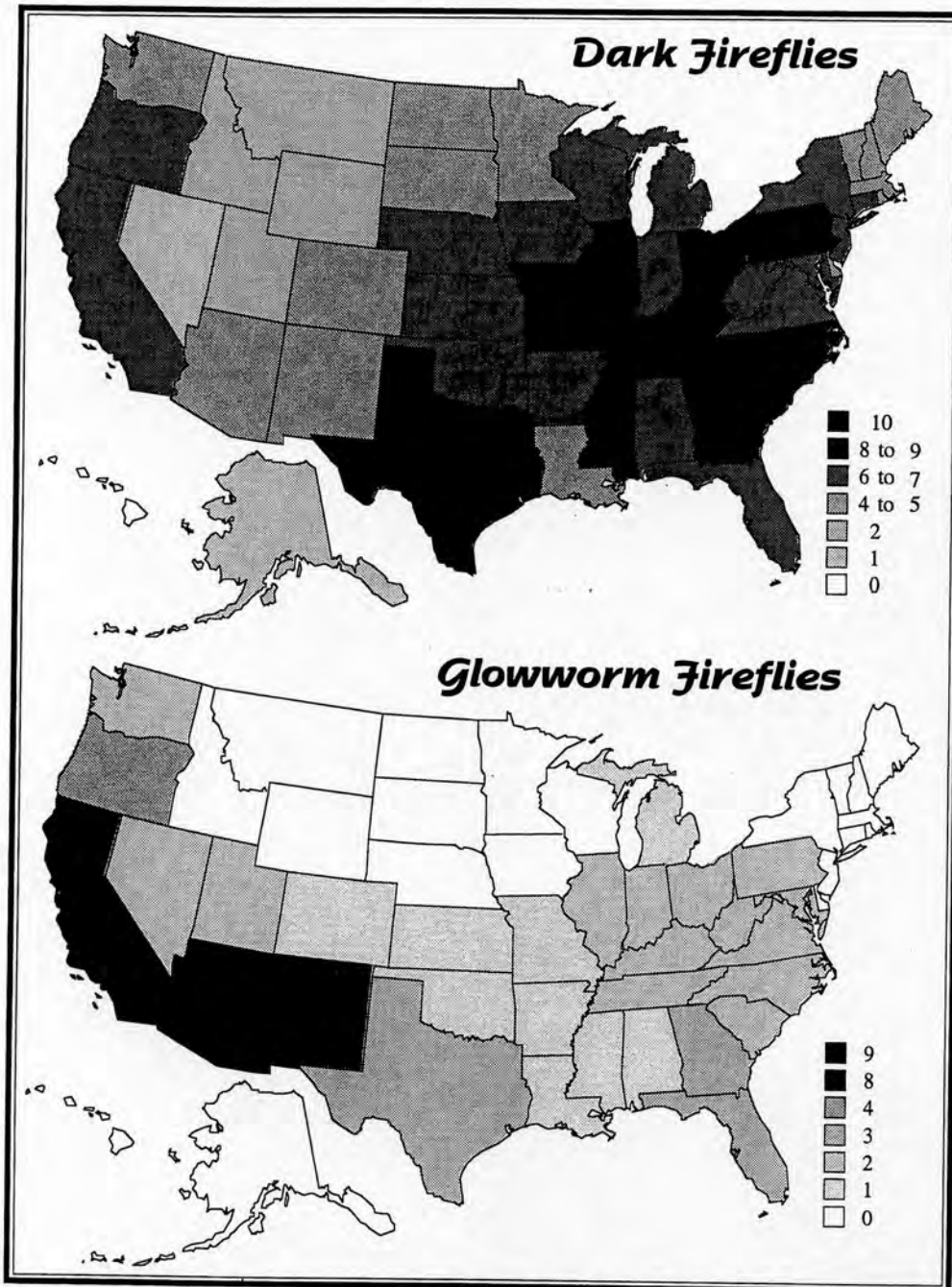
The study of communication in flashing fireflies has decided advantages over research on insects that communicate by chemicals (pheromones) or sound (acoustics). Humans have good eyes and can see in dim light, and their eyes are good analyzers that can detect and discriminate details and nuances of color, timing, spatial patterns, and movements (but remember, human analyzers are subject to certain "optical [analytic/mechanic] illusions" and this must be kept in mind). The fast pace of firefly action — entire sequences take seconds or minutes rather than hours or days — makes firefly study more interesting. Expensive equipment is not needed for such research,

and, in fact, it can easily become a distraction. Finally, for people in the United States living east of the Rocky Mountains, fireflies may be as near as the front lawn or garden. People fortunate enough to live near a marsh, even a little one in an abandoned gravel pit, may find a lifetime study of firefly action and interaction almost on their porch. Here I take a broad view of communication in North American fireflies and outline the three basic modes of communication found among them.

The (Daytime) Dark Fireflies

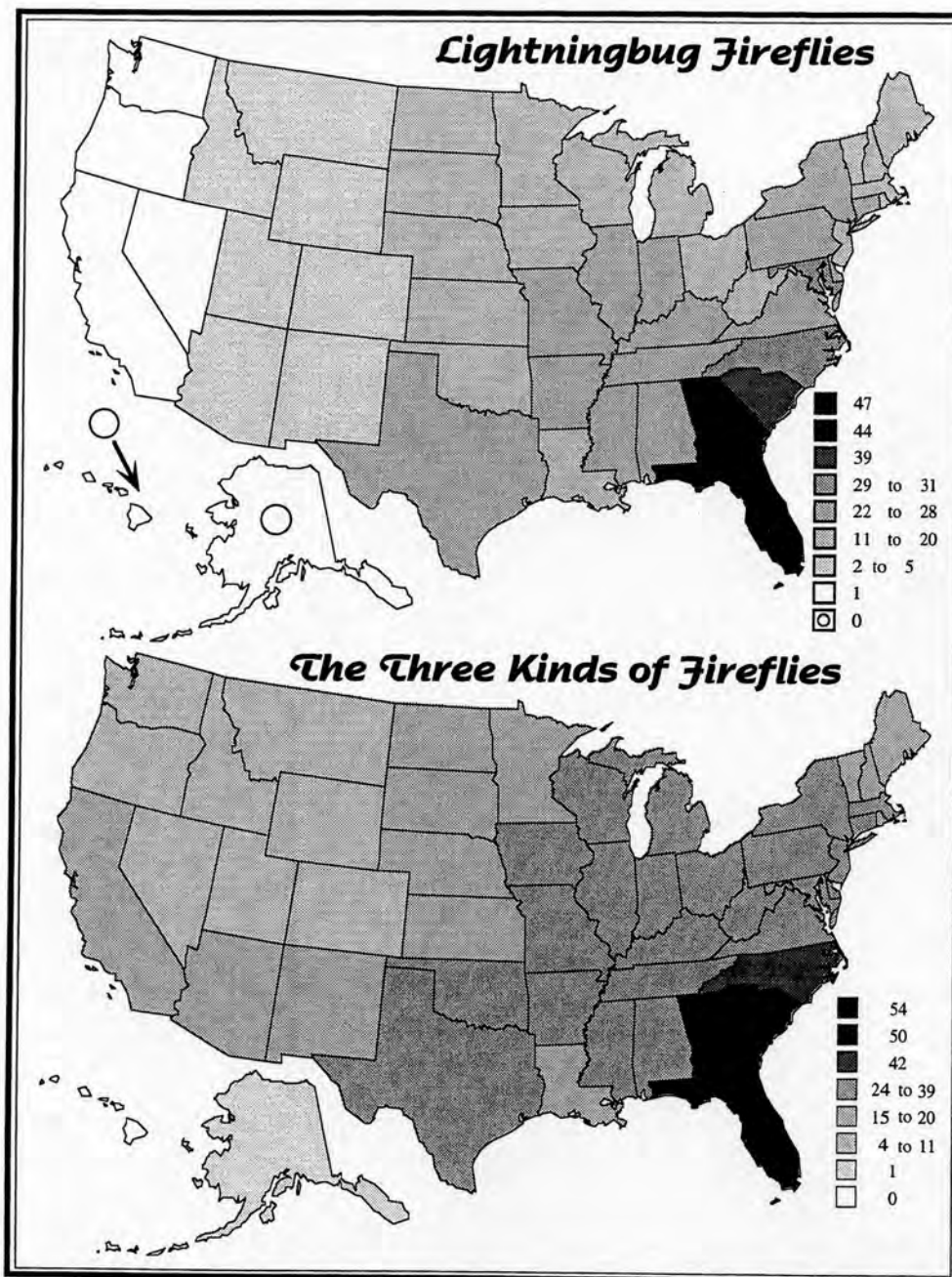
Though adults of our better known firefly species use their own chemically generated light for communication, some firefly species use **pheromones**, perfumes that females emit into the air and that waft downwind in invisible clouds termed **plumes**. Males turn and weave as they track the thin and inter-twisting concentrations (**filaments**) of pheromone within the plumes. When a male locates a plume's point of origin, he has found the female, and he mates with her. A number of nonluminescent species in America use this secretive — "known only to each of them" — communicative system. If a female of *Lucidota atra*, a day-active firefly found in the eastern half of the U.S., is put in a gauze-covered dish (containing an apple to provide moisture and nourishment[?]), and set out in the forest of her origin, she will sometimes attract males at a rate of one per minute for several minutes. If the dish she has been kept in overnight is set out, it too will attract males, showing that the female has left behind some of the essence (of females) of her species.

**Species Counts of the
Lampyridae Beetles
of the
United States of America**

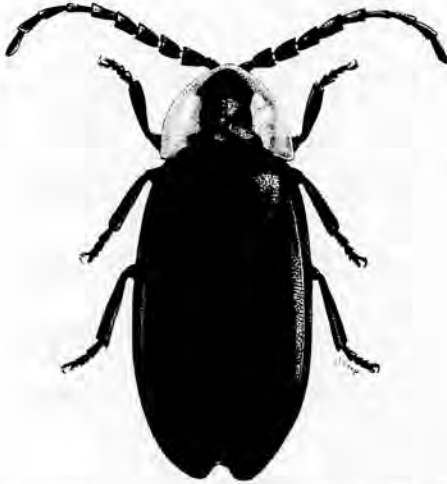


Species totals (tentative/working) for each state are based on: (1) reliable records from published check lists, archived (museum etc.) specimen labels, and field work, and (2) presumption of occurrence based on conservative inference from records for adjacent areas.

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Lucidota atra, a Daytime Dark Firefly

The Glowworm Fireflies

The simplest form of **luminescent** signaling known to occur in fireflies is found in several species of western United States and three rare species in Florida. The females of these **glowworm fireflies** often live in burrows, and after nightfall they appear above ground where they turn on their glows to attract mates. Females of such species are called glowworms, and are usually difficult to identify to species from morphology alone. Males of most kinds of **glowworm fireflies** do not have lights when they reach adulthood — though as far as known all fireflies (family Lampyridae), even daytime Dark Fireflies, have lights when they are larvae. Flying **glowworm firefly** males have especially large, often huge eyes, and find their females by searching for their glows. Apparently a few species use pheromones too, and males first detect females from longer distances than their glows can be seen.

I am surprised that females of all **glowworm firefly** species don't do this. Perhaps they do, but the simple antennae of males and field experience of firefly chasers up till now have not suggested this. Remaining on an advertising station, either near the entrance of their burrow or up on a stem of vegetation, and glowing brightly is dangerous. One female I was watching was quickly grabbed and eaten by a toad and another was carried off by a wolf spider. Thus, it is obvious that a chemical signal that assists the glow and reduces the time a female would be exposed to such predation could often be an advantage. After mating, glowworm females, soon to become single



The Appalachian Glowworm Firefly

mothers, return underground where they lay their eggs and then eventually die, their inseminators having long since flown off in quest of more eggs to fertilize — though this thought is not on their little "minds," males just do it and do it, and . . . and so on.

A very few species of glowworm fireflies incorporate **male** luminescence into their **glow system** of communication. In the Appalachian Mountains males of a firefly long known as *Phausis reticulata* (though I suspect that this name is incorrect), can be seen flying through the forest low over the ground. They look like low-flying hover craft with green running lights. The Appalachian Glowworm Firefly has modified the basic glow system, giving females some protection against light-seeking predators. Females can remain dark and hidden until a lighted male flies overhead, and only then hang out their lamps. The female lanterns in this species are unusual for fireflies, for instead of there being merely a pair of them at and under the tail end, there may be four or six glowing dots positioned in pairs along the back.

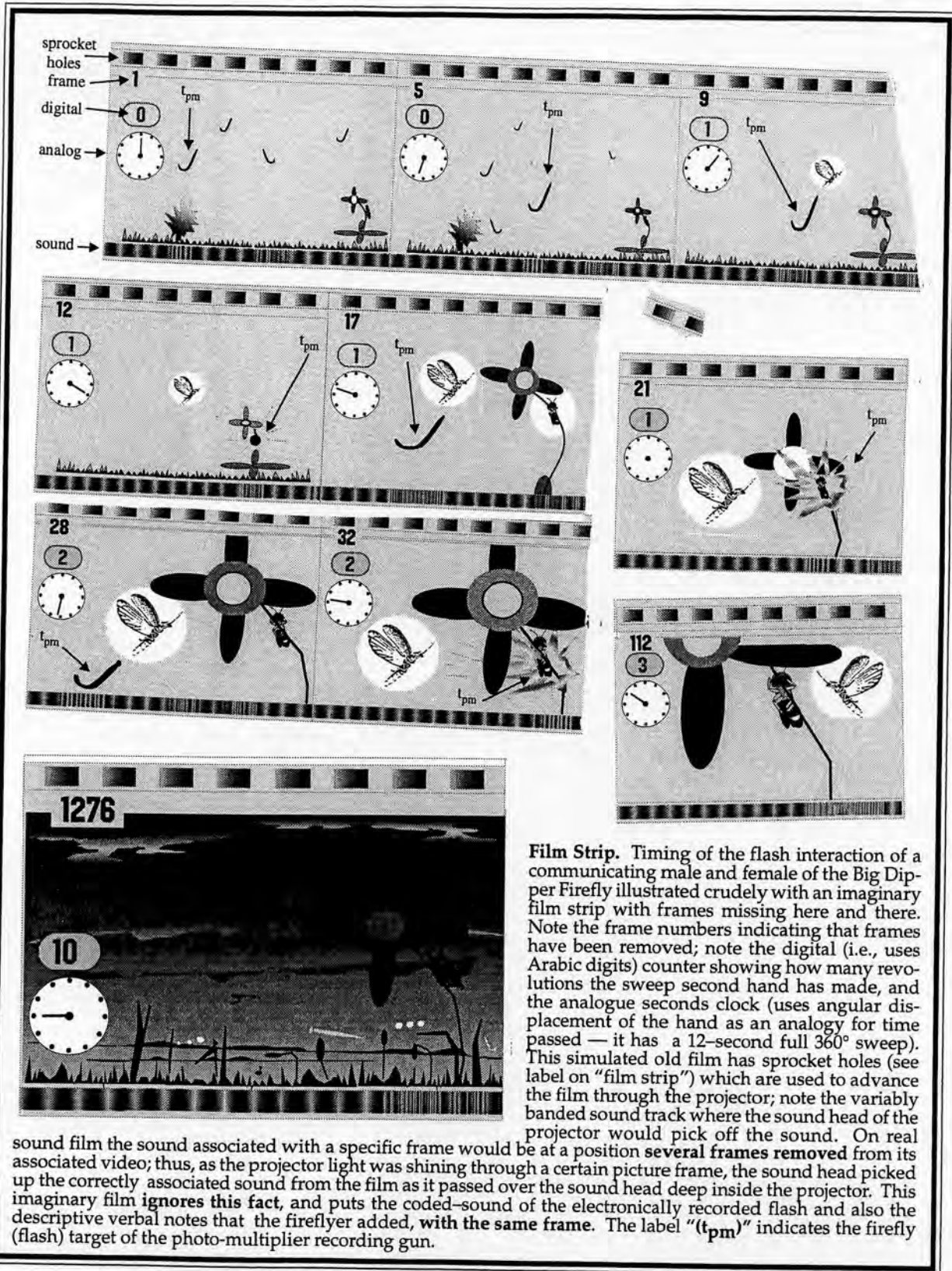
The Lightningbug Fireflies

It is the **Lightningbug Fireflies** that catch our eye! — first I must digress and explain my strange and new terminology. In the United States, beetles of the family Lampyridae are usually called lightningbugs or fireflies, but there is sometimes confusion among observers as to which is the "proper term." Both are correct, but there seem to be regional differences in their usage; the most often used common name for lampyrids in scientific literature is "firefly." I grew up in the glacial hills of central New York State and we called them lightningbugs. Since we wish to unambiguously distinguish among the three mentioned (basic) communication/behavioral types of our North American Lampyrids, it would be a useful and mnemonic to use the following (entomological) etymology: I suggest that we use **lightningbug firefly** for those that flash (like lightning); **glowworm firefly**, for the Lampyridae species whose females emit long-continued glows and are "worm-like"; and **dark firefly** or **daytime dark firefly**, for fireflies that do not use luminescence for sexual communication and that, in known examples, fly during daylight hours. One more thing: note that "bug" and "fly" are connected without a hyphen, in entomological convention, since lampyrids are neither bugs (Hemiptera) nor flies (Diptera).



The Big Dipper Lightningbug Firefly

— **Lightningbug Fireflies** control their lanterns with precision and emit light in short flashes or pulsing flickers that are, if you think about it, dramatic and magic. Before the invention of electric lights their unnatural brilliance must oftimes have been viewed

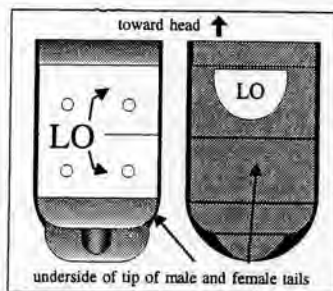


Film Strip. Timing of the flash interaction of a communicating male and female of the Big Dipper Firefly illustrated crudely with an imaginary film strip with frames missing here and there. Note the frame numbers indicating that frames have been removed; note the digital (i.e., uses Arabic digits) counter showing how many revolutions the sweep second hand has made, and the analogue seconds clock (uses angular displacement of the hand as an analogy for time passed — it has a 12-second full 360° sweep). This simulated old film has sprocket holes (see label on "film strip") which are used to advance the film through the projector; note the variably banded sound track where the sound head of the projector would pick off the sound. On real

with awe and mystery, and I suspect jealousy too, for few poets sang their raptures in the old European literature. These lampyrids, our **lightningbug fireflies** have the most complex interactions and stories to tell, and in the eastern half of the United States there are about 130 species of this type. I described the communication of one of them, *Photinus pyralis*, the Big Dipper Firefly, in my first letter as a general introduction to fireflies. The Big Dipper occurs from central Kansas to the Atlantic, from southern Michigan to the Gulf of Mexico, and is an ideal subject for study. It is common and widespread, is active at twilight when it is still quite light outdoors, and it is easy to talk with, using only a penlight. The yellow color of the Big Dipper's flashes is important for enhancing message visibility, that is, it improves the "signal-to-noise" ratio — "yellow" signals against a background of "green" foliage. (can you guess why I put yellow and green in quotation marks? read on and reflect)

At twilight there still is considerable reflected sunlight (ambient, i.e., surrounding environmental light), and much green light is reflected from vegetation. In the geological past when certain species, including the ancestors of *P. pyralis*, became active at twilight, they evolved filters in their eyes to partially remove this green light. And, they shifted the peak color of their luminescence from green, as found in late-evening fireflies, to yellow, thus greatly enhancing their vision for receiving yellow signals at twilight. However, this could make some of them almost blind if they fly late at night when there is very little ambient light available. Note that though they see yellow against a green background, this does not mean that such fireflies have color vision. It means that light energy in the yellow part of the color spectrum is detected and green is filtered out — yellow is seen (as light), green is not seen (is dark) — but the firefly (presumably) sees in monochrome (black and white, "in a manner of speakin").

As males search females perch — on grass and low shrubs and herbs. Morphologically they look pretty much like their males, for they have fully developed wings and wing covers. The most conspicuous difference between male and female Big Dippers is the size of their lanterns (LO in the drawings), which in both sexes are located under the tail. The male organ occupies two full segments, but that of



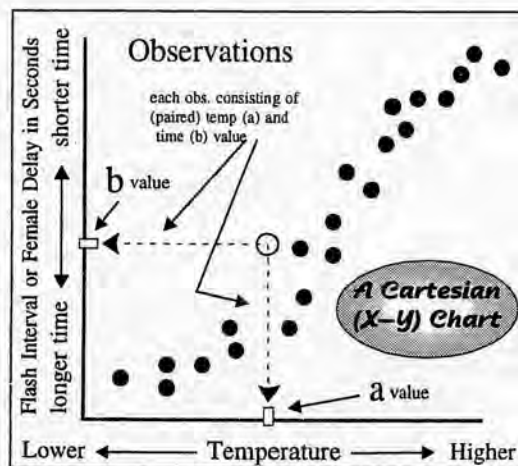
the female is usually only a half-moon in the center of one segment (in *Photinus* species). Males and females also differ in the size of their eyes, with those of males being larger. This gives males a wide field of vision as is appropriate for their flying-searching activity and important for sexual success. One can safely presume that in past generations of fireflies it was the males that scanned their area and aimed their landings better, that found and fertilized more egg-bearing females and put more of their success-promoting "big-eyed genes" in subsequent generations of Big Dippers.

activity and important for sexual success. One can safely presume that in past generations of fireflies it was the males that scanned their area and aimed their landings better, that found and fertilized more egg-bearing females and put more of their success-promoting "big-eyed genes" in subsequent generations of Big Dippers.

When a female sees a male's flash, or the flash of a penlight, or the flare of a match that is of about the correct duration (=0.5 sec), her response circuits are activated, and somewhere in her nervous system a

timer counts off two to four seconds and then triggers/activates her response flash. This time delay is not constant, and the timing of flashing in males and females varies predictably with temperature. On cool evenings the flashes, flash intervals, and female delays are longer than they are on warm evenings. This means that in order to mimic a female flash and attract a male to a penlight, ambient temperature must be (roughly) taken into account.

Temperature curves for male flash intervals and female response delays can easily be graphed by measuring these features (parameters) at different temperatures with a stopwatch. For male flashes this may require that observations be made on several evenings, thus making use of differences in ambient temperature that occur in the field from night to night. A sample of about ten male intervals at each of three or four temperatures between 18° and 27°C (65° and 80°F) is sufficient. At each timing session air temperature is taken in the flight space, away from heat-holding structures such as pavement and buildings.



This discussion of temperature raises a question that I have not seen answered. It would seem that the body temperatures of male and female fireflies must be "roughly" the same if they are to communicate with **time-coded** flashes. For example, when females of *Luciola lusitanica*, an Italian firefly, were warmed more than 20% above ambient (local surrounding) temperature with a small heater, they were unable to attract their males. In nature (real life, outdoors) the metabolism and thus the timing of perched, relatively inactive females may be (is presumed to be) considerably lower than that of their flying males, whose wing muscles are generating heat by their contraction activity. If this is the case, it is surprising that the males and females can maintain communication. Perhaps the males lose heat rapidly, or possibly they have thermally isolated their timers from their warm muscles; or, I suppose the males might measure ambient temperature with a "thermometer" at the remote and cool tip of some part of their body (on the antennae?) and then send ("feed in") a temperature correction into their timing circuits. The simplest explanation is that the signal timing is quite sloppy and allows for sizable discrepancies, but I am also suspicious of this explanation, given the complexity and exquisite detail found in the signal systems of lightningbug fireflies.

Quiet & mysterious trails, *firefly doc*

Tiny Little Firefly

Tiny little firefly at twilight
 Flashing and dancing into the night
 Over marshes and meadows, by ponds and streams
 In glades and thickets by the millions it seems
 Your pale cool glow on a summer evening's breeze
 Sparkles in dim fields and flickers in somber trees
 You bow, you sway, you shimmer and hover
 Desperately longing to discover a lover
 You glow to court, you live to mate
 Will your children duplicate your fate
 Your light is so brief and you are so small
 Soon it will fade and then you will fall
 Warm summer evenings may seem an eternity to you
 But they will pass you by growing shorter and cooler too
 Enemies will feast and lovers will die
 Fewer of you will be seen in a cold autumn sky

Gevin Kenney
 Riverside CA

A Summer Night

My sister-in-law and I
 share secrets and dreams
 on her patio in the dark
 lit by the flashes of fireflies.
 New Jersey butter-and-sugar corn boils on the stove inside
 where our husbands and sons watch TV.
 It gets easier, she says.
 I hope so, I whisper.
 Our sons come out, banging the screen door,
 and run through the dark carrying empty mayonnaise jars
 to capture the magic of the summer night.

Gretchen Fletcher
 Ft. Lauderdale FL

Entheoxicity

How does the tiger run
 In the glow of the good Titan's gift
 Hammered Earth in muscle tone
 And claws of Time's absynth

Saturn as the father
 Soon the tiger slows
 The hourglass of Life is flowing
 All the threads are wove

To Earth the mighty beast
 Will fall with its last breath
 What tremendous Power it must feel
 Of Life before its death

Chris Fillie
 Gainesville FL

Born of the sun
 We all are subatomically one
 Forged in stellar fires
 Of super nova pyres
 Just brilliant bits of light
 Shining bright
 On a warm summer's night.

Chris Tipping
 Gainesville FL

I swoop in the air.
 As the kids try to catch me,
 My mate calls me on the ground.
 I dash to my mate and we swoop from the
 Children as they try to grasp us in their hands.

Sarah Halper, age 6

Fireflies in the sky,
 Where the birds always fly.
 Flashing, Flashing so bright,
 Fireflies make all the light!

Jenny Wang, age 9

[Poem]

It has been said
 thy firefly is part thou
 thy firefly part ghost

Upon speculation
 one shalt see

There inside the firefly

part he
 part she

a lighted thread braids thy shaded back side
 with delights of childhood court
 frolicks from thy figure
 a dirty scamp of sorts

and thou would wonder from those in the crew
 just what kind of lampshade thy Zen will suspend
 among thy chartered brew

or whether
 thy magic will weave once again through rain forest hair

Thy spirit may rejoin
 among ancient people's past
 with portals made of tin
 and cosmic waves of glass

There she will dance on her postcard fern
 holding thou in her unaltered bosom
 rocking thou back
 forth as to rhythm

Watching as thou know

Wondering if thou will glisten

Kim Houck
 Todd NC

Black Robe: A View

[I have used the film *Black Robe* in my Fireflyer course for several years because of its sounds and sights of "wild and natural" North America, and the contrast of the Indian vs European cultural views. Since I first saw it, the film has had an appeal beyond that of any other than I can think of, one that penetrates deep into my psyche. I think Erin Crider has identified part of the magic and mystery that the film has for me that I had not consciously recognized. The opportunity to have students such as Ms. Crider is a reason that I sometimes think that I should pay tuition for the privilege of studying with them! ^[4]

The film *Black Robe* raises many philosophical questions, including concerns about Western society and its concepts of time and language, primarily through the reactions of Native Americans to the Jesuit priests based in Quebec in the year 1644. The technique of exploiting "naive" reactions of those outside society is a well-known literary device; Voltaire's *L'Ingénu*, for example, criticizes 18th century French society when its title character, a young man of French descent raised by Huron Indians, travels to France and to Paris, and experiences a variety of adventures and misfortunes because of his "ingenuous" responses to "civilization." As in Voltaire's work, *Black Robe* employs a young man of French descent born in the colony as a primary critic; this figure, whose position is paradoxically outside and within the Jesuit civilization, speaks the languages of both groups and as such helps articulate many of the differences between French and Native thought.

One of the first differences the film calls into question is the difference between the "Western" notion of time and its importance to society and the Native's view of time. An early scene in the film, the first to present the Native Americans as a group, shows members of the tribe silently seated indoors, as if listening to a sermon or a speaker. After a few minutes spent watching the silent group, the camera finally reveals that the people are attentively watching a clock the priests have carried with them from France. Mystified by this device and its obvious importance to the French colonists, the Natives refer to it as "Captain Clock," who commands the French from Quebec with its chimes. This humorous, seemingly "ingenuous" mistake calls into question the perhaps undue importance Western Civilization places on time, its measurements, and its proper uses. In an era of "time management" crises, ever-pressing deadlines, alarms, and datebooks, perhaps we would be wise to ask ourselves to what extent we really are ruled by "Captain Clock." Stephen Covey, author of the best-selling *The Seven Habits of Highly Effective People* and *First Things First* describes some of the problems Westerners have regarding the tyranny of the clock:

For many of us, there's a gap between the compass and the clock — between what's deeply important to us and the way we spend our time. And this gap is not closed by the traditional "time management" approach of doing more things faster. In fact, many of us find that increasing our speed only makes things worse. (Covey, *First Things First*, p 16)

Covey feels that the problem is due to the predominant Western view of "chronos," the Greek word for time:

Chronos time is seen as linear and sequential. No second is worth more than any other second. The clock essentially dictates the rhythm of our lives. But there are entire cultures in the world that approach life from a kairos — an "appropriate time" or "quality time" — paradigm. Time is something to be experienced. (Covey, *First Things First*, p 27)

Although the comments about "Captain Clock" were certainly humorous, according to Covey they describe a deep problem facing Western society. Perhaps the Natives' observations were more on target than we care to admit.

Another question raised in *Black Robe* is the question of language, in particular written language, as an implement or power. In one scene, a small group of Natives approach one of the priests while he is writing and asks what he is doing. To explain, the priest asks one of the group to tell him something he would not otherwise know. The Native complies, describing the death of his wife's mother, and the priest writes the information down and shows it to another Frenchman, who reads the page and repeats the description to the astonished Native. Although Western society often takes its written language for granted, many modern literary critics and philosophers recognize the need for the Native's astonishment at the power of language in the face of totalitarian regimes and their gross abuses and contortions of language to serve a political end. George Orwell's *1984* is a classic illustration of the power of written language to create its own meanings and its own realities, realities that menace the individual caught within the tyranny of language. Jacques Derrida founded the school of deconstructionism, a school of literary criticism that argues that because language can never correspond to the "reality" it evokes, every text contains the seeds of its own undoing; its very words, he would argue, lead to inherent and insurmountable contradictions that "deconstruct" the work as a whole. Emmanuel Levinas, a contemporary of Derrida, urges his readers to return to the conversation, the act of "saying," the human interaction inherent in speaking or writing a word to another person rather than dwelling on the accuracy of what is actually "said" and its correspondence with truth. In other words, Levinas feels that we need to return to the Native Americans' astonishment at the power of the written language and its ability to connect human beings by revealing things about other people that we never knew before; as in the scene in *Black Robe*, the message conveyed is of less importance than the simple fact of the conveyance and the desire to learn about another person by listening and asking questions.

Perhaps as a culture, we would do well to reconsider the questions raised by *Black Robe*, questions which at first might simply provoke laughter. Although the Native's reactions to Western views of time and language seem startling and humorous, they raise very profound questions about two of the most fundamental — and at times problematic — concepts at the very core of our civilization. Erin Crider, UF.

Erin Crider is an English major in the UF Honors Program and this autumn will be a senior; I hope she will become a regular and long-time contributor to the FC.

Gainesville FL. On the 30th of April '97 the third "annual" firefly lecture and field expedition was held as one of the Outdoor Adventures sponsored in the Community Education Program. Participants first heard a slide lecture on firefly natural history and identification, then set off in a caravan to choice sites near the airport for field observation and experimentation. This year the flash patterns of 7 firefly species were seen, the same number seen last year, according to those with working memories. The class, entitled *A Historical Ecology of Fireflies*, was organized by Dr. Bruce Ferguson, the veterinarian of Micanopy, Florida, and conducted by *id.*

J.E.Lloyd (Ed.), with Joshua Trotter, Flora MacColl, and Greg McDermott. Mailing Address: Fireflies, Department of Entomology, Bldg. 970, Hull Road, University of Florida, Gainesville FL 32601.

Rearing Fireflies: The Agony and the Ecstasy

Sooner or later, it seems, every fireflyer thinks about starting a colony of fireflies. There are a number of reasons why you might want to rear lampyrids. A colony could help you study the biology of a particular species of interest, or you might just want to learn how to encourage their survival in your environment for aesthetic or gardening purposes. If we could start colonies maybe we could reverse the trend of fireflies disappearing in nature (see *Where are the Lightningbugs*, Fireflyer Companion Vol 1; *Fireflies at Risk*, Vol. 2). (Note: another approach that could also help, is to protect their habitats.) At least two major zoos have considered the idea of firefly displays, much like butterfly gardens. There is a chemical company that buys fireflies to extract chemicals for scientific purposes, so why not just colonize them instead? Much of the information that is available on firefly rearing was summarized by Lawrent Buschman in his dissertation (Buschman 1977), from which I have borrowed liberally.

The methods, and consequently the problems involved in rearing a given species are determined largely by the biology of the larvae — recall that fireflies spend most of their lives as larvae. This is because it is during the larval stage that fireflies have their most complex and critical interactions with other organisms, in particular those that they prey upon and those that cause their health problems and diseases, including bacteria, viruses, and nematodes. We need to understand the fine details of how to keep the larvae alive, feeding, healthy, and moving through their instars to successful pupation.

Species with aquatic larvae seem to be easier to culture. In Japan, where fireflies are treasured, there are protected habitats and firefly culture has been going on for decades (Okada 1928, Yuma 1986, and refs.). Two aquatic species have been colonized and mass-reared. Buschman had success rearing a (semi) aquatic species from Florida, *Pyrractomena lucifera*. (Melsheimer). The basic setup in the Japanese method of culturing is an aquatic area for larvae to live in and prey on snails, with a gently sloping "shoreline" where they can leave the water to pupate. Not surprisingly, manipulating environmental parameters affected the duration of the larval stage. The success with rearing aquatic firefly larvae has led to exploration of their use as biocontrol agents for snails (Michelson, 1957).

There seems to be little doubt that terrestrial larvae are more difficult to rear. A species' life cycle in northern United States may even be as long as three years, requiring an extended commitment on the part of the rearer. Furthermore, larval mortality is often high. For example, Buschman cited one researcher who after two years obtained only 3 males and 4 females after beginning with a rather large number of eggs. Among terrestrial larvae, Buschman found that *Photuris* species were the least difficult to rear. These are usually found above ground, which makes it easier to keep track of them. The basic rearing procedure is to keep larvae in a terrarium, covered to retain moisture, and periodically introduce snails, chicken liver, or other food. Food remnants must be removed after the larvae have fed to prevent the growth of infectious organisms. *Photuris* larvae construct igloo-like cells at or near the soil surface for molting and pupation.

We don't know much about the terrestrial larvae

of other North American species, but they seem to have similar biology. *Photinus* larvae, like those of all other known lampyrids, are luminescent, with their light organs occurring on the 8th abdominal segment (Williams 1917, Hess 1920, Balduf 1935, McDermott 1958). The fact that they are luminescent, yet rarely collected, supports the conclusion that they are characterized by mainly subterranean existence. This behavior makes them hard to monitor in captivity. Probably larvae of all lampyrids feed on soft-bodied prey of various kinds, especially earthworms and snails. Larvae of most genera probably pupate in the soil, but those of one tribe (Cratomorphini) which includes several tropical species and our *Pyrractomena* pupate on vegetation, such as tree trunks (Lloyd 1969, 1973, 1997).

To learn to rear fireflies, you can get some experience and have success producing adults if you begin with the larval stage because the most difficult part of the life cycle will have already been completed. Of course you can start with eggs from mated females, and those of many species will deposit eggs if they are kept in a small container, such as a small plastic box (e.g., zipper vial), with moist soil. Eggs of most species will hatch within two or three weeks if they are kept in moist soil or other moist environment. Frequently, a developing embryo can be seen through the chorion ("egg shell") if you have a low-power microscope. The surface of the eggs may at first be luminous and toward the end of embryonic development, just before hatching, the larval light organs may become functional (Harvey 1957, Schwab 1960, Buschman 1977), though you will need to let your eyes completely adjust to darkness in order to observe this extremely faint light.

Once larvae eclose (hatch out) they need to remain in a moist habitat. I have had partial success rearing *Photinus* species larvae in a "ant farm" type of terrarium (Wing 1988). My chambers consisted of two panes of plexiglass clipped to a frame made from 1/8" plywood. The narrow space between the plexiglass panes was filled with soil, tamped to remove air pockets, but not packed. I punched channels on each side with a probe so that I could inject water with an eyedropper. Mated females laid eggs in the soil, and the eggs developed and hatched. Larvae seemed to survive best on tiny earthworms that I placed in the terrarium and that would crawl down the water channels. The first instars would attack as a group and feed on the worms. The narrow thickness of the soil was helpful in that I was able to monitor their activities with a dissecting (i.e., low power) microscope, and kept some alive for over a year, observing them daily as they survived through several instars. However, the thickness of the soil in the terraria was not sufficient to allow them to successfully pupate, and mortality was high despite my efforts. An original clutch of eggs that produced scores of larvae resulted in only one final instar larva that attempted to pupate.

High mortality rates occur in nature, otherwise populations would be conspicuously increasing. For example, an average female may deposit 100 or more eggs; if more than two survive on the average (the number required to replace the female and her mate), the number in the population must obviously be increasing. There are all kinds of mortality factors in nature, including weather, predators, scarcity of food, and disease. However, we should expect to be able to reduce mortality in captivity in environments that we control. We will certainly need high survival rates for successful mass rearing.

You can see that there are many factors to consider when you set up your rearing environment — how tight to pack the soil, how thick to make the soil-holding chamber, how moist to keep the soil, how warm or cool, how often to clean or change, and what photoperiod (combination of daylight and dark periods totalling 24 hours) to use . . . One final and obvious problem worth mentioning is that you will need both males and females to survive and reach adulthood at the same time. Curiously, this seems to be easier with some fireflies than others.

Should you attempt to rear fireflies? If someone can find the secrets to reducing mortality and achieving high survival rates, it could allow us to introduce rare species into "empty" firefly sites in nature, and perhaps prevent their extinction. However, keep in mind that collecting larvae or mated females for such purposes can possibly reduce the chances for survival of existing (source) populations in the wild. Also remember that rearing even a small number of fireflies is a time consuming and long-term project, and re-

commended only for the dedicated fireflyer. Steve Wing, UF, Gainesville.

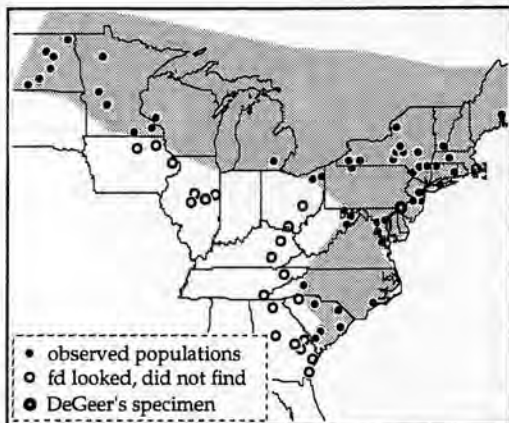
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Firefly Profiles #3

the Pennsylvania Firefly



If you were to use the scientific and popular literature of the past 130 years as a guide you would conclude that *Photuris pennsylvanica* (DeGeer) is the most widely distributed firefly in North America. This is because this one name has been applied to virtually all *Photuris* species in North America, and even some that occur elsewhere in the Americas. Details of the evolution of this compounded confusion are interesting themselves and worth telling, some other time. The real *Photuris pennsylvanica*, that is to say, the firefly to which this name is presently and carefully applied, ranges in a dog-leg distribution across northern United States and adjacent Canada, then southward in and east of the Appalachian Mountains, ending in southernmost South Carolina (see Map).



This Pennsylvania Firefly occurs in low meadows, cattail marshes, salt marshes, soggy hummocky pastures, around the margins of beaver ponds and man-made fish ponds, along streams and in their waterless incised meanders, around old mill ponds and their spillways . . . Presently, the only certain way to identify this (working) species is by the distinctive "dot—long-dash" flash pattern males emit as they



fly about their habitats seeking mates. At low temperatures this pattern may be 2 – 5 seconds long (see illustration); in some populations the break between the dot and dash may be barely discernable. In some (all?) populations males emit only the dot of the pattern at the beginning of evening activity, and then gradually all switch over to the the dot+dash pattern across the next 30 minutes.

One reason there has been so much confusion about this and other *Photuris* fireflies is because of the lack of conspicuous distinguishing morphological characteristics. Thus it is that we must rely primarily upon flashing behavior to recognize *P. pennsylvanica* s.s. (=sensu stricto). Note in the carbon-dust habitus drawing by Laura Line, the anchor-shaped pronotal vitta. This shape may occur more often in the Pennsylvania Firefly than in other *Photuris* species, but **should** not be relied upon for ID. Even the sexes of *Photuris* fireflies are difficult to readily distinguish without a dissecting (low-power, 8–15X) microscope. As a field character, in females the light organ on each ventral plate is surrounded by pale but non-luminous (non-flashing) tissue; male LOs completely cover each of the two light-bearing plates. *Photuris* females, except for those of a few *Photinus*-like species, attract males of other firefly species by mimicking the sexual signals of the males' own females. Then they grab and eat them. "And so it goes." good hunting, fd



Letters

from fireflyers

Dear *fd*, The fireflies are out in numbers in the woods of southern PA (*Ellychnia californica*; 6/V/97). The field guides are ambiguous about their "fire." A couple of them imply that they have fire but another says that *Ellychnia* species have no light organs. I can't find any light organ either. So, who has the right story about these lightless Western "fireflies"? Adalbert G., in the woods in southern PA.

Dear *ff Adalbert*, Your firefly is a member of the confusing *Ellychnia corrusca* species complex (*Ellychnia californica* occurs only on the west coast). Adult *Ellychnia* have no light organs, though larvae and pupae do. Adults probably use pheromones ("perfumes") for sexual communication. The adults you saw enclosed (from the pupal stage) last fall and actually spent the entire winter of 96-97 as adults (as far as we now know). Larvae live in rotten logs, and in my experience pine logs in particular, and especially(?) at the horizon where the log circumference meets the ground level. *illuminating trails, fd*

Dear *fd*, I am interested in doing a photo shoot of a bunch of fireflies this coming summer and would like to know how to do a time exposure in a marsh area — what film and exposures to shoot at. Robert B., New York NY

Dear *ff Robert*, Put your camera on a tripod, use an ASA 400 color film (I use Kodak's Ektachrome), and a lens with an f-stop of f1.4 or faster (I use a 55mm Nikkor with an f1.2 aperture). Such a film and f-stop will record flashes in real time, that is, you will get an instant recording of their luminescence on the film's fast emulsion. Thus, if you use a 10 second exposure you will record two or more flash patterns of each firefly in your camera's view, and on the film record their movement through space during each flash. Your limit in making such exposures will be the amount of ambient light that is present, such as that from a bright moon or bright skylight from reflective clouds near a big city. Hence, too long an exposure on such a night and in such a place will make your marsh of fireflies look like a daytime scene. Try different exposure lengths until you get the hang of estimating light pollution, starting at 5 sec if you are near a city, and more than simply bracketing exposures, go up in 5 sec increments. By the way, I learned this technique from David Lee, a naturalist at the Raleigh N.C. State Museum, who has an article showing exposures he made of *Photuris frontalis* flashes with this technique in *Wildlife in North Carolina* (1990, 54:23). *good luck, and illuminating trails, fd*

Dear *fd*, I've been searching for information on the Jamaican firefly (known to Jamaicans as Peeny Wally), but have been unable to find anything. I came across your name while browsing the Internet. I would really appreciate any info or leads. Prof. Karen A., OR.

Dear *ff Prof Karen*, When I was in Jamaica doing research on fireflies (note, family Lampyridae) in 1967 the term blinky was applied to the Lampyridae (what

we most commonly call fireflies and/or lightning-bugs in the USA). The Jamaican natives I talked with used the term Peeny Wally for glowing beetles of the family Elateridae (what are sometimes called cucujos in Spanish speaking countries; our common name for the family in the USA is "click beetle"). There are many species of nonluminescent click beetles. Today a native Jamaican on our faculty told me that it depends upon the sophistication of the Jamaican one speaks with — "country natives" apparently do not distinguish between the Lampyridae and the luminous Elateridae, though more educated or urban, or whatever, Jamaicans do. If I hear more about this I will let you know. *illuminating trails, fd*

Dear *fd*, Among many of us in New York City there is a renewed interest in fireflies. I would appreciate receiving copies of your "Fireflyer Companion." I am enclosing \$5.00 to help cover the cost. Please let me know if there is an additional charge. The Reverend Norman E., New York, NY.

Dear *ff Reverend Norman*, Thanks for your note with the article that you apparently prepared for your group, *Fireflies of the spirit . . . Signs of hope in modern America*. I am returning your kind donation because at the moment expenses are met by the University of Florida, I presume as part of the "Agriculture Extension" program of this Land Grant University. I must confess, Reverend, that over several years I have been writing a manual on the fireflies of New York City and adjacent regions. With a little pushing I probably might be able to finish it sooner than its present trajectory would predict! *illuminating trails, fd*

Dear *fd*, I am pleased to announce that the 1997 firefly season here in Oskaloosa, Iowa started last night 5/10/97 with the sighting and capture of the first specimen about 9 PM CDT at Keomah Village at Lake Keomah, 5 miles east of Oskaloosa. I find this early date to be amazing, especially since this spring has been cold and wet. This breaks my other all-time early sighting which happened 5/16/94. The specimen is one of those mysterious "orange" fireflies I have written you about in the past. I believe they are *Photinus granulatus*, judging from the flash pattern, but it is still not an exact match. Whatever they are, they are only found in Keomah Village proper on certain lawns and no where else. John S., Oskaloosa, IA

Dear *ff John*, Thanks for the information on your early firefly, and for the "documentation" by your colleagues. I suspect that the species is a *Pyraclomena*, possible *sinuata* or *dispersa*, and not *Photinus granulatus*. *Pyraclomena* species appear earlier in the season than do *Photinus*, and *P. granulatus* is not (yet) known to occur north of central Kansas. Museum records for *Py. dispersa* show the first collection date for ca. your latitude to be 7 May, but museum records span many decades. Yours was an early one! *illuminating trails, fd*

Dear *fd*, Can fireflies survive in the San Francisco Bay area (I have never seen one here), and is there any place where I can purchase fireflies (or eggs), assuming they would survive here? Mary Ann, El Cerrito CA

Dear *ff Mary Ann*, There are fireflies (beetle family Lampyridae) in the Bay area but none of the species in which males fly around at night emitting flashes

of light (i.e., lightningbug fireflies). In the past there have been attempts to introduce flashing species from eastern U.S. into western States but to my knowledge none were well planned or successful. Were I to try I would collect fertile and mated *Photinus pyralis* females from the northern part of this species' range — say, northern Ohio — and release them in a damp, eastern-like grassy grove in a park where insecticides were not used, perhaps an open shady place with a stream and earthworms. I am not familiar with the subtleties of Bay area ecology so perhaps you don't have such places. To my knowledge there are no merchants where you can purchase fireflies or eggs for release. With intensive effort a few firefly fanatics have raised a few individuals, after starting with many eggs, but commercially in North America firefly husbandry has not made it. The Japanese have aquatic species and have had considerable success. Perhaps if Bill Gates put his mind to it he could raise them and it would keep him from meddling with human sociology. *illuminating trails, fd*

Dear fd. Are there any fireflies — hopefully one of the "glowier" sorts — found where I live, which is a semi-arid region of Idaho about 20 miles from the ski resort of Sun Valley? Susan C., Hailey, ID

Dear ff Susan, I know of only one flashing (lightningbug) firefly from your geographic region with any trustworthy record (*Pyrractomena dispersa*), though a second one (*Photinus pyralis*) has been reported from southeastern Idaho. The latter is a well-known and common eastern species and you should look for it in places that can support "lush" grassy meadows and pastures, and along streams and rivers in the drier areas of your region. Look for *Py. dispersa* in somewhat soggy places, and in cattail and other marshes, perhaps as much as a month earlier in the spring than *P. pyralis*. *illuminating trails, fd*

Dear fd. About two and a half years ago my family and I moved to an 18-acre farm in a rural town in southeast Massachusetts. The farm has four fields, three of which are in hay, the other in corn. I was delighted to see that one of the hayfields has fireflies in June. The number seems very low, however, perhaps a couple of hundred. This field is surrounded on two sides by a highway, a third side by our home and outbuildings, and by a thin strip of woods and a shallow pond on the fourth side. The woods are really a 1–20 foot border separating that field from the next one. The trees are mainly maple and ash. The area next to the wooded strip seems to be the most popular spot for fireflies. The hay is made around mid-July. I have no idea what kind of fireflies we have. Do you have any suggestions for improving our firefly population? Danie W., Rehoboth MA.

Dear ff Danie, There are several species of fireflies in your area that occur in habitats such as the one you describe, including members of the genera *Pyrractomena*, *Photinus* and *Photuris*. I would guess that your fireflies are probably a *Photuris*, and a common species in your area is *Photuris* "LIV", a yet unnamed species that I have studied in old fields and at woods edges near Miles Standish State Forest and East Wareham, 30 or so miles east of your farm. Watch them closely for these clues: their luminescence is green, not yellow or orange; when you cup one gently in your hand it flashes and scrambles, rather than remaining dark and relatively motionless; in the field, for the first twenty

minutes (or so) of their activity all emit 2–4 pulse flash patterns, but then more and more of them emit rapidly pulsed flickers (8–15 pulses/flicker) until about an hour after sunset 50–75% are emitting such flickers. As far as improving their lot, all I can say is that we don't know enough about fireflies to say. Old fields are prime firefly areas, and though yours is a hayfield, I suppose it is the next best thing to an abandon field. Cutting the hay once a year keeps back encroaching woody vegetation. A book about restoring natural habitats on a small scale — small farms and suburban 5-acre estates — is *Noah's Garden*, by Sarah Stein. This is required reading in my firefly course. *illuminating trails, fd*

[Questions and original responses to Fireflyers have been edited and sometimes extended to focus on essential points and make improvements on original answers, fd.]

Land of the Light

John McClure

Iowa City IA

At ten o'clock we walk the perimeter of our neighborhood, and out of the tall grasses fireflies show their lanterns in patterns fire: the quarter-second flasher, the four-blinker, the upward-j-stroker, the fast yellow streaker, and the greenish-yellow slow burner.

The last may be *Photuris*, the predatory firefly, who imitates the others and attracts them to their deaths.

I feel a chill when I see her siren light.

The first three scan the lower heights, while the last two seem to favor higher altitude, and *Photuris* reaches even up among the canopies.

On warm summer evenings, the fireflies make a luminaria for our walks.

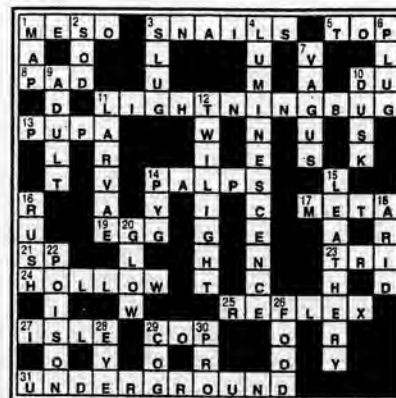
There are unlit lots in the perimeter where owners hire commercial poisoners. Only a desperate few fireflies seek a mate in those small Saharas.

In winter the poison users reverse the lighting of our neighborhood. Their properties emblazon with Christmas decorations, while the tall grasses become vacant, blackened solitudes.

We seek the monoculture of light, as does the firefly, though we care not whether it comes hot or cold, from Prometheus or Lucifer.

It is the light that cheers us on.

Answers to Issue 2 puzzle.



Reports & Observations

Impact of Truck-applied ULV Malathion On Adult Fireflies (Coleoptera: Lampyridae)

by Philip G. Hester

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John A. Mulreanan, Sr. Arthropod Research Laboratory
Florida Agricultural and Mechanical University
Panama City FL

The South Walton Mosquito Control District funded this study to determine whether adult mosquito control practices were having an influence on firefly populations in their county. The District, as many others, had received complaints about dwindling firefly populations. Because mosquito adulticide trucks are very visible with their flashing lights and noisy air blowers, and usually appear at night when most people are home and adult fireflies are active, naturally they are suspect. This study monitored the survival of adult male *Photuris congener* LeConte fireflies after exposure to ultra-low volume (ULV) application of malathion in the field.

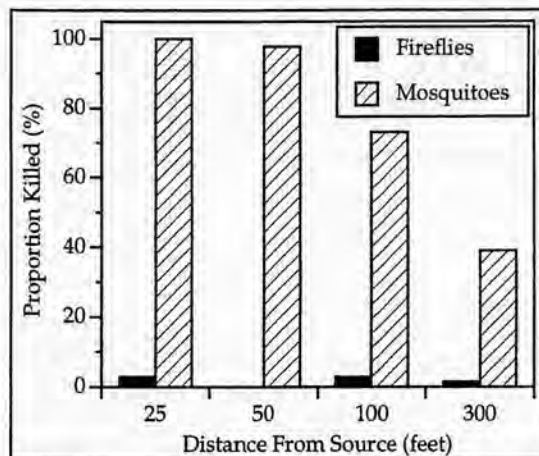
During April and May of 1997, adult male fireflies were collected at Eden State Gardens in Walton County, Florida. Nocturnal collections were made using sweepnets (Bioquip, Gardena, CA) by walking through dense understory of an oak hammock and netting flashing males from the air. The fireflies were transferred to mason jars and provided with grass clippings as a substrate and an apple slice for moisture. Within 24 hours after collecting, the fireflies were aspirated from jars and placed in steel cages in preparation for field tests. Firefly densities ranged 10–15 per cage for three tests. Twenty-five or more adult female mosquitoes (*Culex quinquefasciatus*) were placed in similar cages. After placement of the insects in test cages, the cages were covered with wet cotton pads and a cotton pad containing 10% sugar solution was placed within each cage to provide adequate moisture and an energy source.

Field test sites were selected to take advantage of the prevailing southerly and westerly winds that occur during this time of year. One site had an overstory of slash pine with a moderate understory of palmetto and gall berry. The other site had small planted pines mixed with gall berry. In each site vegetation was sparse within the first 100 feet from the road. Wind speeds varied from 1–4 mph during the test, which was considered adequate for the malathion spray to drift through the area.

Each test [experiment] consisted of exposing caged fireflies and mosquitoes at four distances (25, 50, 100 and 300 ft) downwind from the path of the spray truck. At each distance, cages of fireflies and mosquitoes were hung on stanchions at heights of two and five feet above the ground. Two cages each of fireflies and mosquitoes were placed out of the spray zone as controls. The insects were retrieved from the sites about 20 minutes post-application [after spray trucks had passed] and transferred to clean cages after temporary sedation with carbon dioxide in a "knock-down box." On the following morning, survival of mosquitoes and fireflies was assessed (i.e., ca. 12 hours after treatment) in the laboratory.

The combined results of three tests for firefly mortality [in malathion-exposed cages] was 2.9, 0.0, 2.9

and 1.5% at distances of 25, 50, 100 and 300 ft respectively, after being corrected for check [i.e., control cage] mortality (Abbott 1925). Combined mosquito mortality for these test was 100, 97.8, 73.1 and 39.0%, at distances of 25, 50, 100 and 300 ft respectively.



Based on the data from these tests, minimal mortality would be expected to occur from ground ULV applications of malathion on this firefly species. The mosquito mortality indicated that spray drift through the test area was normal since their mortality was what would be expected in vegetated habitats (Floore et al 1991). In comparison with the firefly collection site habitat (Eden State Gardens), the test sites were far less vegetated and actually represented a worst-case scenario in terms of pesticide exposure.

References: Abbott, W.S. 1925. A method of computing the effectiveness of an insecticide. *Journal of Economic Entomology* 18:265–267. Floore, T.G., C.B. Rathburn, and A.H. Boike, Jr. 1991. Ground ULV applications of Scourge and Cythion against adult *Aedes taeniorhynchus* and *Culex quinquefasciatus* in open and vegetative residential communities. *Journal of the Florida Mosquito Control Association*. 62:1.3. [Emphases and bracketed phrases by fd]

Response of Two Freshwater Snails to LED Light Sources Simulating Predatory Firefly Larvae (Coleoptera: Lampyridae)

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Abstract: The response of two freshwater snails, *Planorbella duryi duryi* (L.) and *Physella hendersoni arionum* Gould, to light-emission patterns of light emissive diodes (LEDs) simulating a predatory firefly larva, *Pyraetomena lucifera* (Melsheimer), was observed. Three LED colors — red, green, and white — were tested with three different lighting patterns: continuous glow, fast blinking (one second on, one second off), and slow blinking (five seconds on, five seconds off). Snail behavior was apparently not altered in response to these illumination patterns.

Introduction: The firefly *Pyraetomena lucifera* (Melsheimer) occurs in freshwater marshes throughout the temperate regions of eastern North America (Buschman 1977, 1984). Both larvae and adults are associated with emergent aquatic vegetation. The larvae are semi-aquatic and feed nearly exclusively on freshwater snails. Buschman reported over ninety-three percent of prey items recorded in the field were snails. He also performed rearing studies using a snail identified as *Helisoma trivolvis* (Say) (F. G. Thompson, personal communication, Florida Museum of Natural History, Gainesville, FL, believes the snail species was *Planorbella duryi duryi* (L.)).

At one time *P. lucifera* could be found in numbers at Lake Alice on the UF campus, and several unsuccessful attempts were made to obtain larvae for experiments. When Buschman investigated this firefly (1972-1977), the Lake was covered with an emergent aquatic weed that no longer is abundant. Consequently I used an artificial light source (LED) to simulate the glow patterns of juvenile *P. lucifera*.

Lampyrid larvae glow spontaneously or when they are mechanically stimulated. Glows are often irregular in frequency and intensity. The significance of larval bioluminescence remains unknown, however many authors have suggested that it provides protection from predators (Lloyd 1971, Buschman 1988), provides illumination (Lloyd 1968), or to lure prey (Lloyd 1973).

Planorbella duryi duryi (L.) and *Physella hendersoni ariomus* Gould, are two common freshwater snails found in lakes and ponds throughout Florida. In areas where *P. lucifera* larvae are found it is not unreasonable to assume that high predation pressure could [genetically, over time/generations] select for snails to respond to firefly glow patterns. These two species of snail were chosen because they are found where *P. lucifera* larvae have been collected in the past.

Materials And Methods: Fifty individuals of *Planorbella duryi duryi* (L.) and *Physella hendersoni ariomus* Gould were collected from Lake Alice, Gainesville, Florida during the first week in March 1995. In a darkened room, from a pool of fifty individuals of *P. d. duryi*, five randomly chosen snails were placed in a 10 cm x 14 cm x 19 cm rectangular plastic box filled half way with 1 liter of pond water filtered through a 32 mesh screen. The plastic arena was divided into equal sized right and left halves by a line along the underside. Snails were allowed to acclimate for five minutes. A green, red, or white¹ light-emitting diode (LED) was placed approximately five millimeters from the surface of the water at the centered extreme right or left side of the arena. An electronic timing generator designed and built for J. Lloyd by Alton Higgins was used to control the LED flash pattern. The patterns for the three LEDs were: constant glowing, blinking with a one second on one second off cycle (fast blinking), and blinking with a five second on five second off cycle (slow blinking). After a five minute interval, snails were observed and the number located opposite from LED was recorded. For example, if the LED was on the left side of the arena for a particular treatment, snails at the right side were counted and vice versa. Each test was replicated three times with a different group of randomly chosen snails. As a control for each LED color, snail position was recorded when LED was unlit. *P. h. ariomus* was then tested in the same manner. Analysis of variance (GLM) was used to evaluate the response of snails exposed to the different treatments (SAS Institute 1982).

Results: *P. d. duryi* and *P. h. ariomus* showed no apparent movement away from LED light sources regardless of color, position, or flash pattern. The control replications did not show a preference for right or left sides of the arena. MiTabs (Micro Tables) 1-3 may be enlarged on a copier for easier reading. They show: Table 1 and Table 2 summarize results of the statistical analysis; Table 3 displays control results.

Discussion: The visual powers of the Mollusca range from simple orientation to light detection in primitive chitons to shape identification in cephalopods (Morton 1958). Aquatic gastropoda [snails & kin] possess eyes at the bases of their tentacles, unlike terrestrial species whose eyes are at the tips of the tentacles (Brown 1991). The visual abilities of *P. d. duryi* and *P. h. ariomus* have not been investigated. Thompson (personal communication, Florida Mu-

seum of Natural History, Gainesville, FL) states that similar groups can detect light direction as well as motion, up to several inches.

There could be many reasons why these two snail species did not appear to respond to the LED lights. Fraenkel & Gunn (1961) state "a response to a given stimulus may not be readily apparent to an observer". The species of snails used in this experiment may have had a reaction to the LED light source that was not apparent. Perhaps detection of the light caused a rise in general activity such as increased locomotion speed. Some organisms respond to stimuli with increased metabolic processes or rates not readily apparent (Alcock 1993). Future studies of snail responses to artificial light sources could measure other such behavioral factors. Perhaps the LEDs produced a frequency [color] of light that was different from the frequency produced by the firefly larvae. Unfortunately filters were not available to modify the light frequency. A potentially ecologically important reason for the snail behavior could be that these two species are not under severe selection pressure from the firefly larvae and therefore have not evolved a response to flash patterns.

Source	DF	Type I SS	Mean Square	F Value	Pr>F
color	2	0.592592	0.296296	0.48	0.6198
position	1	0.074074	0.074074	0.12	0.7298
glocycle	2	1.814814	0.907407	1.48	0.2401
color position	2	1.037037	0.518518	0.85	0.4364
color glocycle	4	2.074074	0.518518	0.85	0.5039
position glocycle	2	0.703703	0.351851	0.58	0.5674
color pos. glocycle	4	1.185185	0.296296	0.48	0.7467

Table 1. Responses of *P. d. duryi* to LED light sources — note source parameters reported independently and then in combination.

Source	DF	Type I SS	Mean Square	F Value	Pr>F
color	2	1.333333	0.666666	1.16	0.3245
position	1	0.462962	0.462962	0.81	0.3751
glocycle	2	2.111111	1.055555	1.84	0.1736
color position	2	1.925925	0.962962	1.68	0.2011
color glocycle	4	2.888888	0.722222	1.26	0.3043
position glocycle	2	0.814814	0.407407	0.75	0.4798
color pos. glocycle	4	4.296296	1.074074	1.87	0.1368

Table 2. Responses of *P. h. ariomus* to LED light sources — note source parameters reported independently and then in combination.

Red LED	Green LED	White LED
3L 2R	2L 3R	4L 2R
3L 2R	3L 2R	3L 2R
2L 3R	2L 3R	3L 2R

Table 3. Control data (i.e., with unlit LEDs).

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Footnote: 1. Apparent color to the human eye; spectral analysis has shown that these light sources should not be used for the analysis of color discrimination.

When Fireflies Flash At Night

When fireflies flash at night, wow they are a pretty sight! The males flash to attract females to mate, but if *Photuris* find them, the males are dead bait! Fireflies taste real bad and their bite will make you mad.

If you step on them they will not smell good at all. When they are all flashing in the field it looks like they are having a ball. Kelly Gordon

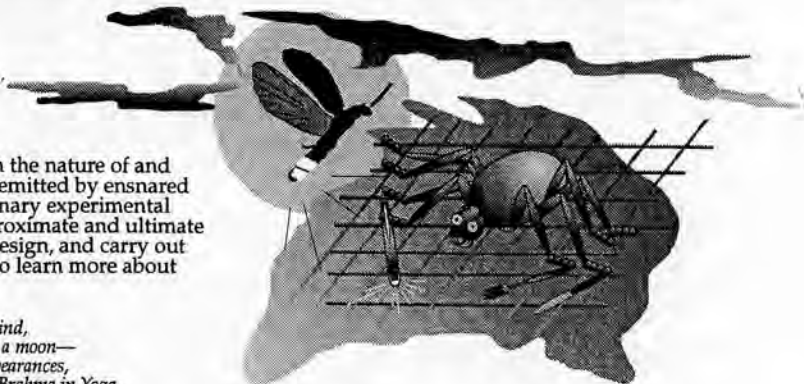
[The firefly teaching manual includes some lab and field projects that give students an introduction to little known or poorly understood subjects, with ideas to get them started on their own research. Here is a project that is fairly easy to do, and lets students explore a fascinating and enigmatic aspect of firefly behavior, and it also lets them wrestle with the evolutionary theoretical framework. Though it may be a little technical and obscure in a few spots, with respect to concepts in adaptation and natural selection, perhaps it will give you an idea of what behavioral ecologists think about. I have kept the manual's format; in future FCs I will include other "FLBs". fd]

Field & Lab 58

Grimm Spiders & Judas Fireflies: Aggressive Mimicry By Proxy?

SYNOPSIS of OBJECTIVES: Become familiar with the nature of and questions about the female-like response flashes emitted by ensnared Big Dipper (*Photinus pyralis* L.) males, and a preliminary experimental analysis of them, via the text; consider possible proximate and ultimate explanations for this behavior. Then, consider, design, and carry out experiments on males of a local *Photinus* species to learn more about this phenomenon.

Fog, smoke, sun, fire, wind,
Fire-flies, lightning, a crystal, a moon—
These are the preliminary appearances,
Which produce the manifestation of Brahma in Yoga.
(The Upanishads)



Introduction. One summer evening while stumbling over the cobbles under ash saplings along the nearly dry bed of Deshea Creek, a little east of Nashville near Gallatin, Tennessee, I saw a male Big Dipper Firefly (*Photinus pyralis* L.) receive a proper answer from three feet up in herbaceous vegetation. There was nothing unusual about the answer; it appeared yellow and was timed about right for a female Big Dipper — a half-second flash at a delay of two or so seconds. It held only passing interest for me because I was looking for a female *Photinus brimleyi*, a brachypterous (short winged hence nonclimbing?) form with a short response delay. When by chance, it would seem, I looked closer I found that the respondent was a male Big Dipper hanging in a spider's web! I then appreciated that his transexual response had been remarkably good (Fig. 1, cf a and b-i). My initial wild notion was that the captive firefly was being used by the spider to attract another firefly, with the only bait that a passing male could not resist, sex. — I then mused: Did the spider inject poison into the male, to make it answer with the proper female-like timing? Did the spider count the firefly species' coded two seconds or so, and then tug on a sticky thread to make the male flash like a female? Did the male firefly do it all himself because if he attracted another dupe, its struggles might help him escape? (no teleology intended here; i.e., read "his hard-wired innate neural circuits made him do it") — perhaps the crash of another male into the web could disconnect some of the sticky threads that held him. Did spiders of her species specialize on male fireflies for a brief window in the Tennessee summer, and during that time position their webs especially to catch Big Dippers?

Before going on I should mention my own experience with spider-wrapped fireflies. I have often unwrapped such prey to identify them for geographic distribution records. Such bound up males are not easily released, even under a dissecting microscope with fine-pointed tweezers! When spiders completely wrap their captives it is not possible that they could get free or be helped by a blundering approach of another *P. pyralis* male.

I have seen luminescent Texas Elateridae (*Dielis later physoderus*, formerly *Pyrophorus texanus*) drawn to a web festooned with glowing captives, and *Photinus pallens*, an aggregating Jamaican firefly, likewise is drawn to the "random" flashing of captive *P. pallens* in webs. I have also noted that fireflies in spider webs, or stuck in the surface of water-puddles, sometimes answer flashlight flashes (they also sometimes flash spontaneously and rhythmically — Fig. 1j). I had even questioned whether neural machinery present in and used by females to emit their own sexual signals, is also present in males, say for recognizing female responses, adopting an idea I heard from Herr Dr. Franz Huber of Tübingen, Germany, when I was a graduate student. Could somehow a reception neural system get turned into a production neural system (i.e., from afferent to efferent neural function). But, I never had seriously or creatively explored possible connections that might exist between the two phenomena, such as, for instance, in a Judas firefly. I once even denied in print that a wolf spider (*Lycosa rabida*?) holding a flashing *Photuris congener* male that attracted additional males, could be using a tool, even in a loose use of the word, or that this was any more than an isolated curiosity and happenstance. Had parsimony, like parsley (hemlock), denied an opportunity for future enlightenment?

Predation on flashing male fireflies by the use of attractive flashed signals is a common tactic of

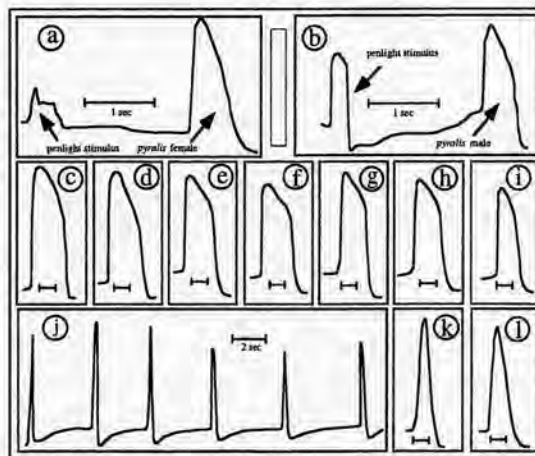


Figure 1. Tracings of pm-recordings of *Photinus pyralis* flashes, showing response delays and flash forms. (a) Response of female to penlight stimulus (16.9°C). (b) Response of male to penlight (20.8°C). (c-i) Response flashes of three males — b-d, e-i, g-i — showing similarity in form to female flashes (20.8°C); cf a & b versus k & l. (j) Train of spontaneous (free-running) flashes emitted by a *pyralis* male in spider web. (k-l) Two flashes from train in "j" showing flash form (20.8°C). Time bar in "a" and "b", 1 second, in "j" 2 seconds, in others 0.25 seconds. Note variation in the trace baselines resulting from the action of the circuit (AFC) that dampens variation in background light but also reacts to the light in flashes and lowers the baselines. This could be removed for illustration but since it does not obscure flash form it is not necessary. Note also the erratic form of the incandescent bulb in "a"; Apparently the switch in the penlight did not make a good electrical contact.

Photuris females, predators with lights of their own. Could it really be that the spider of Nashville and its Judas firefly, each with a different goal and chance of success, were "cooperating" in a grim sporting intrigue! The brothers Grimm of fairy tale fame might have elaborated on this tale, and developed a didactic message for young readers, or, perhaps, Richard Wagner could have developed an opera around a theme in which the spider cynically would give the firefly a small sporting chance to escape if he would but attract others of his own kind to take his place. In reality, one would think that a spider's chances of retaining its Judas firefly and gaining another prey are probably a great deal better than are the chances for escape by a snared betrayer. I must confess that I retain my skepticism and (must?) suspect that the male behavior is merely a lucky break for the spider. I must also, in this context mention the *Naja-Kallu*. Quoting from E.N.

Harvey's *History of Luminescence* (p.22): "It is said that about one cobra in twenty carries around in its mouth a small luminous stone that it places in the grass at night to attract fireflies, which the cobra then proceeds to eat." Aggressive mimicry by proxy, in the eastern hemisphere!

But, the haunting question yet remains. Might some of the observed behaviors in this Grimm-Judas situation have been tuned by a history of natural selection in this specific firefly-spider context? The modern naturalist's Adaptationist's Methodology requires that we tentatively (always reservedly) view such things as evolved adaptations, because perfunctory dismissal of them removes them and what they could teach us, from inquiring view and analysis. Therefore, I shall first describe my observations and experiments, and then make a case for adaptation. Perhaps this will give further insight or ideas for a next step in your own investigation.

Observations, Experiments & Results. The first Judas male was noted on 15 June 1985, and subsequently several more snared, responding males were found (<19 June 1985, and 23 June 1987), and their response delays were timed with a stopwatch or the photo-multiplier-recorder (Figs. 1-3; MiTab [=microtable] below). I timed responses that were flashed by males that I placed in the webs of both free and captive spiders, and males that were held either under strips of library tape or sheets of transparent cling-wrap over window screening. I also timed the responses of three spider-captured males in the field to the flashes of passing male fireflies. Finally, I noted the behavior of males that were attracted to captives to see how their actions might help a Judas male escape.

Some of the spiders were *Eustala anastera* and juvenile *Neoscona hentzii*, (identified by Dr. G.B.

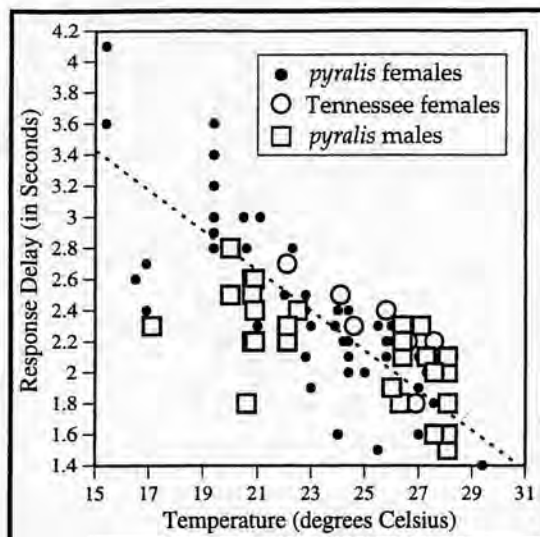


Figure 2. Individual (mean) response delays of restrained males, both natural and experimental, and those of *P. pyralis* females. Females from Tennessee are shown separately. Female data from field records, and lit.: $n = 72+$ females, 792+ response delays. The line is a least squares plot of non-TN females. Male delays are like those reported for females, but note that differences among subsets of females — geographic, age, mating condition, etc., — have not been investigated. Note also that though the delay-time/temperature relationship appears to be linear, it actually is the reciprocal of the delay on temperature (i.e., rate/temp.) relationship that is expected to be (is) linear.

Edwards, arachnid taxonomist with the Florida State Collection of Arthropods), but not all whose prey were observed were captured for identification. Considering the abundance and broad distribution of *P. pyralis*, many other spiders may so also turn their seines into Big Dipper light-traps. I have previously noted 19 separate instances of firefly capture by *Neoscona arabesca* and one by *E. anastera*, and other species (1973, p. 95).

The response-delays of ensnared males were generally within the range of female delays across a broad temperature range (Fig. 2). These included the responses of several classes of males: experimental males in the field and lab responding to penlight flashes, and spider captures in the field responding to the flashes of flying males and penlight simulations of them.

There is more within-individual variation in the delays of males (the conjectured mimics) than is found in the delays of flash-responding females (the presumptive models)².

Flash durations of Judas males also compare well with those of female *pyralis*, and average about 500 mSec at 21°C for males and females (MiTab); But, possibly of more interest than duration similarity is the fact that the shape of pseudo-female flashes is similar to that of their presumptive model (Fig. 1, cf 1a with 1b-i), and unlike that of the flashes of a spontaneously flashing male recorded in a web (Fig. 1j-l).

When attracted males ($n=3$) approached a responding ensnared male, their by-then-miniature flying J-strokes during their flashes, carried them smartly in a darting motion toward the web (Fig. 4). One male approached to 2 inches, then flew away; one struck the ensnared male and fell to the ground. The last observed male went through the plane of the web near the Judas male. Upon examination, the web was found to have a hole in it, made or penetrated by the attracted male. Thus, an unwrapped, hanging male could possibly be knocked free or have a few restraining strands of a web torn loose from him, allowing him to drop and walk free.

Discussion. Questions arising from these preliminary observations go to the heart of the adaptationist's methodology. Are the firefly and spider behaviors in this situation evolved adaptations?; How much modification, that is, natural selection fine tuning from "ancestral" behaviors (so-called "preadaptations") has occurred?; What was the evolutionary sequence, with each new step an adaptive improvement of a pre-existing adaptive behavioral package, and where (elsewhere) might we look to find them in the firefly-spider ecological web?; In the co-evolutionary view of things, what behaviors, directions, and trends might be expected to occur "next" — indeed, where

might they be found occurring now? — in some local population?

I have one somewhat troubling though elementary question: note that I identified the female-like behavior of snared males via the distinctive approximately 2-second delay of their responses; but how can we recognize similar responses in males of species whose code incorporates a very short (<0.3-sec.) female delay? Could not such a delay result (merely) from a "simple neural reflex" and not involve more central neural timing centers? Would this mechanism difference make any difference with respect to the "why" (versus "how") of it? Further, and as a challenge to the Judas-interpretation, I have suggested for *P. pyralis*, female-like responses have been noted in *Photinus macdermotti* males that are competing for females. In this species, Mr. Mac's Firefly, males will emit female-like flashes, along with a variety of others, in the presence of available mates, seemingly to confuse and misdirect nearby rival males. Perhaps, through a comparison of flash forms we will be able to distinguish the two categories (?). Finally, is it actually necessary or useful to experimentally distinguish the two conceptual categories?

Some questions

can provisionally be answered: (1) Is the delay of the Judas-flash timed by the spider and triggered, say, by a tug on the line? Tugs are not required; fireflies in webs with spiders removed, and with artificial constraints, answered similarly. (2) Are injections of venom by the spiders required to induce Judas males to express the female behavior? No, artificial constraint alone caused males to give Judas-flashes; but, a spider's injection might facilitate or fine-tune the response, making males respond more readily or for a longer time, or with more precision or accuracy. There is no evidence that contact with a web (chemicals?) is of significance (Fig. 3). (3) Are there any other situations in which males emit a flash two seconds after an observed flash? Rarely a single male in a jar of several males that were being held for experimental use, flashed at a 2-sec delay, but, more often a male flashed immediately after a flash. Neither of these delays was reported by Maurer (1968), in her extensive experiments on *pyralis*. A (the) "short-delay" re-

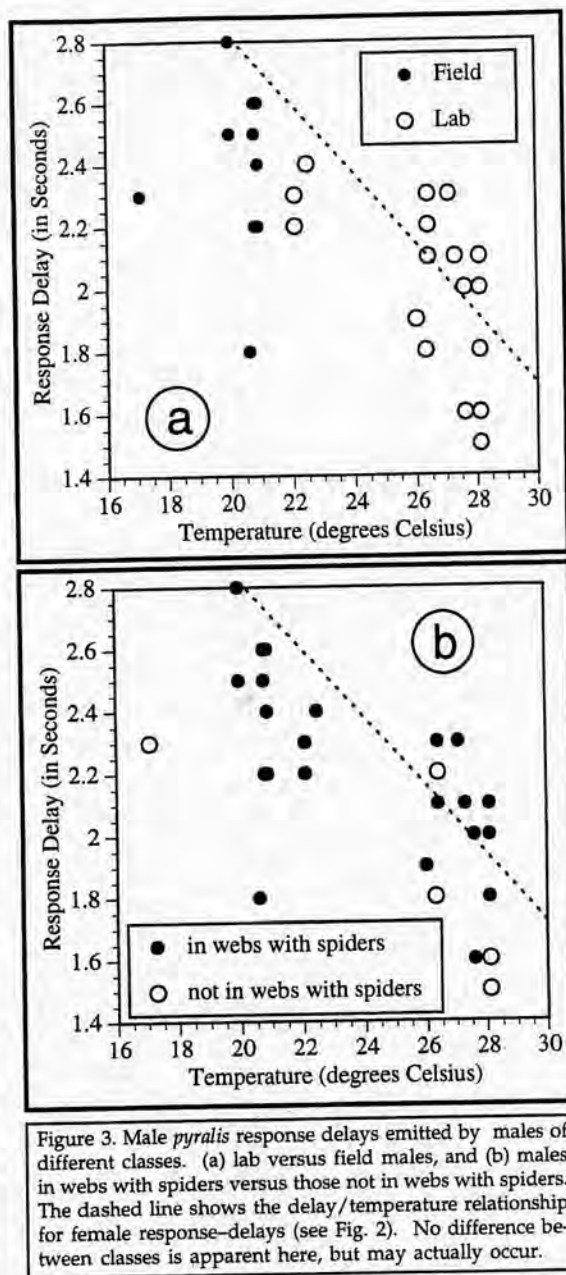


Figure 3. Male *pyralis* response delays emitted by males of different classes. (a) lab versus field males, and (b) males in webs with spiders versus those not in webs with spiders. The dashed line shows the delay/temperature relationship for female response-delays (see Fig. 2). No difference between classes is apparent here, but may actually occur.

sponse was occasionally seen in the field and was emitted by males that had landed near a Big Dipper female or decoy. This response might, as a tentative **explanatory notion**, be a tactic to misinform an approaching male that the responding available female belonged to another species, or perhaps more correctly put, "not my species."

The Grimm encounter: adaptation or accident?: For the adaptation explanation of mimicry by proxy to be conceptually satisfying, spiders must be found to treat Judas-fireflies differently from other prey in some way that enhances spider hunting success in that mode. For example, they might handle early-evening firefly captives differently from late-evening captives, or use a response-enhancing drug, or not wrap thoroughly (say, to avoid inhibiting a useful tarsal response that might block the delay-flash response), or to give differential treatment for fractious fireflies that do not behave properly, etc..

Level of selection?:

Are the fireflies, Judas males and their demates (other members of their local populations), merely victims with no chance for escape, and the spiders adapted to use them? Is there no way for simple natural (individual) selection to remove from

Big Dipper males, their neural program for betrayal of other males of their species? — is this even a useful question? Would a kin (close genetic relative) selection model involving tiny inbred populations be worth seeking in the field? Is a group (interdeme) selection model conceivable — is contemplation of such models worthwhile? At the moment, field research along such lines is not high on my list of firefly things to do, but, of course I hope to be shown wrong in this decision!

Continuing investigation: Research on this project is very simple to initiate. Capture a few *Photinus* species males, restrain them — with library tape, clear plastic wrap, actual spider webs, or something better or gentler — and present them with simulations of their species' flash pattern. Do this during the species' normal evening activity period. Data acquisition should be no problem. The trick is to conceptually recognize and then experimentally distinguish among selection explanations and contexts.

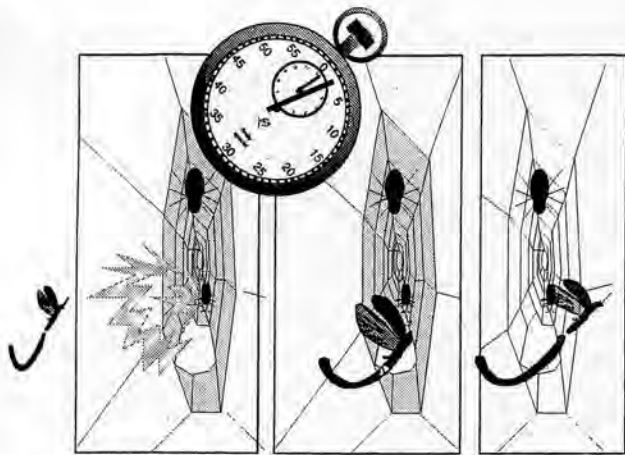


Figure 4. The J-strokes made by flashing males of *pyralis* carry them smartly forward, and in this circumstance, when responding to the flashes of males in webs, the movement can carry them through the plane of the web.

Hint (I think): do free, captive, and restrained males have different responses to their species' flash pattern versus to their species' flash code (= flash pattern plus female response)?

Footnotes. 1. Proximate explanations are those that concern the biological mechanisms involved in the phenomenon under consideration; ultimate explanations are those that concern the adaption and evolutionary considerations involved in the phenomenon under consideration. 2. Statistical treatment: Mean coefficient of variation (V = standard deviation/mean) in the responses (n = 238) of 21 ensnared or otherwise (experimentally) restrained males was 0.14 (23 test bouts; response n 's in samples ranged 2 - 39, x = 10.4; V range = 0.0-0.22); versus 0.04, in the responses (n = 331) of 27 females (43 test bouts; response n 's in samples ranged 2-21, x = 7.8; V range = 0.0 - 0.15). A significant difference is noted in this feature (V) between field (natural spider webs) and lab-tested (various experimental) males: x = 0.13, n = 9 males, 11 tests and 76 responses; versus in the lab, x = 0.16, n = 12 males and tests and 162 responses. (Mann-Whitney, U = 93; $U.05(2)$, 11, 12 = 91; 93>91, thus reject H_0)

MI Tab: JUDAS MALE RESPONSE DELAY SUMMARY: FIELD
 20.0°C [male 1] n =10 x =2.8 s =.46 r =2.2-3.8; n =8 x =2.5 s =.17 r =2.3-2.8; 20.8°C n =6 x =2.6 s =.33 r =2.2-3.2; 20.9°C [male 2] n =4 x =2.6 s =.39 r =2.2-3.1; 20.8°C [3] n =4 x =2.5 s =.47 r =2.2-3.2; [4] n =14 x =2.2 s =.39 r =2.0-2.9; 20.6°C [5] n =12, x =1.8 s =.26 r =1.6-2.6; n =1 x =1.6; 20.9°C [6] n =10 x =2.4 s =.22 r =2.1-2.8; n =1 x =2.2; 17.1°C [7] n =3 x =2.3 s =.23 r =2.2-2.6 not bitten. **LAB** 22.2°C [8] n =18 x =2.4 s =.45 r =1.4-3.0; 26.4°C [9] n =13 x =2.3 s =.41 r =1.4-2.8; 26.3°C [10] n =39 x =1.8 s =.3 r =1.4-2.3; 26.4°C [11] n =6 x =2.1 s =.41 r =1.5-2.6; [12] n =13 x =2.2 s =.31 r =1.5-2.6; [13] n =1 x =2.0; 28.1°C [14] n =31 x =1.8 s =.39 r =1.3-3.1; [15] n =3 x =2.0 s =.3 r =1.6-2.5; 27.1°C [16] n =1 x =2.3; 28.1°C [17] n =3 x =1.5 s =.17 r =1.4-1.7; [18] n =11 x =1.6 s =.29 r =1.2-2.2; [19] n =5 x =2.1 s =.31 r =1.7-2.5; 27.3°C [20] n =12 x =2.1 s =.35 r =1.6-2.6; 26°C [21] n =1 x =1.9; 27.6°C [22] n =8 x =1.6 s =.13 r =1.4-1.8; [23] n =1 x =2.0; 22.1°C [24] n =3 x =2.2 s =.38 r =1.9-2.6; [25] n =2 x =2.3 s =0. **DURATION:** Judas *Photinus pyralis* males: Summer Co. TN. 17-VI-85, 185-4, 20.8°C, ELEC: [2] 52 48 54 46 .60 46; n =6, x =51, s =.05. [3] 48 54 44 48; n =4, x =49, s =.04. [4] 62 54 50 54 54 .58 56 52 52 44 48 46; n =14, x =52, s =.05. **Grand:** n =3 males/24 flashes, x =0.51, s =.07.

References. Harvey, E.N. 1957, *A History of Luminescence*. American Philosophical Society, Philadelphia. Lloyd, J.E. 1973. Firefly parasites and predators. *Coleopterists Bulletin*, 27(3):91-106. Maurer, U.M. Some parameters of photic signalling important to sexual and species recognition in the firefly *Photinus pyralis*. MS thesis, Biological Sciences, SUNY Stony Brook.

What is Malathion Anyway?

Classification of Insecticides. Insecticides are generally grouped into the following seven different classes: Inorganics (boric acid, diatomaceous earth), Organics (limonene, rotenone, pyrethrum, botanicals, microbials), Carbamates (carbaryl, propoxur), Chlorinated Hydrocarbons (aldrin, chlordane, lindane), Organophosphates (acephate, malathion), Synthetic Pyrethroids (permethrin, cypermethrin), and a miscellaneous class that contains most others (horticultural oils, insect growth regulators). Insecticides within the same class generally have the same mode of action. Carbamates, chlorinated hydrocarbons, organophosphates, and pyrethroids are all neurotoxic

but the specific site of inhibition differs among the classes. Inorganic insecticides either cause cuticle abrasion, ultimately resulting in desiccation, or act as stomach poisons. The organic insecticides occur naturally and exhibit a wide variety of activity. The miscellaneous group contains insecticides with a variety of modes of action, but they tend to have low mammalian toxicity and generally are specific to insects. Most insecticides being developed today are in the miscellaneous group.

Mode of Action of Malathion. During normal nerve firing in insects, quantities of acetylcholine (ACh) are released from the terminal end of one neuron into the synapse and picked up by the receiving neuron at specific receptor sites. Through a series of reactions, the receptor sites initiate the production of a nerve impulse which then continues along the length of the neuron, and so on. Many of the ACh molecules are degraded before they reach any receptor sites on the receiving neuron by acetylcholinesterase (AChE). AChE molecules exist freely within the region of the synapse, providing a mechanism that keeps neurons from receiving too much stimulation. Malathion (Fig. 1) binds many of the AChE molecules. This allows a much greater amount of ACh to be transferred to the receiving neuron, causing its prolonged firing, which eventually kills the insect. An insect treated with a lethal dose of malathion will often be found upside-down, twitching, and shaking shortly before death. Because the basics of neuron action are the same for nearly all animals, malathion activity is not specific to insects (See below, Hazards of Malathion).

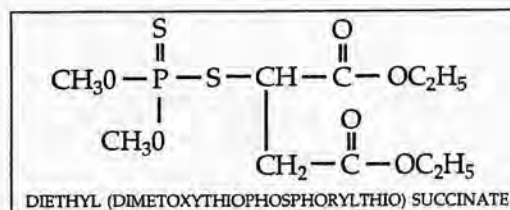


Figure 1. Structural formula for malathion.

Use of Malathion. Malathion is a general-use, non-systemic insecticide. It was developed during the late 1940s and became available during the early 1950s. Because of its relatively low toxicity to mammals, malathion has been used to control many different insect pests. It has most commonly been used to control mosquitoes, flies, household insects, head and body lice, and various sucking and chewing insects on fruits and vegetables. In Florida, malathion use began in 1960 as an adulticide to control mosquitoes, at a dosage of 3 oz per acre. Early on, malathion was formulated with diesel fuel and applied using a large thermal fogger on the back of a pick-up truck. In the late 1970s this method was abandoned and ultra-low volume (ULV) sprayers were used. With this technique, nearly pure malathion is distributed as an extremely fine mist. Treatment for adult mosquitoes is performed during the period between one-half hour before sunset until two hours after sunset. Most insects are inactive during this period but mosquitoes are actively flying about seeking hosts. Most evidence suggests that dragonflies and fireflies are not affected by malathion sprays used in mosquito control. These crepuscular insects are probably not adversely affected by malathion because of their larger size and, possibly, lack of toxin absorption through the cuticle.

Hazards of Malathion and Non-Target Toxicity. Mammals possess a metabolic mechanism that breaks down malathion, rendering it only slightly toxic. No teratogenic, mutagenic, or carcinogenic effects have been recorded from malathion exposure. However,

it is important to realize that it does have some effect and to understand its relative toxicity. Acute toxicity of insecticides are typically reported as LD₅₀ (lethal dose) estimates. This is the amount of toxin required to cause mortality in 50% of test organisms. The amount of toxin is recorded as mg of toxin per kg of body weight of test animal. The lab rat is often used for the test mammal. For comparison purposes, the following rat oral LD₅₀ values are given for four commonly known insecticides: Malathion, LD₅₀ = 2800; Boric acid, LD₅₀ = 3200; Lindane LD₅₀ = 88 - 270; Chlorpyrifos (Dursban), LD₅₀ = 160.

Malathion has very little residual activity and is rapidly degraded by sunlight. It also rapidly degrades in soil, where it has a half-life of six days. It is moderately toxic to birds and highly toxic to honeybees, aquatic invertebrates, and aquatic stages of amphibians, although its toxicity to fish ranges from low to high.

Future of Malathion. Chlorinated hydrocarbons were largely developed decades ago and their relatively high toxicity to humans has rendered most unavailable. Only a few Carbamates remain in use. Overall, malathion is considered to be one of the least toxic organophosphate insecticides available and is effective against many insect pests. However, with continuing development of new materials — such as pyrethroids, botanicals, and super-selective compounds — malathion will ultimately become less popular. Clay Scherer, UF, Gainesville.

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Mr. Scherer is in the Dept. of Entomology and Nematology at UF; he recently completed his Masters Degree and is now working toward the PhD. He assisted in the firefly course two semesters.

Nettie Maria Stevens, Fireflyer; A Pioneer Woman in Science

by Mary Parkhurst

The end of the nineteenth century and the beginning of the twentieth century were exciting times to be a woman of science in America, and in the Western World. Barriers that had previously shut out women from excelling in research and academia were torn down; for the first time, women were admitted to graduate school and female faces began to appear on the academic staffs of universities. This was a time when "a few good women" pioneered the fields of physics, biology, and chemistry, leaving trails blazed for their daughters and grand-daughters. Nettie Maria Stevens, a zoologist primarily interested in the area of cytology, was one of these pioneers who strove to apply her gifted intellect to the fullest of her capability, and succeeded in making an impact through her research and through her personage as a woman of science.

Early Life and Education

What motivated a young lady of the Victorian era to focus her life on science, to forsake the traditional role of the Victorian woman as a wife and a mother, and "angel in the house"? Although Nettie Stevens left no personal memoirs in which she spells out her deepest motivations, the answer appears to be both in her natural ability and in her upbringing, the education that nurtured her talents. Stevens was born

on 7 July 1861, in Cavendish, Vermont, to a "venerable" family of English origin, a family that was not well to do, but had a comfortable amount of wealth. Nettie's family was of sufficient means to provide her with an education that was quite thorough for the age: first Nettie attended elementary school where she "displayed quite early an exceptional ability in her studies," then she advanced to Westford Academy, "where she displayed the same clear visioned attitude," graduating in 1880.

Nettie was a promising student early on. Westford Academy nurtured Nettie's intellect with its rigorous curriculum, and its philosophy that "the school should be free to any nationality, age, or sex." It was also at the Academy where Nettie was introduced to the work of zoologist Charles Otis Whitman, who had previously taught at the school, and left his influence there. It is likely that his influence piqued her interest in the sciences, because after Nettie graduated high school with honors in every subject, she began her college education at Westfield Normal School studying virtually every discipline science offered, including physics, chemistry, physiology, botany, zoology, mineralogy, and geology. Westfield was also a progressive school — the fact that Marian Pyles, who was to become the first black female physician, was a fellow student of Nettie's clearly demonstrates the nature of the college. The liberal and thorough nature of her early schooling combined to give Stevens an excellent background in the sciences, the foundation that would support her career in zoology.

After her graduation from college in 1883, Nettie Maria Stevens worked as a librarian and a school-teacher in Westford, inspiring students in physiology and zoology before she continued her own education at Stanford University in 1896. Although no evidence remains to show that this formative period for Stevens was filled with a great deal of scientific thought, it seems highly likely that her interaction with young minds like her own and her exposure to a wealth of knowledge in the library would inspire creative thought. At any rate, Nettie's work over these thirteen years served the practical purpose of allowing her to save enough money to attend college to further study her love, zoology. Stanford University in California fit the profile of the university where a young female scientist could excel. It was youthful itself, and had a reputation for being innovative.

It was at Stanford University that Nettie truly committed herself to zoology, turning down the path that she would follow toward research and academia. Here she chose to study histology under the tutelage of Frank Mace MacFarland, who guided her in her research over the four summer vacations she spent in California. With MacFarland, Nettie pursued histological and cytological research at Hopkins Seaside Laboratory, Pacific Grove, California, perhaps the ideal location to be immersed for the first time into the methods of biological research, with an excellent variety of marine life and a lovely climate. Nettie Stevens took her A.B. degree in 1900, and soon after she also received her master's degree; her thesis dealt with protozoans — her first paper, published from the thesis, was titled, "Studies on Ciliate Infusoria."

Scientific Career

Nettie thus embarked upon her career as a researcher and later, an academician. Armed with her master's degree, Nettie returned to the East to study for her Ph.D. at Bryn Mawr college, a decision that was a point of inflection in her career. Bryn Mawr offered a unique opportunity to any student of histology or cytology. One of the eminent thinkers in these areas, Thomas Hunt Morgan the "fruit fly guru," was a teaching and research professor there. Stevens studied under Morgan for six months, and

Morgan acted as a mentor to her, until she was awarded a fellowship in Europe at the Naples Zoological Station and the Zoological Institute of the University of Wurzburg, for her excellent work. The trustees at Bryn Mawr recognized the brilliance in Nettie Maria Stevens, and they sent her abroad.

At the University of Wurzburg, Nettie came into in-depth contact with the great mystery that would become her most memorable contribution to science, the role of chromosomes in heredity. Working with Theodor Boveri, Nettie studied the fertilization of sea urchin eggs. It is quite interesting to note that Boveri did not think highly of Stevens, as her superiors in general did, for after her second visit to Wurzburg in 1908, Boveri judged her to be one of the "purest blood-suckers." Apparently Boveri and Stevens did not develop a mentor-student relationship; perhaps they did not share a similar philosophy on science.

Nevertheless, Nettie Maria Stevens must have found the role of chromosomes in heredity to be fascinating, for her most memorable contribution to science was her theory that chromosomes determine sex. She received her Ph.D. in 1903, and was subsequently awarded a postdoctoral research assistantship by the Carnegie Institute in Washington. This enabled her to focus on her work at Bryn Mawr. From 1904-1905, a very focused research period, Nettie observed the chromosomes of a great variety of insects, especially the meal worm darkling beetle, *Tenebrio molitor*, and including certain species of lightningbug fireflies — a species in the *Photinus consanguineus* complex and a species in the *Photuris versicolor* complex (of the *Photuris pennsylvanica* group). Through her meticulous observations of the different stages of fertilization, and the blessed serendipity that sex determination in some of the organisms she chose to study is based on an X/Y chromosome system, she came to the bold conclusion that sex was determined by these chromosomes. This conclusion can rightfully be deemed bold due to the very hot debate at that time over sex determination — her conclusions refuted one side of the argument, that sex was determined by environmental factors present at the time of fertilization.

Nettie Stevens was not alone in her discovery. Much like the parallel work of Darwin and Wallace, Nettie Stevens and E.B. Wilson both arrived at the same conclusions, and in 1905 published their results almost simultaneously but completely independent of each other. However, unlike Darwin, Stevens and Wilson's work did not meet with immediate acceptance in the community of cytologists. According to Thomas Hunt Morgan, the attitude toward the discovery was "skeptical or even antagonistic," due to the "conservatism" of the community. It took a decade or so for cytologists and geneticists to realize the value of the simultaneous discovery Stevens and Wilson had made. By then Nettie had died so she never saw the important role her theory played in confirming Mendelian genetic principles. Much like Gregor Mendel himself, Nettie Maria Stevens died an unsung heroine.

During her career as a cytologist Nettie Stevens did much more than the sex determination discovery for which she is best known. From 1905 to 1912, as an assistant professor at Bryn Mawr, she worked on topics such as regeneration in planarians and discovered two new species of ciliates and detailed their life cycles. Perhaps the reason that her other work in taxonomy did not stand out, was that it was mainly descriptive work; that is, it did not have the broad explanatory power that her discovery about sex determination did. The fact remains, however, that when Nettie Maria Stevens died suddenly of breast cancer in 1912 she left behind a great wealth of de-

scriptive information that laid a foundation for other zoologists, particularly cytologists.

Nettie Stevens as a Person and as a Scientific Mind

The human side to Nettie Maria Stevens is quite elusive. Documents preserved by the Carnegie Institute portray a diligent, conscientious, mobile scholar, but they do not illuminate other aspects of her life. Formal letters reveal some of her personality, but only the concerns that she was willing to express to fellow professors, concerns about her financial situation. It would help a great deal to possess memoirs written by Nettie, or a diary of a close relative, or correspondence with a friend, but none of these seem to be forthcoming. Thus, the humanity of Nettie Stevens remains a mystery.

Nor did Nettie Stevens spell out her philosophy on science, just as she did not record her original motivation for devoting her life to science. However, her absolute devotion to her life's work combines with her superior judgments, to form a picture of a very dedicated, meticulous scientist. She was also a productive scientist. Throughout her scientific career which spanned eleven years, she published at least 38 papers, covering topics ranging from ciliates to chromosomes. However, productivity does not necessarily imply creative thinking. According to her superiors, Stevens seemed to lack the ability to synthesize her observations into a theory. Thomas Hunt Morgan wrote that Stevens was able to achieve what she did because of her "keen powers of observation" and "her single-mindedness and devotion," but that her work was "wanting in that sort of inspiration that utilizes the plain fact of discovery for wider vision." Perhaps this is why Stevens is not remembered in the general history of science as the major contributor to the discovery of sex chromosomes. However, the fact remains that Nettie Stevens did make the connection between observation and theory in the case of the sex chromosomes, and this fact is testimony to her mind's capacity for creative thinking; it is also testimony to her potential to have become a great cytologist of the twentieth century, if only she had lived to develop her mind further.

Conclusion

Although Nettie Maria Stevens will not be remembered as one of the greatest scientists of the twentieth century, she is certainly remembered by those who pay attention to the details of the history, as a strong, hard-working woman of science. Stevens was a prolific, meticulous taxonomist and a cytologist who managed to make the quantum leap from observation to theory in at least one instance when it really mattered. Perhaps less important than her actual discovery of the role of chromosomes in the inheritance of sex is her devotion to science as the center of her life. This devotion helped her overcome the expectations of Victorian society, and to seize the day for all the new opportunities that were opening up to women. This devotion made her a pioneer, an example to all women of science who come after her.

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