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COMMON EASTERN FIREFLY

(*Photinus pyralis*)



The common eastern firefly thrives in Center City despite the light pollution.

Figure 12.1 Male and female common eastern fireflies on the rear wall of our house. They were on top of each other before I disturbed them to take this photograph.

In 1774 Baron Charles De Geer described and named an American firefly sent to him by Israel Acrelius, a Swedish clergyman in Christina (now Wilmington), Delaware. At the time Delaware was under the jurisdiction of the governor of Pennsylvania, and De Geer named the beetle *Lampyrus pensylvanica*.¹

In 1851 John L. Leconte was the country's authority on fireflies. Referring to De Geer's firefly as *Photuris pensylvanica*, he wrote in the *Proceedings of the Academy of Natural Sciences of Philadelphia* that the species is abundant in every part of the United States.² This firefly has since been designated the official state insect of Pennsylvania.³ It is absent in Center City, where another firefly thrives, the common eastern firefly, *Photinus pyralis*.

Deciphering firefly flashes

Frank Alexander McDermott succeeded Leconte as the regional expert on fireflies. In 1911 he published his findings on the flashes of *Photinus pyralis*.⁴ He hypothesized that the flashes of light emitted by males signal females. To test this, he lit safety matches in the evening near females. During the flare of ignition, he swung the matches in imitation of the characteristic arc made by the flash of a male of this species in flight. He blew out the matches as soon as the flares ended. He described his findings:

In each instance the flash of light from the match was followed, within two to five seconds, by the flashes of females of *pyralis* in the surrounding grass and weeds. Most of them flashed at the end of about four seconds. They did not flash in the intervals between the lighting of matches, except in response to the flash of a passing male.⁵

He then repeated his experiment, except this time he used an electric lamp to simulate the answering flash of females, which flash while at rest, typically on a blade of grass.

If the male is in a position to see the light of the bulb, he will almost invariably drop, and repeating the process will bring him up to the bulb; usually he will crawl around and over it excitedly for a few minutes, and then fly away. Sometimes males would crawl up grass stems above the bulb, and apparently looking over the edge of the blade, hold perfectly still for a moment, and then flash; the instant the bulb was flashed in answer they would commence to wave their antennae rapidly, and crawl quickly down the blade and toward the bulb. Early in the flying period of an evening, as many as a dozen males have been thus attracted in a few moments.⁶

McDermott reproduced these findings for two other species of *Photinus*. He demonstrated that each of the three species has its own flash code, which he simulated with his electric light. He tried to do the same for *Photuris pensylvanica*, but failed:

Although a quite close watch has been kept on *Photuris pensylvanica* Deg. for a considerable number of nights, nothing definite can be said as to the possible relation of its light emission to its reproductive life. A large number of these insects fly about in the trees and bushes, emitting their light in the various ways that have been described for it, and yet apparently paying no attention to each other.⁷

Discovery of femme fatale fireflies

Six years after McDermott's paper, Francis X. Williams, working in New England, unlocked the mystery surrounding the flashes of *Photuris* fireflies. He observed *Photuris* females eating males of another species of firefly. The victims were members of the genus *Photinus*, which includes Center City's common eastern firefly.⁸

One evening six females were disturbed at such meals. The fact that the victims were always males, though the females were nearly as abundant in this locality, and that the feeders were invariably females, strongly suggests that the weak *Photinus* males were drawn to their untimely ends by the lure of the greenish-yellow light of the female *Photuris*. When bottled up with *Photinus* they would readily devour the latter, despite its active exudations.⁹

Half a century later, James E. Lloyd at Cornell University extended these findings in a classic paper, "Aggressive Mimicry in *Photuris*: Firefly Femme Fatales."¹⁰ Lloyd's findings were serendipitous. In the course of his research on fireflies, Lloyd needed to collect *Photinus* females, so he searched for them by signaling with a flashlight that mimicked flashes of *Photinus* males. He was essentially applying McDermott's methods as a tool to locate female *Photinus* fireflies. He discovered *Photuris* females flashing in answer to his flash simulating male *Photinus pyralis*, the common eastern firefly. He then observed that *Photuris* females not only answered the flashes of *Photinus* males, but they lured them in, seized them, and ate them.¹¹ Later he showed that *Photuris* females have repertoires of flashes; they match the particular flashes of different species of *Photinus*, depending on which is available as potential prey.¹² Lloyd reported that *Photuris* males (which do not eat) mimic the flashes of the prey of *Photuris* femme fatales; he speculated that *Photuris* males use this mimicry to seduce *Photuris* femme fatales.¹³ He and Steven Wing showed that *Photuris* females hunt *Photinus* males not only by luring them, but also by directly attacking them in midair, guided by their prey's flashes.¹⁴ The measures and countermeasures that fireflies use to signal each other have been called an evolutionary "arms race."¹⁵

Discovery of firefly poisons

The ecological toxicologist Thomas Eisner and his colleagues showed that *Photinus* fireflies synthesize defensive poisons that *Photuris* fireflies do not produce; *Photuris* females acquire chemical protection by eating *Photinus* males and sequestering their poisons.¹⁶ *Photuris* females themselves avoid the toxicity of the poisons they eat while endowing their eggs with high concentrations of these poisons.¹⁷ Selective pressure due to *Photuris* predation may be responsible for an evolutionary switch from nocturnal to diurnal behavior in some members of the firefly family, Lampyridae. The light-producing organs in these diurnal "fireflies" are only vestigial.¹⁸

Revision of firefly taxonomy based on flashes

In retrospect, McDermott's initial bafflement over the function of the flashes of *Photuris pennsylvanica* can be appreciated in the context of femme fatales. Female *Photuris* fireflies respond to the flashes of male *Photuris* fireflies only before mating. After mating, they become femme fatales, ignoring the flashes of male *Photuris* fireflies.¹⁹ McDermott continued to delve into *Photuris* mating signals for fifty years and discovered cryptic species, based on differences in mating flashes and other

traits not detectable in museum specimens. He and an associate, H. S. Barber, concluded that *Photuris pennsylvanica* is a complex of cryptic species distinguished by their flashes.²⁰ McDermott surmised that the *Photuris* species that Baron Charles De Geer named *pennsylvanica* was probably another species, *Photuris versicolor*,²¹ which today in Delaware is more common.²² In describing the flashes, Acrelius, the pastor who sent De Geer the firefly, had told him only that “they glow and appear to viewers as thousands of sparks, but they shine even more when they fly”²³ (my translation of the French). Acrelius’s specimens are lost.²⁴

Photinus pyralis in Center City

During the latter half of June and early July in Center City, I have watched fireflies flashing in Rittenhouse Square, Fitler Square, and Schuylkill Park. They are abundant in our courtyard garden and the College of Physicians garden, which was first planted in 1914 and later converted to a medicinal herb garden.²⁵ From mid-June to early July, they start flashing around dusk, and in twenty minutes the flashing ends, except for rare stragglers. The J-shaped arc of the flash of males about a meter or less above the ground is characteristic of *Photinus pyralis*. In Center City I have yet to see *Photuris* fireflies flashing, although in a suburban garden just outside of Center City I have seen them flashing high in trees late at night.



Figure 12.2 Benjamin Rush Medicinal Plant Garden of the College of Physicians of Philadelphia, where fireflies are common. Cultivation of this site began almost a century ago. Photographed July 1, 2012, just before renovations.

The abundance of *Photinus pyralis* in Center City is surprising, even if one concedes that their flashing may make the fireflies appear more numerous than they actually are. They thrive here despite streetlights and light pollution. At night they fly to door lamps; in the day they rest exposed on doors and walls.

Diet of *Photinus pyralis* fireflies

What accounts for their abundance in Center City is unknown. Their larvae are predaceous and live underground, but their subterranean habits have proved difficult to study. Parasites of larval *Photinus* fireflies include mites and maggots from two families of Diptera (Tachnidae and Phoridae).²⁶ Conceivably Center City protects *Photinus* from parasites that do not tolerate urban conditions.

In 1868 early American entomologists deduced that *Photinus pyralis* larvae eat earthworms:

It lives in the ground where it feeds on other soft bodied insects. At times these “fire-fly” larvae must subsist almost entirely on young earth-worms, for we have found them abundantly in soil, on which no vegetation had grown for at least one year, and where in consequence there was scarcely another animal to be found, besides these two— the “fire-fly” larva feeding upon the earth-worm, and the latter subsisting on the earth itself.²⁷

McDermott reared *Photinus* larvae on earthworms.²⁸ The population density of earthworms in soil has been found to be higher in urban than rural and suburban forests,²⁹ and to increase as urban parks age.³⁰ In our backyard, two introduced species are common, the rosy-tipped earthworm (*Aporrectodea rosea*) and the common nightcrawler (*Lumbricus terrestris*). The rosy-tipped earthworm has developed tolerance to contamination of soil with lead³¹ and zinc.³²



Figure 12.3 Earthworm under a log in our backyard. Populations of earthworms take time to build up in soil. Center City’s nineteenth-century row houses are well endowed with old gardens and earthworms, prey of larvae of the common eastern firefly.

Photinus fireflies flash in large numbers over grass in Schuylkill River Park's older sections, which were completed several decades ago, but not in newer sections along the bike path, completed only six years ago. The lawn that hosts an abundance of fireflies consists of a mixture of weeds and grasses that have not been subjected to pesticides and herbicides. I do not find fireflies flashing over perfect carpets of weed-free grass, probably because of the chemicals required to achieve such perfection. Center City's rich legacy of nineteenth-century courtyards with gardens may have contributed to its abundance of fireflies. Flashes of fireflies, like songs of tree crickets, may be favorable indicators of environmental health.



Figure 12.4 Turf containing white clover (*Trifolium repens*), plantain (*Plantago*), and diverse grasses in Schuylkill Park, where fireflies are common. Fireflies are rare over “perfect” lawns—grass monocultures—dependent on pesticides and herbicides.

Light pollution as protection against femme fatale (*Photuris*) fireflies

Center City may have an abundance of *Photinus* fireflies because, among other reasons, it affords them safe haven from their primary enemy, *Photuris* femme fatales, which are absent here. Such an urban safe haven may benefit *Photinus* fireflies in much the same way as urban refuges benefited ailanthus silkmoths before their enemies moved in. *Photuris* larvae, unlike subterranean *Photinus* larvae, can be found on the ground surface.³³ Perhaps in Center City, pedestrian trampling takes a heavier toll on *Photuris* than on *Photinus*.

I presented this thought to Sara Lewis, one of the country's leading experts on fireflies. I noted that *Photinus* fireflies in Center City flash at dusk near artificial lights. She offered alternative hypotheses:

It's quite unusual to find such high firefly density in an urban environment. I'm intrigued by your idea that some environmental condition might differentially affect *Photuris* predators, and thus indirectly increase *Photinus* abundance.

It seems like there are a couple of possibilities here: soil conditions (as you suggest) or artificial lighting. As for soil conditions, I'm not convinced that *Photinus* & *Photuris* larvae are all that different in their habitat requirements (although we know remarkably little about this because they're so hard to raise in captivity). Both groups live & pupate underground, although *Photuris* larvae do forage more actively on the surface at night. Based on my own anecdotal observations, *Photuris* larvae are more generalist scavengers—for example, they'll eat cat food. In contrast, *Photinus* larvae appear to specialize on eating earthworms. Any urban gardens nearby?

Another possibility is they may have different reactions to artificial lighting—I assume these are streetlights? Because for many *Photuris* species, courtship takes place when it's fully dark, artificial lighting might be more disruptive for these than for crepuscular *Photinus* species.³⁴

The possibility that light pollution might contribute to the abundance of fireflies is counterintuitive. James E. Lloyd has pointed out multifarious ways that nocturnal artificial lighting harms fireflies, particularly by confounding and whitening out their flash signals and disrupting their nocturnal navigation systems.³⁵ Light pollution may constitute another example of “creative destruction,” in which habitat degradation benefits one species at the expense of another. Urban lighting acted this way in the case of the bridge spider, *Larinioides sclopetarius*, which feeds on insects attracted to municipal lights.

A group of firefly investigators who trained under Professor Lewis at Tufts University has collaborated with the Museum of Science in Boston to engage volunteers in the study of fireflies. It provides protocols for volunteers to collect data on firefly abundance and behavior.³⁶ Such an undertaking may clarify whether artificial lighting favors *Photinus* at the expense of *Photuris*.

Fireflies as an artifact of urbanization

In Center City, artificial lighting may protect common eastern fireflies while old gardens support their larvae. In his poem “Philadelphia,” Rudyard Kipling viewed fireflies as a natural heritage:

If you're off to Philadelphia this morning,
And wish to prove the truth of what I say,
I pledge my word you'll find the pleasant land behind
Unaltered since Red Jacket rode that way.
Still the pine-woods scent the noon; still the catbird sings his tune;
Still autumn sets the maple-forest blazing.
Still the grape-vine through the dusk flings her soul-compelling musk;
Still the fire-flies in the corn make night amazing!
They are there, there, there with Earth immortal
(Citizens, I give you friendly warning).
The things that truly last when men and times have passed,
They are all in Pennsylvania this morning!³⁷

Although fireflies may evoke the primordial past, neither Kipling's cornfields nor Center City's gardens nor artificial lights belong to that past. And in Pennsylvania, less than a quarter of the species of earthworms, which *Photinus* fireflies feed on, are native.³⁸ One would have to conclude that the abundance of fireflies in Center City is at least in part a legacy of man-made disturbance.