

ON RESEARCH AND ENTOMOLOGICAL EDUCATION II: A
CONDITIONAL MATING STRATEGY AND RESOURCE-
SUSTAINED LEK(?) IN A CLASSROOM FIREFLY
(COLEOPTERA: LAMPYRIDAE; *PHOTINUS*)

JAMES E. LLOYD

Department of Entomology and Nematology, University of Florida, Gainesville 32611

ABSTRACT

The Jamaican firefly *Photinus pallens* (Fabricius) offers many opportunities and advantages for students to study insect biology in the field, and do research in taxonomy and behavioral ecology; it is one of my four top choices for teaching. The binomen may hide a complex of closely related species and an interesting taxonomic problem. The *P. pallens* population I observed gathers in sedentary, flower-associated swarms which apparently are sustained by the flowers. Males and females remained together on the flowers for several hours before overt sexual activity began, and then pairs coupled quickly and without combat or display. Males occasionally joined and left the swarm, some flying and flashing over an adjacent field in a manner typical of North American *Photinus* species.

Key Words: Lampyridae, *Photinus*, mating behavior, ecology

RESUMEN

La luciérnaga jamaicana *Photinus pallens* (Fabricius) brinda muchas oportunidades y ventajas a estudiantes para el estudio de la biología de los insectos en el campo y para la investigación sobre taxonomía y también sobre ecología del comportamiento; es una de las cuatro opciones principales elegidas para mi enseñanza. Este nombre binomial puede que incluya un complejo de especies cercanamente relacionadas, que es un problema taxonómico interesante. La población de *P. pallens* que observé se reúne en grupos sedentarios asociados con flores los cuales son aparentemente mantenidos por dichas flores. Machos y hembras permanecieron juntos sobre las flores por varias horas antes de que evidente actividad sexual comenzara, y luego las parejas se aparearon rápidamente sin combate ni exhibición. Los machos ocasionalmente se juntaron y abandonaron al grupo, algunos volando y alumbrando sobre un campo contiguo en una forma típica de las especies norteamericanas de *Photinus*.

As in days agone, I take certain truths to be self evident: 1) that the connection between academic research and teaching is that professors who do research maintain their intellectual interest in scholarship and infect their students with a passion and love for a lifetime pursuit of knowledge; 2) that students properly taught become living repositories of this civilizing Ideal of western culture; and 3) that a true academician understands the expression "publish or perish" to mean that he publishes to give evidence that he has not mentally perished, and thus failed in his unique and special responsibilities to his students and civilization. It is in this context that I introduce fireflies that I have met, and suggest research that students can conduct, through Letters similar to those I use as substitutes for lectures in my firefly courses. The one offered here follows through on an observation that I made in last year's symposium (Lloyd 1997), that insect taxon-

omists in particular have a wealth of anecdotes and observations, and even “thumbnail” studies, that can be useful to students and phenomenon-oriented biologists—in keeping with John Sivinski’s original introduction to this symposium series. This sketch concerns the quest for an explanation for the long-puzzling congregations of a Jamaican firefly, and for an evolutionary connection between the mating behavior of this firefly and that of its mostly prosaic North American congeners.

One of the puzzles that confronted early fireflyers was the significance of the huge swarms of sedentary fireflies that were reported to occur in some exotic places in the world such as southeast Asia and Jamaica. Once pioneer Frank McDermott had discovered how the flash signal system operates in North American fireflies (McDermott 1917, see Lloyd 1990), sexual attraction in fireflies was understood to be a one-on-one operation. (Recall that in general, the male firefly searches throughout his habitat/site while flashing his species-specific signal, and when a female of his species sees, from her perch below, the appropriate signal [flash pattern] she flashes an answer, and the two maintain a pattern-answer dialogue until he reaches her.) Thus, while the huge gatherings and displays of *Pteroptyx* fireflies long reported to occur along tidal rivers and in mangrove swamps in southeast Asia made little sense, the swarming of a *Photinus* firefly in Jamaica was probably even more inscrutable—should not a *Photinus* species, no matter where it occurred, follow the same general signaling routine and mating protocol? What were the Jamaican *Photinus* doing? Specifically, if their gatherings actually were mating swarms, how did such a signaling system work, with such visual cacophony and all?; and, what was the evolutionary connection between such behavior and the general pattern observed in *Photinus* species in North America?

After the 1985 FES meeting in Jamaica I had a chance to spend a week in the field with this enigmatic firefly, and make observations on swarms along the Rio Grande River, between the Blue Mountains and the John Crow Mountains (Fig. 1). There were many gatherings in the trees and fallow fields along the river and the road that followed it up toward the highlands. The following Letter outlines key observations, provides tentative answers for the two basic questions, and suggests a working model for *P. pallens*’s mating system. In the future Lesley Ballantyne and I will publish data on morphological comparisons and luminescent emission patterns.

The Internet (electronic) publication of this paper has additional figures as AuthorLink attachments to illustrate the text; these are color slides of the study region and site, and various firefly behaviors. These are cited in text here by their number as ALR figures. For example, the figure citation in the preceding paragraph should read (Fig. 1; ALR 1998, fig. 1) because the first AuthorLink illustration is a view of the Rio Grande River and the road paralleling it. Legends for AuthorLink figures are included here in this printed version in the End Notes section. These copyrighted illustrations may be used freely with this citation: J. Lloyd, Univ. of Florida.

LETTER 23
THE UNIQUE MATING BIOLOGY OF
A CONGREGATING FLOWER-LOVING FIREFLY

Dear Fireflyers, the Jamaican firefly *Photinus pallens* (Fabricius) is one of the most interesting and curiously different species that you may ever see, and it is the best reason for going to Jamaica that I can think of. What sets *P. pallens* apart is that its sexual behavior is very different from anything yet found in any species, in Jamaica or any place elsewhere in the Americas. Recalling lessons on the comparative method in biology, this means that this firefly can provide an interesting exploration

into “adaptive” radiation, and may reveal subtle elements in the behavior of other *Photinus* that we now observe, but don't really see.

P. pallens is certainly one of the “World Class Big Four” apropos of firefly research opportunity, and I have several arguments in support of this nomination. 1) It has the richest, most complex mating protocol yet seen in any *Photinus* species, for it apparently involves a conditional sexual strategy, prolonged mate evaluation, conspicuous mutual luminescent displays with “obvious” resource acquisition, and perhaps biparental investment in offspring; 2) this flower-loving firefly with its esoteric sexual charm, commonly occurs in easily accessible, sedentary, and manipulatable swarms—I saw populations numbering in the thousands in fallow fields on the blossoms of the introduced Asian ginger-lily—and the fireflies show varying degrees of site fidelity, which seemingly is related to the number and nutritional value of the arena-plant's blossoms.

3) *P. pallens* is a large and robust firefly, and this makes field observation easier and permits marking for individual recognition, and it also simplifies dissection for analyses of individual mating and nutritional conditions that may be connected with mating behavior; 4) *P. pallens* is widely distributed in time and space, can be found throughout Jamaica and the year (Fig. 1), and it is easily identified by non-coleopterists (Fig. 2); it is readily located in the field and described to residents if help is needed in finding active populations; and 5) *P. pallens* has a taxonomic mystery about it, for though I have referred to it in the singular, as “it”, so-called *P. pallens* may actually be an array of closely-related species, incipient species, and sister and cousin populations, diverging through mechanisms of sexual preference while in micro-geographic and/or temporal isolation. On a trip to Jamaica in the 1960s I observed and recorded “a *P. pallens*” with a completely different flash pattern and saw no huge gatherings of them.

My first doctoral student, Ed Farnworth, reviewed what was known about *P. pallens* when he made an extensive study of Jamaican fireflies (1973), and made a number of observations on its behavior, ecology, and distribution. He pointed out the fragmentary nature of current knowledge, alluded to the complexity of the puzzle, and suggested that what was needed were detailed observations on the behavior of lo-

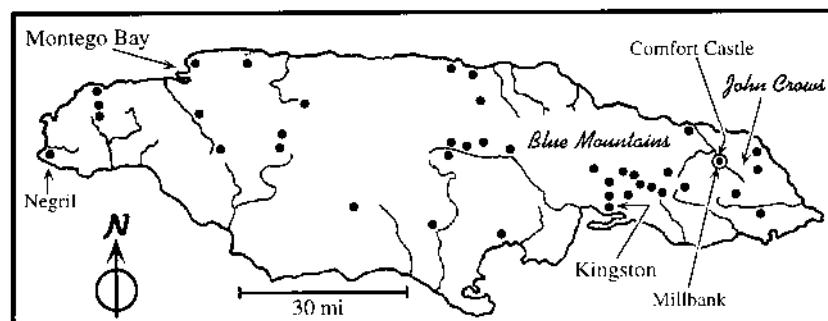


Fig. 1. Known localities of *Photinus pallens* (s.l.) in Jamaica. Elevations range from sea level to 5000 feet; there are records for every month except May. Records are primarily from Farnworth (1973), but also Leng and Mutchler (1922), and personal observation. The circled dot at the eastern end of the island, in the valley of the Rio Grande River between the Blue and John Crow Mountains, is where the observations reported here were made, near the villages of Comfort Castle and Millbank.

cal populations. In August of 1985 the Florida Entomological Society held its annual meeting in Montego Bay, and after the required formalities and speeches, two of us took to the hills, “your present author” with the *P. pallens* puzzle firmly in mind. I found a good population in a ginger lily field between Comfort Castle and Millbank, on the Rio Grande River at an elevation of about 1000 feet—but this jumps ahead in the story.

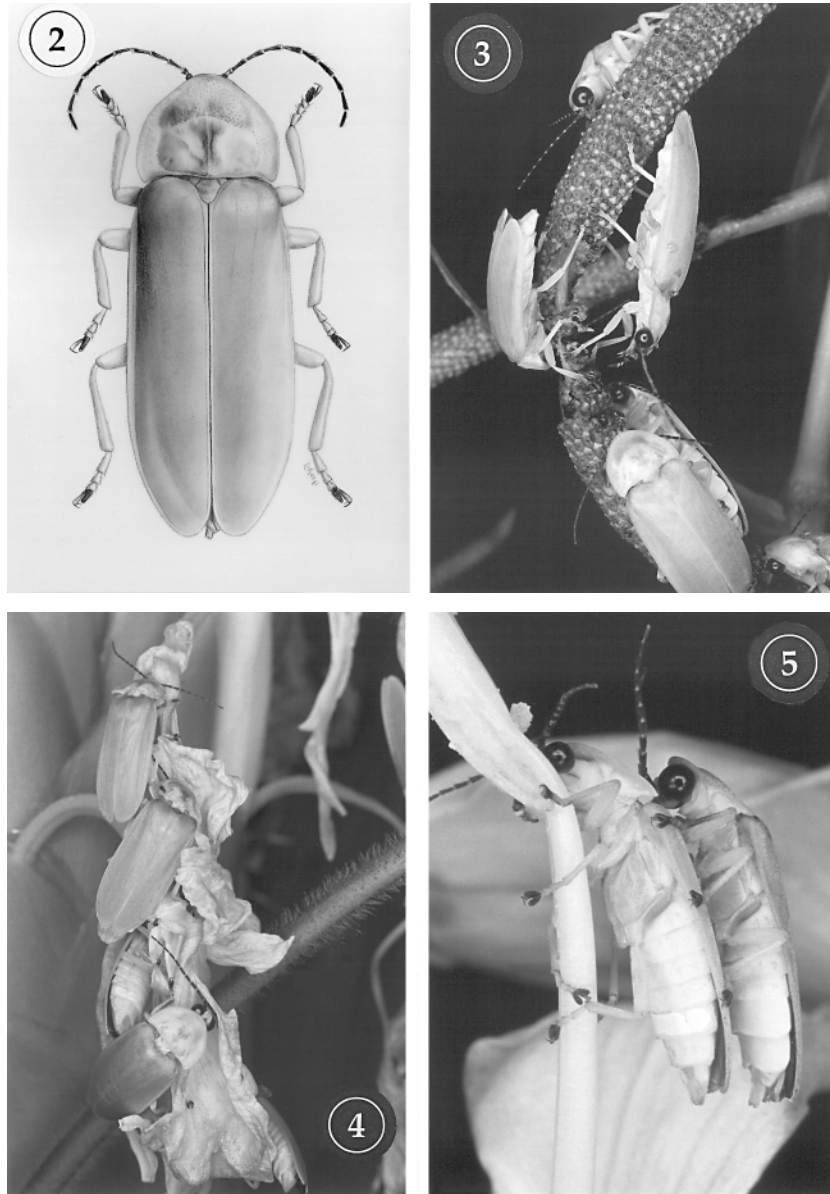
From the literature and my observations it is clear that *P. pallens* congregates on many different plant platforms: almond, rodwood, jointers, water mahoe, thistle, and others, and sometimes in such numbers that the apparition of a swarm can be seen from some dark distance. I saw several in trees along the creek called the Rio Grande River, and could see their light from distances nearly as great as the combined lengths of two football fields. Commonly such gatherings occupied only a portion of a tree, a single branch, or a discrete “patch” in the foliage, but sometimes the entire crown of a tree was occupied with flashers.

Though they occurred on a wide variety of plants and foliage types, walking along stems and on and around the edges of leaves, it was clearly the blossoms of the plants that were of special importance, for on them males and females remained motionless with their mandibles buried in the flower parts. This resulted in an interesting illusion when you looked up through the foliage of a jointers tree; individual flashing lights on the vegetative parts of the tree were separated and in motion, but points of light on the flowers were clustered and fixed along the elongate, curved spikes (Fig. 3; ALR 1998, fig. 2), and appeared as scattered Pleides star constellations in a fluid universe.

With respect to the initial formation of a swarm there can be little doubt that a single flashing individual can seed a gathering. Flashers on a patch of low grass as in a pasture, captives in spiders webs (ALR 1998, figs. 3-5), and even the red-filtered light of a head lamp being used by an entomologist who was digging singing crickets out of their burrows, attracted *P. pallens*. Though swarms formed easily, only those with flowers were sustained for very long. At blossom-rich sites such as jointers trees and ginger lily fields (ALR 1998, fig. 6), many fireflies could be seen at dusk entering the flower-arena from daytime retreats in the grass beneath the plants; “certainly” these were swarmlers from the previous night rejoining their swarm.

The Comfort Castle-Millbank region was a mosaic of agricultural and fallow fields, with borders of tall grasses and other herbs and hedgerows of various trees and shrubs. The study-site was a patch of the invasive Asian wildflower, the ginger lily (*Hedychium corium*; ALR 1998, figs. 6-7). Each flower spike had several blossoms, but it was the recently-drooped petals of mid-level flowers, not the top fresh nor the severely withered ones at the bottom of a spike that the fireflies chose to stand on and sink their mandibles into (Fig. 4). Curiously, these petals were of about the same pale color as the fireflies themselves (Fig. 4; ALR 1998, figs. 8-10), and a naturalist’s reflex would be that a protective coloration model could be proposed—but, considering the relatively recent introduction of the flower and that the beetles do not remain on the flowers during daylight, this is not likely. The site I finally chose to watch had been a taro field, was about 50 by 75 feet in dimensions, and had been plowed but not disked (harrowed) level, and with its corduroy ridges and ditches it often put me down upon my knees in the dark. Immediately adjacent to this patch was a 5-acre taro field (*Colocasia esculenta*, dasheen), over which *P. pallens* males flew, primarily very late at night, as I will soon describe.

Flashing began at the ginger-patch at dusk, in dark, well-shaded places at the ground beneath the fairly dense canopy of lilies and large leaves. Then, three to five minutes later flashing had moved up onto the flowers. As darkness deepened, a few fireflies flew in and landed on the flowers, and for a few minutes at twilight unlit flyers could be seen by silhouette. During the first hour of flashing there was some move-



Figs. 2-5: 2. Habitus of *Photinus pallens*; a carbon dust drawing by Laura Line. 3. Flowering spikes of a jointers tree, with six *P. pallens* at the blossoms. 4. Five *P. pallens* on wilted petals of a ginger lily. 5. A male *P. pallens* mounted on a female. Note the difference in lantern topography.

ment within the patch, as fireflies glowingly flew from perch to perch, and occasionally even several yards out from the swarm before returning to a flower-spike perch. Contrary to what you might expect, fireflies and other beetles are not necessarily clumsy bunglers when it comes to flying, and they sometimes fly to and from perches in very dim light with considerable precision. On the Pacific island of Espiritu Santo I once saw a large luminescent click beetle fly slowly up to the top wire of a barbed-wire fence, illuminating it with his ventral light-organ, and delicately land on the wire—the equivalent of landing a rowboat in the dark, on a powerline, crosswise, using a kerosene lantern!

Here are a couple of examples of field notes that I made during early firefly flight at swarm trees and the ginger patch: “glow start 2' out, go in and land. See another start and fly few feet to another spot . . . rise with glow, go 1 m up, go 3 m and arc down . . . 4 m high, arc back, fishtail . . . male fly from 1 plant to another, like a projectile trajectory. Like [as though] thrown . . .” During the first hour of activity many fireflies joined the swarm from elsewhere: “watch glower approach firefly tree. 80' out . . . as it got closer it got brighter . . . one in from outside [above], made a corkscrew for 4 cycles, 5" diameter . . . long glow 1/4 bright, 10-15' out, went in to tree and landed . . . occasionally see glower coming down, not know if a recruit coming in or one changing positions . . .” There also were exchanges between the swarm and nearby vegetation: “out from tree, flew around periphery in meandering zigzag course, and landed in an adjacent tree . . . out from tree, glowed and glowed, gradually touched down, 1 m high vegetation 2 m out from tree . . .”

Male flash patterns were of two major types, excluding landing flashes and glows. Males that were perched in swarms emitted fairly short flashes at very irregular intervals. In trains of these flashes, a few or several pulses were given in rapid succession and then the rate slowed and they were emitted at irregular and longer intervals. Whether each male has his own individually unique train, a signature you might say, remains to be seen. Occasionally, a flashing male on a flower walked about with his tail turned down. This resulted in his light being directed forward, and it also dragged his abdomen tip along the substrate; perhaps chemical signals and markers were being deposited?

When *P. pallens* males flew over the nearby taro field they emitted bright flash patterns, consisting of a single flare-like flash. (Such flashes were only uncommonly emitted by perched males or those mounted on females.) Photo-multiplier analysis of these flashes revealed them to be symmetrical in form, and to average about one-quarter second in duration; they were emitted at roughly 3-sec intervals. One would obviously presume that these flashes are comparable to the flash patterns emitted by mate-seeking males of our North American *Photinus* species. Males flying over the taro could be attracted to a penlight by answering their flash patterns with a quarter second flash immediately after their flash, which probably approximates their females' responses.

Females in swarms emitted trains of flashes that were visually indistinguishable from those of males. However, photomultiplier-recordings reveal some differences and careful analyses of lengthy, continuous pm-records are needed. There is one curious aspect of male and female flashing that I find especially interesting, and revealing. The sexual difference in light-organ topography of *Photinus* fireflies is well known; the lantern of males occupies two ventral segments and that of females, only a portion of one segment. As expected, when *P. pallens* males emitted flaring flashes they flashed both segments of their light organ brightly. But, when perched and emitting flash trains males emitted light from only one segment of their lantern. And, when this segment was flashed, light sometimes seemed to scintillate across or race around it, and sometimes only the middle section of it was illuminated. In other words, when

perched and flashing in swarms, males and females have similar emission surfaces—and luminous output(?). Thus the loudness of a male's statement is seemingly not of importance to him as he (apparently) competes in each little flower group, nor is his light a competing beacon for the attraction of passing females. The whispered messages of twinkling fireflies on the flowers are a key to the mating system, and it is their meaning that we must seek, to understand *P. pallens* communication and mating system.

From time to time when watching fireflies and stumped for what to do next, as a matter of habit I compulsively quantify; it may help me see and think. I counted stationary points of light in the ginger-patch by slowly scanning across the top of the arena, punching a hand tally counter with my thumb and pointing through (azimuth) space with the index finger of the tallying hand. When I compared scan-samples of flashes with actual beetle counts for several flower-spikes I found that there were 4-5 times more fireflies flashing than I could count from my stand (a 1-ft earthen hummock), which would indicate that sometimes more than 2,000 fireflies could actually have been present in the ginger lily patch!

I made such scan samples of flashing *P. pallens* at various times during several nights (Fig. 6). They began flashing on the flower spikes about 30 minutes after sun-

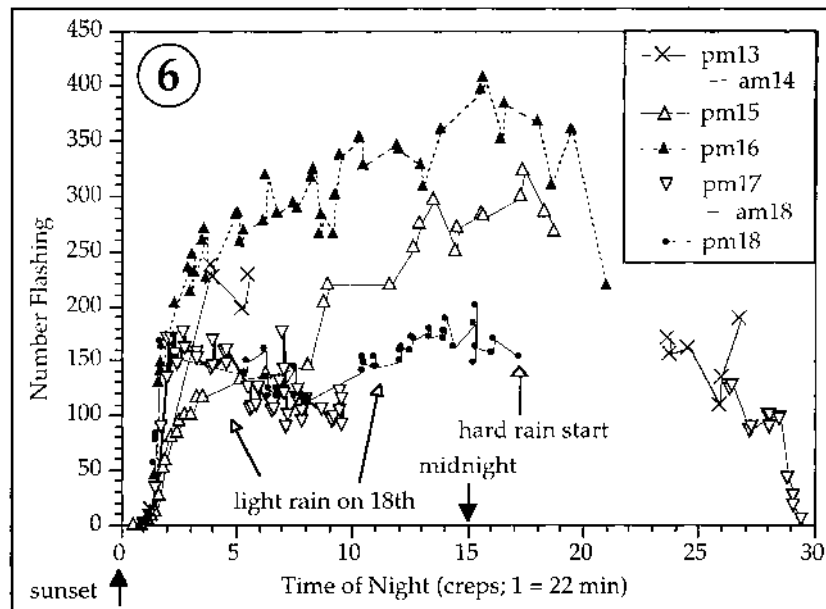


Fig. 6. Scan samples of fireflies flashing in the ginger lily field at various times during five nights. Flashing on the flower spikes began about 25 minutes after sunset, though flashing could be seen in the deep shade at the stem bases a few minutes earlier. An activity peak occurred shortly after midnight (ss + 390 min.) and activity then fell off, ending about 30 minutes before sunrise—about the time birds began singing. The biggest night was on 16 August (pm16). The last two days of observations had the least activity: one followed a warm, dry day, the other, an overcast day with light rain; perhaps the ginger blossoms or the “season” of mating activity in the local *P. pallens* population had reached a peak and was falling off.

set, and the number flashing rose sharply for the next 20+ minutes. Such flashing peaked about midnight (sunset + 360 min.) and completely ended about 25 minutes before sunrise (ss+650). At the end, with the dawn singing of birds, nearly all of the fireflies had left the flowers, most of them apparently having moved down the stems and out of sight, for I saw none in flight.

Up till now though I have alluded to reproduction, and we have come to expect sexual behavior whenever we see adult fireflies flashing, I have not actually mentioned intromission or the physical flowing of sperm and genes. Your suspense should have been mounting, and now it is time for *P. pallens* males to successfully do so—keep in mind that the time of mounting and mating in a local population or swarm could be of considerable significance for recognizing local subpopulations and even presently unrecognized sibling/sister *P. pallens* species.

In another quantification routine, I carefully scrutinized a “trap-line” of (tagged and numbered) individual flower-spikes (ALR 1998, fig. 7) at various times during the night from dusk till dawn seeking recognizable sexual activity. I finally saw it, and it began late, ca 200 minutes after sunset. Before this time of night, though “pairs” were often especially close together, mandibles buried in the same withering petal—even with cuticles touching and standing head-to-head, side-by-side, or lying across each other—nothing conspicuously sexual was noted. In fact, flower-spike samples of “touchy-touchy pairs” had various sex combinations, male/male and male/female and female/female.

Recognizable sexual pairing began when males actually mounted females (Fig. 5), and probed their terminalia with extruded aedeagi (ALR 1998, fig. 8). Males sometimes repeatedly inserted and withdrew the tip or distal portion of their aedeagus (ALR 1998, fig. 9), and at such time both individuals often flashed continuously. Perhaps it is such flashing that is responsible for an increase in overall flashing that seems to occur at about ss + 180 (Fig. 6). Also, at such times males sometimes emitted flare-like flashes, and mounted flaring males could be spotted from some distance in the ginger patch—could such flaring be “desperation arguments” being used on reluctant females? (But this suggestion biases expectations—perhaps it is the males that are the discriminating mate choosers?) The flare-flash has the same form and apparent intensity as the flare-like flash patterns that are emitted over the adjacent taro field. Females easily avoided intromission by bending the tip of their abdomens downward.

Copulation was first observed at ss + 317 minutes (Fig. 7; ALR 1998, figs. 9-10), and sketchy notes and fragmentary observations suggest that pairs may remained attached even until dawn. Soon after connecting, pairs rotated to a tail-to-tail copulation position, and some abandoned the flower petals for adjacent foliage and bracts, with one partner dragging the other backward (ALR 1998, figs. 11-12). At a dawn count, coupled pairs separated abruptly at a touch of their flower or when illuminated by the beam of the headlamp. Males that were rejected apparently did not remain mounted long nor show aggressive behavior toward other males, though I once saw a male briefly butt another that was mounted on a female.

From the aerial traffic I observed it would appear that male *P. pallens* sometimes left their ginger patch flowers and behaved like other (“normal”) *Photinus*, seeking females via search over adjacent fields. The temporal appearance of this behavior suggests that there was an intimate and functional relationship between the two activity spaces, between the ginger lily arena and the taro field, and that these two tactics are part of a conditional sexual strategy in this flower lover—conditional in the sense that on condition of mating failure on the flowery platform, or failure to find a swarm, a male (“flashingly”) takes to the air to seek a mate afield.

Male *P. pallens* flew over the taro field at altitudes up to 15 feet and their flash patterns could be seen at distances of 75 or more yards. I made a few scan-samples of

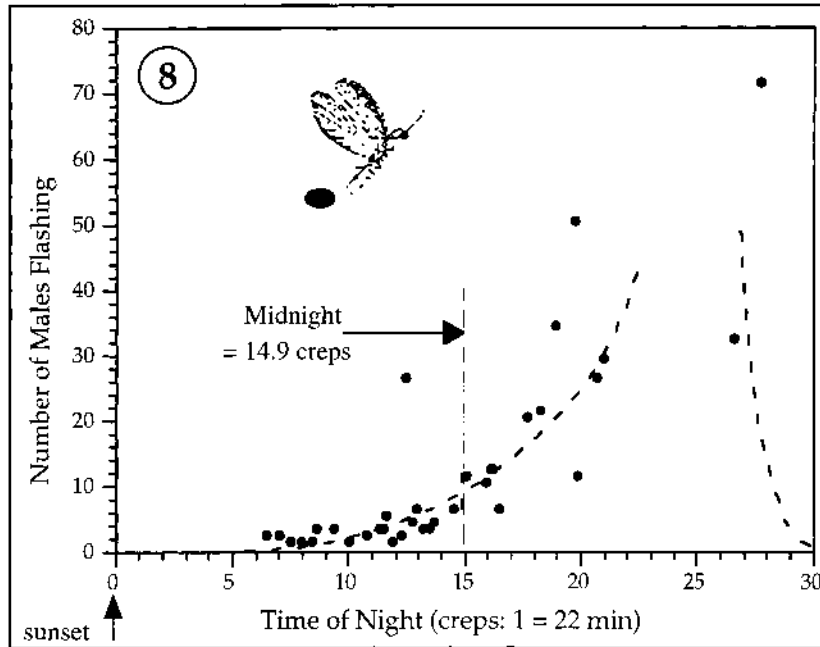


Fig. 8. Scan samples of male *P. pallens* emitting flash patterns over the taro field adjacent to the ginger lily study patch. Males flew up to 5 meters in altitude and emitted their single bright flashes each 2-4 seconds. The beginning of the sharp rise at about 12 creps coincides with the onset of overt sexual activity in the adjacent ginger lily field. Curve segments drawn by eye.

tion—in the flower-borne swarms fireflies find and observe prospective mates and they take on food and water.

The answer to the second question is problematic. We can see that to make a reasonable evolutionary connection, an acceptable historical transition from a typical *Photinus* to the *P. pallens* mating system, we need to insert a stage of lengthy precopulatory association. We might be seeking a *Photinus* species that has prolonged platonic associations at watering or sapping or nectaring holes. Although adult fireflies of various species are occasionally seen at flowers, and captives can be kept alive up to a month by providing them with honey or slices of fresh apple, only the flower-lover *P. pallens* has been found in nature in prolonged association with blossoms. You will need to peek in on the lives and sexual behavior of species that seem to be *P. pallens*' closest relatives, and *pallens* itself (i.e., s.l., in a broad sense) at other Jamaican retreats. Call your travel agent, and when you go, plan ahead to put identifying marks on adults to see, for example, whether sexual associations endure more than one night; and to provide artificial blossoms with various kinds of enriched (e.g., carbohydrate, protein) "juices" to see if they are especially valued; and to see whether molecules of nutrients that males imbibe from flowers wind up in the eggs that their mates lay—could this actually be what the long-delayed copulation and mate choice is all about? Personally, I am most curious about the possibility that the trains of flashes emitted by perched males and females are individualized signatures, because this

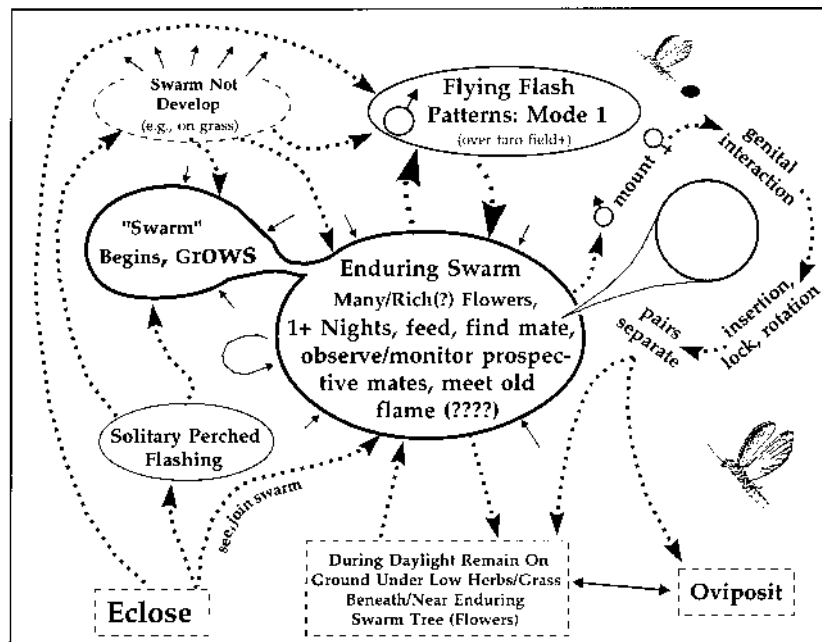


Fig. 9. Flow chart model of *P. pallens* sexual behavior, integrating observations at the ginger lily patch, the taro field, and other sites in the Comfort Castle-Millbank region along the Rio Grande River.

would connect with other insect behaviors I have found puzzling (Lloyd 1981). And, my thoughts return again and again to the fundamental taxonomist's question—just how many *P. pallens* species are there throughout Jamaica and her calendar?

ENDNOTES

I thank John Sivinski and Steve Wing for reading the manuscript. Florida Agricultural Experiment Station Journal Series Number R-06152.

The following enumerated statements are figure legends for color illustrations (slides) that appear as AuthorLink attachments to this article in the electronic publication of this issue of the *Florida Entomologist*, and which are cited in text here as ALR 1998, fig.#: 1. A view southeast along the gravel highway and upstream toward the Highlands. The Rio Grande River flows in the valley between the Blue Mountains and the John Crows. 2. Curved spikes on a jointers tree with feeding or sipping *P. pallens*. 3. A flashing *Photinus pallens* hanging and being wrapped in a spider web. The flashes of single fireflies in webs or on the ground, and even continuous emissions of light as from a flashlight attract *P. pallens*. 4. A patch of grass atop a hill above the Rio Grande River, where a few *P. pallens* gathered and flashed one evening. Apparently swarms that form at sites without many flowers do not become large nor long endure. 5. Flashing *Photinus pallens* at flowers on a spike in the grass. Though a few fireflies were attracted, large swarms were not seen at such sites. 6. A view of the ginger lily patch. Samples of flashing fireflies in this field indicate that 2000 or more may have

been present. Note the red plastic tags here and there. These mark flower spikes that were periodically sampled for firefly sexual activity. 7. A tagged ginger lily spike number 10, in the series of spikes that was sampled for sexual activity. 8. A mounted *P. pal-lens* male with extended aedeagus probing the abdomen tip of his mate to be. 9. The male in 8 and 9 (above) with partially inserted aedeagus. This connection seemingly indicates mate acceptance and requires the mechanical cooperation of both, though it is of course conceivable that males have some coercive leverage or that females can avoid using sperm that males have injected into them. 10. The connection (initiated in 8 and 9 above) is now complete, judging from external appearances, though inside the female's reproductive track there certainly are other significant events unfolding. 11. A pair partially rotated to a tail-to-tail position. 12. A pair has now completed rotated to a tail-to-tail position. Such pairs sometimes leave their flowers, where their lengthy(?) association presumably began, and remain on nearby leaves and bracts. Note the sexual difference in light organ topography.

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