Conversations with Fireflies: A Case Study of Mimicry and Defense

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Moving In

Joe sighed as he sank into the overstuffed chair in what had once been the library of Dr. James E. Lloyd, a former entomology professor at Cornell University. Joe had graduated from college in May and was excited to begin his new life as a graduate student in entomology. His new apartment was in the old house that had belonged to Dr. Lloyd, and there had been plenty of cleaning to do.

It was raining outside and he didn't feel like moving, so Joe decided to relax and take a peek at the old, tattered field notebook he had found behind a pile of junk in the garage. He settled in and opened the notebook to reveal the long-hand scribbling from long ago.

"13 June 1963. Fife, Goochland County, Virginia," read the first entry. Walking through a grassy field at dusk with a flashlight in hand, Dr. Lloyd had been hunting fireflies that warm, humid June night.

Joe's interest was piqued. He thought fireflies sounded interesting and that it must have been fun to tromp around in the field studying them. He wouldn't mind doing some research on the natural history of such magical creatures. Intrigued, Joe continued reading:

> *13 June 1963. Fife, Goochland County, Virginia.*
> *While searching in the site of* Photinus ignites, *I received a single-flash response to a quick flash of the flashlight after a delay of 5.5 seconds at 14°C. This is the delay time and flash of* P. ignites *females.*

Joe sat up straighter in his chair. Had he read that right? Did that mean what he thought it meant? Had Dr. Lloyd "talked" to the firefly? Joe knew that males flash their lights in a species-specific pattern as they fly around to attract mates. He also knew that females of the same species respond with a flash pattern of their own from their perches in the grass, thus alerting males to their presence and willingness to mate.

Joe mused that if it were true that the delay time and flash pattern were species-specific, then Dr. Lloyd had not only "called" to the firefly, but he had called specifically to the female of that particular species! Dr. Lloyd was an entomological Dr. Doolittle!

Joe's mind was tired but alert, and he wondered if the males and females of the same species have the same flash pattern. He was intrigued, but awfully sleepy. He looked at his watch and, seeing it was after midnight, decided it was time to head to bed. He put the notebook on the table, still musing about talking to fireflies. He didn't notice the next sentence of Dr. Lloyd's faded entry:

> *When collected after several more similar flash responses, this female was found to be* Photuris.

Question

1. What does this last sentence in the notebook tell you about the fireflies that Dr. Lloyd was observing?

Two Weeks Later

It had been a long but exciting two weeks as a new graduate student. Even though it was Friday night, Joe decided to spend a quiet night at home, with his mind back in 1963 with Dr. Lloyd and his fireflies. He settled into the overstuffed chair by the window and opened the tattered field notebook. As the light faded outside, his attention was caught by the following entry:

> *24 July 1963. Red Hills State Park. Lawrence County, Illinois.*
> *During the early period of activity of* Photinus pyralis *I located a* Photuris *female in a* P. pyralis *site by her flash, given 2.2 seconds after a flash from my flashlight at 21°C. This is the time delay my colleague Buck found for* P. pyralis.

Joe rubbed his eyes hard and looked at the entry again. Had he read it wrong? No, *P. pyralis* was a species in the genus *Photinus,* but the female Dr. Lloyd had found using the *Photinus pyralis* flash pattern was a female of the genus *Photuris.* That's what it said all right.

"That doesn't make sense," Joe said aloud. "I thought I read last time that the flash pattern was species specific. What's a Photurus female doing responding to a Photinus signal?" He turned the page and found the following entry:

> *24 May 1964. Gainesville, Alachua County, Florida.*
> *In the site of a large population of a species in the* Photinus collustrans *complex, two* Photuris *females repeatedly answered my single flash with a single long pulse, 1 second in duration, after a delay of about 1 second (the flash-and-delay-characteristics of this* Photinus *species). No* Photuris *males were seen.*

Joe thought things were getting stranger still. What were females doing responding as if they were a different species? Was Dr. Lloyd seeing things? Joe turned out the light and went to bed.

Three Months Later

It was raining again, and Joe felt depressed and discouraged. He had been working on his own research for three months, but so far none of his experiments had been successful. He decided to visit with Dr. Lloyd and his troublesome research. Maybe the fireflies would cheer him up on this dreary evening. He turned to the following entry:

> *6 April 1965. Gainesville, Florida.*
> *The flash pattern of males in one species of the* Photinus consanguineus *complex consists of two short pulses separated by about 2 seconds. This phrase is repeated every 4 to 7 seconds. While searching for females I received a response from the direction of a low weed along a stream. The flash appeared greener and brighter than usual, and upon investigation I found a large (14-mm) black* Photuris *female. One 11-mm black* Photuris *male was later caught which emitted single, ragged, flickering flashes at intervals from 3 to 5 seconds in duration.*
>
> *I watched this female for the next half hour, and during that time she responded to 12 passing males of the* Photinus *species with a single-flash response similar to that of the females of this species—a single pulse about 1 second after the second male pulse. All of these males were at least partially attracted to her. One flew into the stream. Two flew into the grass below her and*

then she stopped answering them; presumably she couldn't see their flashes. Eight of the males were attracted to within 1 meter of her and then she stopped answering them.

While answering, she would occasionally flash after the first male pulse and then again after the second pulse. Usually she answered only after the second pulse. I also noted that, as the males neared her, she greatly reduced the intensity of her flashes. The last male attracted, after three or four flash exchanges, landed about 7 cm from her. After another flash sequence I turned on my light and found him 15 cm from her. Following the next flash exchange, after a pause of 10 to 15 seconds, I checked and found she was clasping him and chewing on him!

Joe's eyes lit up as bright as a firefly. He thought he saw what was going on, and if he were right, it would be the coolest thing he had learned about insects yet! And if those fireflies were doing what he thought they were doing, he had an awful lot to learn about how their behavior had evolved, and why they were doing it. He decided to see if there was more information on this in the library because surely there were unanswered questions. Maybe he could dump his research project and revive Dr. Lloyd's research.

More Questions

2. What further research questions regarding the behavior of the Photuris females are raised by these observations?

3. Propose two hypotheses explaining how this behavior might be advantageous to the Photuris females.

4. Design an experiment to test one of your hypotheses. Be sure to identify your dependent and independent variables and control treatment.

References

Lloyd, J.E. 1965. Aggressive mimicry in Photuris: Firefly Femmes Fatales. *Science* 149 (3684): 653–654.

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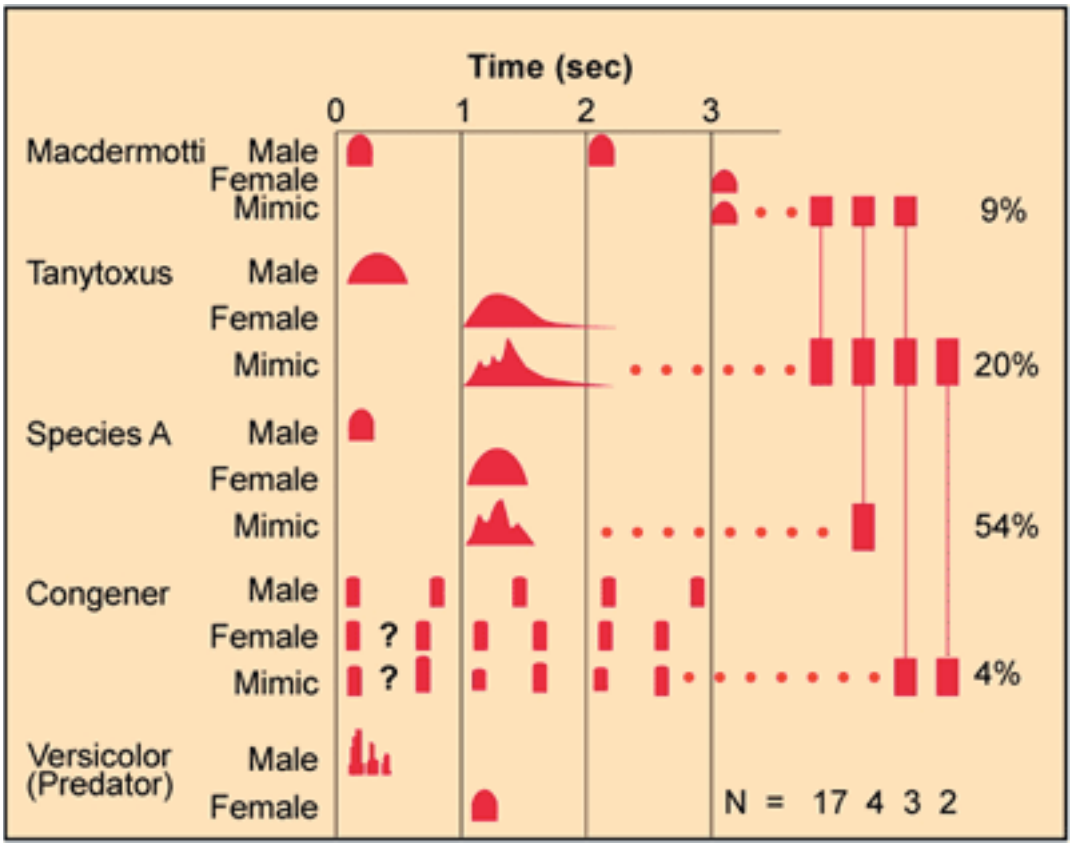
Handout 1

The figure below portrays the luminescent signals of selected fireflies. The response used by the predator is shown beneath the female it mimics. Vertical bars at right indicate observed individual repertoires; N is the number of females exhibiting the repertoire. Capture rates (percentages) are adjacent to prey species. The flash rate of the congener female is variable, and the specific nature of the coding is unknown.



Prey species:
Photinus macdermotti
Photinus tanytoxus
Photuris sp. A
Photuris congener

Predator/mimic:
Photuris versicolor
(i.e., femme fatale)

Questions

1. What do the black horizontal humps represent in the body of the graph?
2. In general, what information does this graph convey?
3. Compare the normal mating flash-response pattern of the femme fatale with that of the mating signals used by her prey species.
4. How perfect does the mimic have to be?
5. What are the potential benefits of this predation strategy?

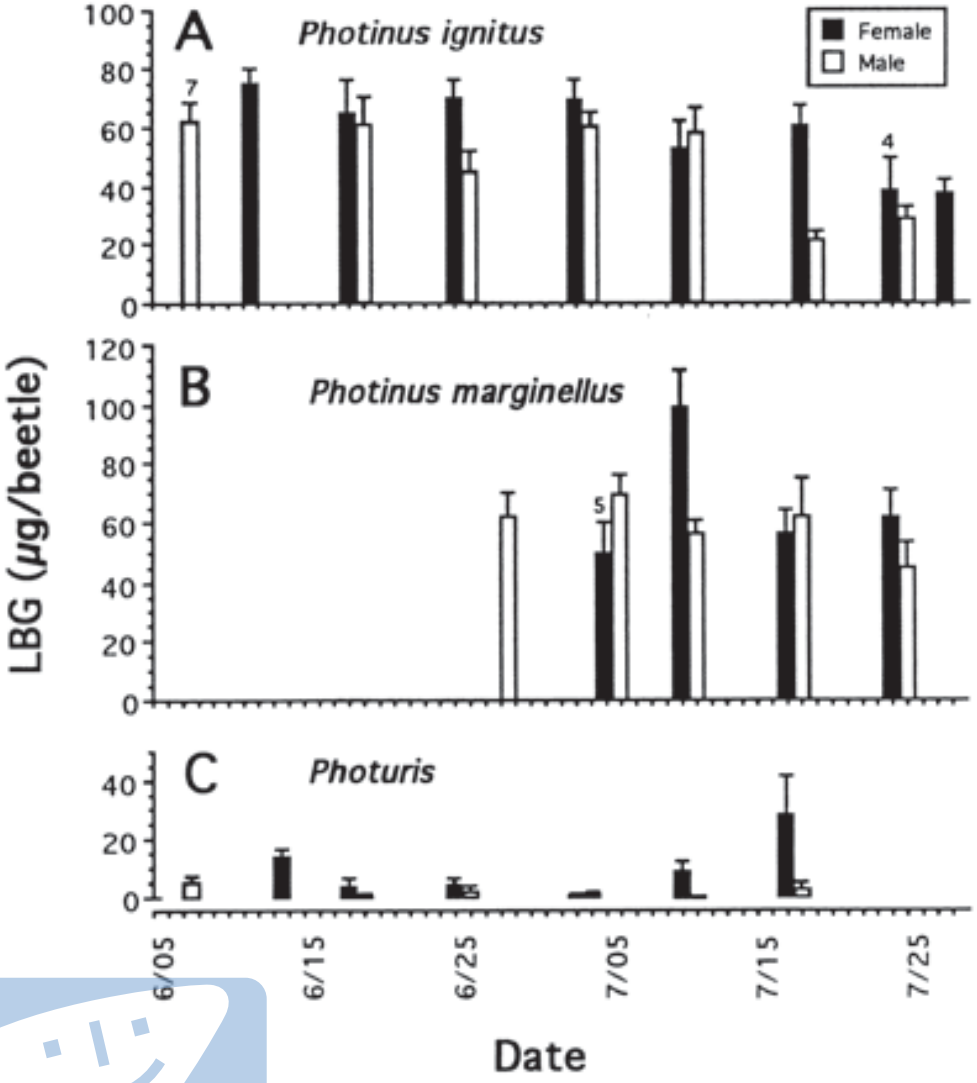
Image Credit: Figure adapted from "Aggressive mimicry in Photuris Fireflies: Signal repertoires by femmes fatales" Lloyd, J. E. (1975) *Science* 187(4175): 452–453.

Handout 2

Firefly femmes fatales acquire defensive steroids (lucibufagins) from their firefly prey.

Body LBG* content of field-collected male and female fireflies, plotted as a function of date of collection (Ithaca, NY); n = 10 per column, except where otherwise indicated. Note: *P. marginellus* appears later in the season than the other two fireflies, accounting for the absence of samples of this species for most of June.

** LBG = a chemical class of cardiotonic steroids known as "lucibufagins." These compounds are structurally similar to steroids produced by Chinese toads (*Bufo *spp.), which are known to be toxic to many vertebrates. The name "lucibufagin" is a combination of the name of the chemical that produces the light in fireflies (lucferin) and the toad's name (bufo).*



Questions

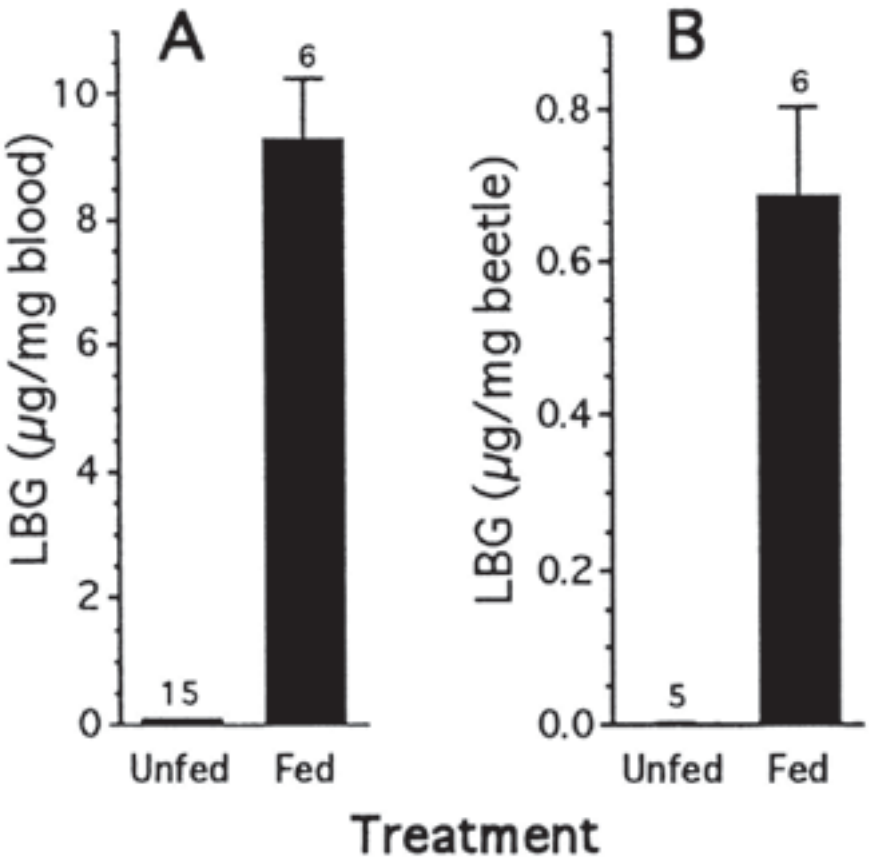
1. How do Photinus spp. compare to *Photuris* spp.?
2. How do males compare to females (*Photinus* spp.)?
3. How do males compare to females (*Photuris* spp.)?

Image Credit: Figure from Eisner et al. (1997) *Proceedings of the National Academy of Sciences* (USA) 94: 9723–9728.

Handout 3

LBG content of *Photuris* females that ate two *P. ignites* males (n=6) or were kept unfed (controls; n=15).

LBG values are expressed as concentration (in blood [Graph A] and body [Graph B]). In both cases, differences were significant (t tests, $p<0.01$).



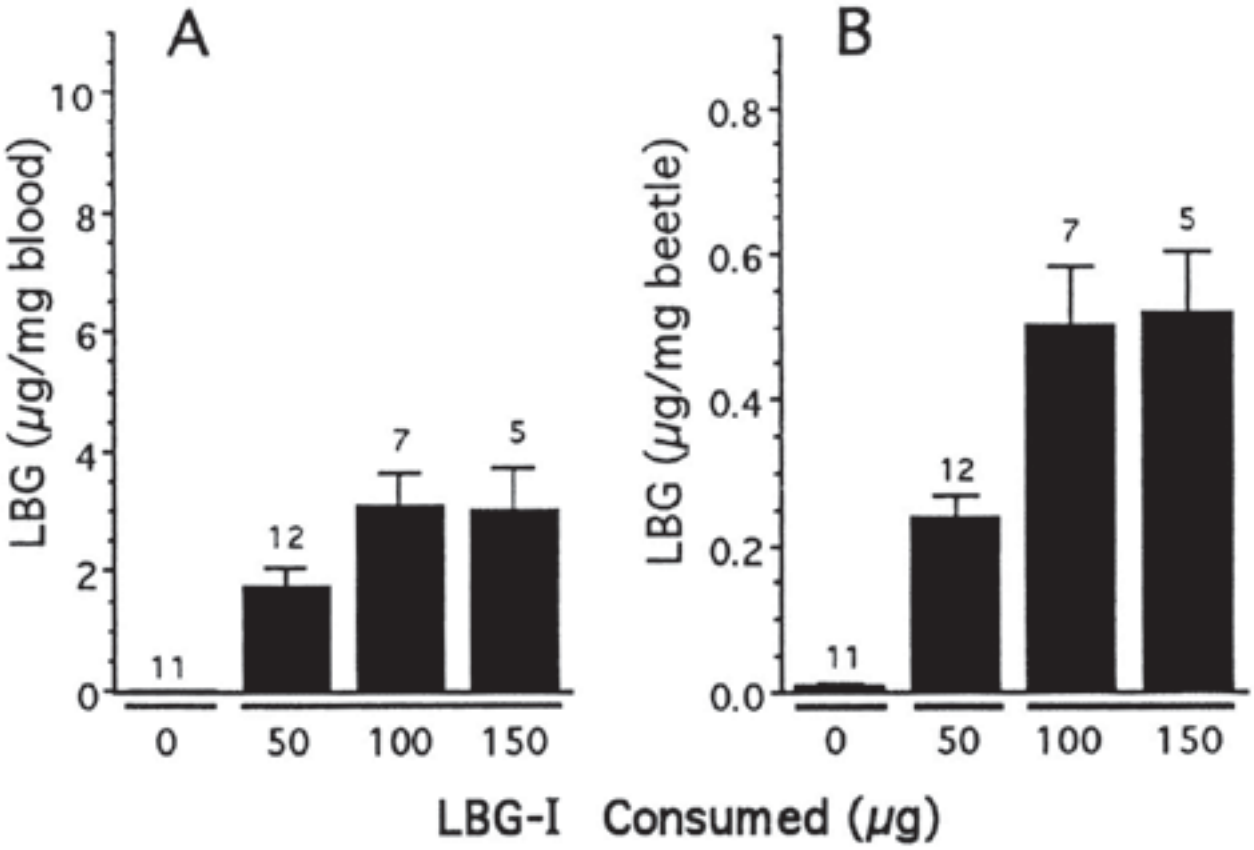
Questions

1. What can you conclude about the presence of LBG in Photuris spp. females?
2. Given that Graph B represents the concentration of LBG in a whole beetle that was ground up (so it includes both blood and other tissues) and that Graph A represents the concentration found in the blood alone, what can you conclude about how the LBG is distributed in the tissues of the fed females?

Handout 4

LBG content of *Photuris* females, plotted as a function of LBG-I consumed.

Data are presented as concentrations as in the previous Handout 3. In both cases, significant differences were detected [ANOVAs of log (x + 1) transformed data, $P<0.0001$]. Within a plot, columns not sharing underlining are significantly different (experiment-wide alpha = 0.05).

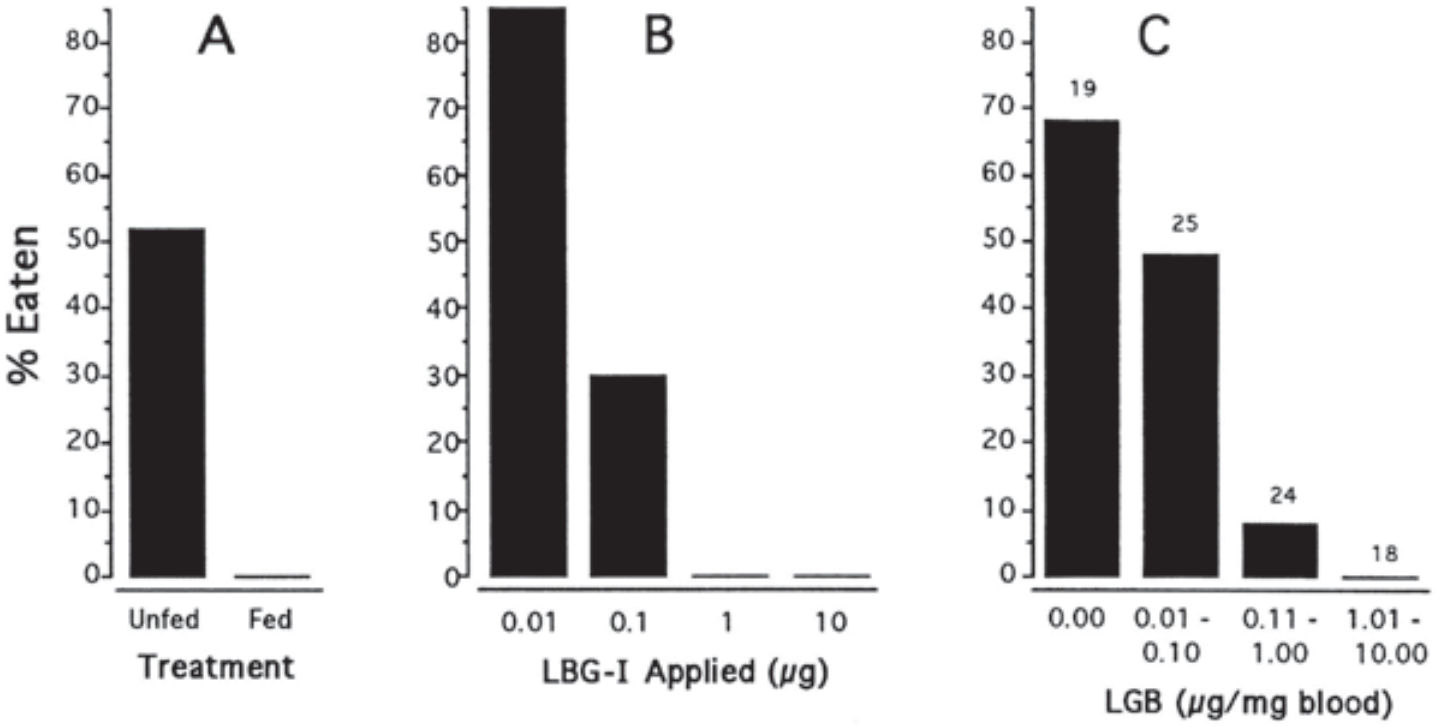


Questions

1. What conclusions can you draw based on these data?
2. In this experiment the scientists fed Photuris spp. different LGB concentrations. Why was this a necessary experiment?

Handout 5

Predation tests with *Phidippus* spiders (Graph A and Graph C, *P. audax*; Graph B, *P. regius*).



Graph A—Acceptability of *Photuris* females, plotted as a function of whether or not they had eaten two *P. ignitus* males (n=29 per category) [i.e., unfed are *Photuris* females who have not eaten the *P. ignitus* males, and fed are those who did eat them].

Graph B—Acceptability of the fruitfly *Drosophila melanogaster*, plotted as a function of quantity of LBG-I added topically (n=20 per category). Note: *D. melanogaster* are small flies that are readily available for purchase and are easily reared in the laboratory. By using them as a stand-in for the fireflies, the scientists ensure that the results can be attributed to the LBG and not something else in the fireflies.

Graph C—Acceptability of field-collected female *Photuris*, plotted as a function of LBG concentration in blood. Acceptability was dependent upon treatment (A and B) or blood LBG content (C) (G-tests, in each case, $P<0.00001$).

Questions

1. Given the fact that *Phidippus* spiders are common predators of fireflies, interpret these graphs.
2. What result would you predict if you offered male *Photuris* to the spiders?

Homework Assignment—Putting it all together

Write an abstract for a paper based on this case. Emphasize the following points:

- the behavior;
- how the system might have evolved (what pre-existing conditions were the foundation for selection of this behavior?); and
- why the system might have evolved (what advantages are conveyed by predation?).