ON RESEARCH AND ENTOMOLOGICAL EDUCATION, AND A DIFFERENT LIGHT IN THE LIVES OF FIREFLIES (COLEOPTERA: LAMPYRIDAE; *PYRACTOMENA*)

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ABSTRACT

Research at institutions of higher education could be restored to at least a shadow of its original role through publication in a manner appropriate for immediate classroom use, with questions that pique and direct the interests and activities of students. Studies on basic natural history may be good candidates for such publication and an example is drawn from fireflies: Two woodland species show directional orientation in their pupation sites on the trunks of trees; one uses southerly exposure and the other occurs on the north side of smaller trees, and much lower on the trunks. These contrasting positions have different thermal consequences, as demonstrated with a physical model, which possibly have a role in reducing interspecific sexual contact or prey competition.

Key Words: fireflies, behavior, life history, orientation, ecology

RESUMEN

La investigación en instituciones de educación avanzada podría ser restaurada parcialmente a su rol original a traves de publicaciones, de manera tal que las mismas puedan ser usadas para enseñar, con preguntas que atraigan el interés de estudiantes y que se relacionen con sus actividades. Los estudios de historia natural básica pueden ser buenos candidatos para ese tipo de publicaciones, y un ejemplo del mismo se puede obtener con luciérnagas: Dos especies de luciérnagas muestran diferencias en la ubicación de sus pupas en los troncos de los árboles; una especie las ubica expuestas hacia el sur y la otra usa el lado norte de árboles mas pequeños y en la zona mas baja del tronco. Estas posiciones contrastantes tienen diferentes consecuencias térmicas, como se demuestra con un modelo físico, las cuales podrían tener un papel en reducir el contacto sexual o la competencia por alimento entre las dos especies.

In times past it went without question that the connection between research and teaching was that professors who did basic research maintained their intellectual interest in scholarship and passed on to their students an inquisitive attitude and love of the pursuit of knowledge as the essence of life and a life-sustaining spirit. Students thus became living repositories of what was then acknowledged to be a civilizing Ideal of western culture. An academician of the time translated the expression "publish or perish" as meaning that if he did not publish he had mentally perished, and in doing so was failing in his professional responsibilities to his students and his civilization. Over the past 30 years this fundamental understanding and connection has been eroded and forgotten, and a great deal of what is now done as "scholarly publication" has little direct bearing on a "civilizing education."

The essence of scholarly research is discovery and originality. In my experience, good students find it more interesting to actively participate in doing something that relates to discovery than to see someone else do it on TV. It is worth exploring to determine whether some primary publications in science could be written directly for the classroom, rather than for the narrow and generally disinterested "readership" of a scientific journal, even leaving some obvious refinements for students to manage. Original research papers could be used as texts, and beginning students have direct contact with researchers themselves—who could speak directly to them in their papers, and then perhaps personally through the internet, thus achieving a quasi-oral tradition of wide dimensions! Students would use an original publication as a source of information and to stimulate their imaginations for initiating their own school-time and life-time pass-time research. What once might have been a scarcely read, esoteric and expensive "contribution to . . ." could be an informative introduction and background with suggestions and questions for personal projects and class discussion. Though it pains me to admit it, fans of electronic publication may be the first to see the desirability and simplicity of doing this.

There is another twist to this notion. Since I have chased fireflies for about a third of a century, I am often asked by citizens and reporters, by letter and phone, "what is happening to the fireflies, I don't see them anymore?" Only people who once knew and pursued fireflies can ask such a question, because those who have never known them cannot miss them. Similarly, might not students who learn by reading and doing original research and see it in connection with their personal education, understand and care more about what we have long considered to be the intellectual values and strengths of an enlightened civilization? The irony, the flip side of this is that here I address this notion to many who have never seen a firefly.

Obviously, some research subjects lend themselves to such instruction better than others, because of technical complexity and expense, but there are many available sources of inspiration. As John Sivinski has pointed out, one unfailing repository of observations and ideas worth developing are the anecdotes, sketches, and speculations that insect naturalists accumulate. From my search for new sources and angles, I would add that many taxonomists especially know what is lost to lab-bound and urban biologists, because of their solitary hours of collecting and observing their quarry in the field, which are as basic field investigations, typically followed by solo hours of contemplation as they curate their specimens. I have found that much of what can be done with firefly taxonomy and behavior can be used almost immediately in the classroom. It should be as a personal goal and measure of scholarly accomplishment and fulfillment to see the development of some significant area of insect research begun and developed by undergraduate students in a teaching/research connection. Think of the satisfaction that graduates would enjoy when they subsequently saw their own studies used in a general entomology text.

For several years I have taught a general biology course entitled *Biology and Natural History With Fireflies* in which every class meeting is a field trip or lab and involves some research-related activity. Instead of giving oral lectures, I write the students letters; instead of laboratory and field exercises with recipes and empty lines to write on, I give them a background text on a subject, the material and equipment they may want to use, and directions so they can do some things they will find interesting. English, religion, architecture, microbiology, German literature, journalism, pre med., and animal science majors, to mention a few of the represented fields, experience first hand the basics of biological research, including the design of empirical studies and the gathering of data, the use of statistical analysis, and the value of models and theoretical perspective. During class meetings students are only required to be focused and interested, and try to accomplish what they recognize with increasing skill as sound biology.

As an example, the "Letter" below provides the introduction and background for a number of field studies that students can make in winter in a flood plain forest in Gainesville, about two miles from the indoor classroom. The Letter is modified for use here. Scientifically, this Letter is the first publication of the outlines of a seemingly simple but perhaps very complex element of firefly biology. The Letter omits statistical descriptions and analyses, which are a field/lab experience themselves, but illustrates the observations and raises questions that students anywhere in the geographic range of the species can discuss and independently or jointly pursue in the lab and woods (Fig. 1). More than this, when students begin to address specific questions about this apparently simple behavior of mere beetle larvae, they discover that it is potentially so complex that it may never be completely understood, and for them this itself is encouragement to continue, to enjoy the study, and sometimes to see such biology as also of the arts and humanities.

LETTER XIII: A DIFFERENT LIGHT IN THE LIVES OF FIREFLIES

Dear Fireflyers, When fireflies and light are mentioned in the same breath, one reflexively thinks bioluminescence, and of the use that fireflies and taxonomists have made of pulses of living light for species recognition, that behavioral ecologists have made of firefly flashes for studying mate competition and mate choice, and finally, of the use that biochemists, cell biologists, and physicians now make of bioluminescence chemistry for enzyme analysis, cell physiology, exobiology (extraterrestrial life searches), and medical diagnoses. Our knowledge of firefly flash communication in nature began with the incidental observations of a chemist, Frank McDermott, who went to the field to observe fireflies out of an interest in the mechanism of their luminosity, but stayed to discover that some lightningbug species can be distinguished by their flashed mating signals. What I will tell here began with a taxonomist's interest in getting a photograph, and became an enigma in the realm of what some might call environmental physiology. It is about a connection that some fireflies have with light other than through their remarkable ability to generate it.

The larvae of one species may use sunlight to hasten or perhaps, maybe, even to manipulate their pupal duration and adult eclosion time ("date"). *Pyractomena* fireflies, and perhaps all of the fireflies in their tribe (Cratomorphini), unlike other lampyrids that do it in hidden chambers underground, climb up on vegetation to pupate. Aerial pupation was reported by Francis Williams near the beginning of the passing century and observed in some detail by Lawrent Buschman, who examined this behavior in the marsh-inhabiting species *Pyractomena lucifera* (Melsheimer). Aerial pupation would seem to be a reasonable adaptation for larvae that live on emergent vegetation over water and hunt the aquatic snails below, or that could have their habitat submerged by the flood water of a creek or river spilled out of its banks onto adjacent flood plain. *Pyractomena borealis* (Randall) pupae hang on tree trunks, by means of laterally projecting points that extend into their cast larval skins they previously glued to the trunk by the tail-end. At eclosion, the pearly-white, teneral adults walk a few centimeters leaving behind the larval and pupal skins and dangling tracheal linings, and remain motionless until their cuticle has tanned. Sometimes adult males are found waiting next to or on top of pupae (female only?; Fig. 2).

In the winter of 1982-83 I visited the flood plain forest along Possum Creek in Gainesville to get photographs of pupating *Pyractomena borealis*, whose adults I had seen flying and flashing there in considerable numbers the previous March. I found one, then several, then numbers of them, and it soon became obvious that they did not occur randomly over the tree trunks. Sometimes pupae occurred together, sometimes alongside vines or in crevices, and occasionally below twig bases. They used trees of several species and bark textures, usually anchoring themselves between knee and basketball-rim height. I returned again and again for more photographs, notes, and measurements of pupation locations. Then, larvae and pupae of another woodland

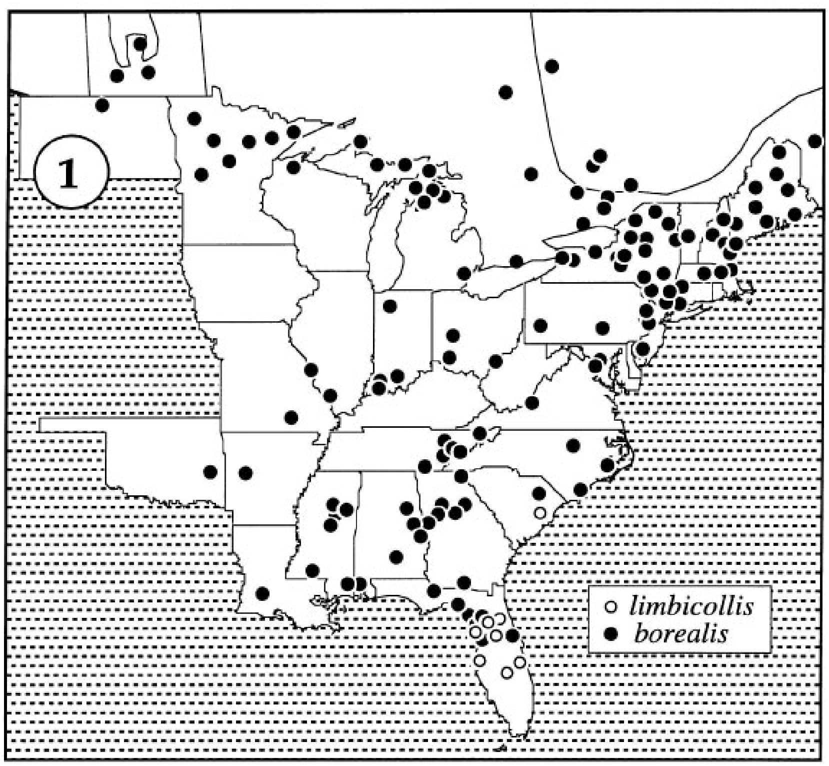

Fig. 1. Locations of specimen-label records for *P. borealis* and *P. limbicollis* from several North American collections. Woodland *Pyractomena* species in addition to these two probably also pupate up on the trunks of trees or shrubs.

Fig. 2. Male *P. borealis* with a *P. borealis* pupa, sex unknown.

species, *Pyractomena limbicollis* Green, began to appear up on trees and in many respects this species was as a foil for *P. borealis*, providing a useful and informative and certainly puzzling contrast.

P. borealis pupae show a surprising directional orientation in their choice of pupation sites on the trees. In a sample of 240 pupae during three winters, the mean direc-

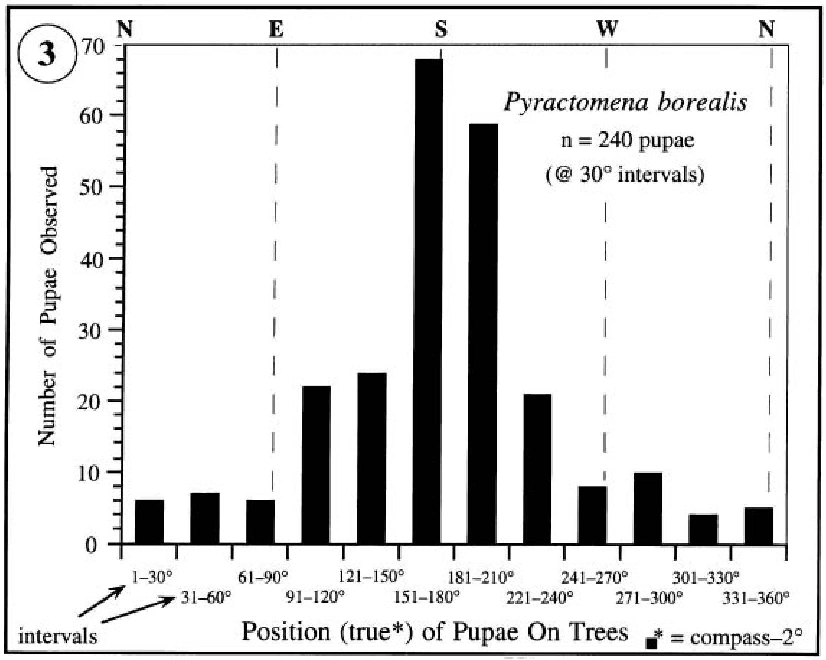

Fig. 3. Directional orientation on tree trunks of *P. borealis* pupae during three winters, at the Possum Creek-Hog Town Creek flood plain site.

tion was southerly, that is, about 180° true (= compass -2°; Fig. 3). But sunlight is more than illumination and a suitable directional cue for orientation—if indeed the larvae are using sunlight for orientation—because it warms what it shines upon. By choosing a pupation site at or near the south side of trees in January, when ambient temperature may be low for many days and even drop below freezing, *P. borealis* pupae raise their body temperature during pupal development by several degrees, presumably decreasing the duration of pupation. One potentially dangerous thermal consequence of the sun-exposing behavior of *P. borealis* is that they must be able to survive extreme temperature changes over a very short period of time; on a clear and sunny winter day the temperature of a dark-barked tree may reach over 90° F (32° C) at three in the afternoon, and by midnight drop well below freezing (32° F, 0° C). One wonders how they manage this!

Pupation up on trees has another conspicuous variable that has thermal consequences. Were the adaptive significance of aerial pupation merely the avoidance of rising flood water, we might expect their vertical distribution on the trees to be rather limited, with pupal distribution clumped around some height—perhaps just above a residual high-water mark left by previous flooding, possibly cueing upon chemical residues left by the water, or algal growth encouraged by flood borne nutrients. Not so; the vertical distribution has considerable spread (Fig. 4). Height may have thermal significance because (1) in winter the ground below may be a heat sink and have a tendency to hold lower-trunk temperatures down, and (2) with increasing altitude there is less shading from sunlight by the trunks, branches and leafless twigs of adjacent

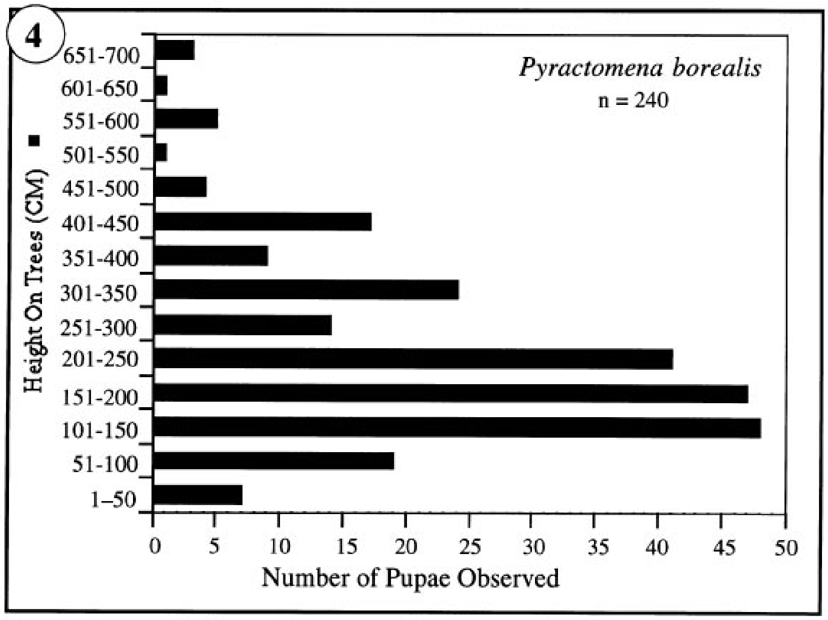

Fig. 4. The height of *P. borealis* pupae on tree trunks.

trees. Obviously then, vertical as well as circumferential positioning on a tree could potentially be used by larvae for manipulating the timing of their metamorphoses. And, there are other possible though more subtle influences on the thermal relations of these pupae. For example, larvae use different species of trees, species that vary in the smoothness of their bark and in the water content of their wood, and these are probably not independent in their effects.

The bark on beech trees is smooth and presents few cliffs and side-directing channels; the bark on oak is rough, with the crevices seemingly the equivalent of four story buildings and presenting an obstacle course for short-legged, prostrate larvae. I comparatively ranked the bark of each tree that larvae selected for the energy and time I expected would be required to climb over (up) them. Beech and sugarberry were typically toward the least expensive end of the ranking, and red maple and oak were at the most expensive end. In consideration of the difficulty of climbing, one would expect that pupae might be found higher on smooth than on rough trees, and perhaps there would be fewer of them. This is what I observed. Trees with smoother bark had more, and species with coarser bark had fewer pupae and they were not as high on the trees (Fig. 5).

Because trunks of different tree species vary in their water content, in sunshine a tree with more water will take longer to warm up, and remain warm longer into a cooling winter evening. Tree-water will also dampen temperature changes, preventing rapid extremes—only two pupae were found on dead (dried out?) trunks. Bark coarseness and thickness could have an influence through the insulation it places between a hanging pupa and the warm water held in the tissues of the trees. On the other hand, rough bark and its crevices provide protective and perhaps thermally amplified niches that provide dead air pockets and radiating walls.

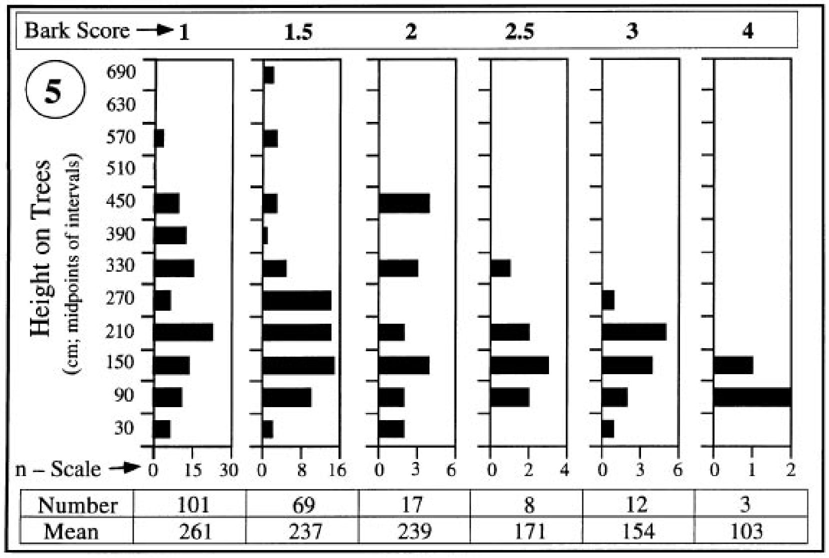

Fig. 5. The height of *P. borealis* pupae on trees with different bark roughness.

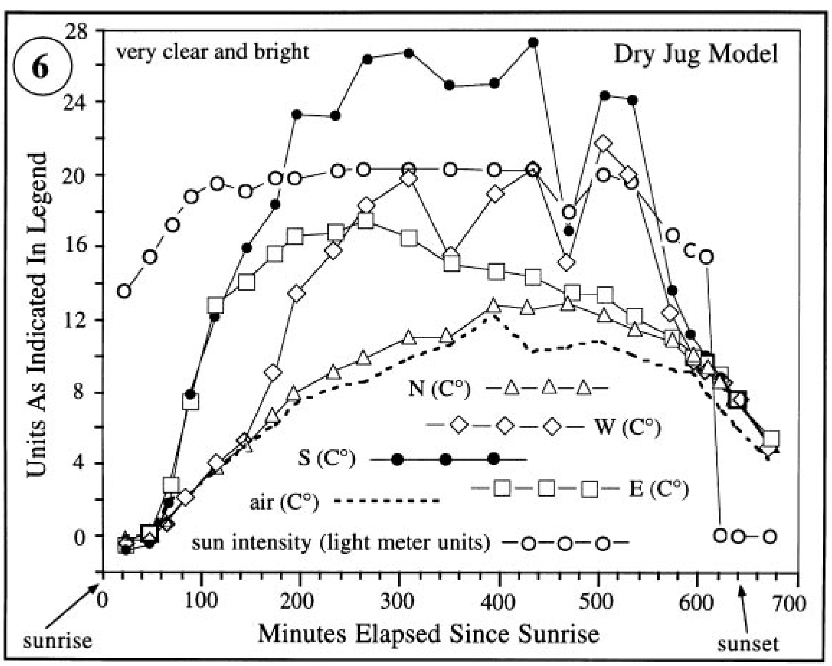

Fig. 6. The basic physical model of a tree with pupae. The tree was a photographic chemical jug filled with dry sand, painted flat black up to the sand level; the model fireflies were 1 cm clay spheres, painted black, each with a thermocouple inside.

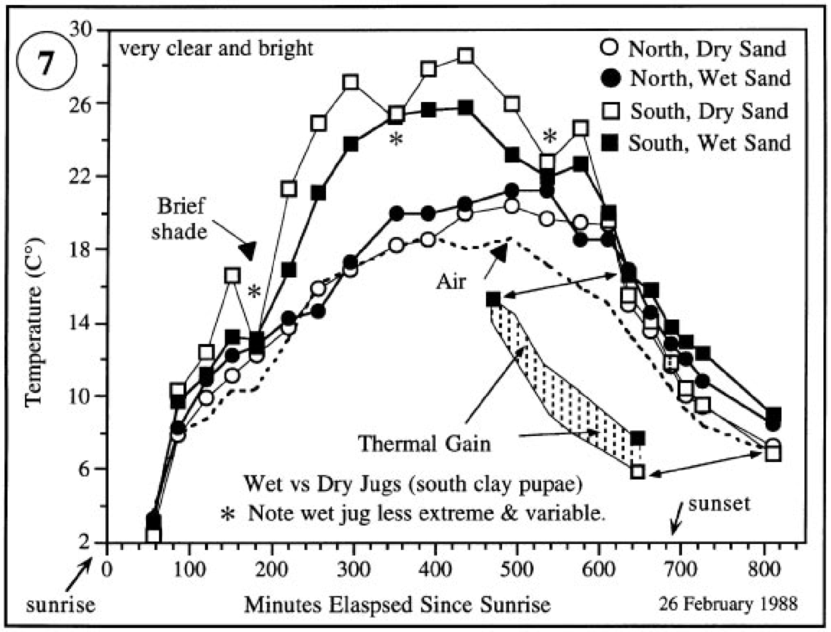

Fig. 7. The comparison of temperatures of model pupae at north and south positions on a dry-sand jug and a wet-sand jug; a physical model examining the influence of tree water content on pupal temperature.

Questions of water content and heat storage can be explored with a simple physical model. I made artificial tree trunks of plastic jugs used to store photographic darkroom chemicals, and hung them in the sun on cool winter days. Each bottle had a 1 cm clay sphere with a thermocouple inside, at each of four directions (N, S, E, W); spheres were painted flat (i.e., not enamel) black and held against the surface of their jug with an elastic band around the jugs and passing over the thermocouple wires. Jugs were of two "trunk" sizes, some contained dry sand and some water-saturated sand, some were hung near the ground and others more than a meter above the ground. Results were generally as expected. Figure 6 shows the temperatures recorded from the basic physical model, a large dry-sand jug, on a cold winter day, with air temperature for comparison, and also sunlight intensity as measured with a photographic exposure (visible light) meter.

Note that the temperature/time courses of clay spheres (model pupae) on different sides of a tree are not the same: the S (south) clay sphere (black dots) warmed more and climbed from freezing to nearly 28° C; the N sphere (open triangles) closely followed air temperature; and that a brief shading at 460 min. affected the S and W spheres but the E and N spheres scarcely if at all. Many comparisons among such spheres and jugs are possible; Figure 7 shows temperature/time plots for N and S clay pupae on wet and dry jugs, with the moderating effect and thermal gain from "tree water." However, one photographed pupa was discovered to be conspicuously arched out away from the tree, suggesting that it should not be presumed that pupae fastened to trees have no control over their body temperature; perhaps they press

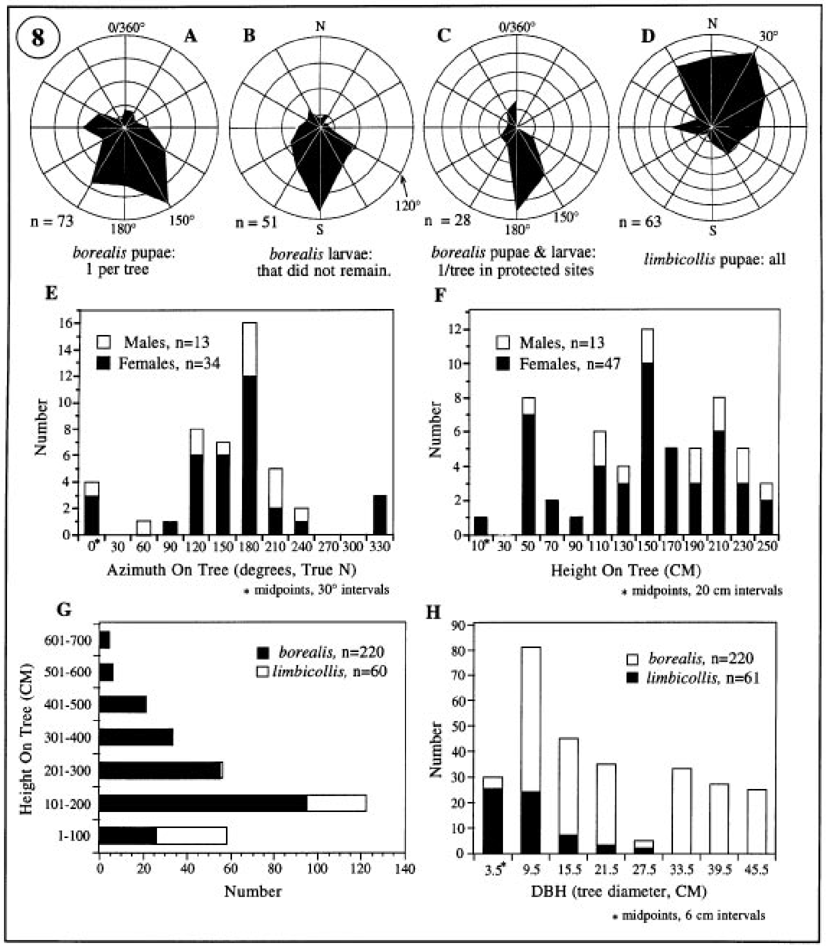

Fig. 8. Graphs illustrating data that are pertinent to some basic questions about *P. borealis* pupation biology, and the remarkably contrasting behavior of *P. limbicollis*. (A) Azimuth positions of solitary *P. borealis* pupae that presumably were not influenced by others; (B) Azimuths of *P. borealis* larvae that did not remain in position, showing that they abandoned what would seem to be a good angle—though they may have moved to fine-tune their positioning(?); (C) positions of *P. borealis* larvae and pupae situated in sheltered locations showing that the shelters did not have highly deviant azimuths; (D) The north-easterly azimuth orientation of *P. limbicollis* pupae; (E, F) Azimuth and height positions of male and female *P. borealis*. (G) Heights of pupal positions of both species; (H) Trunk diameters (DBH, diameter breast height) of pupation trees of both species.

against a warm tree to warm up, or arch out away to cool down by increasing air insulation and circulation between them and their too-warm tree.

The behavior of these juvenile fireflies raises many questions that students can approach. Do larvae actually manipulate with some precision their thermal gains from azimuth and height?—how about thermal conditions in pockets between the ridges of a muscle tree (Carolina beech)? Would a larva select a pupation site 15° from a "precise target position" or "ideal directional site," if other pupae or a sheltering vine were positioned there? Could a *P. borealis* juvenile be expected to integrate all or some of the variables noted or discussed, to control the moment when it, as an adult enters the competitive reproductive environment? Would a male-to-be larva that was late getting to a tree accelerate its development? Of course it would be absurd to ask whether a larva could control its gender by adjusting its developmental temperature.

Fundamental to comparing observations and sets of observations, and of interest to the mathematically-minded, note the problem of calculating statistical descriptions such as mean positions and amount of spread in circular data, that is, of angular positions around a tree—consider this: the average position of a pupa 5° west of north and another 5° east of north, is half of 355° + 005° and thus 180°, which is true south! Nor is it simple and straightforward to compare the means and deviations (spread) of samples to determine the likelihood that they are "identical" (drawn from the same population). Were my samples properly made?—my data show that more larvae climbed smooth-barked trees (Fig. 5), but were there more smooth trees in the woods; but, perhaps it is not relative abundance that should be considered, but rather the identity of nearest neighbors to trees actually climbed, because individual larvae may not move far in the days or weeks before pupation. If you are interested in physics or photo-journalism, can you suggest a better method of measuring insolation (solar radiation), or a way to see infrared patterns on and among the trunks of the trees that might be available to tree-seeking larvae?

Figure 8 illustrates data that bear on several questions: do azimuths of solitary *P. borealis* pupae show the same directionality? (Fig. 8A); did hanging larvae that subsequently moved, have the same near-southern azimuth? (Fig. 8B)—this question of course relates to the (proximate) mechanism of orientation; do solitary larvae and pupae that occur in protected sites deviate appreciably from an approximate southern azimuth? (Fig. 8C).

On several occasions I found adult *P. borealis* males attending pupae (Fig. 2). This raises questions related to mate finding and competition: are males able to recognize female pupae?; would guarding a sexually unidentified pupa have a better long run payoff than searching with a signal light at night, and would this probability and payoff change through the mating season?; might males accelerate their eclosion to appear earlier in the season to be ahead of and be waiting for unfertilized (high value) females? This last speculation presently finds no support in the azimuth and height data, assuming that accelerating males would show different pupation azimuths and heights than females (Fig. 8E and F). Perhaps *P. borealis* fireflies in north central Florida accelerate their seasonal appearance to avoid predaceous *Photuris* species, which pupate in the soil and thus are stuck in a cold cellar.

The pupation behavior of the smaller species *P. limbicollis* stands in such contrast to that of *P. borealis* that it reinforces the suspicion that there really is something significant occurring in *P. borealis*, providing both encouragement to proceed and another firefly subject for a comparative study. In my sample, *P. limbicollis* pupated toward the north (Fig. 8D) and much lower on smaller trees (Fig. 8G and H)—being low down on the north side of small trees would result in a cooler-than-air temperature regime.

The adult season of *P. limbicollis* is about three weeks later than that of *P. borealis*, and *limbicollis* adults appear with a versatile firefly predator belonging to the *Photuris versicolor* complex. The (sexual) flash pattern of *P. limbicollis* males is virtually identical with one flash pattern emitted by the males of this *Photuris*, an instance of the pattern-matching phenomenon seen in males of many *Photuris* species. What would *P. limbicollis* gain by synchronizing with a pattern-mimicking predator, or is *limbicollis* manipulating its adult season to avoid a critical seasonal overlap with its congener *P. borealis*? If this is the case, is the avoided overlap that with mate-seeking adults or with first instar larvae that must find soft-bodied and perhaps only minute gastropod prey in the same forest litter?

These fireflies clearly present sufficient questions with respect to proximate mechanisms and ultimate consequences, to provide fireflyers many years of intriguing "off-season" field work. Find quiet and mysterious trails.

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