

ON RESEARCH AND ENTOMOLOGICAL EDUCATION IV:
QUANTIFYING MATE SEARCH IN A PERFECT INSECT—
SEEKING TRUE FACTS AND INSIGHT (COLEOPTERA:
LAMPYRIDAE, *PHOTINUS*)

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ABSTRACT

Male *Photinus collustrans* LeConte fireflies fly over their grassland habitats flashing and seeking their flightless females. I followed individual males, measured, and took note of various aspects of their behavior. Then, from a sample of 255 male runs, with a total distance of 13.9 miles and 10,306 flashes, various sets of these males, those seemingly directed by other than search flight-plans, were removed to leave a sample to characterize "pure" search flight. Fireflies are good subjects for students to study foraging ecology and sexual selection, and from studies of common grassland fireflies it will be clear to students that even simple behavior by males of a single species, under seemingly uncomplicated and homogeneous conditions, can be complex, but provide opportunity for theoretical and empirical exploration. Among factors identified here as influencing male mate-seeking behavior were ambient temperature, ambient light level, and time of night. Other influencing factors, enigmas, and student explorations are indicated.

Key Words: Lampyridae, *Photinus*, mate search, sexual selection, foraging, teaching

RESUMEN

Las luciérnagas machos de la especie *Photinus collustrans* LeConte vuelan sobre los pastizales destellando su luz y buscando a las hembras que no pueden volar. Seguí a los machos, los medí y tome notas de varios aspectos de su comportamiento. Luego, de una muestra de 255 vuelos de los machos, con una distancia total de 13,9 millas y de 10.306 destellos, varios grupos de estos machos, esos dirigidos aparentemente por alguna otra razón que la de un vuelo de búsqueda, fueron removidos para formar una muestra que caracterice el vuelo de búsqueda "puro". Las luciérnagas son buenos elementos de estudio para los estudiantes de ecología del forraje y selección sexual. Del estudio de las luciérnagas comunes de los pastizales quedara claro para los estudiantes que, incluso el comportamiento simple de los machos de una sola especie, bajo condiciones aparentemente sencillas y homogéneas, puede ser complejo, pero proporciona la oportunidad para la exploración teórica y empírica. Entre los factores identificados aquí que influyen el comportamiento de búsqueda de la hembra, están la temperatura, el nivel de luz ambiental y la hora de la noche. Otros factores influyentes, enigmas y exploraciones de los estudiantes son incluidos.

In this symposium series I have passed along notes on the natural history of fireflies I have met in the field while exploring their species-level taxonomy, in the form of written lectures (Letters) to an introductory biology and natural history class. On the face of it, this Letter is an attempt to quantify the mate search of flashing males over a pasture, and apply this information toward understanding mate competition. In actuality it reveals the biological complexity of this seemingly simple behavior, and finds a num-

ber of difficulties that students can appreciate and avoid in their turn. The study was stimulated by papers in a symposium moderated by Dan Otte in the mid 1970s, which surely introduced many naturalist/systematists to a different view of insect signaling and associated behavior. The symposium was a timely event in my life with fireflies, for it offered new perspectives that fit in naturally with what I had learned from reading papers of pioneer fireflyers F. A. McDermott and H. S. Barber, and discussions with systematists T. H. Hubbell and W. L. Brown, and especially, R. D. Alexander.

A pictorial moment of firefly search flight and its variation among species is seen in the illustration orthopterist Otte created as *Frontispiece for a Photinus* behavioral-taxonomy paper (Fig. 1; note his surreptitious acridid), a graphic used not long ago as cover illustration for a mathematical (and for some naturalists an abstruse and mystical) treatise entitled "Quantitative Analysis of Movements" (Turchin 1998). This book has a number of useful considerations even for such an elementary study as reported here, and views individuals to develop models for understanding populations. In "the present study" individual fireflies were watched closely to learn something of their (adaptive) programs for mate search flight. The two views, individual and population, overlap, then merge when mate-seeking fireflies leave or enter local populations and these "migrations" influence population vigor, independence, and fate. Other relevant books and teachers that students may wish to consult are: "Foraging Theory" (Stephens and Krebs 1986), "Spatial Ecology" (Tilman and Kareiva 1997), and "The Ecological Detective" (Hilborn and Mangel 1997).

My leaves-of-grass-top project began with the naive notion that it would be easy to collect some few data on males of each of several low-flying species, and make a ready comparison of species that have different flash (signal) patterns and fly in somewhat different ecological situations. Innocent at inception, results were reminder that raw nature is not as it is often condensed for textbook generalizations, theoretical modeling, and taxonomy, a discovery students will make when they try to quantify mate-seeking behavior. It was great fun to follow individual fireflies through a twinkling of their nocturnal careers, and to see them in another dimension for the first time, and so closely that I saw individual—but nevertheless yet nameless—males quit searching and in climbing flight enter the boughs of the scattered pines in the study site. I even saw some that crashed into herbs and shrubs fall to the ground, lights burning, marking meteor-like descents. Decades ago when spinning tackle was introduced into the U.S., an expert noted that spin-fishing was a soothing, meditative experience, to be compared with making thread at a spinning wheel (though I wondered how he knew this). Chasing fireflies across a meadow while pushing a measuring wheel is also good for contemplation—and data just roll in.

It is of course obvious to almost anyone, today, that there is variation among the phenotypes of individuals even within local populations, due to a number of "innate," experiential, and of-the-moment inputs to each firefly's central processing system. After miles in pursuit of males of a near-perfect species, I was reminded that simple variables in method, equipment, and assistants can also mess-up tidy results. In the end, the chase provided previously unknown and eye-opening facts and basic statistics about firefly search behavior, and it suggested interesting, short-term studies that students can do in night-time labs (Appendix). Best of all, it incidentally dramatized an important source of selection pressure that "must" often have led to divergence of local populations, toward and, maybe, even to . . . speciation.

In summer any teacher in the range of a grassland firefly, such as the widely distributed and very common "All American Firefly" *Photinus pyralis* (L.) (Fig. 1: flash-path #8), will find that with stopwatches and foresters' measuring wheels students can acquire a new understanding of sexual reproduction in the animal kingdom, and discover that males often share a lonesome misery. They will learn to focus on details

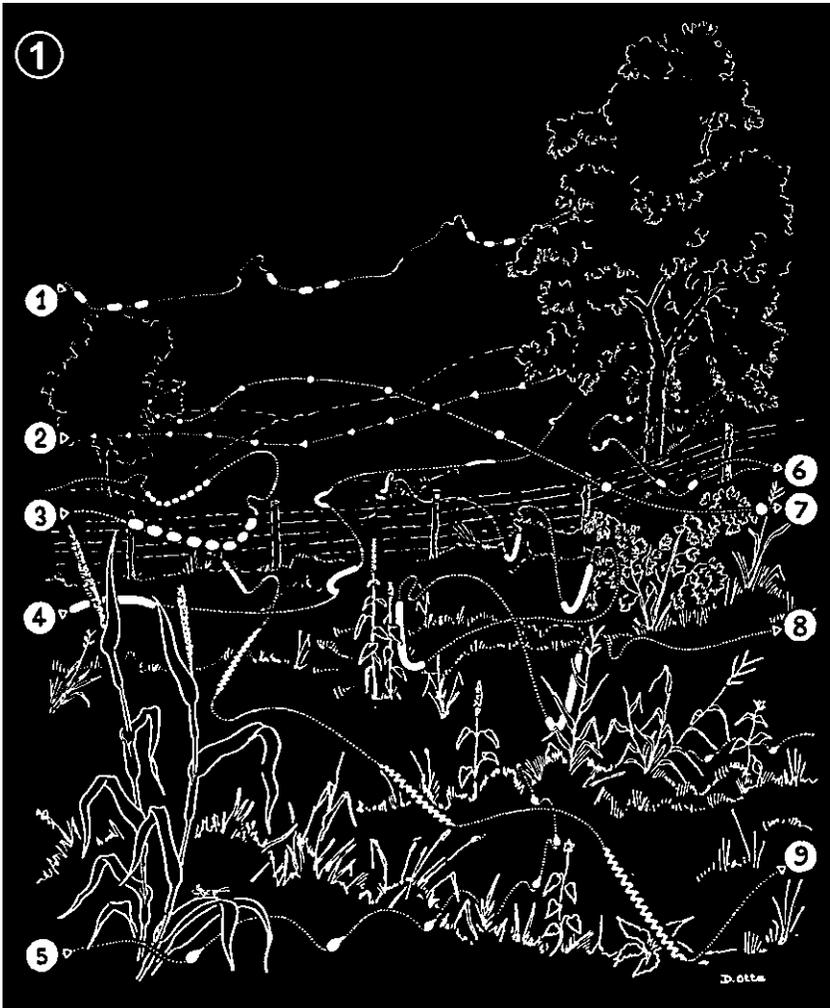


Fig. 1. Flashes and flight paths of males of several different *Photinus* species as they would appear in a time-lapse photograph. Arrowheads indicate direction of flight. The species illustrated are not all sympatric; number 4, *Photinus collustrans*, with its low arcing flight is the species of focus here. (1) *P. consimilis* complex (slow pulse sp.), (2) *P. brimleyi* Green, (3) *P. consimilis* complex (fast pulse sp.) and *P. carolinus* Green, (4) *P. collustrans*, (5) *P. marginellus* LeConte, (6) *P. consanguineus* LeConte, (7), *P. ignitus* Fall, (8) *P. pyralis* (L.), and (9) *P. granulatus* Fall.

of behavior and quantify elements against an array of variables and distractions, and discover sources of variation that they themselves introduce into their data. In my own use, this Letter serves as an introduction to a field problem for a “biology with fireflies” class—a companion guide has instructions for observing and quantifying firefly search behavior, analyzing data, dealing with ecological variables, and devel-

oping experiments for new-found questions—it provides a challenge for engineering majors to conceive of a system of aiming devices, servos, and a portable computer to quantify the 3-dimensional search paths of arboreal, crown-cruising fireflies.

The Internet (electronic) publication of this paper has additional figures as Info-Link attachments to illustrate the text. They are cited here by their number as ILR figures and their legends are included in the End Notes section. These copyrighted illustrations may be used freely with the citation: J. Lloyd, Univ. of Florida.

LETTER XXVII

In Search Of “The Pure-Seeker” Male—Following Sex-Driven Fireflies Through Pastures For the Mind (Lampyridae: *Photinus collustrans*)

“... many a requisite we see must be fulfilled in living things ere they avail to propagate their kind ...”

(Lucretius, 95-52 B.P.E.)

“You can observe a lot just by watching.”

(Yogi Berra, 1925–P.E.)

Dear Fireflies, Luminescent fireflies are good subjects for the study and quantification of mate-seeking behavior. I realized this somewhat belatedly when attending a scientific gathering on sexual selection and mate competition in insects. It came to me, with some embarrassment, that all the while I had been viewing firefly flashes exclusively from the standpoint of a biological-species-seeking taxonomist, merely as signals that were involved in mate recognition and reproductive “isolation,” they were intimately connected with mate competition among conspecific males. Suddenly it was potently clear, the competitive mating context had probably been a major force of selection pressures on signaling behavior, and if I were to understand firefly signals and their evolution, and use them taxonomically, I would need to get some sense of how sexual selection might have influenced them. With information on several species, comparisons might even give clues to adaptations in signaling behavior that are tuned to specific features of the mating arena. Could there be a general theory of flash patterns, perhaps even a descriptive and predictive equation that a mathematical modeler could formulate?

Some of our commonest species in North America occur in grassland habitats where mating flights of males occur in a thin volume of air, sometimes an almost 2-dimensional space, low over the ground, and individuals can be followed and watched closely with relative ease. It was not difficult to select a prime subject that occurs in north central Florida that has characteristics that would especially lend themselves to such study. *Photinus collustrans* LeConte is a twilight firefly of fields, pastures, lawns, and savannas (Figs. 1: flash-path #4, and 2; ILR 2000, Figs. 1 and 2). The male flash pattern is a single, short, yellow flash that is emitted about each 2 seconds of flight, with flash rate varying predictably with ambient temperature (Figs. 3 and 4). Male flight paths are diagnostic, for during each flash males typically arc to the right or left (ILR 2000, Figs. 3 and 4). These arcs may enable them to see the species-typical flash-then-glow responses they have just elicited from females, and perhaps also to scan more broadly for female responses that nearby, rival males have stimulated.

Female *P. collustrans* are flightless and found on the ground or very low on grass stems near their burrow's entrance (ILR 2000, Fig. 5); their sedentary, virtually sessile “search” for passing airborne mates, and other aspects of their biology has been studied in intimate detail by Steve Wing). They respond to male flashes with a single

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Fig. 2. Habitus of *Photinus tanytoxus* Lloyd, a sibling species of *P. collustrans*, differing conspicuously in external appearance only in the black rather than pale elytral sutural bead in the apical third or so of its length. Length, ca. 7 mm. Searching flight in this species will make an interesting comparison with that of *P. collustrans*, because it begins about 5 minutes after *P. collustrans* ends, at full darkness, and continues for one-half hour or more. This photo-like illustration is actually a carbon-dust drawing by Laura Line.

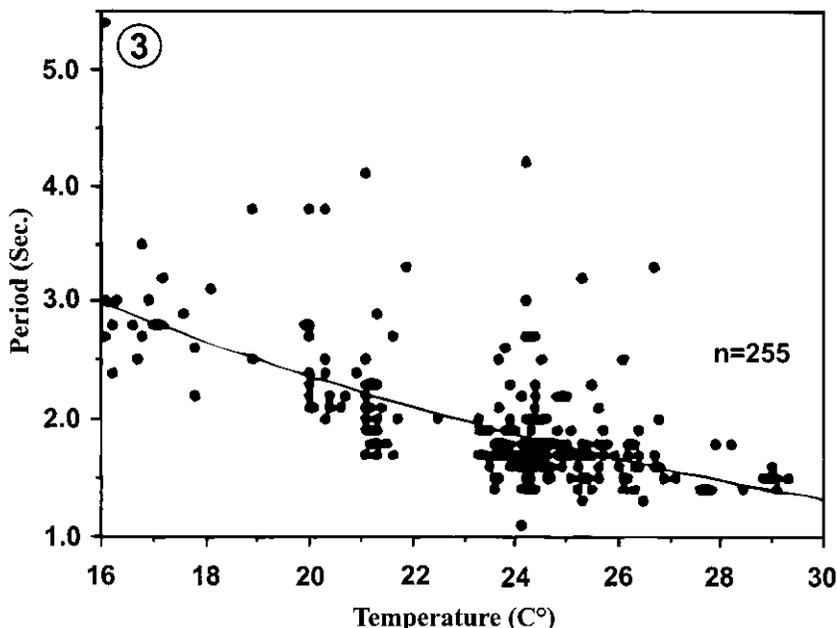


Fig. 3. Flash period duration (in sec) as a function of ambient temperature (in C°). A chart such as this can be useful for species identification in the field. However, flash rate (= 1/period) is better for comparing species because its regression is approximately a straight line, and can be plotted with fewer data points, see Figure 4.

flash that begins about a half second after the male flash, and ends in a briefly persistent, tapering glow. Males of each local, conterminous population (patch, deme) are active for about 20 crepuscle (twilight) minutes each evening, though each individual may only fly during a part of this already narrow window (note circles in Fig. 6). Such flight “compaction” in time is great for fireflyers because it makes each night’s flight window a discrete and comfortably-managed sampling unit, reducing the number of environmental, behavioral, and human variables that must be considered. Also, *P. collustrans*’ flight straddles one especially significant ecological event, the rapid decrease of ambient light known as twilight (“tween” light).

Is it possible to characterize, to describe the ideal, the optimum mate-seeking flight for male *P. collustrans*? That is, can we sample the behavior of males, and then describe a “pure” search flight that will have evolved because it is *the most* appropriate and efficient (competitive) for males under the ecological conditions they live with? Not likely, and the fallacy behind this notion is that there actually could be a *most* efficient or *most* appropriate search flight. Males, their genetic constitutions and the individual circumstances they experience through their lives are not identical. And, on any given day some are older and have less search time remaining before they die—males may be programmed to take more risks as they age, say, risks in where, when, and how fast they fly; also, sometimes males experience high levels of competition, with rivals always within “eyeshot”—males may be programmed, upon detection of such conditions, to employ different, more concealing flight and flash tactics, and such flight would certainly reduce their measured efficiency as “ideal searchers.”

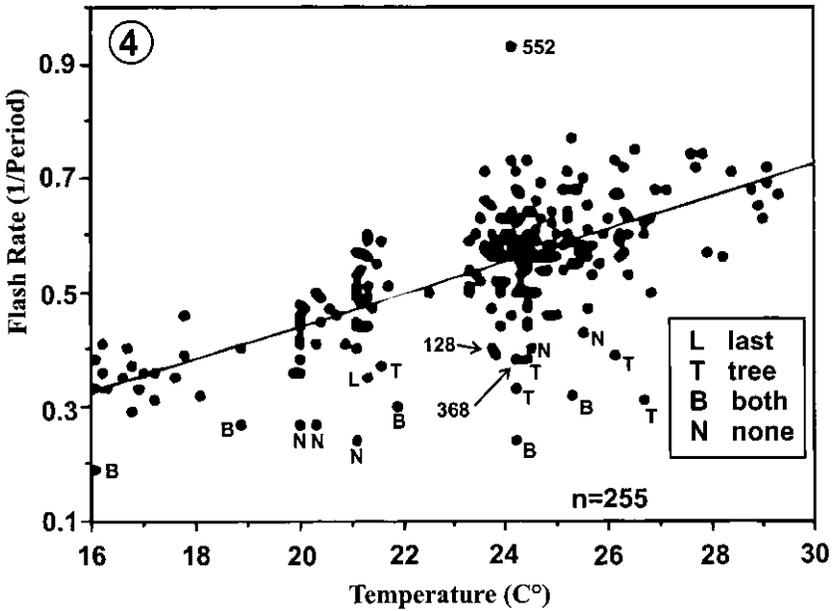


Fig. 4. Flash rate (1/period) as a function of ambient temperature (in C°); data points were converted from those in Figure 4. A “hurry up” flash period regression for field use can be approximated by converting mean flash periods from two remote temperatures to rates, drawing/extending a line through their plots, converting several points to rates, drawing/extending a line through their plots, converting several of letter and number dot tags.

Also, we intuitively understand that what might well be the best flight program for the discovery of females in an ideal grassland could also be more dangerous when occasional tall spikes of wing-tearing thistles are present, and an unfortunate flight accident could, with some calculable level of statistical probability, reduce the total number of days a male has to search. Thus, we expect “imperfections” in search adaptation to arise from various trade-offs, and for other reasons, too. Nevertheless, we might determine the overall search-flight characteristics of “our average male” across the (mostly unspecified and little understood) range of conditions that prevail during the evenings that data are recorded. Parameters of such a search plan, when visualized as axes of XY charts will frame a cloud of “slightly-off” as well as more deviant searches clustered ‘round a mean. These are the (dots of) males with different phenotypic characteristics and whose control systems are processing different inputs. Perhaps we can find clues for some of the observed differences among males, and speculative notions that can be developed into formal hypotheses for testing by carefully focused research. (How could one construct, and then place in a meadow, 100 fake thistle spikes, and quantify male responses and losses to them?)

On Firefly Trails

To collect data I followed individual *P. collustrans* males as they flew and flashed over a pasture grassland, pushing a measuring wheel through each subject’s curves and turns—I trailed a few meters behind them and never saw any indication that my

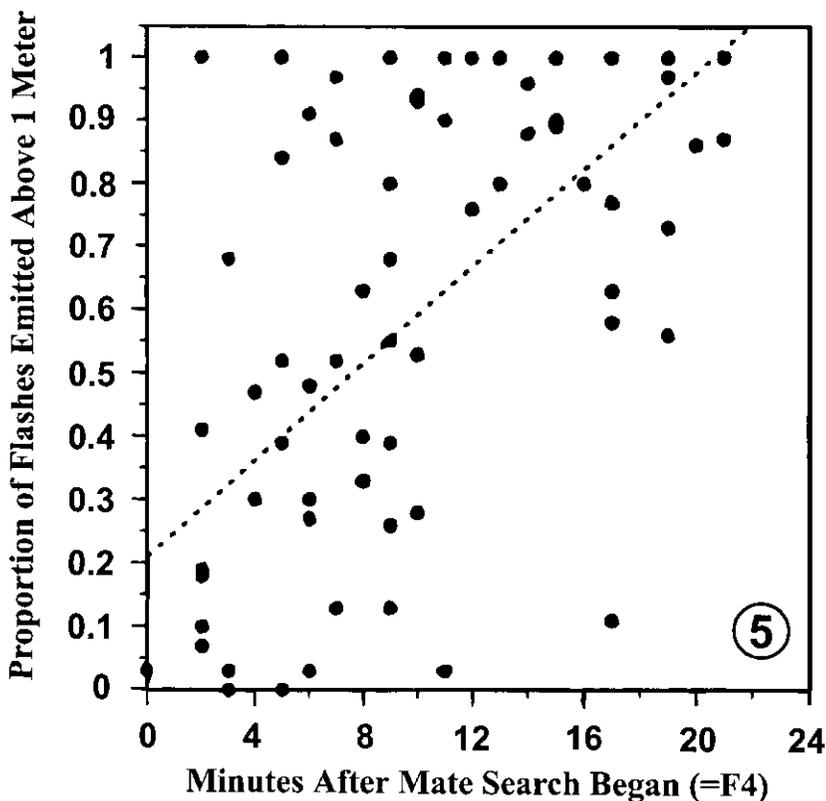


Fig. 5. Height of flight flashes of 74 male *P. collustrans*, given as the proportion of flashes (Y axis) that were emitted above one meter altitude. The ratio (above-1-meter/all altitudes) for each male is marked. The X axis shows the number of minutes after evening flight began, "marked" when four males had begun flashing flight (F4). This convention was adopted as an attempt to avoid biasing by idiosyncratic males, such as those embarking on their evening flight from especially shady places. Other conventions are possible, perhaps even better? Samples were made during 38 evenings.

delayed presence influenced their flight. A 2-channel event (blood-cell) counter mounted on the handlebar was operated by thumb and stored certain "digitized" data (ILR 2000, Fig. 6). For example, I had noticed that males fly at somewhat different altitudes over the ground, and altitude seemed to be connected with the time of evening, so in each of 74 individual followings (i.e., runs; during 38 evenings) my thumb kept track of the flashes emitted above and below 1 meter altitude. I found that during the first few minutes each evening males generally flew lower than 1 meter, but gradually through their twilight window, ever more of their flashes were emitted from above 1 meter (Figs. 5 and 6). That this change is in response to diminishing ambient light is suggested by the observation that in early evening when males fly into shady spaces beneath trees they fly conspicuously higher, and then fly lower again as they move out under open sky. The scatter seen in the plot of individual records (Fig. 5) occurs in part because males flew in or through the shade of trees.

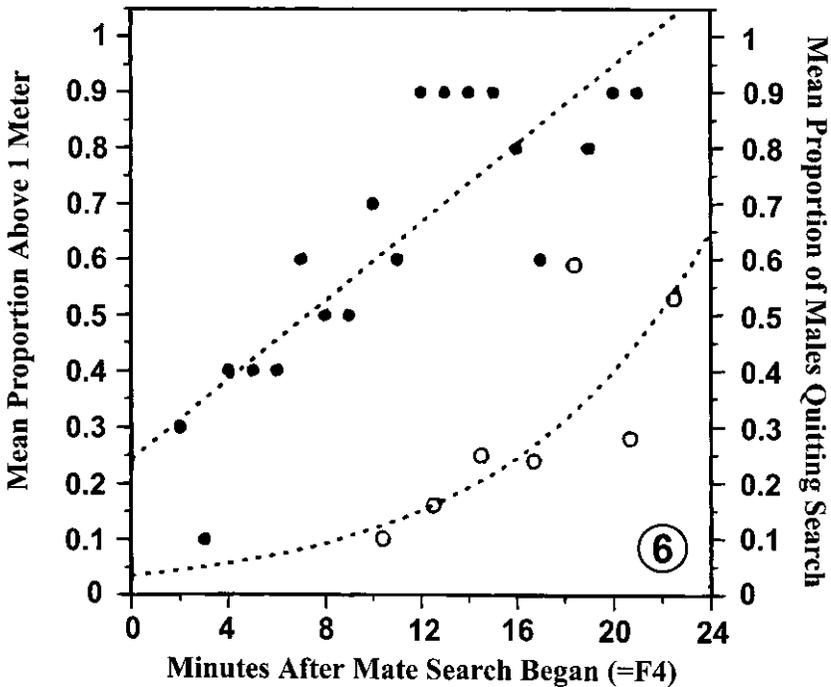


Fig. 6. Mean height ratio of males for each minute (left Y axis). With increasing darkness males tend to fly higher, possibly to avoid unseen spikes of herbs, or to see further, or to spread their light further?; can these notions be demonstrated, or be differentiated experimentally? The figure also shows (open circles, right Y axis), the proportion of followed males that quit search during consecutive brackets of time, beginning 10 minutes after evening flight began (n = 138, 24 males quitting). Lines were fitted by the graphing program, linear in dots of 5 and 6, and exponential in circles of 6.

Among the categories of data recorded for each run were: duration in seconds, from the first flash to the terminating one; number of flash periods per run, with the starting flash counted as zero and the count at the run's terminating flash giving the number of flash periods; distance flown, as read from an automatic counter clicking feet at the rim of the wheel; and time of day at the end of a run. I also made written notes of unusual flight features and the reason for ending the run; for examples, runs were terminated because males flew to a perch apparently ending their evening flight (Fig. 6, circles), because followed males intersected paths with another and I was uncertain which male I had been following, and because the run was sufficiently long (>30 flashes).

First and simpler questions to be answered by the wheel-pushing data are, what are the flash-rates and flight speeds of mate-seeking males? Next, do these parameters vary through the activity window (period)? Then, when interactions of these parameters are viewed, are there any generalizations or predictions to be made, any puzzlements or surprises? The total data set from the pasture is from 255 males, followed on 43 evenings, during the years 1976-7, for a distance of 22,356 meters (13.9 miles); this required 5.25 hours of actual following, during which time the males emitted 10,306 flashes. The longest run was 0.49 miles, and the fastest, 4.8 mph. I should

note that of all of my firefly field studies only this one seemed to demand professional, knee-length snake boots; but they were not called into their intended service.

On nine occasions males flew into vegetation and fell with lights burning to the ground, each losing a few seconds of search time (= 1 crash per 1.54 miles); males found two females and coupled with them (= 1 per 157.5 min, per 7.0 miles!). Statistically speaking, if each male should actually search 20 minutes per evening, on average, only one in eight of them would find a female? More realistically, but still statistically, if individual males average only 16 minutes of search per evening, only one in 10 will find a female! (How many males find none in their entire adult lives ($7 \pm$ days?), and how many find two or three—and, beyond some degree of good fortune, do exceptionally successful (super) males share an uncommon set of mate-finding features? How could you determine this, and how big a sample would it require?)

Flash rate. The period of consecutive flashes (period = time between beginning of one event to the beginning of the next such event) emitted by flying searching males decreases with increasing ambient temperature, and ranges between 3 seconds at 16° and 1.5 seconds at 29°C (Fig. 3). There is a curvilinear relationship between flash period and temperature, but between flash rate (1/period) and temperature the relation can be considered linear for our purposes (Fig. 4). Observe the slower, individually labeled runs in Figure 4. When field note (written) descriptions of these slower runs were examined it was obvious that several of these males may have been in an “activity-terminating mode” rather than a “mate-seeking mode,” because they flew up into the scattered pines or down to the ground, apparently quitting flight for the evening. To characterize “pure-seeking” behavior, runs that represent alternative or mixed behavior modes, such as this set would appear to represent, must be culled from the data set. (But, note that the data set is shown in its entirety before any purging of “bad” data; Figs. 3 and 4; $n = 255$ runs).

Selecting pure seekers. To get statistics for presumptive “pure-seeking” flight-parameters, I culled runs when field notes suggested the males might be following mixed or other flight plan directives. Thus, I removed: all flight terminating runs (when followed males flew up into tree boughs or down into the grass and stopped flashing, “T” in Fig. 4); all last-of-the-evening runs (such males were always the last one or two that could be seen flying and flashing in the population, “L” in Fig. 4—the rationale being that they may already have been slowing down); runs during which males behaved “erratically” (flying up then down, conspicuously slowing and then speeding up); runs when the males crashed into vegetation (males can be seen glowing brightly as they fall down on the approached-side of herbs and bushes); and runs when males noticeably paused in flight, as they do occasionally over small sandy patches and pale flowers. A few very short runs were also removed, those comprising fewer than 8 flash patterns.

As examples of purged sets, note labeled run #368 (Fig. 4), in which the male paused in flight and hovered over one place for 8-9 sec; and in run 128, the male ran into a twig, fell down and lost about 2 seconds on the ground. The male of run 552 rapidly approached a 50-meter wooded sinkhole, momentarily stopped flashing at the wall of foliage at the edge, then abruptly flew back over my head. His headlong dashing flight makes me suspect that his measured parameters were not those of even an extreme “pure” search flight plan. Finally, note that there are several runs at the slow edge of the clustering marked “N”, meaning that I made no relevant verbal notes at the end of the run. I must interpret these as representing the slow tail of a “normal” distribution of a pureseeker flash rate, and retain them in the hopeful set. In every case, all of the males of a given rejected category were culled, and not merely those that were conspicuous outliers on the chart. Figure 7 shows the flash-rate/temperature regression of the now much reduced, remaining sample of 123 runs. The correla-

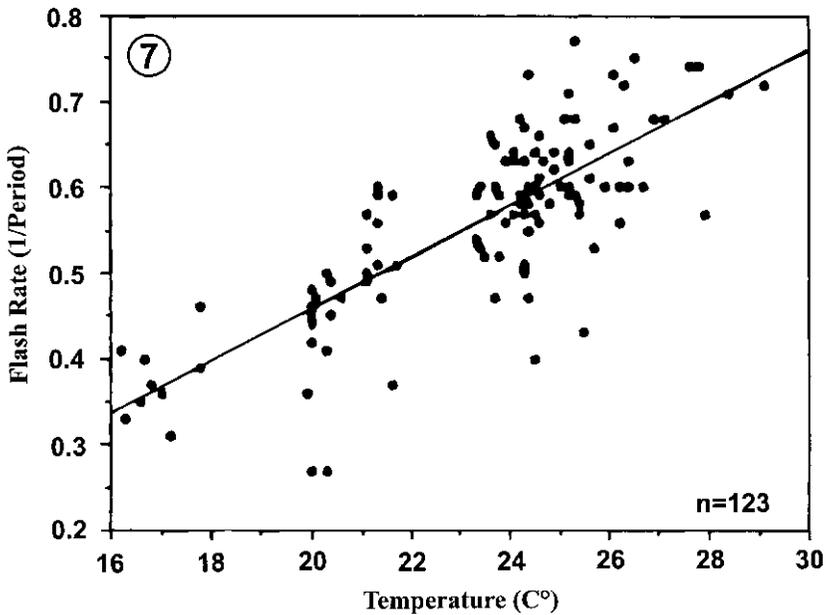


Fig. 7. "Purified" flash rate regression, with all males in categories mentioned in text removed (see outliers and key in Figure 4), as a function of ambient temperature (in C°); compare with Figure 4.

tion coefficient (r) for the complete data set in Figure 4 is 0.69, and for the selected set in Figure 7 it is 0.80, though the slope remains about the same.

Flash-rate revisited. The slope of the "purified" data in Figure 7, can be used to adjust ("correct") the flash-rates of the selected runs to what they would be at 25°C. The temperature-adjusted rates can then be plotted as a function of the time-of-night (i.e., sun-time of run midpoint) they were measured (Fig. 8). This regression slope (of flash-rate/midpoint), reveals no time-of-night effect, and nearly zero correlation (i.e., $t = 1.25$, slope not significantly different from flat; $r = 0.12$, on a scale of 0 to 1). In other words, twilight time with its ever increasing darkness, and other changes such as a (probable?) reduction in the availability of unmated females and perhaps even the number/proximity of rival males, does not appear to influence the rate of male flash pattern repetition).

Flight-speed of this "purified" set of mate-seekers increases slightly with temperature (Fig. 9; $t = 2.975$), significantly different from flat, though the correlation is pretty weak ($r = 0.26$). Then, when speed data are adjusted to 25°C and plotted as a function of the time of night, flight-speed is seen to increase through the activity period (Fig. 10: $t = 5.285$; $r = 0.43$). But, to the naked eye and common sense, the chart's dots do not really lie along a straight-line. A linear regression was imposed on the data by the graphing program, but the data points clearly increase linearly to about 1.3 creps, remain flat to about 1.5 creps, and then decline slightly.

Before addressing this, I want to whack some more outliers. Note the several faster runs especially after 1.6 creps (Fig. 10); might they indicate the presence of yet another search tactic or influence? Field notes reveal that the data for four of them were taken by a young family member (unpaid assistant) who had used a measuring

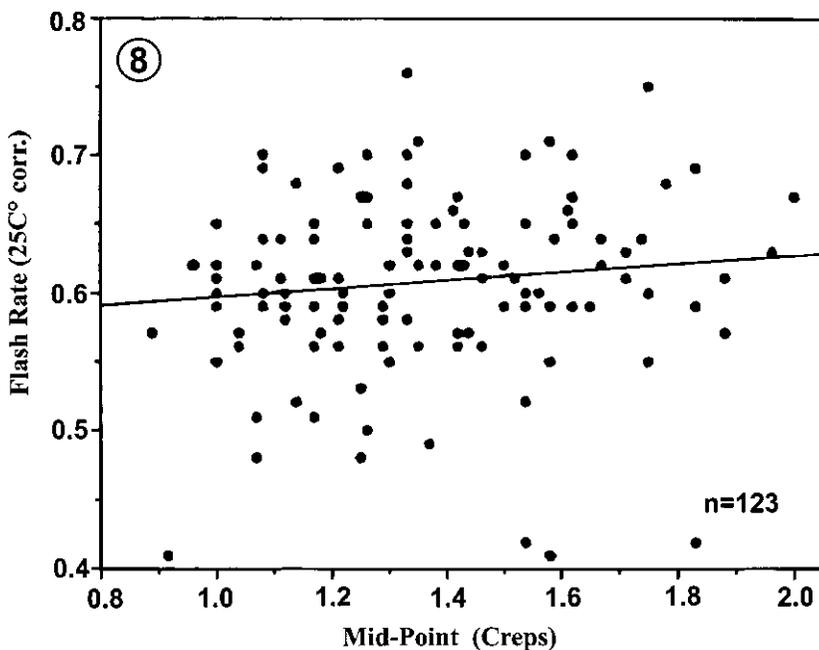


Fig. 8. Flash rate, adjusted to 25°C, as a function of time of night (in crep units, where 0 is sunset; a crep unit, which varies with date and locality, is the duration of Civil Twilight).

wheel with a smaller diameter (ILR 2000, Fig. 6—one that would probably roll more tightly over the surfaces of smaller humps and bumps, going further per linear distance and unit time. These data points thus suffered from two additional variables; consequently, all data collected by this apprentice fireflyer were purged. One outlier was a last run that escaped notice during the first culling, and another was a penultimate run that ended three minutes before the end of evening activity. These two were also removed from the data set, though purging the last mentioned point was not legitimate, not statistically proper—unless I were to remove all penultimate runs (and replot, beginning with Figure 3). The data set is now reduced another 7 percent ($n = 114$, down 55 percent from the original 255!). This refinement hopefully, theoretically in a loose sense of the word, should reveal the best glimpse of search behavior yet achieved, and show speed adjustments made by males through their twilight window about as well as I can now sketch them (Fig. 11). A verbal summary of what the graph suggests would be: flight speed increases at first, while twilight darkness deepens rapidly (causation?), and then after 1.5 creps there appears to be a slight downturn, indicating that males that remain active fly (flew) a bit more slowly.

Distance-flown per flash-period (flash rate melded with flight speed), decreases with temperature (Fig. 12; $t = 6.630$, $r = 0.52$). This is to say, the cooler it is, the greater the distance along the flight track, out in front of the male, the flash is “expected/required(?)” to cover (“to stimulate?” Tom asked, illuminatingly). Though flight speed appears to decrease slightly as temperature decreases (Fig. 9), flash rate decreases considerably (i.e., period lengthens, Fig. 7), and this results in a longer distance flown between flashes. This

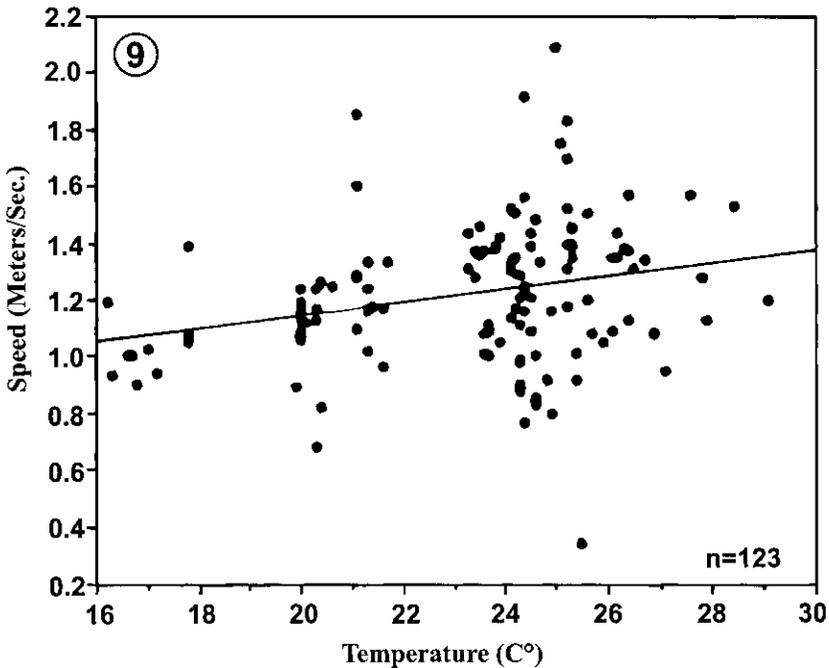


Fig. 9. Flight speed (in meters/sec) as a function of ambient temperature (in C°).

would seem to indicate that with decreasing temperature, flashes “are required to” stimulate progressively larger areas. There are too many unknowns to interpret this: we do not know and cannot easily determine whether the intensity (photons emitted) of flashes remains constant at lower temperatures, or, whether the angular spread of the light leaving the lantern remains constant—some luminescent click beetles apparently control the spread of the light beams emitted by their ventral lanterns!

Predator Pressure and Deme Divergence. Females of many, seemingly most Nearctic species of the genus *Photuris* prey upon mate seeking males of other species. They perch in the activity spaces of their prey and mimic the flash responses of the males’ own females, attract and eat them. No such deceivers were seen at the pasture site, and this makes for a very interesting contrast with data from another site. The latter was a narrow, roadside, pine savanna with a nearby mesic hammock and marshy catch-basin and drainage ditch. These habitats produce the predators *Photuris versicolor* (Florida form) and *Photuris bethaniensis* (Florida form). Females of these two species occurred in the *P. collustrans* site and flashed responses to *P. collustrans* males I was following. Thirteen such predators were observed to answer them, and though some males landed and lost search time, none were caught by these femmes fatales. What makes these statistics especially noteworthy, was that the savanna sample of measured runs was a great deal smaller than that from the pasture—40 males were followed for a total of only 3,550 meters (2.2 miles). The score card: pasture, 2 mates and no predators; savanna, no mates and 13 predators! Converting this to a numerical comparison: if, during the next instant such a predator had been found at the pasture (I need one predator to avoid the unworkable zero), mimicking the re-

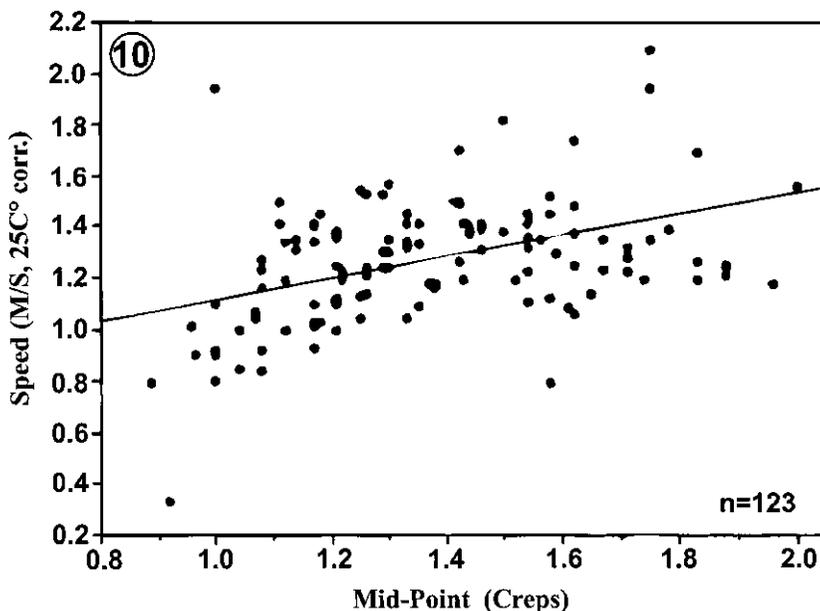


Fig. 10. Flight speed (in meters/sec, adjusted to 25°C), as a function of time of night (in crep units), with a forced linear regression line that even to the eye is not a good fit; note the rise then fall of data points.

sponses of *P. collustrans* females, the hunter-exposure rate in the savanna would have been nearly 69 times that of the pasture site (3.10 vs. 0.045 predators/kilometer). In other words, in this predator connection, this savanna was “immeasurably”, virtually “infinitely” more dangerous than the pasture for male *P. collustrans*. This really brings home the fact that local populations (demes) can be under grossly different selective pressures, pressures that must be expected to have a significant influence upon mate seeking and code-recognition behavior of males—and this is a phenomenon that can be measured and compared!

Other Conclusions and Explanations. At the outset of this study, it seemed that for a number of reasons mentioned in the introduction, it might be fairly simple to describe the mate-seeking flight of *P. collustrans*, and identify characteristics that made it well-tuned, “optimal” for finding mates in a competitive environment. Each of the sets of male runs that was distinguished and then removed at some point in the analysis, including quitting, crashing, and last-of-the-night runs, and runs whose measurements may have had technical inconsistencies, not only produced a tidier sample, but more importantly identified sources of influence and variation for future reference. Some of the culled sets revealed something about *P. collustrans*’ biology, whether tentative explanations were correct or not. But, it now is clear that to characterize the simple search flight of *P. collustrans* for comparison with that of other species will require a great deal more intraspecific comparative study. Studies must first be comparable at the technical and deme levels, and find and identify the influences of: (1) the mechanical aspects of sampling techniques, including different wheel sizes, different wheel operators, and different bump and hummock sizes (with consideration given to

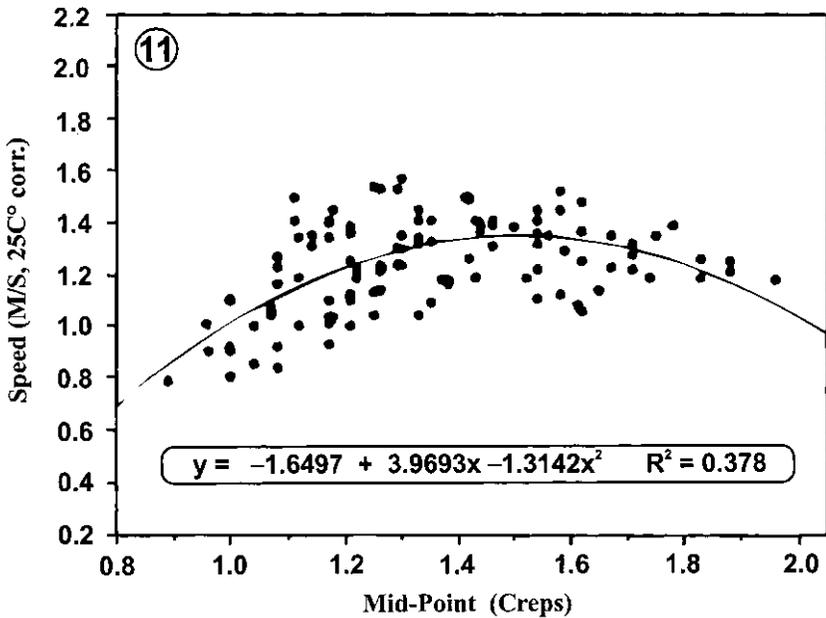


Fig. 11. Flight speed (in meters/sec, adjusted to 25°C), as a function of time of night (in crep units), with a regression line and equation for a second-order polynomial plotted and calculated by the graphing program.

varying flight speed) on over-the-ground measuring accuracy and precision; (2) different ecological conditions, including vegetation, predator and rival-density, ambient light, and season; and (3) (presumptive) population genetic differences—for example, by comparing contiguous pairs of demes, pairs of more remote demes such as those in different drainage systems, and pairs of demes from extreme ends of the species' geographic range. The fact that females of this species are flightless and burrowing means that any gene flow that occurs must be either through male flight, female or larval dislocation/dispersion through flood waters, or flight by as yet unknown macropterous females, which I have unsuccessfully sought for many years. The fact that sex determination in fireflies does not involve a Y (male) chromosome may mean that we do not have a simple male versus female genetic marker to use to differentiate the mechanics of gene flow among local populations.

The proper study and characterization of but one aspect of the biology of but one presumptively simple, ground level firefly species could take a person a lifetime; or the efforts of an insect behavioral ecology course for generations of students. It is fortunate that wheel pushing is a rewarding and a relaxing thing to do in itself, especially in high-stress times.

ENDNOTES

I thank Cindy Weldon Lasley, for making the hundreds of data sortings and manipulations that were necessary for this analysis, and Steven Lasley, Department computer specialist, who gave us considerable instruction and wrote essential analy-

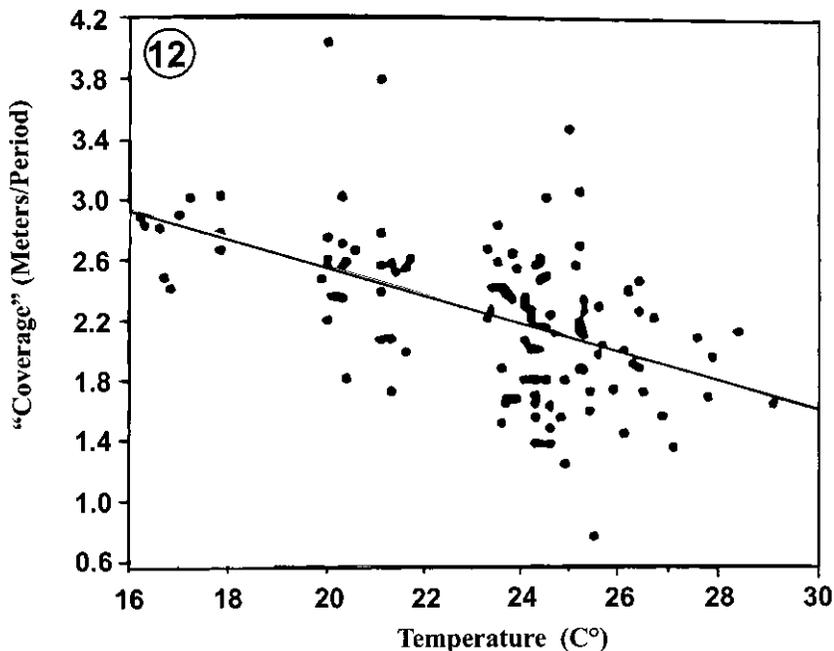


Fig. 12. Meters flown per flash period as a function of ambient temperature (in C°). But what of actual area illuminated in front of the male by each flash? See text.

sis programs. The late Harry A. Lloyd made modifications on the wheel to make it more suitable for the special application required for this study; Robert S. Lloyd followed and measured some males. I also thank Tim Forrest, John Sivinsky, Steve Wing, M. I. Montenegro, and Jade Williams for comments on the manuscript at various stages of its development. Flora MacColl and the late Barbara Hollien provided considerable technical expertise and assistance. Jenny Gavilanez-Sloan for translating the abstract. Florida Agric. Exp. Station Journal Series No. R-07406.

Measuring wheels were Rolatape® Models; Model 623 was the larger and used for all but the few exceptional runs mentioned in the text. The event counter was a Clay Adams 2channel. For analysis, the midpoint time of each run was calculated by halving run duration and subtracting this quotient from the day-time of the run's end. This time, expressed in minutes after sunset, was then converted to Crep Units by dividing by the duration of Civil Twilight for that date and place (Nielsen 1961). Sunset times and C.T. durations were determined from a computer program, "Sunset", written by J. P. Oliver with modifications by T. Forrest. Early and partial summaries of certain data have previously been reported (Lloyd 1979).

The following enumerated statements are figure legends for color illustrations (photographic slides) that appear as InfoLink attachments to this article in the electronic publication of this issue of the Florida Entomologist, and are cited in text here as ILR 2000, Fig.#: 1. Copulating pair of *Photinus tanytoxus* Lloyd, a sibling species of *P. collustrans*, which except for the dark coloration of the elytral bead is morphologically indistinguishable. The female was perched just off the ground near her burrow. 2. A copulating pair of *P. tanytoxus* on the ground, with attentions from a second (top)

male. Wing (1984) made several interesting discoveries concerning this situation, and the competitive and defensive tactics of males. 3. Twilight on the lawn of a lakeside house near Gainesville, Florida, with several *P. collustrans* males searching for females. Note their arcing, slowing flight while flashing, and the thin slice of space they use over the ground. 4. A firefly student observing the flashing flight of a single male *P. collustrans*, along the grassy roadside on the west side of Newnans Lake, Gainesville. 5. A female *P. collustrans*, showing her short elytra and large and thinly cuticled abdomen, with her burrow's entrance at the tip of her abdomen. 6. Large and small measuring wheels. The wheel at the right has the "event counter" mounted on the handle bar; the smaller one was used by an assistant and seems to have been responsible for somewhat different values. Another wheel model has a solid rather than spoked wheel and would work better in brushy areas.

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APPENDIX

Field studies for consideration.

1. How long should a sample run be (number of flashes) to adequately sample the behavior of an individual male?
2. How much agreement is there between consecutive samples (e.g., 30 flashes) of an individual's search behavior—i.e., between a 30-flash sample and the next consecutive 30-flash sample?
3. Do older males take more risks in their flight? Do they fly longer each evening, earlier or later, or faster and lower? Is it possible to sample an individual's search behavior when he is young and then again when he is elderly?
4. Is flight altitude smoothly proportional to ambient light level, and what (physiological) mechanism of altitude determination is involved?
5. From what distance are males able to competitively approach female flashes given in response to a rival male's flashes? (see Otte and Smiley 1975?)
6. Is the direction of the arcing flash-trajectory of males influenced by the presence of nearby males or other aspects of the natural environment, such as large or dark herbs, shrubs, or the brighter (western) horizon?
7. Are local activity patches (deme sites) as delineated by observing the flights of males, constant in space occupied, or do "hot spots" change from moment to moment, night to night, or with the number of males active in the site?
8. Can patch-entering and -leaving males be detected by their flashes, or do they fly flashless, and can be found only with flight-interception traps (e.g., window-pane traps)?
9. Do crashing males always light up, or do the data reported here need to be adjusted (calibrated)?
10. Do run-terminating males as observed in this study here actually end flight for the evening or do they return to aerial search?
11. When males fly into a space just previously searched by another male in their presumptive vision-space do they adjust their direction of flight?
12. What is the adaptive significance (function) of the higher flight altitude observed in later-flying males? That is, when it is darker will they see and broadcast further? Or, is it that they cannot see to avoid tall plants and higher flight is safer? Which of these, either or both, is the actual explanation, and can these two be tested and separated simultaneously?
13. What is the adaptive significance of the (apparently) smaller area coverage of flashes at higher temperatures? For example, at higher temperatures might neighboring males react to female response flashes and interlope faster, so (the apparent) smaller flash coverage is a defensive tactic?