ON RESEARCH AND ENTOMOLOGICAL EDUCATION III: FIREFLY BRACHYPTERY AND WING "POLYMORPHISM" AT PITKIN MARSH AND WATERY RETREATS NEAR SUMMER CAMPS (COLEOPTERA: LAMPYRIDAE; *PYROPYGA*)

JAMES E. LLOYD
Department of Entomology and Nematology
University of Florida, Gainesville 32611

ABSTRACT

The origin, evolutionary malleability, and sometimes loss of insect wings, gossamer structures whose existence has reshaped the natural world, is one of the most interesting and enigmatic dramas of insect biology. Lampyridae have long been known for the reduced wings that occur in females of some genera, but in all previously known examples it is a *fait accompli*, with little or no intraspecific variation. Such variation occurs in and among populations of the little daytime firefly *Pyropyga nigricans*, and also, among these populations there appears to be variation in sexual involvement in the phenomenon, with brachypterous males also occurring at some localities. This firefly provides an opportunity for students, both in summer classes and as solitary individuals, to study the evolutionary biology of wings, from adaptive significance to sexual selection and population ecology and genetics, to speciation, and in a variety of habitats from strands on northern glacier lakes to southwestern montane stream sides and beyond, to west-coast marshes.

Key Words: Lampyridae, *Pyropyga*, brachyptery evolution, deme divergence, speciation

RESUMEN

El origen de las alas de los insectos, su maleabilidad evolutiva, y algunas veces su ausencia, son unos de los más interesantes y enigmáticos dramas de la biología de los insectos. Los Lampyridae se reconocen desde hace tiempo por las alas reducidas de las hembras de algunos géneros, y en todos los ejemplos conocidos anteriormente en esta familia las alas reducidas son un hecho con poca o ninguna variación. Sin embargo, polimorfismo en las alas ocurre entre poblaciones y entre individuos de una misma población de la pequeña luciérnaga diurna *Pyropyga nigricans*, y también dentro de estas poblaciones parece haber variación en la participación del fenómeno en la atracción sexual. Esta luciérnaga brinda una oportunidad a los estudiantes tanto en clases de verano como individualmente para estudiar la biología evolutiva de las alas desde su significancia adaptativa en la selección sexual, en la ecología poblacional y en la genética, hasta la especiación, y además en una variedad de hábitats desde las orillas de los lagos glaciares del norte hasta los bordes de riachuelos montanos en el suroccidente y más allá en los pantanos de la costa este.

In this symposium series I have passed along notes on the natural history of fireflies I have met in the field, as I might in written lectures (Letters) to an introductory biology class, in the spirit of the initial introduction by John Sivinski. I continue here with the story of a firefly that has no adult lantern nor nocturnal activity, but instead uses pheromone communication in broad daylight. This is another illustration that taxonomists—in this example the late John Wagoner Green—have valuable observa-

tions and speculations on their taxa that go unnoticed indefinitely, hidden away in esoteric papers, perhaps archived in personal field books after their authors have passed on, unless we make special effort to help them out into the open. An informed teacher can place such memorabilia in a larger biological context and use them as vehicles to introduce, sketch, and add human interest to a general subject area. Publication of such lessons makes these useful notes and essays available to others to initiate projects at several levels of biological sophistication, beginning with field exploration in particular, and should be encouraged as a legitimate method of primary publication. This is what I do here, though the background and related information is abbreviated.

In this example, a cryptic treasure buried in the revision of a small and "not especially interesting" genus of Lampyridae was recalled by a teacher/researcher ("your present author") who recognized the phenomenon in specimens collected by a student doing a summer project. It involves shortcomings, so to speak, of firefly wings and elytra, and why it is that such valuable adaptations as flight and protective body armament can be traded away or lost. The subtexts of the phenomenon, the "whys" of selection and adaptation, and the "wheres" of population divergence should invite the attention and investigation of student and professional biologists.

In known cases of wing reduction in fireflies members of a species are short-winged to approximately the same degree. In other words, the transformation events are passages of the past, and in our time each is seemingly complete, a done deed as they say. Cantharoid taxonomist Green discovered unique and perhaps yet unfinished examples when he revised the genus of "little daytime fireflies," *Pyropyga*, in 1961. The nominal species of interest occurs across North America and individuals of both sexes are typically long winged. Green's two populations in which wings were shorter than typical for this firefly were 2500 miles apart, embedded it would seem in an infinite number of local populations of long-winged individuals. In 1973 Terry Butler invited my attention to some unusual specimens that she had found along the shore of Douglas Lake in northern Michigan, at the University of Michigan Biological Station (UMBS), near Pellston. With this as introduction, let us begin the lesson . . . after this brief message: The Internet (electronic) publication of this paper has additional figures as InfoLink attachments to illustrate the text; these are color slides of the fireflies and their sites. These are cited in text here by their number as ILR figures. Legends for InfoLink 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 XIX

On Becoming A Glowworm—The Disappearance Of Firefly Wings and Flight, Over Time and Space (Lampyridae: *Pyropyga nigricans*)

> When I am working on a problem, I never think about beauty. I think only how to solve the problem. But when I have finished, if the solution is not beautiful, I know it is wrong.
>
> (R. Buckminster Fuller, architect)

Dear Fireflyers, The wings of insects fascinate many entomologists before their futures catch up with them and they become entomologists. I can imagine that soon after the painful light of conscious thought first glimmered in a hominids head, he and she envied the wings of dragonfly and butterfly, for with them they would not have to walk over rough ground all the way to a watering or wintering place. Entomologists

attribute some of the great success of their beloved subjects to wings, whether success is measured by the phenomenal number of species or the equally unbelievable number of life-styles and niches taken by them, or by their diversity of form. Insects do more than fly with their wings. They rub them and broadcast rap, they wave them and push molecules of sex pheromones toward potential mates, and in southeast Asia tree-swarming fireflies use them as upper jaws of clamps that hold partners tightly, against intrusions of pushy interlopers perched all 'round (Fig. 1).

With the adaptive advantages offered by wings, one must wonder why it is that over evolutionary/geological time the females of several firefly species have greatly reduced and sometimes even lost theirs. How could such a conspicuous handicap be favored by natural selection? Unfortunately, in known cases of wing reduction in fireflies all members of a species are short-winged to approximately the same degree. This means that in each of these lineages the happening is in the past, and we can only observe products, not the process as it is occurring. Probably this is to be expected, for it may require only a few tens or hundreds of generations to go to completion.

But, remarkably, there is one North American firefly that today, even now as you read this, appears to be in the process of losing its wings, and this reduction seems to be proceeding differently, to have reached a different condition in each of the few local populations presently known to exist. If this is correct, this firefly is a living model for evolution/adaptation studies, with something to teach us about how wings may sometimes be lost by fireflies. It may also show us how the gene pools of local populations may become isolated from nearby parent populations, with each being a living experiment and a unique step in a passage of possibility toward becoming a new species.

Fig. 1. Copulation clamp employed by a male of *Pteroptyx valida* in a firefly tree near Bangkok, Thailand. The tip of the male's elytra are pushed under those of his female (at right) and tightly down against the top of her abdomen; at the same time the tip of his abdomen is pushed up against hers from below, holding her in a vice-like grip.

The named species of promise is *Pyropyga nigricans* (Say) (Fig. 2), and as presently understood, this little daytime firefly occurs across northern United States and southern Canada, and southward in the west into Mexico (Fig. 3). My education by this firefly began in 1973 when Terry Butler, a student doing a project under my direction at the University of Michigan Biological Station collected some remarkable specimens with much-shortened wings along the shore of the "Bug Camp's" Douglas Lake (Fig. 4). When I saw them I recalled that master taxonomist John Wagoner Green (Fig. 5) had mentioned this phenomenon in his 1961 taxonomic revision of the genus *Pyropyga*. In the section on *P. nigricans* he noted:

> "In an interesting series [of specimens] collected by Peter Rubtzov at Pitkin Marsh in Sonoma County, California, the elytra in both sexes are definitely shortened, exposing several abdominal segments. In another series, collected by the author on the shores of Lake Champlain, near Plattsburg, NY, the same incipient brachyptery [short wingedness] is evident in the females but not in the males. Possibly this phenomenon is associated with permanent moisture." (page 68)

The Pitkin marsh fireflies were collected during a botanical survey of the marsh in 1951-52. In 1990 Rubtzov sent me photos and additional information about the site; Fig. 6 shows the spot where the fireflies were abundant. He wrote: "(the beetles were especially numerous in an open, marshy area with very wet, soggy ground covered by sedges and other wetland herbs . . . there was *no* significant open water . . . only a very narrow, sluggish creek, overgrown by wetland vegetation, in the vicinity)" Green's own Lake Champlain locality was probably a cobble beach, such as or perhaps even the same one shown in Fig. 7 (ILR 1999, Fig. 1), where I found the fireflies in June 1998, 62 years after Green collected his series of specimens.

To put a repeatable, quantitative method into the evaluation of the wing-reduction phenomenon, measurements are needed. This presents two problems, but both seem to be manageable: (1) to see and measure flight wings of preserved dry specimens, they first must be softened (relaxed), then one wing removed from beneath its elytron, unfolded, and placed on a microscope slide. Fortunately there is a strong correlation between elytra and flight wing lengths (Fig. 8). Thus, elytral length can be used as a rapid and reliable indicator of flight wing length, and no dissection or specimen mutilation is needed. (2) Flight wing and elytron lengths vary with specimen size; thus, their lengths must be calibrated for overall body size. To do this, I divided the elytral length of a each specimen by that specimen's pronotal width—body dimensions are commonly used for such calibration in taxonomic keys (see sketch in Fig. 9). I will use this ratio (quotient) to compare wing reductions among *P. nigricans* specimens of diverse body sizes. (Ear lengths in certain breeds of show dogs, when laid forward must not reach the nose, to demonstrate appropriate "conformation to breed"!)

I borrowed and measured Greens two series of specimens from Pitkin Marsh and Lake Champlain. In Fig. 9 note the vertical dotted line at ratio 2.25, which I placed to separate Greens short- and long-winged specimens, cueing on and quantifying the evaluation he made. I will use this line for reference in charts of measured *P. nigricans* from other localities. What initially made Green's discovery especially interesting, in addition to the virtual certainty that his two populations had not been in genetic contact for some geological time, was that there was an apparent sexual difference in the occurrence of brachyptery. Let your mind run with this for a moment—does this indicate significant differences between the two populations in alleles, genes, strength of selection favoring brachyptery, immigration and the degree of isolation from neighboring demes, mate choice and sexual selection, number of generations since the initial appearance of brachyptery in each population, stage of

Fig. 2. Habitus of *Pyropyga nigricans* (Say), a carbon dust drawing by Laura Line. This firefly was named *Pyropyga fenestralis* by Melsheimer in 1846, but Thomas Say's name of 1823 has priority (see Green 1961).

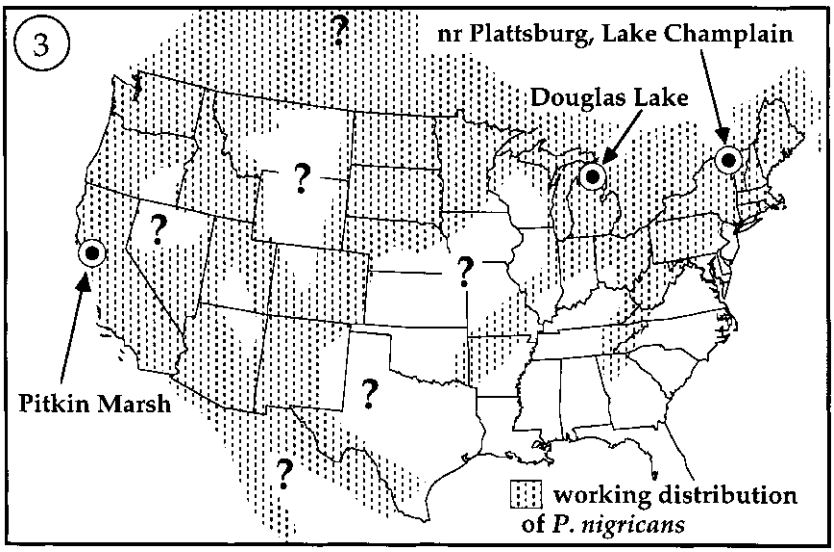


Fig. 3. Distribution map of *Pyropyga nigricans*, with general distribution based on locality labels of identified specimens. Green's two localities, Pitkin marsh in Sonoma County, CA and Plattsburg on Lake Champlain in Clinton County, NY, and the location of Douglas Lake in Cheboygan County in northern Michigan, are indicated. Question marks indicate areas of uncertainty of occurrence — perhaps only temporary gaps in my specimen data.

ecological succession of the site . . . or is it merely the result of sampling error (i.e., Green's small samples)?

Figure 10 shows the elytral ratios of specimens that Butler and I collected and measured from various locations along the shoreline around Douglas Lake in 1973, and Fig. 11 shows ratios of a sample I made 25 years later (ILR 1999, Fig. 2). Note that the sexual involvement is different from that observed in either of Green's two samples, that the female ratio is bimodal (has two peaks) with separation falling near Green's line, and that male ratios range broadly but never as low as those of females. This pattern is also shown by Cheboygan County specimens that are archived in the University of Michigan Museum of Zoology (Fig. 12). These specimens were collected between 1917 and 1969, many from the Douglas Lake vicinity.

Are there more variations around unexplored lakes and marshes in North America? In the course of identifying fireflies for several museums I have viewed many specimens of *P. nigricans* and measured some of them, to have size records, and have found a few other brachypters. Some were archived in the American Museum (NYC) collection, and were collected in 1961 and 1964 at McMillan Camp near Silver City, NM, by lepidopterist Frederick Rindge and his family (Fig. 13). Specimen labels indicated that they were collected at 6800 feet elevation. Rindge replied to my letter of habitat inquiry, after consulting his field notes, that the camp was "situated in a rather small river bottom, with a profusion of ponderosa pine, oak and junipers, plus a great assortment of smaller trees and shrubs. But being in this rather narrow canyon, the stream was always nearby." This location sounds to me as though it shares features with shoreline strands, with unfriendly and isolating habitats on each side! Figure 14 shows the ratios of all of the other North American specimens I have measured.

Fig. 4. A brachypterous female *P. nigricans*, originally photographed for me by Gary Williams at the Bug Camp in 1973; this print was made from the original and is of lesser quality. Note that the dorsal tip of her abdomen (pygidium) is narrowly rounded; those of males are truncate. Her elytral ratio is 1.6.

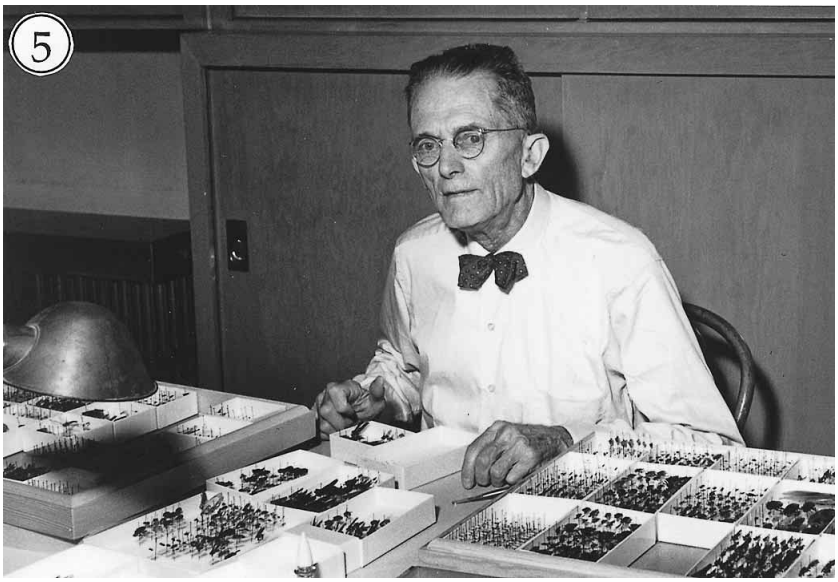


Fig. 5. Taxonomist John Wagoner Green at his desk, about 1960. This photo was provided by the California Academy of Sciences, where Green had taxonomized.

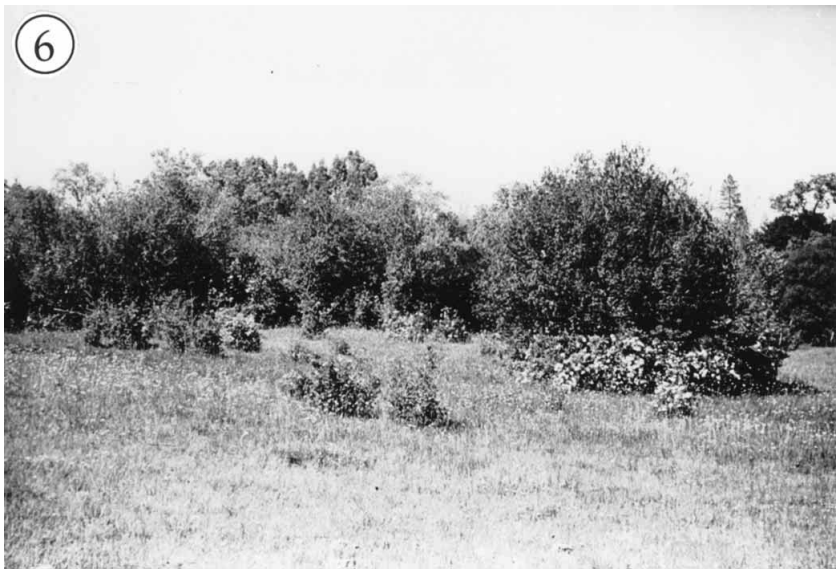


Fig. 6. *P. nigricans* site in Pitkin Marsh, Sonoma County, CA; this photograph was taken by the late Prof. William Hovanitz and provided to me by botanist Peter Rubtzov (see text). Fireflies were most numerous in the area in front of the large shrub at the right.

Fig. 7. *P. nigricans* 1998 site near Plattsburg, NY on Lake Champlain. Green's site was near, perhaps even this one. Fireflies occurred within a few feet of the water, on sand and cobbles. This print was made from a color slide, and lacks the quality that a monochrome negative would have given.

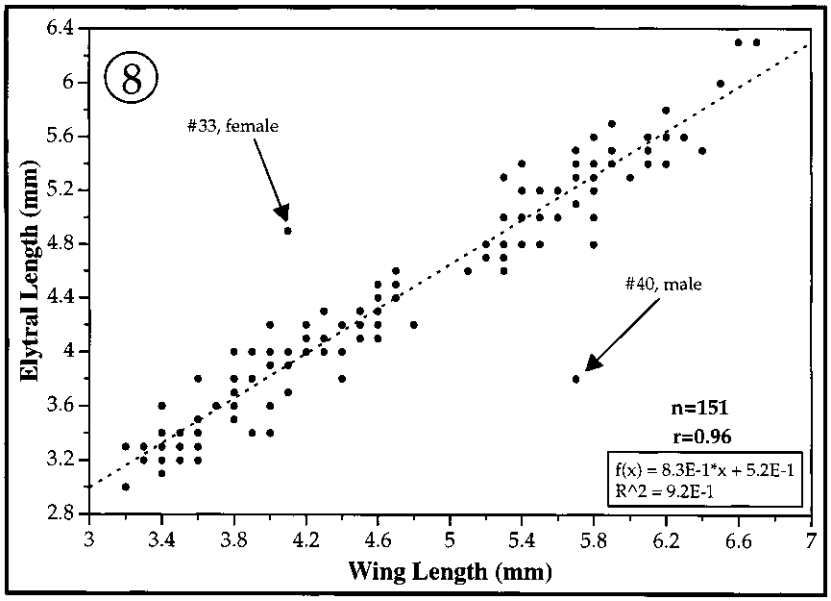


Fig. 8. Elytron length as a function of wing length, showing their strong correlation. This permits the easily measured elytral length to be used to assess wing reduction. Measurements were made by Terry Butler and me.

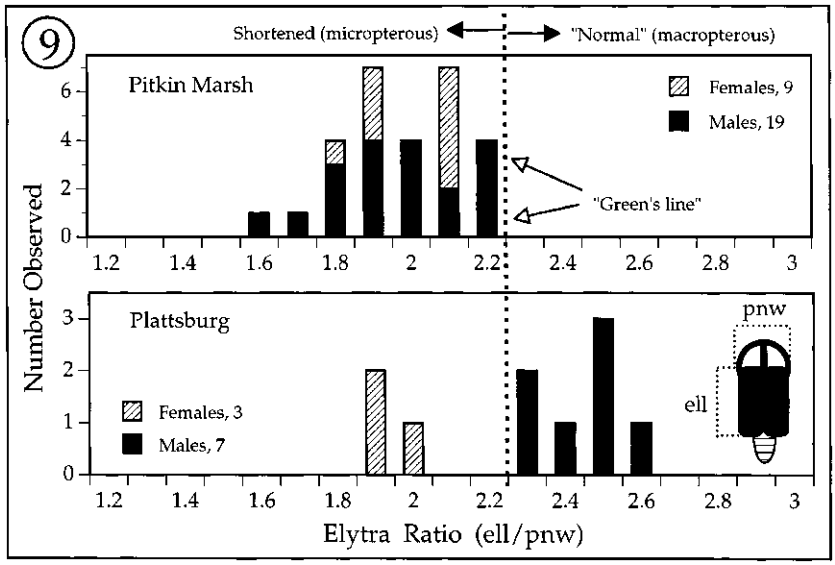
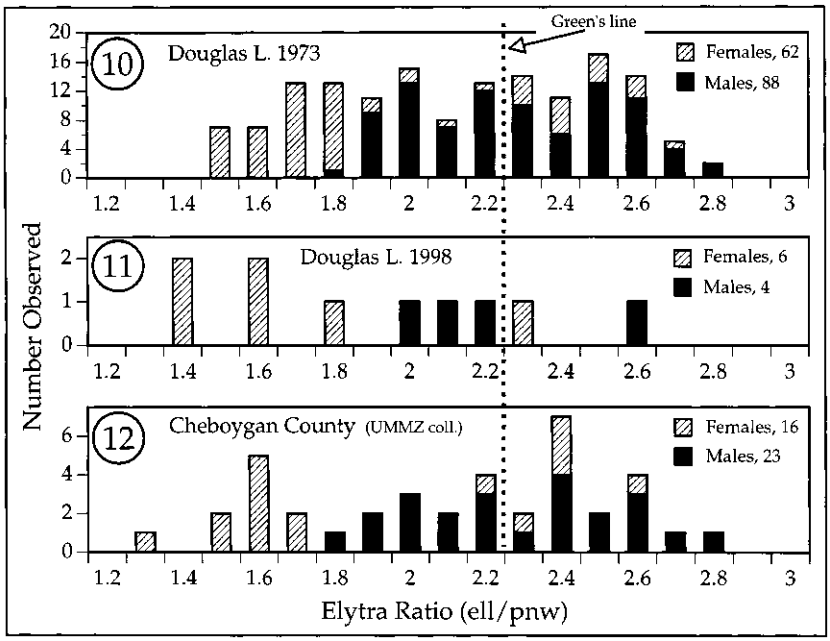


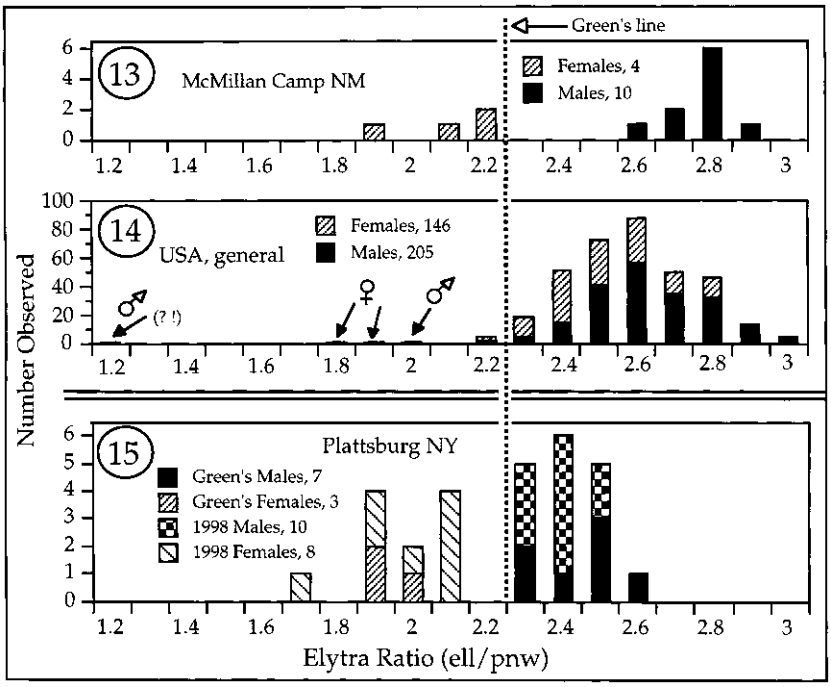
Fig. 9. Quantification of elytral reduction occurring in each of Green's specimen series. Elytra ratio is the quotient of elytral length divided by pronotal width; note sketch. Note that sexual involvement is different in the two samples.



Figs. 10-12. Quantification of elytral reduction in Douglas Lake fireflies and vicinity. Elytra ratio = elytral length/pronotal width. Note that sexual involvement is different from that seen in Green's two samples, shown in Fig. 9 (see text).

Now I excitedly ask, with anticipation, if we are seeing wing length in evolutionary transition, are there brachypterous populations of different ages out there to be sampled for comparison, to be found by wading around marshes and lakes in old tennis shoes? One especially interesting exploration would be to follow the outlet of Douglas Lake—the Maple River—and see whether (a younger population of?) brachypters occur at its mouth where it enters Burt Lake on its water's way to the St. Lawrence and Atlantic (ILR 1999, Fig. 3). I found none where I looked near a boat ramp, nor at another and unspoiled but accessible strand on this lake. Recalling Green's personal field discovery, Lake Champlain has a long shoreline and many islands and streams. My 1998 sample from near Plattsburg is similar in ratio to his 1936 sample (Fig. 15). The map in Fig. 16 shows suspicious localities identified by ratio values (ratios < 2.25) shown in Fig. 14.

There are many places to look, when you consider all of the thousands of glacier lakes advertised by Minnesota, Wisconsin, and Michigan, to say nothing of lakes and canyons scattered throughout the general range of *P. nigricans* (ILR 1999, Fig. 4). Over the past century geologists have learned that the space that became Douglas Lake began as a large, long-lasting chunk of ice, broken from the terminal end of a melting, brittle glacier, leaving a pit (kettle) in the gravel, and that what is now firefly shoreline has been developing in wind and waves and a changing water level for 9500 years. They also know that the climate has changed from cold and damp to warm, and the surrounding forests, from spruce to pine to oak and other hardwoods. They also tell us that Douglas Lake will eventually drain out the Maple River to Burt Lake. So many lakes, so much happening, so little time . . .



Figs. 13-15. Charts showing (13) elytral reduction in *P. nigricans* from a site in New Mexico; (14) elytra ratio in a general sample of *P. nigricans*; and (15) a 1998 Plattsburg sample combined with Green's original sample. Elytra ratio = elytral length/pronotal width. (see text)

I made a few observations on *P. nigricans*' mating behavior at Plattsburg and Douglas Lake. Mating occurred from sunrise to midday, with males and possibly females too being attracted to female pheromones (Fig. 17; ILR 1999, Fig. 5). Adults remained within a few feet of the shoreline and after coupling they turned tail-to-tail; though tiny, pairs were conspicuous on sand, gravel, and stones (ILR 1999, Figs. 6 and 7). Winged males rarely flew, and when they did their flights were short, typically less than a meter in length; I saw only one flying in 1998. Figures 18-20 show activity "profiles" made along beaches at the two localities. Larvae were found walking along beaches at Douglas Lake within a meter of the waterline on damp sand (ILR 1999, Fig. 8). I never found nocturnal activity by juveniles or adults.

To conclude and highlight, questions of natural selection happily arise—why are individuals with shorter wings better at reproducing, at leaving offspring with their alleles in such ecological situations, than are individuals with longer and flight-capable wings? This phenomenon in insects has been noted and considered by a succession of naturalists for more than a century. The strand habitat, that is, the shorelines of lakes, rivers, and oceans, and around islands, has often been associated with wing reduction and loss. Among possibilities that have been considered and that could fit here: if this firefly gains little or nothing from flight, allelic substitutions from strong selection in pleiotropic contexts could substitute alleles that produce reduced wings; energetic savings realized by not building wings could be diverted into eggs or mate

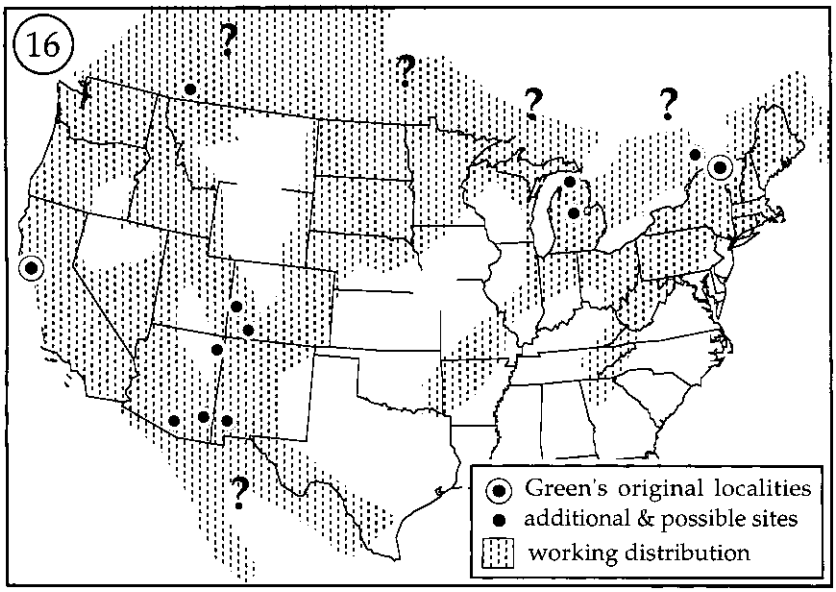


Fig. 16. Known and suspected *P. nigricans* brachypter locations. Isolated lakes and montane canyons are promising situations.

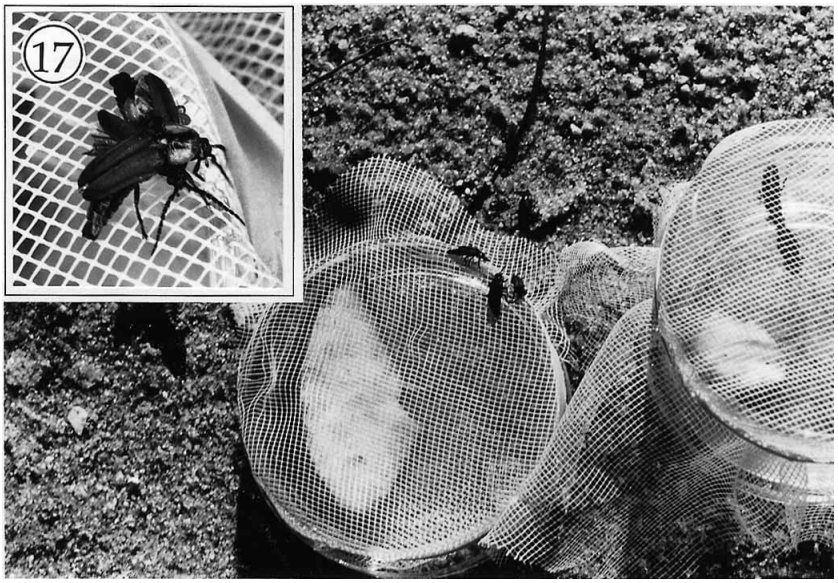
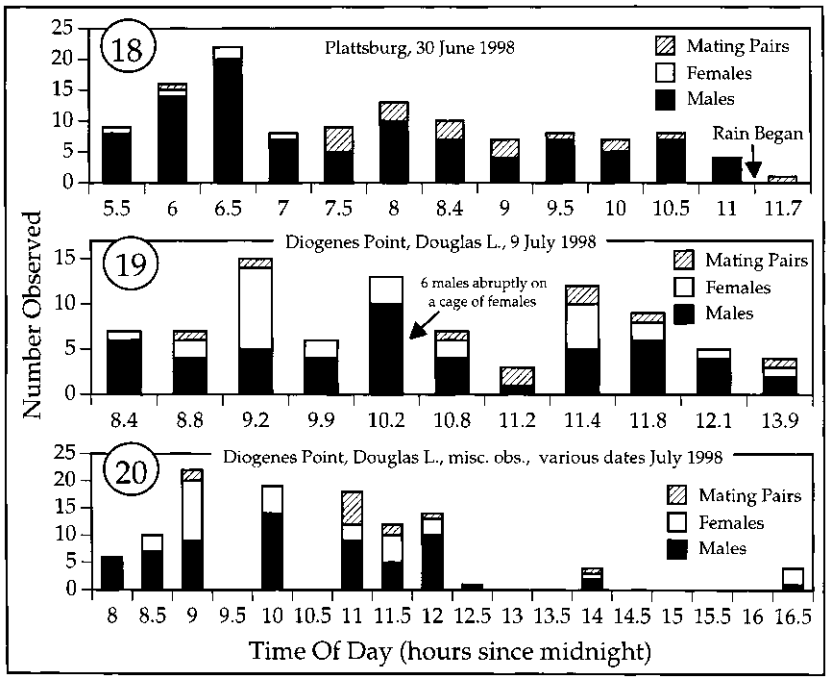


Fig. 17. When females were placed in a net-covered dish on the Douglas Lake beach males and females quickly approached (appeared) and walked up onto the net. Inset shows male atop another, and their spatulate pygidia. Red mites are common on these fireflies; there is one in the inset, spreading the lower male's wings.



Figs. 18-20. Adult activity profiles for two sites. (18) A systematic census in the site at Plattsburg; (19) a systematic census at a site on Douglas Lake; (20) a nonsystematic collection of incidental counts made on several days at the Douglas Lake site.

search (and provide an advantage over short geological time); because flyers can be blown over open water away from limited or narrow habitats, having wings may often be fatal (a genetic lethal!) in such situations.

Of special interest in strand inhabiting *P. nigricans*, is whether their genetic isolation from nearby, say, just-inland demes is primarily geographical (spatial), or if mate choice and sexual selection have become involved and promote genetic isolation. This consideration properly enlarged brings fireflyers into the realm of sympatric speciation models, which, in my view, is a too-neglected aspect of taxonomic thought for insect fancying naturalists afield.

Perhaps it will be found that the population of fireflies in Pitkin Marsh, interpreted for sake of mental jogging as nearing maturity, has proceeded further toward wing reduction stability than other *P. nigricans* now known. Maybe this population is very old and began somewhere else, within walking distance of course, on a strand around a now dried up pond or lake? Surely, when we have more data on these little daytime fireflies, and now I explain this letter's obscure title, we will understand more of the evolution of wing reduction and loss in luminous glowworm and lightningbug fireflies.

ENDNOTES

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for preparing the InfoLink attachments; Juan Manuel Alvarez for translating the abstract into Spanish for the resumen, Peter Rubtzov for photographs and ecological information on the Pitkin Marsh site; and Frederick Rindge for ecological information on the McMillan Camp site. I thank the staff and administration of the University of Michigan Biological Station (UMBS) in 1973 and 1998, for use of their outstanding facilities and equipment, for bringing key references in their library to my attention, and for their unstinting cooperation. I especially want to thank Terry Butler, the student who saw something "peculiar" about the Douglas Lake brachypters and brought them to me, and then collected and measured many of them; Gary Williams, for taking the photograph of the firefly in Fig. 4 and teaching me the fundamentals of darkroom photography; and Jack Burch for his kind hospitality, answers to snail questions, and barge piloting during the 1998 survey of sites along the circumference of Douglas Lake.

Archived specimens from several collections have been viewed over several years, and I thank each of the curators and collection managers for loan of these specimens. Their institutional affiliations and collections are here indicated by name and "Arnett coden": Lee H. Herman, American Museum of Natural History (AMNH); Mark F. O'Brien and Richard D. Alexander, Museum of Zoology, Univ. of Michigan (UMMZ); Hugh Powell, Staten Island Museum; Norman D. Penny, California Academy of Sciences (CASC); Jerry Pilney and Alan Morgan, Dept. of Earth Sciences, Univ. of Waterloo, Canada; Robert E. Lewis, Dept. of Entomology, Iowa State Univ. (ISUI); Brett C. Ratcliffe and Charlie Messenger, Systematics and Research Coll., Univ. of Nebraska (DEUN); the late Floyd G. Werner, Dept. of Entomology Coll., Univ. Arizona (UAIC); Roland L. Fischer, Michigan State Univ. Coll. (MSUC); Bruce Gill, National Museum of Natural Sciences (CNCI), Canada; Robert H. Turnbow, Jr., Dept. of Entomology Coll., Univ. of Georgia (UGCA).

The following enumerated statements are figure legends for color illustrations (slides) that appear as InfoLink attachments to this article in the electronic publication of this issue of the *Florida Entomologist*, and which are cited in text here as ILR 1999, Fig.#: 1. The strand on Lake Champlain near Plattsburg where I made behavior observations in June 1998, and probably near and similar to Greens 1936 collection site. 2. Diogenes Point on Douglas Lake; the July 1998 observation site was the open strand seen to the right. 3. The Maple River, looking downstream just inside the outlet at the southwest corner of Douglas Lake, where the stream begins its woodsy flow to Burt Lake, 118 feet lower in elevation and a mile and a half in distance. 4. A stony strand on the Ontario side of the Ottawa River in Canada, at about 46 N Latitude; to my eye it looks much like the Plattsburg locality, but I found no *P. nigricans*. 5. A shorter-winged male *P. nigricans* that has been attracted to a cage of females. Note the spatulate pygidium that readily identifies him as a male, and a female's silhouette in the cage below the net. He feeds at least four red mites (Acarini), common parasites of shoreline insects. 6, 7. Coupled pairs of *P. nigricans* on a cobble and on a twig on the shore of Lake Champlain. Such pairs are easily spotted, and some (all?) remain coupled for hours. 8. A wind-swept beach on North Fish Tail Bay, Douglas Lake, where 14 larvae were seen (hunting?) along three feet of the shoreline on damp sand; all were within two feet of the waters edge. Florida Agricultural Experiment Station Journal Series Number R-06817.

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