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BIOLOGY OF THE FIREFLY *PYRACTOMENA*
LUCIFERA (COLEOPTERA: LAMPYRIDAE)

LAWRENT L. BUSCHMAN¹
Dept. Entomology and Nematology
University of Florida, Gainesville, FL 32611 USA

ABSTRACT

The firefly *Pyractomena lucifera* (Melsh.) occurs in fresh water marshes throughout the eastern half of temperate North America. Larvae captured prey both above and below the water surface and dragged it above water to feed. Prey records included: snails (n = 38) (Gastropoda: Pulmonata), freshwater limpets (n = 5) (Gastropoda: Ancyliidae), a jumping spider (Salticidae), a damselfly nymph (Odonata) and a leech (Annelida: Hirudinea). Cryptically pigmented pupae were found on emergent vegetation and did not glow when probed. The pupal stage lasted 6.8 days for males and 6.4 days for females. At dusk males flew over the vegetation emitting single flashes (0.2 sec long, 27°C) at 2.9-5.1 sec intervals (17-24°C). Females answered male flashes with single flashes (ca. 1 sec long) at delays of 0.7-1.5 sec (17-27°C). Mated females seldom answered male flashes. Females oviposited when they were 5-6 days old, but 2-4 days after mating. They laid 30-194 eggs (mean = 102) and the number of eggs laid correlated with pupal weight of the female (correlation coefficient = 0.82). Eggs measured 0.8 mm and hatched in 15 days. They became faintly luminescent 2 or 3 days after oviposition and remained luminescent until they hatched. Six predators of this firefly were recorded: wolf spiders (n = 2) (Lycosidae), an orb weaver spider (Argiopidae), a harvestman (Phalangida), a giant water bug (Belostomatidae) and a tree frog (*Hyla* sp.).

RESUMEN

La luciérnaga *Pyractomena lucifera* (Melsh.) ocurre en pantanos de agua dulce a través de la mitad este de la zona templada de Norteamérica. Las larvas capturan la presa arriba y debajo de la superficie del agua y la llevan arriba del agua para comérsela. Se han reportados como presas: caracoles (n=38) (Gastropoda:Pulmonata), "limpets" de agua dulce (n=5) (Gastropoda:Ancyliidae), una araña saltadora (Salticidae), una ninfa "damselfly" (Odonata) y una sanguijuela (Annelida:Hirudinea). En vegetación nueva se encontraron pupas crípticamente pigmentadas y no brillaron cuando se tocaron. El estado pupario duró 6.8 días en los machos y 6.4 días en las hembras. Al anochecer, los machos volaron sobre la vegetación emitiendo destellos individuales (0.2 segundos, 27° C) a intervalos de 2.9 a 5.1 segundos (17-24°C). Las hembras le contestaron a los machos con destellos individuales (aprox. 1 segundo de duración) con demoras de 0.7-1.5 segundos (17-27° C). Hembras que habían copulado, rara vez le contestaban al destello de los machos. Las hembras pusieron los huevos cuando eran de

¹Current Address: Dept. of Entomology, Kansas State University, Garden City Experiment Station, Garden City, KS 67846 USA.

5-6 días de edad, pero después de 2-4 días de haber copulado. Ellas pusieron de 30-194 huevos (promedio = 102) y el número de los huevos puestos está correlacionado con el peso de las pupas de las hembras (coeficiente de correlación = 0.82). Los huevos midieron 0.8mm y nacieron en 15 días. Dos o tres días después de puestos los huevos, eran vagamente luminiscentes y se mantuvieron así hasta que nacieron. Se han reportado 6 rapazes de esta luciérnaga: arañas "wolf" (n=2) (Lycosidae), una araña "orb weaver" (Argiopidae), un "harvestman" (Phalangida), un "water bug" gigante (Belostomatidae) y una rana de árbol (*Hyla* sp.).

The bioluminescent behavior and flash communication of many North American fireflies have been described (Lloyd 1971), but other aspects of lampyrid ecology and life history are poorly understood. The limited information available on the biology of immature lampyrids relates to a few species that occur in northeastern United States (Williams 1917, Hess 1920, McDermott 1948, and McLean et al. 1972). In this paper, I report the biology, ecology and flash behavior of the firefly *Pyroactomena lucifera* (Melsheimer) in northcentral Florida. This firefly was a common local species and the larvae responded readily to laboratory rearing efforts.

P. lucifera was originally described in 1854 (Green 1957), but this name has been used in referring to several different taxa. McDermott (1911, 1948) used this name when he described the flash communication of fireflies which were later described as *P. dispersa* Green (Green 1957). Williams (1917) associated observations of Wenzel (1896) with *P. lucifera*, but Wenzel was working with *P. ecostata* (LaConte). Barber (1951) describes 2 populations of *P. lucifera* in a marsh, one emitting single flashes, the other producing 5 flashes per flash pattern. Green (1957) found both *P. dispersa* and *P. lucifera* in the series collected by Barber and concluded the single flash specimens were *P. lucifera* and the 5 flash specimens were *P. dispersa*.

METHODS AND MATERIALS

A large population of *P. lucifera* occurring in marsh areas associated with Lake Alice on the University of Florida campus (Gainesville, Florida) was visited at least once a month 1970-1973 and 1976. Daily or weekly visits were made during the summer. In this marsh, the emergent vegetation was dominated by cattail (*Typha* sp.) and sawgrass (*Mariscus* sp.) and the floating vegetation was dominated by water hyacinth (*Eichhornia crassipes* [Mart.]). In the laboratory all firefly stages were maintained in 177 ml (6 oz) jars containing a filter paper folded into an upright cone. The filter paper was kept saturated with water and replaced when moldy. In flash responsiveness tests, jar lids were replaced with polyethylene wrap. Larvae and other life stages were observed and collected in the marsh usually at night on warm evenings when they could be located by watching for their glows. Additional observations were made in rearing jars or in aquaria. Prey records were compiled for larvae found with prey in the field.

The ability of lampyrid larvae to survive under water was examined in 2 experiments. First, 2 groups of 14 medium-sized *P. lucifera* larvae were placed in vials with screened ends. The vials were submerged in each of 2 beakers of water. Bottled nitrogen was bubbled through the water in one beaker to remove the dissolved oxygen. Bottled air was bubbled through the

water in the other beaker to aerate it. The vials were arranged so the water circulated through them continuously but the larvae were not exposed to the bubbles. In the second experiment, larvae were held under water as described above for an extended period. Air was bubbled through the water continuously as described above. Five large and 5 small *P. lucifera* larvae, 4 large and 4 small *Photuris* sp. (non-red) larva, 2 large *Photuris* sp. (red) larvae, and 1 larva of *Pyrractomena limbicollis* Green were all held under water for 31 days. A larva of *Photinus consimilis* Green was added later and was held for 26 days. Snails were offered as food.

Flash behavior of adults was recorded verbally on a tape recorder and the timing of events was subsequently measured using a stopwatch or an event recorder. The flash exchange between caged males and females was also recorded electronically in the laboratory using equipment described by Lloyd (1968). Female responsiveness to artificial flashes was tested with a pocket flashlight. Male responsiveness was tested with the modified flashlight and with a flashing device which produced a flash and a prolonged afterglow. This device was mounted on the end of a 1.5 m pole so it could be activated beneath an advertising male.

A mark-recapture experiment was conducted in which males were marked with individually coded spots of airplane dope paint. The length and weight of each firefly were recorded before release and after recapture. The flight period was only 15-30 min, so this time was devoted to collecting as many males as possible. Since they could not be released during the flight period in which they were captured, they were held and released the following evening. Holding them for 24 h did not affect their physical condition since they survived for several weeks under these conditions. The number of days between release and recapture is reported and does not include the 24 h holding period.

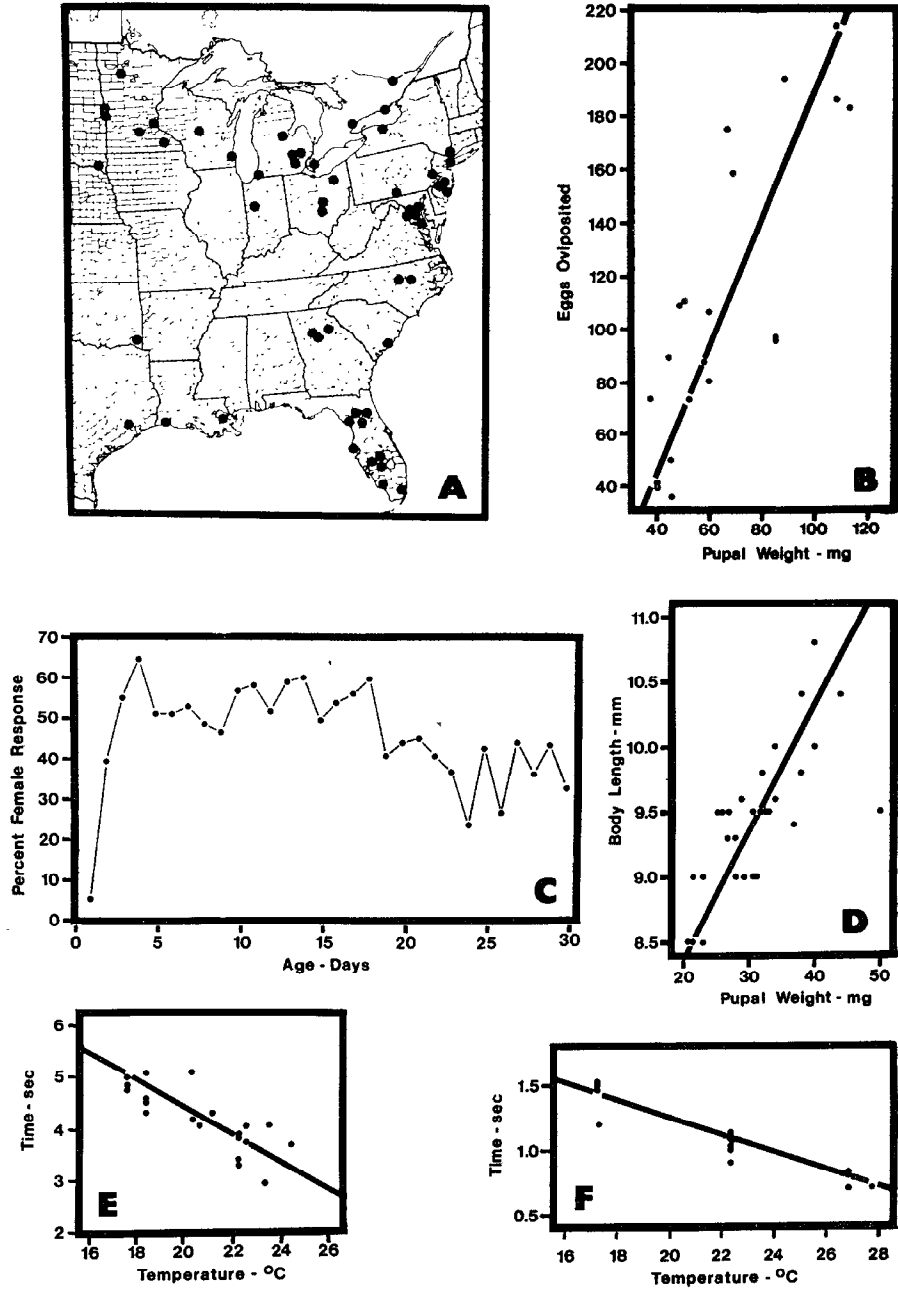
Females of known age and mating status were tested daily to detect changes in responsiveness to flash signals. Four to 6 responsive females in individual jars were placed in each of a series of cardboard boxes. The responsiveness of females in each box could then be tested without disturbing the whole population. Initially, artificial flashes were used, but female responsiveness was poor, so spontaneous male flashes were used in the main experiments. Male flashes were obtained by holding several jars, each containing 1-10 males, over the females in a box until a male flashed spontaneously. The response of each female was recorded. Five such flash stimuli were presented to each female during each of 5 test periods for a total of 25 stimuli per evening. The first test period started 15 min after room lights went out (1300 h) and subsequent test periods started at 15 min intervals thereafter. Spontaneous flashing by males lasted about 10 min, usually long enough for 1 test period. Several groups of males were maintained in a lighted holding room so a different group could be used for each test period. Females were considered 1 day old the first evening after they enclosed.

The duration of copulation was determined by checking mated pairs every 12 h. A mating pair was considered to be in copula if they did not separate when touched with a probe. Oviposition was recorded daily. The development of the female reproductive system was determined by dissecting virgin females at 1, 2, 4, 6, and 8 days and recording the number of mature oocytes in the oviducts.

RESULTS AND DISCUSSION

GENERAL INFORMATION

The firefly *P. lucifera* occurs in fresh water marshes throughout eastern temperate North America (Fig. 1A). In Florida, I observed this firefly in Alachua, Marion, and Levy Counties. I also observed it near Charleston,



South Carolina and Wilson, North Carolina. At all locations this firefly was associated with emergent and floating aquatic vegetation such as water hyacinths and cattails.

BIOLOGY OF LARVAE

Larvae of *P. lucifera* (Fig. 2A and 3D) were consistently found on aquatic vegetation at Lake Alice. They were particularly abundant in and around cattail stands, but larvae were found throughout the extensive mats of water hyacinths that covered large areas of the lake. They spent most of their time near the water surface but when the vegetation was wet after a rain or when dew was present they could be found on vegetation 1-2 m above the water. During the day larvae were found in crevices between the leaves of the hyacinths and cattails. Larvae could be collected at night by watching for their glows. Glowing by these larvae was observed most frequently when they were crawling.

Larvae of *P. lucifera* were observed to crawl in and out of water both in the field and in the laboratory. The caudal grasping organ (described by Balduf 1935) was used to grasp the substrate during locomotion (Fig. 3A). This organ was also used in grooming. No other North American lampyrid is known to have such aquatic habits, but several Asian and Jamaican lampyrids are known to be aquatic (McDermott 1953, Annandale 1900, Blair 1927, Okada 1928).

Two experiments demonstrated the ability of lampyrid larvae to survive under water. In the first experiment *P. lucifera* were held under water that was aerated with air or deaerated with nitrogen. After 20 h all larvae were alive and clinging to the surfaces of the vials. The flow of gases was increased and 6 h later all larvae exposed to bubbling nitrogen had released their grip on the substrate and were lying on their backs, apparently dead (most later revived). Larvae exposed to bubbling air were still alive and clinging to the vial surfaces after being submerged 26 h. In the second experiment only 2 of 10 *Photuris* larvae died during the 31 day period under aerated water. The 10 *P. lucifera* larvae and the *P. limbicollis* larva survived for 31 days under water. The *Photinus consimilis* larva survived 26 days under water. These larvae apparently were able to absorb oxygen through the membranous cuticle or through the caudal grasping organ. None of these larvae have special aquatic adaptations such as gills as have been reported for other aquatic lampyrid larvae (Blair 1927, Okada 1928).



Fig. 1. A, The geographic distribution of *Pyraetomena lucifera* in North America. Each dot represents a county record (data from Green [1957], J. E. Lloyd [personal communication], and personal observations). B, The relationship between pupal weight of females and numbers of eggs laid ($y = 11.04 + 1.66x$, $r = 0.820$, $n = 18$). C, Percent female responses to 25 male flashes at female ages 1-30 days. D, The relationship between pupal weight and body length of males ($y = 7.67 + 0.06x$, $r = 0.733$, $n = 31$). E, Interval between male advertising flashes at various temperatures in the field ($y = 8.02 + (-0.18)x$, $r = -0.678$, $n = 20$). F, Response interval between male flashes and female responses at various temperatures (solid dots = field observations timed with stopwatch, open dot at 28° = laboratory observations timed electronically) ($y = 2.45 + (-0.06)x$, $r = -0.889$, $n = 15$ combined observations).

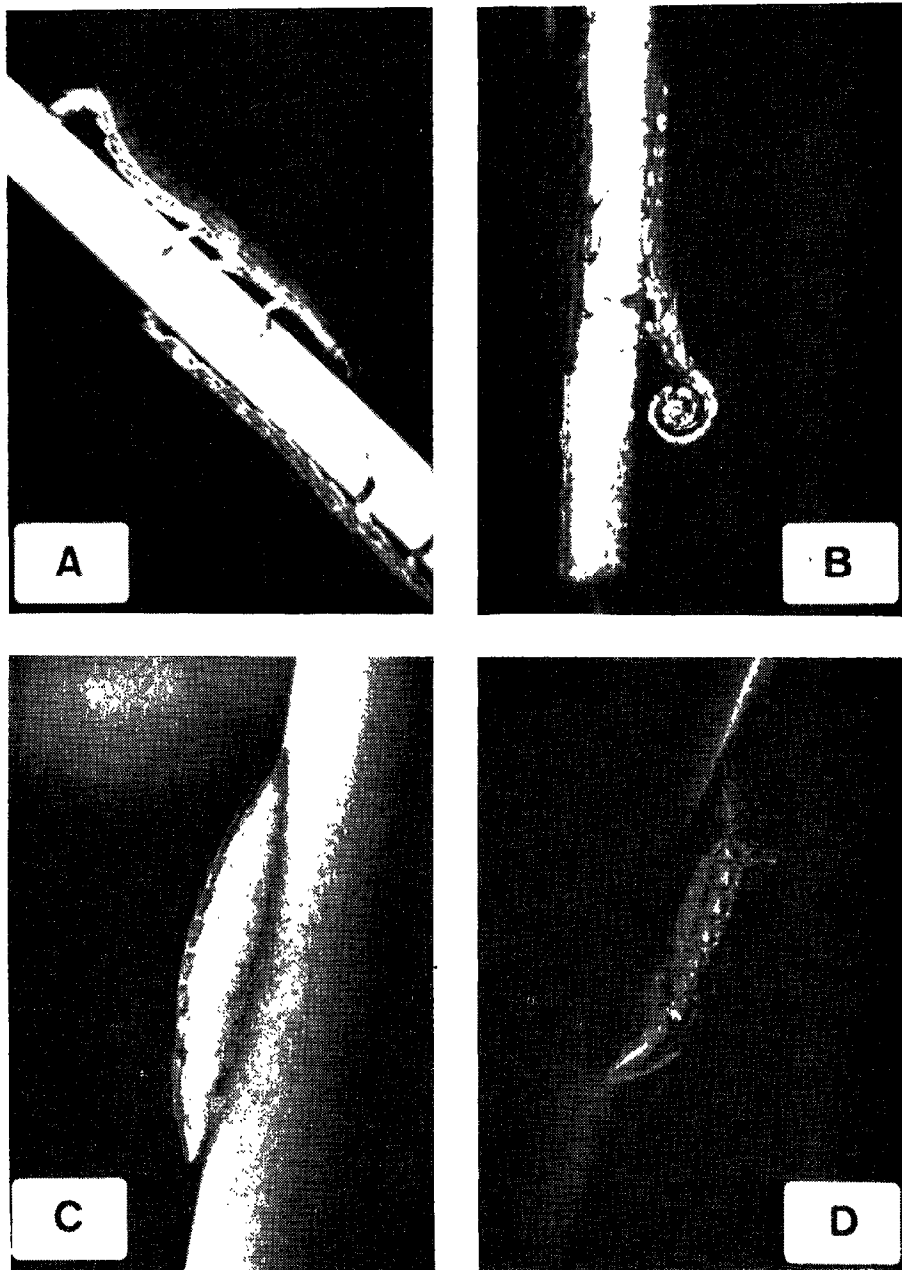


Fig. 2. A, Larva of *P. lucifera* crawling with thoracic legs and caudal grasping organ. B, Larva feeding on a snail which was captured under water and pulled out of the water. C, and D, Prepupa and pupa hanging from aquatic vegetation.

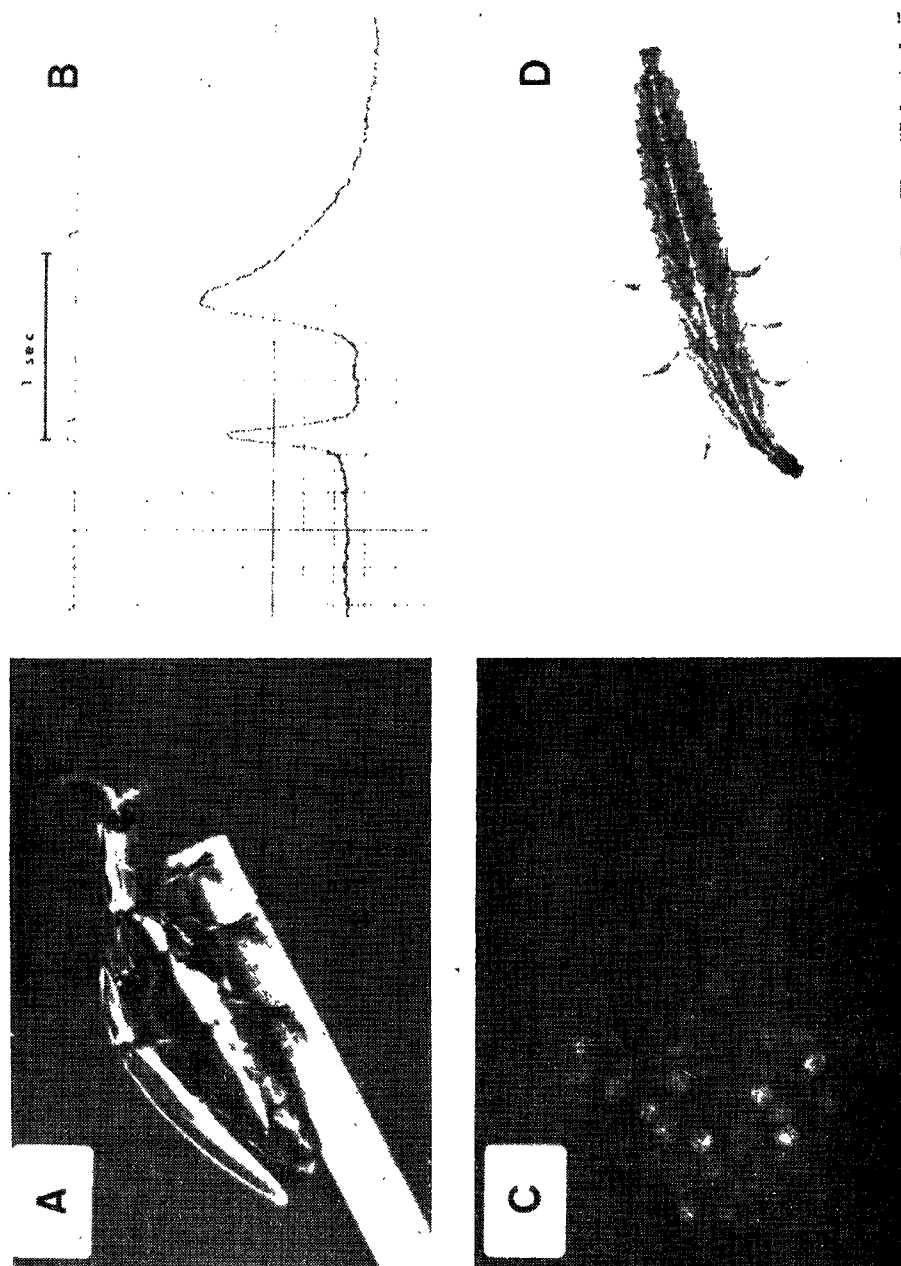


Fig. 3. A, A mating pair of *P. lucifera*. B, A flash exchange between a male (left) and female (right) recorded electronically 28°C. C, Luminescence of eggs which were nearly ready to hatch in which the embryonic light organs are visible (24 h exposure on Kodak recording film developed at ASA 1000). D, Dorsal view of a larva with head extended.

Photuris and *Photinus* larvae are generally terrestrial species found in wet habitats but are seldom found in water. Red *Photuris* larvae are found in relatively dry areas and *P. limbicollis* larvae are arboreal.

Larvae of *P. lucifera* seem to prey primarily on snails. Larval prey records were as follows: snails (n = 38) (Gastropoda: Pulmonata), freshwater limpets (n = 5) (Gastropoda: Ancyliidae), a small jumping spider (Salticidae), a damselfly nymph (Odonata: Coenagrionidae) and a leech (Annelida: Hirudinea). The following snail species were recorded: *Physa pumilia* Conrad (n = 20), *Pseudosuccinea columella* (Say) (n = 3), *Polygyra* sp. (n = 1), *Lymnaca cubense* (Orbigney) (n = 1), *Promenetus* sp. (n = 1), *Helisoma duryi* (Wetherby) (n = 1), *H. trivolvis* (Say) (n = 1), and *Zonitoides arboreus* (Say) (n = 1). The damselfly was identified as *Anomalagrion hastatum* (Say). There are only 2 previous prey records of *Pyraetomena* sp. larvae. Farnworth (1973) found *Pyraetomena gamma* Jac. larvae feeding on snails and Lloyd (1973a) photographed a *Pyraetomena limbicollis* larva feeding on a snail.

Larvae of *P. lucifera* captured snails as prey both above and below water (Fig. 2B). Larvae pulled snails out of the water by climbing backwards, reaching upward and backward with the caudal grasping organ and pulling the snail 10-20 cm up the emergent vegetation. Larvae spent considerable time patrolling the water edge and sometimes stuck their heads into the water. This behavior would allow larvae to detect prey both above and below the water surface. Snails were frequently observed crawling upside down on the surface film and under water on aquatic plants. Only occasionally were snails observed crawling above water on emergent vegetation.

There was no evidence of cooperation between 2 or more larvae in attacking snails. Only once did I find more than 1 larva feeding on a single prey. In the laboratory, several larvae would often feed on the same prey, even when other prey was available. Observations indicated that larvae were attracted by chemicals released from the prey when the first larva began feeding (see also Buschman 1984). There was no indication that larvae oriented to snail slime trails. Schwalb (1960) demonstrated that *Lampyrus noctiluca* L. could follow snail trails, but did not respond to the odor of snails.

P. lucifera larvae attacked snails by climbing onto the shells and reaching under them to bite and chew at the snail body. There seemed to be no preference for a specific part of the snail body. Schwalb (1960) reported that *L. noctiluca* larvae attacked snails in the head region, injected a toxin and retreated; they did not begin feeding until the snail was immobilized by the toxin. There was no such hesitation in the attack of *P. lucifera* larvae; they followed the snail into the shell biting and chewing continuously. *P. lucifera* larvae did not release their prey as do other terrestrial lampyrids (Schwalb 1960, Buschman 1984). In this habitat released prey would fall away and might be impossible for the larva(e) to retrieve.

BIOLOGY OF PUPAE

Mature larvae became sedentary and adhesive secretions from the caudal end fastened the abdominal sternites to the substrate. Such larvae (prepupae) were usually oriented head-down and were found 2-45 cm above water on emergent vegetation (Fig. 2C). At this stage the filaments of the

caudal grasping organ were withdrawn, the legs did not grip the substrate, the body was bloated and there was no response to tactile stimuli. The prepupal stage lasted for 3 to 5 days. At pupation, the larval cuticle split around the lateral edge of the pronotum, the pupa wiggled forward inside the exuviae and anchored itself in the exuviae with adhesive secretions and hooks on the tip of the pupal abdomen. The exuviae remained covering the tip of the abdomen (Fig. 2D). The pupae became cryptically pigmented in a pattern similar to that of the larvae. The pupae of *Pyractomena* differ from other lampyrid pupae in several ways: 1) they occur on vegetation in exposed situations instead of in soil, 2) they become cryptically pigmented instead of becoming milky white and 3) they did not glow as did other pupae when disturbed or handled roughly. The pupal stage lasted 6.8 days ($n = 63$, standard deviation = SD = 0.77) in males and 6.4 days ($n = 35$, SD = 0.70) in females at room temperature (22-28°C). The pupal stage was significantly longer in males than in females (T-test, $p = 0.05$).

BIOLOGY OF ADULTS

Adult Behavior. Males began flashing 32 min after sunset (23 dates, SD = 6.2) and flash activity reached a peak about 5 min later. Flash activity was intense for 10-15 min then decreased rapidly. The last flashes were usually seen 15-30 min after flashing began. At dusk, males flew among the plants or up to 0.5 m above the vegetation but after dark they flew only above the vegetation and up to 2 m high. Males did not fly over the shore except when the vegetation was wet. Flight activity was reduced when it was windy or when there was bright moonlight. Males produced single advertising flashes as they flew over aquatic vegetation. The duration of the male flash recorded at 27°C averaged 0.21 sec ($n = 39$, SD = 0.032). The interval between male flashes averaged 2.9-5.1 sec depending on temperature (17-24°C) (Fig. 1E) ($y = 8.02 + (-0.18)x$, $r = -0.678$, $n = 20$). Gravid females were too heavy to fly and remained on the aquatic vegetation. They answered male advertising flashes with a single flash having a measurable duration of 0.96 sec ($n = 33$, SD = 0.287) followed by a prolonged afterglow lasting several seconds (Fig. 3B). The interval between male flashes and female response averaged 0.7-1.5 sec depending on temperature (17-27°C) (Fig. 1F) ($y = 2.45 + (-0.06)x$, $r = -0.889$, $n = 15$) for 6 responsive females (at 14°C females did not answer male flashes). Flying males that received response flashes hovered and repeated the flash exchange before landing. Approaching males climbed up and down the vegetation to reach the female. Males flashed at irregular intervals and females answered these flashes occasionally. Two caged responsive females placed in the field answered 6 of 7 flashes from flying males that flashed within 1-2 m. These females answered 3 of 11 flashes from males that were climbing in the vegetation and they answered 12 of 17 flashes of males that were within 10 cm of the females. Males located each female jar within 15 min. The flash dialogue between these fireflies continued for an hour (when observations were terminated), at least 30 min after male flight activity had stopped.

Both sexes responded poorly to artificial flashes: females answered artificial flashes only occasionally and males could not be decoyed with artificial response flashes even when the flashlight was modified to simulate female flashes. When flashlight flashes and spontaneous male flashes were presented alternately to a group of 9 responsive females, only 3 answered

flashlight flashes, but all 9 answered male flashes. In this test, 5 flashlight flashes received a total of 5 response flashes, whereas the 5 male flashes received 24 response flashes.

The response rates of 43 virgin females, 1-30 days old, to male flashes are presented in Fig. 1C. Of 29 females tested on day 1, only 8 were responsive. On day 2, 25 of 30 responded. By day 3 all females were responsive, answering 55% of test flashes. On day 4, the response rate reached a peak of 64.5%. From day 3 to day 18 the rate of response remained fairly constant and averaged 54.5%. From day 19 to day 30 the response rate decreased slowly, but erratically. The response rates for days 1-5 were analyzed using the Student's T-test (unequal variance, percent response data were adjusted using the arc-sine transformation). The rates for days 1, 2 and 3 were significantly different from each other ($p = 0.05$) while days 3, 4, and 5, were not.

Lloyd (1979) suggests that as a female ages her response pattern may change as the likelihood that she will remain unmated increases (He notes that aging females of *Lampyrus noctiluca* glow more brightly and change glowing stations more frequently than young females). This hypothesis does not seem to apply to *P. lucifera* since the response rate of mature females declined as they aged. It is possible, however, that older females might remain responsive longer during the evening. The distribution of female response during the evening was analyzed for 11 females which had been tested on days 3-8 consecutively. In a 2-way factorial analysis of this data, there was no significant interaction ($p = 0.05$) between response rate during the evening and the age of female, indicting no change in the distribution of female responses during the evening.

Of 20 mated females exposed to flashlight or male flashes every day as long as they live, 15 never answered male flashes after they had mated. These 15 laid one or more batches of fertile eggs beginning 2-5 days after mating. Five of the mated females began answering male flashes at ages 12, 14 ($n = 2$), 21 and 22 days. Four of the 5 females laid at least one batch of eggs 2 or 3 days after mating. Three of the 4 egg batches were fertile. The response rate of these 4 females was low and erratic (less than 20%). The 5th responsive mated female failed to oviposit normally. Her responsiveness was suppressed for 10 days, but then for the next 32 days she answered 12-56% of male flashes. This female laid a small clump of infertile eggs on day 26 (virgin females frequently began laying small groups of infertile eggs when they were over 20 days old). These observations indicate that mated females seldom respond to male flashes and they are therefore unlikely to mate a second time under field conditions.

Other Mating Biology. Mated pairs remained in copula for extended periods (Fig. 3A). In the laboratory males remained on the female almost continually even when the genitalia were not engaged. Sometimes pairs appeared to be in copula, but when touched with a probe they quickly disengaged. The mean duration of copulation was 33 h ($n = 14$). One mated pair was found in the field during the day. This pair had apparently mated the previous evening about 18 h earlier. Prolonged copulations (up to 24 h) do not appear to be laboratory artifacts. Lloyd (1972) also observed mated pairs of *Luciola* sp. during the day and at dusk that had apparently mated the previous evening.

The number of mature oocytes in female oviducts on days 1, 2, 4, 6, and

8 averaged: 0.0 (n = 4), 5.3 (n = 6), 24 (n = 4), 57 (n = 7), and 72 (n = 8). Females that mated on day, 2, 6, and 9-16 oviposited 4.0 (n = 7), 3.1 (n = 10), and 2.3 (n = 9) days after copulation started. Females did not oviposit before they were 5 or 6 days old even when they mated early, but oviposition was delayed when they mated late. The delay in oviposition may be related to the extended period of copulation. Males appeared to prevent or delay oviposition of older females by remaining in copula. Females begin oviposition soon after copulation terminated.

The delay between mating and oviposition may have caused the female to shift her peak flash responsive period forward in time. Females are ready to oviposit on day 5 or 6 (the full complement of mature oocytes is present in oviducts at this time). Any delay in oviposition beyond this time unnecessarily subjects females to natural hazards. If there is to be a long delay (2-4 days) between copulation and oviposition, it would be advantageous for the female to begin copulation several days before eggs are ready to be laid. This would explain why females become fully responsive by day 3 although their eggs are not ready until day 5 or 6. If a female was successful in attracting a mate on day 3, she would be ready to oviposit 2-4 days later at age 5-7 days when her eggs were ready to be laid.

Females oviposited 1 to 5 times over a 20 to 30 day period. Most ovipositions (71%) occurred at intervals of 2 to 7 days and averaged 5.1 days (n = 20). Eggs from each oviposition were placed on the substrate in a group (egg mass). Many eggs were in contact with each other and each was covered with a transparent secretion. In the laboratory, females placed eggs on glass as often as on filter paper. Females also laid eggs between layers of filter paper. Females laid an average of 2.6 egg masses (n = 31). The hatch rate for all eggs averaged 96% and was about the same for early and late ovipositions even though females mated only once. Two females had lower hatch rates of 74 and 65%. The number of eggs laid by 32 females averaged 67, 28, 19, and 15 in the first through fifth egg masses respectively. The total oviposition averaged 102 eggs (n = 29, SD = 41.9) and was related to the weight of the female pupa; larger females laid nearly twice as many eggs as the small ones (Fig. 1B) ($y = 11.04 + 1.66x$, $r = 0.82$, $n = 18$).

Of 46 females that were mated and maintained during these experiments, 42 laid fertile eggs. Three of the infertile females failed to lay eggs normally, but expelled a small mass of infertile eggs at death. The fourth female mated with 2 males and laid 5 apparently normal egg masses (a record 214 eggs), but they did not hatch.

In the laboratory females lived up to 53 days but it is doubtful that they approach that age in the field. Females laid most of their eggs by day 20 and none were laid after day 31. Mated egg-laying females lived an average 31.5 days (n = 19, SD = 9.9). Unmated non egg-laying females lived an average 32.1 days (n = 12, SD = 12.4). Female life span was significantly ($p = 0.05$) correlated with pupal weight (unmated $r = 0.645$, $n = 9$, mated $r = 0.492$, $n = 26$).

Males were capable of multiple copulations. In the laboratory, males often mated with more than one female. One male mated with 4 females which laid 178, 154, 84 and 134 eggs which hatched normally. In the field multiple matings by males would be more limited since each copulation ap-

parently takes 24 h or more and it may take several days of searching to locate a female (Lloyd 1979).

The life span of male fireflies in the laboratory averaged 20 days ($n = 16$, $SD = 3.5$), but this is undoubtedly much longer than in the field. Of 198 males marked and released, 24 males were recaptured (ca. 12% of the marked-released population) after 1 day ($n = 11$), 2 days ($n = 3$), 5 days ($n = 1$), and 10 days ($n = 1$). The longest interval between release and recapture was 10 days. It therefore appears that the maximum life span of these males was 11 or 12 days since they were probably at least 1 day old when first captured. This is almost twice as long as the life span recorded for *Photinus tanytorus* Lloyd which appeared to have a life span of 6 or 7 days (Buschman 1977).

Males emerging from large pupae were larger than males emerging from small pupae (Fig. 1D) ($y = 7.67 + 0.06x$, $r = 0.733$, $n = 31$). Adult male fireflies seem to depend primarily on energy reserves accumulated during the larval stage (occasionally fireflies have been observed to drink dew or flower nectar). Large pupae transmit larger energy reserves to the adult than small pupae and therefore should live longer, search larger areas and thus have greater probabilities of finding females. The 2 males recaptured after 7 and 10 days were among the larger males captured during the experiments. However, male life span in the laboratory was not correlated significantly ($p = 0.05$) with pupal weight ($r = 0.137$, $n = 16$).

BIOLOGY OF EGGS

The pale yellow-orange eggs of *P. lucifera* were laid in groups of 20-100 and measured 0.8 mm ($n = 12$). They were covered with a transparent secretion which acted as an adhesive. Since the egg chorion was transparent, the developing embryo was visible inside the egg. Eggs hatched in an average of 15 days ($n = 31$, $SD = 0.92$) when reared at room temperatures (22-28°C). Eggs of *P. lucifera* were found in the field on 2 occasions: once on a waterlogged hyacinth leaf and once on a hyacinth leaf ca. 15 cm above water. Gravid females were often found between leaves at the base of cattail and hyacinth plants and they probably oviposit in these areas also. Eggs became luminescent 2 or 3 days after they were laid and remained luminescent until they hatched (Fig. 3C). The luminescence was faint; it took 15-20 min to dark-adapt the eyes sufficiently to see it. Eggs laid by unmated females were not luminescent.

The oviposition of eggs in large groups on vegetation is unusual among lampyrids. Most lampyrids lay their eggs singly or in small clusters in the soil among plant roots (Williams 1917, Hess 1920, McLean et al. 1972, Kaufmann 1965, Schwab 1960, Kiichiro 1961).

NATURAL ENEMIES

Only a few natural enemies of *P. lucifera* were observed. A wolf spider (Lycosidae) and a giant water bug (*Belostoma testaceum* (Leidy), Belostomatidae) were observed feeding on larvae. A tree frog (*Hyla* sp.), an orb weaver spider (*Acanthepeira* sp; Argiopidae), a wolf spiders (Lycosidae) and a harvestman (Phalangida) were observed feeding on adults of *P. lucifera*. Surprisingly, I did not find *P. lucifera* captured as a prey by the aggressive mimic *Photuris* females which were common in the vicinity. In

the laboratory *P. lucifera* larvae were cannibalistic when severely starved. They attacked dead larvae, and live prepupae and pupae. Small larvae attacked unsclerotized newly hatched larvae. No insect parasites were recovered from the hundreds of field-collected larvae reared during these studies. Only a limited number of parasites and predators of fireflies has been recorded (Lloyd 1973b).

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MALE-MALE INTERACTIONS IN CARIBBEAN FRUIT
FLIES, *ANASTREPHA SUSPENS*A (LOEW)
(DIPTERA: TEPHRITIDAE): TERRITORIAL FIGHTS
AND SIGNALLING STIMULATION

THEODORE BURK

Biology Department, Creighton University, Omaha, NE 68178, USA

ABSTRACT

Laboratory experiments were made on 2 aspects of male-male interactions in Caribbean fruit flies, *Anastrepha suspensa* (Loew). Observations of males involved in territorial contests on a lab-caged grapefruit tree revealed that large size and residence gave males advantages in fights; large intruders usually were able to oust small residents. In a second experiment, groups of individually-caged males began to emit sex pheromone and produce acoustic signals earlier in the daily sexual display period when in contact with other males than when isolated from them.

RESUMEN

Se hicieron experimentos en el laboratorio sobre 2 aspectos del comportamiento entre machos del "Caribbean fruit flies", *Anastrepha suspensa* (Loew). Observaciones de machos, en un árbol de toronja enjaulado en el laboratorio, envuelto en disputas territoriales, revelaron que los residentes de mayor tamaño y tenían ventaja en las peleas; los intrusos de mayor tamaño usualmente podían sacar a los pequeños residentes. En un segundo experimento, en su diari despliegue sexual, machos individualmente en-

