BIOLOGY AND BIOLUMINESCENCE OF SELECTED FIREFLIES IN THREE GENERA: PYRACTOMENA, PHOTINUS AND PHOTURIS (COLEOPTERA: LAMPYRIDAE)

By

LAWRENT LEE BUSCHMAN

A DISSERTATION PRESENTED TO THE GRADUATE COUNCIL OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1977

Larva of Pyractomena lucifera feeding on a snail.

In memory of my mother,

Clara D. (Lohrenz) Buschman

who died June 26, 1976.

Official emblem of the

Florida Entomological Society

designed by

Lawrent L. Buschman

ACKNOWLEDGEMENTS

This dissertation could not have been completed without the support and assistance of my wife, Rose. I am particularly grateful for her editorial assistance and for typing the manuscript.

I would like to express appreciation to the professors who served on my graduate and examining committees: J. E. Lloyd (chairman), J. E. Brogdon, P. S. Callahan,D. H. Habeck, S. H. Kerr, J. Reiskind, R. E. Waites, and T. J. Walker. I also acknowledge the extensive discussions with J. E. Lloyd and T. J. Walker which have influenced this research.

The following individuals provided taxonomic determinations: F. W. Mead (Hemiptera, Homoptera) and R. E. Woodruff (Coleoptera), Dept. Agric. & Cons. Services, Division of Plant Industry, Gainesville, Florida; M. J. Westfall (Odonata) and J. Reiskind (Spiders), Dept. of Zoology; D. H. Habeck (Lepidoptera), L. A. Hetrick (Lepidoptera, Bibionidae), J. E. Lloyd (Lampyridae), L. P. Kish (Fungi), G. B. Edwards (Spiders), Dept. of Entomology and Nematology; and Richard Franz (Snails), Florida State Museum, University of Florida, Gainesville.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Abstract of Dissertation Presented to the Graduate Council of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

BIOLOGY AND BIOLUMINESCENCE OF SELECTED FIREFLIES IN THREE GENERA: PYRACTOMENA, PHOTINUS AND PHOTURIS (COLEOPTERA: LAMPYRIDAE)

By

Lawrent Lee Buschman

March, 1977

Chairman: Dr. J. E. Lloyd
Major Department: Entomology and Nematology

In northcentral Florida the firefly Pyractomena lucifera (Melsh.) occurred on freshwater marshes. At dusk males flew over the marsh emitting single flashes (0.2 sec long, 27°C) at 2.9 - 5.1 sec intervals (24 - 17°C). Flight started 31 min after sunset and continued for 15 - 30 min. Females answered male flashes with single flashes (ca. 1 sec long) after delays of 0.7 - 1.45 sec (27 - 17°C). Female responsiveness to male flashes increased from 5.1% on day 1 to 55% on day 3 and averaged 54.6% from day 3 - 18. Females seldom answered flashlight flashes and males were not successfully decoyed with artificial flashes. Mated females seldom answered male flashes. Mated pairs remained in copula 12 - 72 h. The number of mature eggs in the female lateral oviducts increased from 0 on day 1 to 71.25 on day 8. Females oviposited when they were at least 5 - 6 days old but 2 - 4 days after mating. Females oviposited 101.8 eggs (r= 39 - 194) in 1 - 5 batches at intervals of 3 - 8 days over a 20 - 30 day period. The eggs were oviposited in clusters on aquatic vegetation. Eggs measured 0.75-0.9 mm and hatched after 14.8 days (ca. 25°C). Larvae captured prey above and below

water and dragged it above water for feeding. Snails (n=38), freshwater limpets (n=5), a jumping spider, a damselfly nymph and a leech were recorded as larval prey.

Larvae matured in 65 days (males) or 80 days (females) and consumed 15.3 (males) and 20.0 (females) snails when reared under 16:8 h light-dark cycles. Larvae matured after 175-177 days when reared under 11:13 h light-dark cycles and consumed 25 (males) and 33.2 (females) snails. Short photoperiods acted on mature larvae to prevent pupation but the larvae continued to feed and grow. In field-rearing experiments larvae reared during the summer completed development in 9 weeks. Larvae did not pupate after Sept. 18 but continued to feed and grow until March. Field populations of larvae developed rapidly during the summer and some larvae probably completed development in fall. Most larvae overwintered and completed development the following year. Larvae pupated on the vegetation above water, adults emerged after 6 - 7 days and were present from April to October. Males lived ca. 10 days.

Three different populations of Photinus consimilis Green were observed in northcentral Florida: "slow pulse" males emitted 1- to 4-pulsed flash patterns (1.0-1.9 sec intervals) repeated at 10 - 20.5 sec intervals (24-15^{o}C), females answered with 1 - 5 flashes after delays of 5.7 sec (18^{o}C); "slow-fast" males emitted 4- to 11-pulsed flash patterns (0.4 - 0.6 sec intervals) repeated at 14.2 - 25.2 sec intervals (25 - 15^{o}C), females answered with 1 - 8 flashes after delays of 8.8 sec (21^{o}C); "fast-fast" males emitted 3- to 9-pulsed flash patterns (0.3 - 0.44 sec intervals) repeated at 7.1 - 12.0 sec intervals (25 - 14^{o}C), female responses were not observed. Larvae were found on mats of decaying aquatic vegetation. An earthworm and a leech were recorded as larval prey.

Larvae of Photuris congener LeConte had a reddish or rufus dorsal pigmentation (other larvae were brown-black) and were collected in fall in well-drained areas. Larvae of Photuris "A" were collected throughout the year on poorly drained soils. Larvae of Photuris "B+D" were collected in spring and fall mostly in forested areas. Larvae of Photuris "W" were collected in Jan. and March in rotten logs. Larvae of Photuris "V" were collected throughout the year on poorly drained soils. Fall and winter collected larvae did not pupate as quickly as did spring and summer collected larvae. Cold and photoperiod treatments had little effect on pupation. Larvae of P. congener did not pupate even after cold and photoperiod treatments. Snails and slugs (n=5), insects (n=11), fallen fruit (n=4) and an earthworm were recorded as larval prey.

INTRODUCTION

Fireflies have fascinated man for centuries and have become a part of his mythology, folk-lore, fashion, medicine and literature (Lloyd 1971). To children the firefly presents the challenge "catch me"; they spend many enjoyable evenings catching "lightning bugs" to fill jars which they can then use as lanterns. To biologists and naturalists the twinkling fireflies that light up an evening landscape present the more intellectual challenge: "How do they do it?" and "Why do they do it?". Even though answers to these two questions have been accumulating over the years many mysteries remain.

The question of "how" fireflies produce light has dominated the attention of biochemists and physiologists studying insect bioluminescence. The biochemistry of bioluminescence has been reviewed by Harvey (1952), McElroy and Seliger (1966), McElroy and DeLuca (1973) and is summarized in many biochemistry and cell physiology text books. The anatomy and physiology of the firefly light organ has been reviewed by Buck (1948), Harvey (1952), and McElroy and Seliger (1966).

The question of "why" fireflies produce light has received the attention of biologists and naturalists. They have demonstrated the role of bioluminescence in sexual communication. This information has recently been reviewed by Lloyd (1971). Bioluminescence also occurs in immature lampyrids but since the biology and ecology of the immature stages is poorly understood the function of luminescence in the immatures is unknown.

In spite of the attention lampyrids have received over the years, many aspects of their biology remain unexplored and many species are known only taxonomically. In these studies I have chosen to study the biology, ecology, development, life cycle and behavior of the firefly Pyractomena lucifera (Melsheimer). This firefly occurs throughout eastern North America and could become a useful experimental animal. During these studies I also made observations on the biology and flash behavior of fireflies in the Photinus consimilis Green complex and on the ecology and behavior of Photuris spp. larvae. This information gives us a better understanding of the biology and ecology of Florida lampyrids and their relationship to other elements in their ecosystems.

LITERATURE REVIEW

Bioluminescence in Adult Fireflies

Bioluminescent communication

The primary function of bioluminescence in the adult firefly is sexual communication between males and females. Two major signal systems have been described (Lloyd 1971). In signal system I, one sex (usually the female) remains stationary or sedentary and broadcasts a species-specific signal to which the other sex is attracted. The well-known European glowworm, Lampyris noctiluca L., utilizes this system. Among fireflies utilizing this system the female is usually flightless and the light organ is large and bright. The male is a strong flier but often lacks a light organ. The communicative function of luminescence in L. noctiluca was recognized as early as 1557 (Harvey 1957). Schwalb (1960) experimentally analyzed the communicative parameters and found that the male was attracted to a light source and that he recognized a female of his species by the configuration of the female light organ. The sexual function of bioluminescence was often questioned because in many other fireflies both sexes were luminescent and did not follow the above pattern. In signal system II, one sex (usually the male) flies about broadcasting a species-specific signal to which the female responds with a species-specific signal. The advertiser (male) then flies or climbs to the responding female as the flashing continues. Most American Photinus and Pyractomena fireflies utilize signal system II. In these fireflies the male has a light organ larger than the female's. Both

sexes may be strong fliers. Osten-Sacken first described sexual communication using signal system II in 1861 (Harvey 1952). Lloyd (1966a) experimentally analyzed the communicative parameters of this communication and found that females discriminate on the basis of pulse length, pulse interval and pulse number; males discriminate on the basis of response delay time.

The flash behavior of some lampyrids is intermediate between these two signal systems and reflects various stages in the evolution of flash behavior (Lloyd 1966a). The female Phausis reticulata (Say) begins glowing when it sees a glowing male fly overhead (Lloyd 1965b). In Luciola discicollis Laporte (Kaufmann 1965) and Luciola sp.(Lloyd 1973d) the males emit trains of flashes as they fly about and are attracted to females who emit trains of flashes at a slightly different flash rate. Recently, a third and much more complex mating system has been proposed for Luciola obsoleta (E. Oliv.)(Lloyd 1972b). This mating protocol includes 5 distinct phases or stages: (1) sedentary signaling, (2) chasing, (3) walking-luminescing, (4) mounting and (5) copulating.

Synchronous flash behavior of Asian fireflies in the genus Pteroptyx has received considerable attention from Western naturalists but its role in mating behavior remains uncertain. Lloyd (1973c) proposed the following model for the mating protocol for synchronously flashing fireflies: "(1) Both sexes are attracted to the flash rhythm of males of their species. (2) Males in swarm trees detect approaching females and modify their luminescent behavior in ways that stimulate females to land near them. (3) Recognition cues other than flash rhythm (such as flash intensity) are detected as flying males and females near swarm trees. (4a) Females land near and observe males. (4b) Males land and

flash in synchrony with nearby males. (5) Other behaviors (flying and walking) bring males and females closer together. (6) A change of communicative channel (chemical communication) occurs in the terminal stage of courtship before a male and female make physical contact." In this model a male increases his fitness (probability of mating) by participating in synchronous flash behavior. Previous models by Buck and Buck (1966), Case et al. (1972) and Wynne-Edwards (1962) did not account for natural selection of individuals (Lloyd 1973c). Buck and Buck (1976) present a popularized summary of synchronously flashing fireflies.

Other proposed functions of adult luminescence

Several secondary functions have been suggested for bioluminescence in adult lampyrids. Female Photuris fireflies are aggressive mimics. They use their flashes to answer males of other firefly species and prey on the fireflies they attract (Lloyd 1965a). Lloyd (1968) has suggested that Photuris fireflies also use flashes to illuminate landing and take-off areas. Since many fireflies flash when handled it has further been suggested that these flashes might have a negative effect on possible natural enemies (Lloyd 1969a).

Bioluminescence in Immature Fireflies

Bioluminescence is found in all the life stages of fireflies: eggs, larvae, pupae, as well as adults. Since only the adult stage is sexually active, bioluminescence in the immature stages cannot function in sexual communication. Moreover, luminescence is present in the immature stages of species in which adults are non-luminous, eg. Ellychnia corrusca(L.), Pyropyga nigricans (Say), and Lucidota atra (G.A. Oliv.)(Williams 1917 and Hess 1920).

Eggs

Bioluminescence in the lampyrid egg was noted as early as 1557 (Harvey 1957) and has since been observed repeatedly (Harvey 1952). Although it was thought the luminescence was due to the adhesive secretion with which the female covers the eggs at oviposition (Newport 1857), it has now been shown that luminescence is internal (Schwalb 1960). The luminescence of a group of L. noctiluca eggs was photographed by Schwalb (1960). The luminescence in freshly laid eggs is usually described as a faint diffuse continuous glow. However, later in incubation, 3-4 days before hatching, the luminescence is concentrated in the light organ of the developing embryo and becomes periodic (Harvey, 1957). The eggs of E. corrusca, P. nigricans, Photinus spp., Photuris spp. and Luciola spp. are luminous after oviposition but seem to lose this luminosity for a time; it returns again about the time the light organ of the embryo appears (variously Williams 1917, Hess 1920, Kiichiro 1961). The eggs of L. noctiluca apparently remain luminous throughout development (Schwalb 1960).

Larvae

All known lampyrid larvae are luminescent (Balduf 1935, McDermott 1958), even the larvae of species whose adults are non-luminous (Williams 1917, Hess 1920). The larval light organs occur rather uniformly in all instars and throughout the family as 2 spots, one on each side of the 8th abdominal segment. This is the situation in the following genera: Photuris, Photinus, Pyractomena, Ellychnia, Lucidota, Pyropyga, Luciola, and Lampyris (variously Williams 1917, Hess 1920, Okada 1928, Balduf 1935, Schwalb 1960, Kiichiro 1961, Kaufmann 1965). Only two larvae are known

to have light organs that differ from the above pattern: Lamprohiza delarouzei Jacq-DuV. larvae have 2 pairs of luminescent patches, one on the abdominal segment 2 and another on segment 6 (Balduf 1935); L. splendidula L. larvae have 3 - 12 luminous spots on abdominal segments 2 - 6 (Schwalb 1960). The uniformity of the larval light organs stands in sharp contrast to the variety of shapes and locations of light organs in the adult stage (Harvey 1952, Lloyd 1971). The shape and location of adult light organs are used as taxonomic characters at the generic level.

Lampyrid larvae are reported to glow spontaneously or when they are disturbed or stimulated in various ways. Spontaneous larval glows, lasting several seconds, are repeated at irregular intervals. The significance of larval luminescence is unknown although many authors have suggested that it provides protection from predators or that it is used to lure prey (Lloyd 1973e).

Pupae

Lampyrid larvae generally form a cell in the soil in which to pupate. The pupa is generally milky white with a little yellow or pink pigmentation. The eyes and wings often blacken as the pupa nears eclosion. The whole pupa often has a dim glow or "effulgence" which is independent of the light organs. The larval light organs continue to function in the pupa and sometimes for 1 - 2 days after eclosion. The larval light organs of the pupa generally glow brightly at the slightest disturbance or vibration. The adult light organ is present in the pupa but does not function until 1 - 2 days after eclosion. In the genus Pyractomena, the larvae do not pupate in the soil but on vegetation in

exposed situations (Williams 1917, Lloyd 1969c, 1973a). The pupa is cryptically pigmented and is much less likely to glow even when stimulated tactually (Lloyd 1973a).

Biology of Old World Lampyrids

In spite of the extensive literature on lampyrids our knowledge of their biology and development is restricted to a relatively small number of species that have been studied.

Lampyris noctiluca and Lamprohiza splendidula

In Europe many naturalists have recorded observations concerning the "glowworm" L. noctiluca. The larvaform female glows continuously and attracts non-luminous flying males (signal system I). When a male locates the glowworm and copulates with her, the glowing subsides. In the next few days the female oviposits 60 - 90 eggs in the soil under leaf litter. The eggs hatch after an incubation of 27 - 55 days depending on temperature. The larvae live in moist grass and leaf litter where they prey on various snails and slugs. The larvae locate snails by following their slime trails. They attack a snail by repeatedly biting the head region of the snail and injecting a toxin. They are able to subdue snails 15 times their weight. When the snail is paralyzed it is dragged to a sheltered location before feeding begins. Newport (1857) and Vogel (1915) believed that the secretion that was injected into the snail through the hollow mandibles also accomplished extra-intestinal digestion and that the digested tissue was ingested through the mandibular canals. Schwalb (1960) demonstrated that tissue fragments were ingested through the mouth and he discounted extra-intestinal digestion. The larvae molt 4 - 6 times while growing from 5 mm to 33 mm long. Female larvae generally molt

one more time and grow considerably larger than male larvae. Mature larvae pupate in the soil under leaf litter from May to September. The pupal stage lasts 10 - 11 days (female) and 13 days (male). The duration of the life cycle of L. noctiluca is variously reported as 1 year, 2 years and 3 years (Schwalb 1960, Naisse 1966). According to Naisse (1966) the life cycle is probably 1 year in most warmer parts of Europe but is extended to 2 or 3 years in cooler northern regions. Development of individuals within a brood is variable, and they probably reach maturity in different seasons. Only 2 workers have succeeded in rearing this insect from egg to adult: Naisse (1966) was able to rear 2 generations of larvae each year and Wootten (1976) obtained 3 males and 4 females after rearing a group of larvae for 2 years.

The biology of L. splendidula, another glowworm found in Europe, differs only slightly from that of L. noctiluca (Schwalb 1960).

Lamprigera tenebrosus

Another glowworm, Lamprigera tenebrosus (Walker), occurring in India and Ceylon, has been studied by Paiva (1919), Bess (1956) and others. The larvaform female glows to attract the flying male (signal system I). After mating she digs a chamber in the soil in which she lays 30 - 101 eggs and broods them until they hatch 7 weeks later. The larvae emerge and live in the leaf litter. During their development, male larvae consume 20 - 40 snails and female larvae consume 40 - 60 snails. When the larvae mature they excavate a cell in the soil in which to pupate. The pupal stage lasts 16 - 23 days for the male and 7 - 10 days for the female. Larvae mature in 8 - 9 months in an insectary, but the life cycle probably takes a year in the field. Because they prey on the giant African snail, Achatina fulica Bowdich, a serious crop pest in many parts

of the world, the glowworms have been shipped to several Pacific islands as biological control agents against the snail (Peterson 1957, Bess 1956).

Luciola cruciata and Luciola lateralis

In Japan the 2 most common fireflies are Luciola cruciata Motsch. (the Genji firefly) and Luciola lateralis Motsch (the Heike firefly). The biology and life cycles of these fireflies have been reported by Okada (1928) and Kiichiro (1961). The Genji firefly is found only along clear flowing rivers, whereas the Heike firefly is found along the muddier canals and in flooded rice fields. In both species flashing and flickering behavior leads to copulation, but the flash communication system is not understood. At times large numbers of the Genji fireflies are observed to flash in unison. After copulation the female Genji firefly oviposits 300 - 500 eggs (in a cluster), and the female Heike firefly oviposits 70 - 100 eggs (singly) in moist soil and moss within 50 cm of the water. Eggs hatch after 26 - 27 days (Genji) and 21 - 22 days (Heike), and larvae crawl into the water. Larvae live underwater where they prey on various snails. Genji larvae undergo 6 molts while growing from 1.5 mm to 30 mm long and, Heike larvae undergo 4 molts while growing from 1.7 mm to 15 mm long. In spring the larvae emerge from the water in large numbers and climb on shore where they dig pupal chambers in the soil. After about 2 months in the cells they emerge as adults. The life cycle covers 1 year. In Japan fireflies are collected and mass-reared to be sold as exotic pets and to be released during festivals. The government has designated several firefly habitats as national monuments to preserve them from the environmental insults by man.

Luciola discicollis

In West Africa Luciola discicollis Laporte is one of the most common fireflies,and was studied by Kaufmann (1965). During the rainy season it occurs in large numbers over moist grasslands and marshy areas. Both sexes engage in extensive flashing which leads to copulation but the parameters of this flash communication are not understood. The female oviposits up to 50 eggs laid singly in moist soil. The eggs hatch after 7 - 13 days,and the larvae live in the leaf litter. They feed on soft bodied insects, earthworms, slugs and animal carcasses. They do not eat snails. The larvae grow from 1.5 mm to 12 mm long and have 5 molts. The mature larvae construct a pupal cell in the soil. The pupal stage lasts about 8 days. Larvae reared by Kaufmann (1965) matured in about 5 months. The life cycle of L. discicollis apparently lasts less than one year,and there may be 2 generations a year in favorable habitats.

Lampronetes mauritanica

Larvae of the lampyrid Lampronetes mauritanica (L) are believed to live as inquilines in nests of harvester ants in the genus Messor in southern Europe and northern Africa. Their relationship with the ants is not clear (Balduf 1935).

Biology of North American Lampyrids

In the New World the variety of lampyrids is much greater than in Europe. In North America 3 genera include the majority of the species. The genus Photinus as revised by J. Green (1956) includes 28 species. The genus Pyractomena as revised by J. Green (1957) includes 16 species. The genus Photuris as revised by Barber (1951) and McDermott (1967) includes 20 species. Numerous other genera with fewer representatives are also present. The flash behavior of North American fireflies has received considerable attention due to the taxonomic diversity and the

species-specific flash behavior of these fireflies (Lloyd 1966a,1971). Most North American fireflies utilize signal system II in their flash communication. Other aspects of the biology, life cycle and ecology of fireflies occurring in northeastern United States have been recorded by Williams (1917), Hess (1920), McDermott (1958), Keiper and Solomen (1972) and McLean et al. (1972).

Photinus spp.

Several notes on the biology and life cycles of Photinus fireflies have been recorded by Williams (1917), Hess (1920) and McDermott (1958). Photinus females may be brachypterous or fully winged (Green 1956), but they are seldom taken in flight. The female generally remains sedentary and attracts a male utilizing signal system II (Lloyd 1966a, 1971). After mating the female lays eggs singly in moist soil. The eggs hatch 13 - 21 days later. The larvae are believed to live in the soil since very few are found on the surface. Feeding behavior in the field is unknown, but in the laboratory larvae are reported to feed on earthworms, cut-up flies and snails. The larva pupate in cells in the soil, and the pupal stage lasts 9 - 15 days. Photinus fireflies have not been reared from eggs. They are believed to have a 2-year cycle in New England (Williams 1917, Hess 1920) because some of the larvae collected in spring seemed to be too small to mature the same year. McDermott (1958) has suggested a 1-year life cycle for a Photinus sp. in Delaware.

Pyractomena spp.

The biology of Pyractomena fireflies is unique among lampyrids in several respects. Larvae pupate in exposed situations, on vegetation or on tree trunks or branches (Williams 1917, Green 1957, and Lloyd 1969c, 1973a), instead of in the soil as do other lampyrids. Since the

pupae are exposed they are cryptically pigmented while other pupae are white or milky colored. Some Pyractomena larvae are found on tree trunks and branches and are believed to be arborial (Williams 1917, Green 1956, Lloyd 1973a). Other larvae are found in marshy areas (Wenzel 1896, Farnworth 1973). Larvae of P. gamma (Jacq.-DuV.) were found feeding on snails (Farnworth 1973), and a larva of P. limbicollis Green was photographed feeding on a snail (Lloyd 1973a). Larvae of P. angulata Say were found on trees infested with aphids and scales (Green 1957). McDermott (1953) found a larva which he believed to be P. gamma on sea-drenched rocks in Jamaica. (Farnworth,1973,concluded that they were not P. gamma.) Pyractomena females are fully winged but remain sedentary and attract males using signal system II. The flash behavior is similar to that of Photinus fireflies except that in some cases the male lands immediately after the first female response and the subsequent dialogue and approach is protracted. Flash behavior of Pyractomena fireflies has been described by Wenzel (1896), McDermott (1911, 1958) and Lloyd (1964, 1966b).

Photuris spp.

Photuris fireflies are found in a variety of habitats and are among the most common fireflies. Photuris fireflies appear to utilize signal system II in courtship; the flash dialogue, however, is more complex than in other American fireflies (Lloyd 1969a, Buschman 1972, 1974). Flash communication in these fireflies is complicated by aggressive mimicry practiced by some Photuris females. They answer the advertising flashes of other species, mimic their females, and eat the males they attract. Both males and females are active fliers. Females oviposit in the soil and eggs hatch 15 - 27 days later. Larvae

live in the soil and leaf litter where they prey on earthworms and snails (Williams 1917, Hess 1920). In the laboratory they also prey on various soft-bodied insects and eat a variety of laboratory foods (Hess 1920, McLean et al. 1972). Mature larvae build cells in the soil in which they pupate. The pupal stage lasts 16 - 20 days. In New England, Williams (1917) and Hess (1920) concluded that Photuris fireflies had a 2-year life cycle because they found both mature and half-grown larvae in the spring. McLean et al. (1972) obtained 1 female Photuris lucicrescens Barber from larvae they reared from eggs over a period of 14 months. They concluded that since the larvae were inactive during the winter the life cycle must be 2 years in Maryland. Lloyd (1969a) reported that he and D. Minnick obtained an adult Photuris sp. in September from eggs laid in April. Since adults of this species are found in spring and fall there may be 2 generations each year in northcentral Florida.

Other Lampyrids

Three lampyrids, Ellychnia corrusca, Lucidota atra and Pyropyga nigricans, are unusual in that the adults have diurnal habits and do not utilize luminescent signals in courtship (Williams 1917, Hess 1920). In these fireflies the female releases a pheromone to attract the male (Lloyd 1972a). E. corrusca are also unusual in that they hibernate as adults under stones, in rotten logs and under loose bark (Williams 1917). According to Hess (1920) larvae of P. nigricans were active during the day and were found feeding on snails and earthworms. In the laboratory they also preyed on several soft-bodied insects. These larvae were collected under rocks and on wet sand along a stream. P. nigicans appeared to have a 2-year life cycle because half-grown larvae were found when adults were present. Larvae pupated in the soil and the pupal stage lasted 7 - 8 days.

SITE DESCRIPTIONS

Most of the research presented here was conducted on a large population of Pyractomena lucifera occurring in the marsh areas of Lake Alice. The lake is located in the southwest part of the University of Florida campus, Alachua Co., Gainesville, Florida. According to Cason (1970) the lake occurs in a solution basin on Ocala Limestone in a fault zone underlaid by multiple fractures and caverns. Formerly the lake drained into a sinkhole to the east of the present lake but this drainage was blocked by a dam in 1964 and 2 discharge wells were drilled 235 and 450 ft deep at the west end of the lake; the water is currently pumped deep into the Floridan Aquifer. A thick accumulation of silty clay and sand on the lake bottom prevents drainage through the natural solution channels in the limestone beneath the lake. The lake receives water from 3 sources: surface drainage from the university campus, discharged cooling water from the Health Center steam plant, and effluent from the campus sewage treatment facilty.

Lake Alice covers ca. 33 ha (Center 1976), but a catwalk and submerged fence built across the lake in 1970 divides it into 2 parts (Fig. 0.1). The east end, ca. 21 ha, is a shallow marsh up to 2 m deep and is covered with aquatic vegetation: 1) emergent vegetation dominated by cattail (Typha sp.) and sawgrass (Mariscus sp.), and 2) floating vegetation dominated by water hyacinth (Eichhornia crassipes (Mart.)). The west end, ca. 12 ha, is 2 - 5 m deep. It was completely covered with mats of floating vegetation in 1969 but

continuous mechanical removal of the aquatic plants since that time has maintained extensive areas of open water. However, the nutrient-rich effluent from the sewage plant continues to encourage rapid and extensive growth of aquatic vegetation in the lake. The catwalk and fence were built across the lake to prevent the floating vegetation from drifting into the western part of the lake. The catwalk served as a convenient platform during the course of this research. The water level of the lake fluctuated between 22 and 26 cm at the catwalk (Center 1976). The water level was usually high after heavy rains but was also artificially manipulated for various reasons. Experimental agricultural fields are located south and west of the lake; woodlands and the University of Florida campus are to the north and east of the lake (Fig. 0.1).

I made most of my observations of Pyractomena lucifera (Melsheimer) from the catwalk (Fig. 0.1A) and while wading along the edge of the lake (Fig. 0.1B). Photinus consimilis fireflies were studied in these 2 areas (Fig. 0.1A,B) and at the east end of the lake (Fig. 0.1H).

Photuris larvae were collected in a variety of sites. Occasionally they were collected while wading among the aquatic vegetation (Fig. 0.1B) but more frequently along the stream (Fig. 0.1C) and along the trail (Fig. 0.1D) in the flood-plain forest between the lake and the Medicinal Plant Garden. Photuris larvae were also collected in the Medicinal Plant Garden. This was also a wooded area but the underbrush had been removed and the grass was mowed occasionally. The southwest corner (Fig. 0.1E) was fairly low and wet most of the year. Frequently there were 2 - 5 cm of water standing in puddles in this area after a rain. The drier area in the Medicinal Plant Garden (Fig. 0.1F) was up to a

meter higher and was better drained. This area was usually covered with hardwood leaf litter and grass.

Photuris larvae were also collected in several other sites. The Archery and Gun Club sites are located in northeast Gainesville just east of the Municipal Airport. At these sites larvae were collected on the roadsides and in wet ditches where the road passed through mesic hardwood forest along a stream. Highway 329B follows the west shore of Newnans Lake (east of Gainesville) through a mature mesic hardwood forest. Photuris larvae were collected along the road and ditch, on the forest floor and in rotten logs found in the forest.

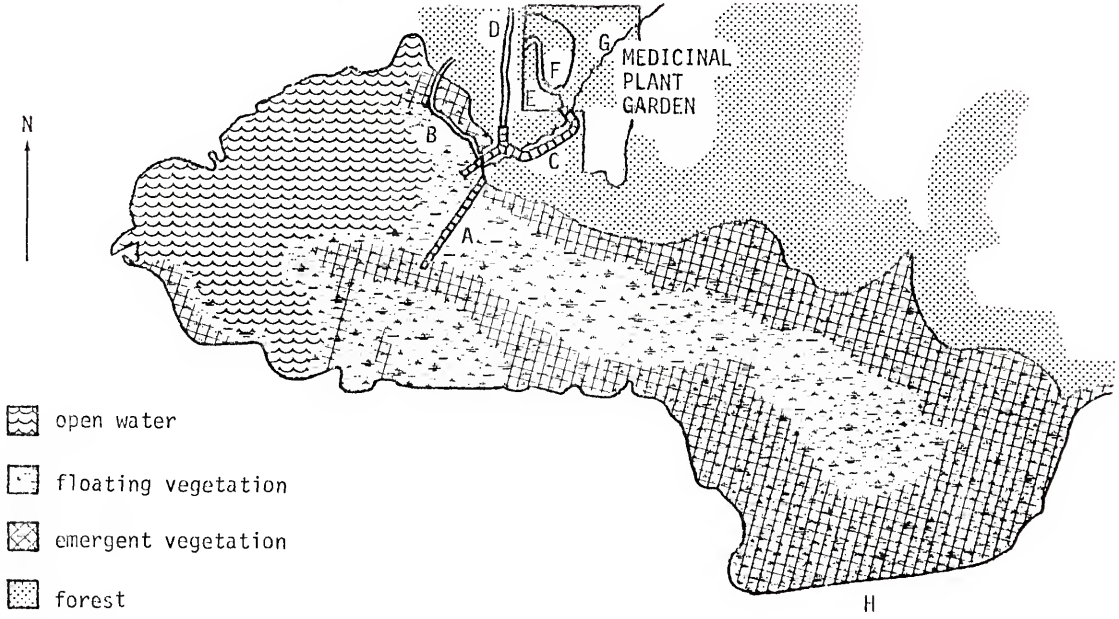

Fig. 0.1 Map of Lake Alice and the Medicinal Plant Garden on the University of Florida campus, Gainesville, Fla. Most of the lake is covered with aquatic vegetation.

CHAPTER I
BIOLOGY AND FLASH BEHAVIOR OF THE FIREFLY *PYRACTOMENA LUCIFERA*

Over the years considerable information has accumulated concerning the biochemistry and physiology of firefly bioluminescence (Buck 1948, Harvey 1952, McElroy and Seliger 1966, McElroy and DeLuca 1973). Recently the communicative function of firefly luminescence has also received considerable attention and the flash behavior of many American fireflies has been recorded (Lloyd 1971). In spite of the attention lampyrids have received, many aspects of their biology remain unexplored. For this reason I have chosen to make a more detailed analysis of the behavior, biology and development of the firefly *Pyractomena lucifera* (Melsheimer). This firefly was chosen for study because it was a common local firefly, the larvae were available year-round, adults were present throughout the summer, and the larvae responded readily to laboratory rearing efforts.

The firefly, *P. lucifera*, was described in 1854 by Melsheimer (Green 1957); the usage of this name in literature is misleading, however, because the name has been used in referring to several different taxa. McDermott (1911, 1958) used this name when he described the flash communication of fireflies which were later described as *Pyractomena dispersa* Green (1957). Williams (1917) referred to observations by Wenzel (1896) using the name *P. lucifera*, but Wenzel was referring to *P. ecostata* (LeConte). Barber (1951) found 2 populations of *P. lucifera* in a marsh, one emitting single flashes, the other producing 5 flashes

per flash pattern. Green (1957) reviewed the genus Pyractomena and found one specimen collected by H. S. Barber who recorded the male flash pattern as a "short sharp flash at irregular intervals". P. lucifera occurs throughout eastern North America (Fig. 1.1). In Florida I have observed this firefly at the following locations: Lake Alice, Bivens Arm, Paynes Prairie and Newnans Lake, Alachua Co.; Orange Lake, Marion Co.; and near Cedar Key, Levy Co. I also observed it near Charleston, South Carolina and Wilson, North Carolina. At all of these locations this firefly was associated with the emergent aquatic vegetation, water hyacinths and cattails in marshes. J. E. Lloyd originally informed me that adults and larvae of P. lucifera occurred on the aquatic vegetation on Lake Alice, Gainesville, Florida.

Description of Life Stages

Male P. lucifera are 7.5 - 10.5 mm long and weigh 6.1 - 20.3 mg (Fig. 1.2). The pronotum is tan with a median and 2 lateral black stripes. The reddish-pink pigmentation of the prothorax is visible through the base of the pronotum. The elytra are pigmented black, with medial and lateral tan margins. The flight wings are black, and when folded under the elytra intensify the black color of the elytra. Ventrally, the body is pigmented light brown to black except for the prothorax which is reddish-pink. The yellowish light organs are located on the ventral side of abdominal segments 6 and 7. The head with its 2 large,black compound eyes is retracted under the prothorax

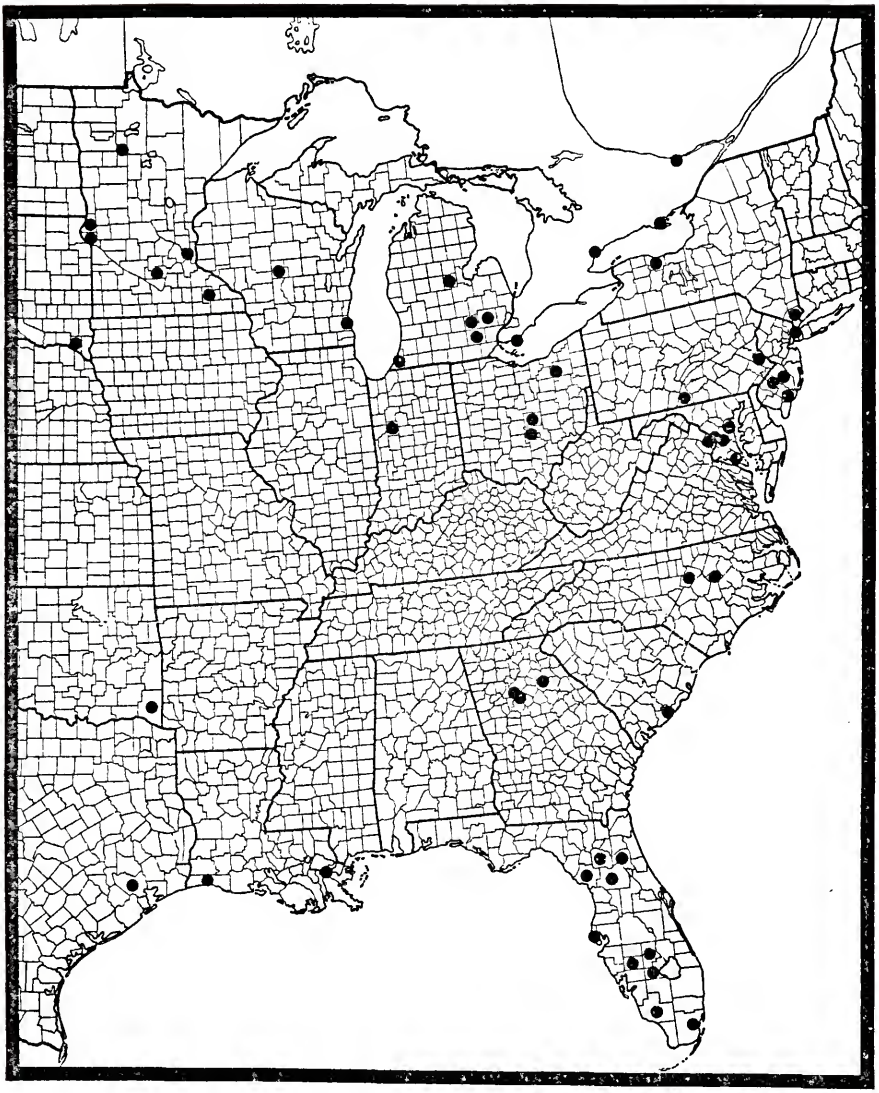

Fig. 1.1 Geographic distribution of Pyractomena lucifera in North America. Each dot represents a county record: Green (1957), J. E. Lloyd (personal communication) and author's observations.

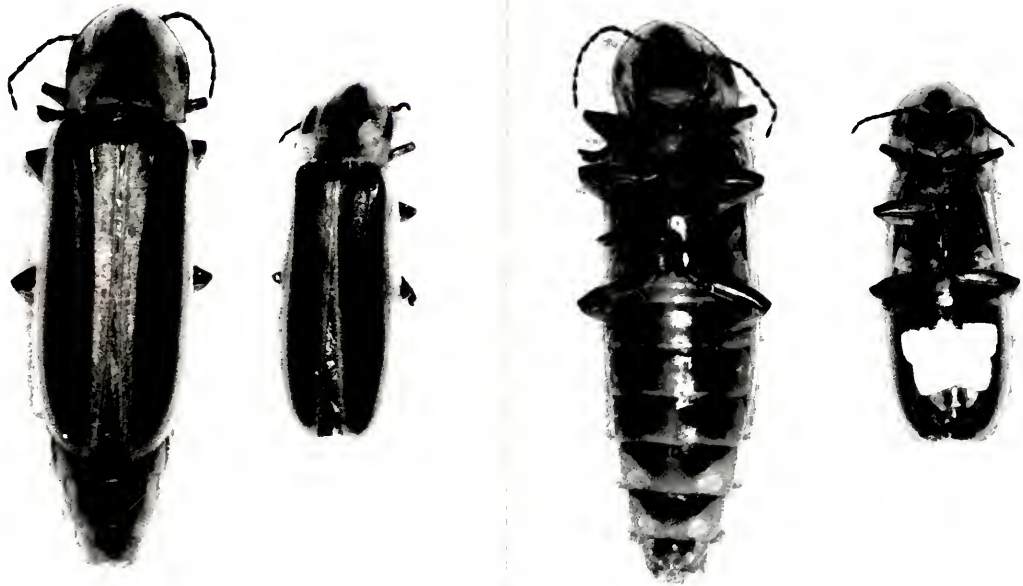

Fig. 1.2 Pyractomena lucifera male and female fireflies; left, dorsal view, right, ventral view (larger insect is female).

when the insect is resting but is extended beyond the anterior margin of the prothorax when it is active. The mouthparts of both sexes are functional; the mandibles are curved and tapered smoothly.

Females are 9.0 - 10.0 mm long and weigh 37 - 112 mg. The overall shape and color of the female is similar to that of the male (Fig. 1.2), but the abdomen of a newly emerged female is greatly distended and the elytra do not cover it. After the first batch of eggs is oviposited the abdomen often fits under the elytra. The light organ of the female consists of 2 pairs of lateral spots on segments 6 and 7 (Fig. 1.2). The head of the female is also extended when the firefly is active. The eyes of the female are much smaller than those of the male.

Eggs are pale yellow-orange and measure 0.8 - 0.9 mm by 0.75 - 0.8 mm (Fig. 1.3). They are oviposited in groups of 20 - 100. The female covers each egg with a transparent secretion which apparently acts as an adhesive. The egg chorion is transparent and the developing embryo is visible inside the egg.

Newly hatched larvae are nearly white with black eyes. They weigh about 0.35 mg and measure about 6 mm long. Within a few hours the cuticle becomes sclerotized and the tergites become pigmented a light tan with brown- or rufus-brown markings. The ventral surface is a much more pale grayish brown. The larvae grow and molt 4 or 5 times, but the general body color and proportions remain about the same. The mature larvae weigh 20 - 89 mg and measure about 17 mm long. The body is rather elongate, tapering bluntly anteriorly but gradually posteriorly (Fig. 1.4). The pigmentation of field-collected larvae is quite consistent, but light and dark individuals are encountered occasionally. The larvae are flat dorso-ventrically except when well-fed.

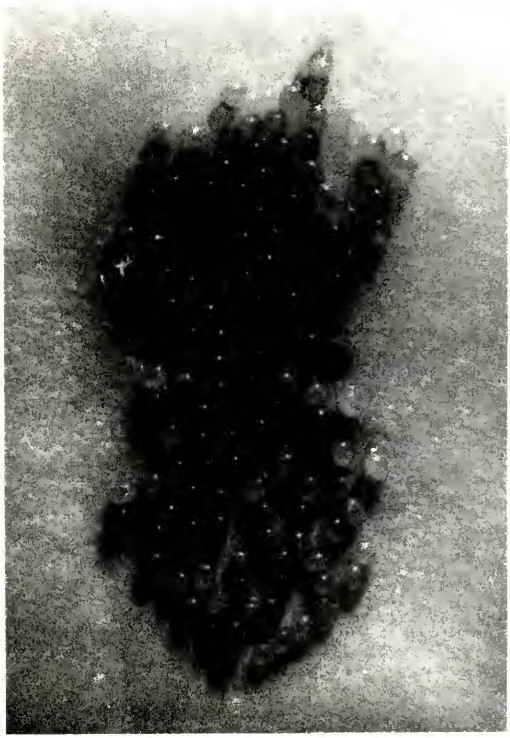

Fig. 1.3 Eggs of Pyractomena lucifera.

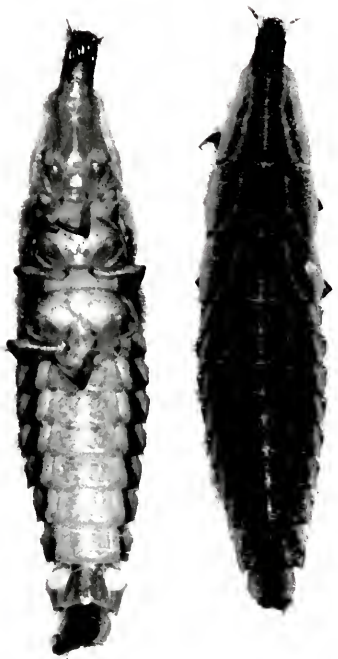

Fig. 1.4 Large larvae pf Pyractomena lucifera. left: ventral view, right: dorsal view.

As larvae approach pupation they become decreasingly active, and finally secrete an adhesive substance (from the anus?) which glues the abdominal segments to the substrate. This is the prepupa. At this stage the filaments of the caudal grasping organ are withdrawn, the legs do not grip the substrate and the body becomes bloated (Fig. 1.5). The prepupa does not respond to tactile stimuli. After several days the cuticle splits around the lateral edge of the pronotum and the pupa wiggles forward inside the exuviae. It anchors itself in the exuviae with adhesive secretions and hooks on the tip of the pupal abdomen. The exuviae covers part of the abdomen of the pupa (Fig. 1.6). In contrast with pupae of other lampyrids, the pupae retain the cryptic pigmentation pattern of the larvae. Pupae also have pairs of dorsal spines on the lateral margins of each abdominal segment.

Biology of Adults

Flash Behavior

Field Observations. Male P. lucifera emit single advertising flashes as they fly slowly over aquatic vegetation. In the early part of their activity period they tend to fly within 0.5 m of the vegetation or even among the plants. Later, after it is dark, they fly up to 2 m over the vegetation. At Lake Alice males did not fly over the shore except when the vegetation was wet, but at other locations they seemed to fly over the shore more readily. The flight activity of P. lucifera was reduced when it was windy or when there was bright moonlight.

The male flash pattern is a single short flash emitted at intervals of 2.9 - 5.1 sec depending on temperature (Fig. 1.7). Male flash activity starts an average of 31 min after sunset (n=23, s=6.2). The flash activity increases to its maximum about 5 min later. Flying males can

Fig. 1.5 Prepupa of Pyractomena lucifera.

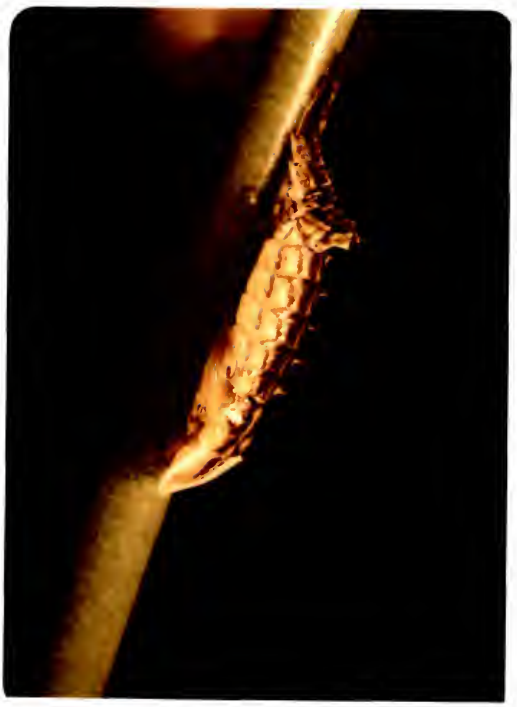

Fig. 1.6 Pupa of Pyractomena lucifera.

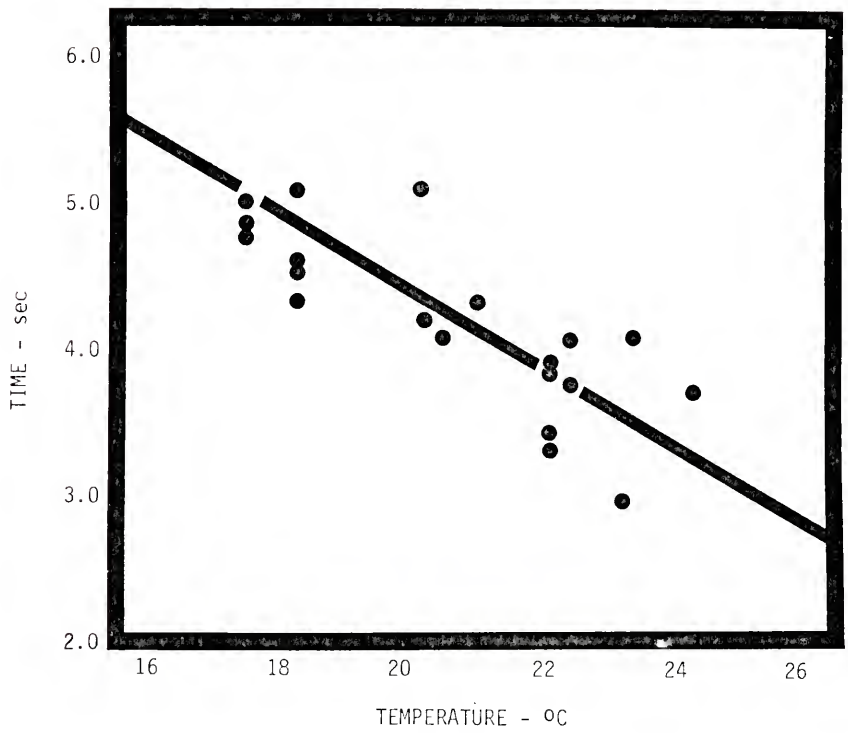

Fig. 1.7 Interval between male advertising flashes at various temperatures in the field.

be seen for 15 - 30 min, but the major flash activity lasts for only about 10 min.

Gravid and responsive females are found on the aquatic vegetation and they answer advertising flashes of males. The female response to a male flash consists of a single flash ca. 0.5 sec long with a prolonged afterglow. The response interval is about 1 sec. Flying males that receive response flashes land immediately after receiving a response or hover over the female and flash again before landing. The male climbs up and down the vegetation to reach the female and flashes at irregular intervals; the female answers the flashes occasionally. Two caged responsive females placed in the field answered 6 of 7 flashes from flying males who flashed within 1 - 2 m. These females answered 3 of 11 flashes from males that had landed on the vegetation. The females probably did not see all of these male flashes. Males located each female after about 15 min. The females answered 12 of 17 male flashes when the males flashed in the immediate vicinity. The flash dialogue between these males and females continued for an hour, at least 30 min after male flight activity had stopped, when observations were terminated.

Both sexes respond poorly to artificial flashes: females answer artificial flashes only occasionally and males do not approach artificial response flashes even when the flashlight is rigged to produce a prolonged afterglow and the color is adjusted with a yellow-green filter.

On several occasions I collected non-gravid females that had apparently oviposited most of their eggs. These females were very active and were found on vegetation 1 - 3 m above the water. I believe these females were about to begin dispersal flights. Kaufmann (1965) observed dispersal flights by Luciola discicollis females after they had

oviposited. Since oviposition had already occurred such a delayed dispersal greatly reduced the risk of complete reproductive failure should the female fail to find another suitable habitat. Should the female locate in another suitable habitat she would still be capable of ovipositing 1 - 2 dozen eggs.

Laboratory observations. The flash exchange between caged male and female fireflies was recorded in the laboratory with the following equipment. Flashes were detected with a photomultiplier tube and transduced to a frequency-modulated signal that varied proportionally (9 - 12 K Hertz) with light intensity much like an audio signal. This signal was recorded on magnetic tape by a Uher 4000 Report-L tape recorder at 19 cm/sec (7.5 in/sec). The transducing equipment was custom designed and built for J. E. Lloyd by Alton Higgins, Gainesville, Fla. For analysis, the recorded signals were transduced to a variable DC voltage that fed into a Gould Brush 220 chart recorder, Clevite Corporation, operating at a chart speed of 25 mm/sec. Measurements of the signals were based on the intersection between the baseline and a line extended through the transients of the signals.

The flash exchange between a caged male and female recorded electronically is presented in Fig. 1.8. Duration of male flashes recorded at 28.0°C averaged 0.21 sec (s=0.032, n=39). Intervals between male flash and female response flash for 12 females at 28°C averaged 0.70 sec (s=0.114, n=50) (Table 1.1). The duration of the female response flash was more difficult to measure because it dimmed gradually to a steady glow that lasted several sec and was difficult to distinguish from the base line. At 28.0°C the measurable duration of the female response flash averaged 0.96 sec (s=0.287, n=33) (Table 1.1). The

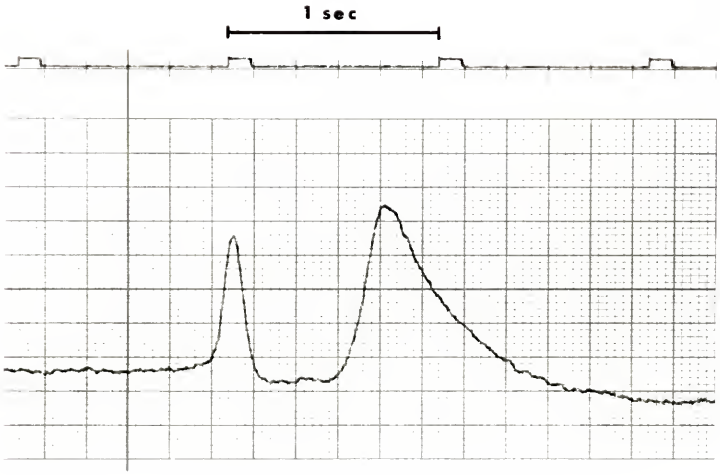

Fig. 1.8 Flash exchange between a caged male and female recorded electronically, 28°C.

Table 1.1 Response interval between male and female flashes and female flash duration recorded electronically, 28°C.

Females		Flash duration, sec		Response interval, sec	
No.	age in days	mean	measurements	mean	measurements
918	15	1.00	0.90, 1.00, 0.90, 1.18	0.78	0.66, 0.74, 0.75, 0.67, 0.72, 0.74, 0.94 0.95, 0.89
916	14			0.62	0.62
1140	9	0.86	0.80, 0.78, 0.86, 0.90, 0.85, 0.92	0.69,	0.53, 0.78, 0.59, 0.58, 0.63, 0.73, 0.86, 0.71, 0.83
Z	8	1.38	1.32, 1.38, 1.45	0.67	0.53, 0.76, 0.71
981	20			0.68	0.68, 0.67
1114	18	0.78	0.64, 0.92	0.64	0.62, 0.62, 0.68
988	17	1.21	0.96, 0.80, 0.98, 1.48, 1.22 1.46, 1.55	0.63	0.56, 0.55, 0.56, 0.67, 0.71, 0.62 0.75
X	16	0.85	0.80, 0.88, 0.72, 0.50, 1.34	0.76	0.89, 0.58, 0.78, 0.69, 0.88, 0.73
1093	25	0.80	0.80	0.52	0.46, 0.57
1116	22	0.68	0.84, 0.58, 0.62	0.65	0.68, 0.57, 0.70
1012	12			0.67	0.62, 0.72
977	21	0.70	0.70, 0.70	0.79	0.70, 0.93, 0.74
Mean for all females 0.96 (s=0.287, n=33)				0.70)s=0.114, n=50)	

response intervals of 6 females to male flashes at several temperatures was recorded with a stopwatch. The response intervals averaged 0.7 - 1.45 sec (Table 1.2 and Fig. 1.9). There were no responses to male flashes at 14^{o}C.

The responsiveness of females to flash signals was analyzed in the following experiments. Individual females of known age were reared from field-collected or laboratory-reared larvae. They were maintained in babyfood jars containing a moist filter paper cone and covered with polyethylene wrap. The females were considered 1 day old the first evening after they eclosed from the pupae. Unmated females were used to determine the effect of age on responsiveness. Some females were mated when they were 2 or 6 days old to determine if mated females were responsive to flashes. Initially, I presented flashes produced by a penlight covered with a yellow-green filter to virgin females. The female responsiveness to flashlight stimuli was low, seldom more than 1 or 2 responses per evening. I observed that females that did not answer the flashlight, readily answered spontaneous flashes by males in nearby jars. To confirm this observation I presented flashlight flashes and spontaneous male flashes alternately to a group of 9 responsive virgin females. Only 3 answered flashlight flashes but all 9 answered male flashes. After 5 pairs of flash stimuli, flashlight flashes received 5 response flashes and male flashes received 24 response flashes. Since females seemed to reject flashlight flashes, spontaneous male flashes were used in subsequent tests. Groups of females were placed in a series of cardboard boxes so their responsiveness could be tested without disturbing other females. Several groups of males, 1 - 10 per babyfood jar, were held over the females. When a male flashed spontaneously the responses of females were recorded. Five flash stimuli

Table 1.2 Response intervals of 6 females to male flashes at 4 temperatures in the laboratory, measured with a stopwatch.

Date	May 4, 22.3°C		May 5, 26.8°C		May 9, 14°C	May 10 & 11, 17.2°C	
Females	mean	measurements	mean	measurements		mean	measurements
1	1.1	1.0, 0.9, 1.1, 1.3, 1.2	--	--	--	1.5	1.7, 1.4, 2.0, 1.3, 2.0, 1.1, 1.3, 1.5
2	1.1	1.1, 0.9, 1.2, 1.2, 0.9	--	--	--	1.5	1.7, 1.5, 1.2, 1.7
3	1.0	1.0, 0.8, 1.1, 1.0, 0.9, 0.8, 1.4	0.7	0.8, 0.6, 0.8, 0.9, 0.8, 0.5	--	1.5	1.0, 1.9, 1.7
4	0.9	0.8, 0.8, 0.9, 1.0, 0.7, 0.9, 1.2	0.8	0.7, 0.7, 0.8, 0.7, 0.8, 0.8	--	1.2	1.1, 1.1, 1.0, 1.0, 1.7
5	1.0	0.8, 0.9, 1.0, 1.0, 1.3, 0.9	0.8	0.9, 0.6, 0.7, 0.7, 1.0	--	--	--
6	1.1	1.3, 1.0, 1.3, 1.0, 1.0	1.1	1.0, 0.9, 1.0, 1.2, 1.2	--	--	--
Totals	1.0	s=0.177, n=35	0.82	s=0.180, n=22	--	1.45	s=0.341, n=20

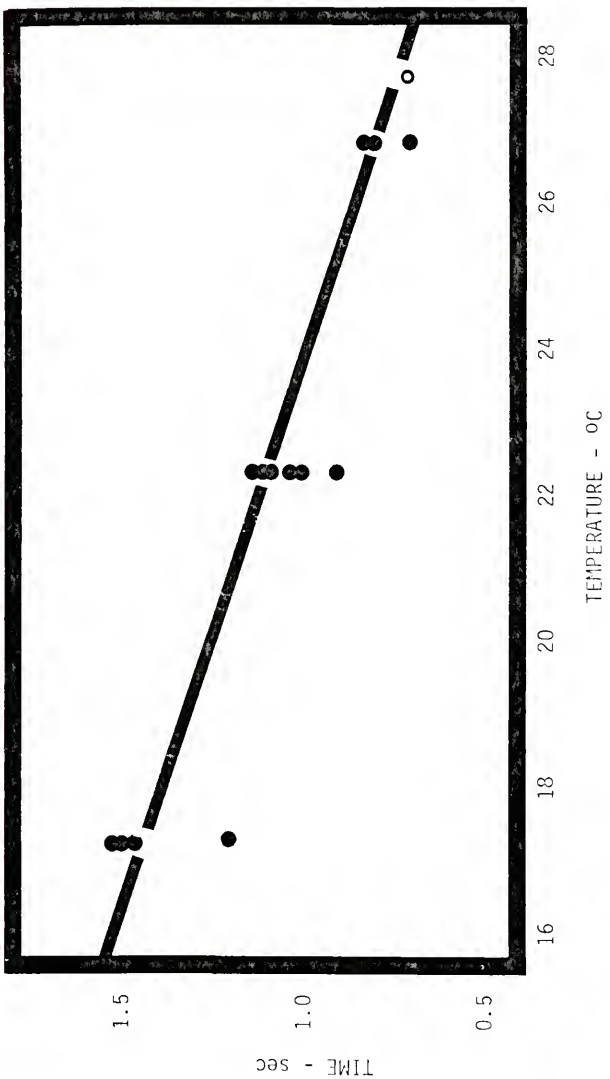

Fig. 1.9 Response interval between male flashes and female responses at various temperatures.

were presented during each of 5 test periods for a total of 25 stimuli. The first test period started 15 min after the light went out and subsequent test periods started at 15 min intervals. During the experiment several groups of male fireflies were kept in a lighted room. A group of males was taken into the darkened experimental room at the beginning of each test period. Spontaneous flashing by males lasted about 10 min, but if they were returned to the light for ca. 30 min, they would again flash spontaneously.

The responsiveness of 43 virgin females to male flashes is presented in Table 1.3 and the mean responsiveness for females on day 1 - 30 is plotted in Fig. 1.10. Of 29 females tested on day 1, only 8 were responsive, answering an average of 5.1% of male flashes. By day 2, 25 of 30 females responded, answering an average of 39.5% of male flashes. By day 3 all tested females were responsive, answering an average of 55% of male flashes. On day 4 the responsiveness reached a peak of 64.5%. Peak responsiveness of individual females occurred on day 2 (n=6), day 3 (n=8) and day 4 (n=8). From day 3 to day 18, female responsiveness remained fairly stable and averaged 54.6%. From day 19 to day 30, female responsiveness seemed to decrease slowly but erratically. The data on female responsiveness, days 1 - 5, were analyzed using the student's t test (unequal variance). The percent response data were adjusted using the arc-sign transformation. The female responsiveness on days 1, 2 and 3 were significantly different from each other ($p=0.05$) while days 3, 4 and 5 were not (Table 1.3).

The distribution of female responses to male flashes during the evening was investigated by examining the responses of 11 females in the previous experiment that were tested on days 1 to 8 consecutively.

Table 1.3 Responsiveness of females at different ages to male flashes (percent response out of 25 stimuli).

Age in days	Female identification numbers																						
	920	935	927	975	897	1004	923	1094	929	1054	1046	912	1048	1093	952	977	981	1074	1114	988	X	918	916
1	-	-	-	-		-	-	-	+	0						40	0	4	0	0	0	0	0
2	-	+	+	-		+	-	+	36	12	32	48	33*	50*	67*	76	32	76	52	0	0	40	50
3	-	+	+	+			32	60	20	12	80*	93*				76	60	80	44	48	16	75	40
4	-	+	+	+		+	72	56	24		60	68	40	68	72	60	24	76	28	96	50	44	60
5	+	+	+	+		+	68	48		8	40	52	36	44	48	36	60	72	28	83	32	60	44
6	-	+	+	+		+			36	0*	28	84	56	40	60	48	36	48	44	92	8	36	48
7	+	+	+	+		+	64	52	47*	0	75*	92*	76	48	80	56	16	88	44	72	32	64	40
8	+	+	+		-	+	53*	80*	40	0			56	60	84	28	56	92	20	96	16	52	56
9	+	+	+	+	-	+	44	52	48	8	44	96	4	44	56	56	28	56	12	80	36	68	72
10	+	+	+	+	+	+	64	48	24	33*	64	88		56	76	44	32	76	0	68	48	68	96
11	+	+		+			92	48	67*		40	72		52	80	32	0	72	20	72	76	76	80
12	+		+	+	+	+	75*	92*		24	72	84		52	64	32	0	92	4	96	56	44	
13	+	+	+	+	+	+			42	8	44	80		58	67	48	56	84	100	64			
14	+	+	+	+	+	+	100	64	28	28	56	92		64	20	24	28	80	100				
15		+	+	-	+	+	92	52	32	4	68	76		36	48	20	28	88					
16	+	+	+	+	44	60	76	48	40	28	72	88		48	52	36	28	80					
17	+	+	+	+	36	84	84	48	28	20	79	75		36	56	76	28	76					
18	+	+	+	-	32	80	92	68	20	40	76	80		44	72	52							
19	+	+		+			80	48	8	16	9	52		48	64								
20	+		+	+	28	52	44	64	20	28				52	64								
21	+	+	+	52	60*	53*		60	25	33				48	52								
22	+	+	+	60	16	40		54	33	42				44	36								
23		+	+	52	24	56		48	17	24													
24	+	+	8		8	44		35	21	24													
25	+	72	40	52	0*	58*		46	13	32													
26	+	44	8	60*				48	12	20													
27	+	48		52	28	84		68	24	4													
28	64		16	24	40	68		12	12	52													
29	36	68	13*	48	20	48			20	64													
30	12	73*	4	30*	36	52				60													

* partial sample; + at least 1 response to flashlight stimuli; - no response to flashlight stimuli

Table 1.3 - continued

Age in days	Female identification numbers 1012	919	1040	1117	Y	933	1128	1121	1140	A	Z	1118	1143	1142	1147	B	1127	1146	991	1136	Mean	n=
1	0	0	0	0	0	0	0	0	13	48	4	0	0	4	12	0	0	24	0	0	5.1a	29
2	0	0	0	92	74	13	80	64	76	96	8	8	84	28	16	20	8	64			39.5b	30
3	16	12	72	80	68	52	92	100	96	96	36	32	88	40	44						55.0c	27
4	76	56	88	80	64	100	100	88	56	92	44										64.5c	27
5	60	0	84	96	12	100															51.0bc	23
6	76	0	96	84																	51.1	18
7	64	4	96																		52.7	17
8	56	12	52																		48.5	16
9	80	0																			46.5	19
10																					56.8	15
11																					58.8	14
12																					51.6	12
13																					59.1	11
14																					60.1	12
15																					49.5	11
16																					53.8	13
17																					55.8	13
18																					59.6	11
19																					40.6	8
20																					44 0	8
21																					45.0	6
22																					40.6	8
23																					36.8	6
24																					23.3	6
25																					42.5	6
26																					26.4	5
27																					44.0	7
28																					36.0	8
29																					43.4	7
30																					27.3	6

Letters indicate results of "t tests" (p=0.05): different letters indicate differences are statistically significant.

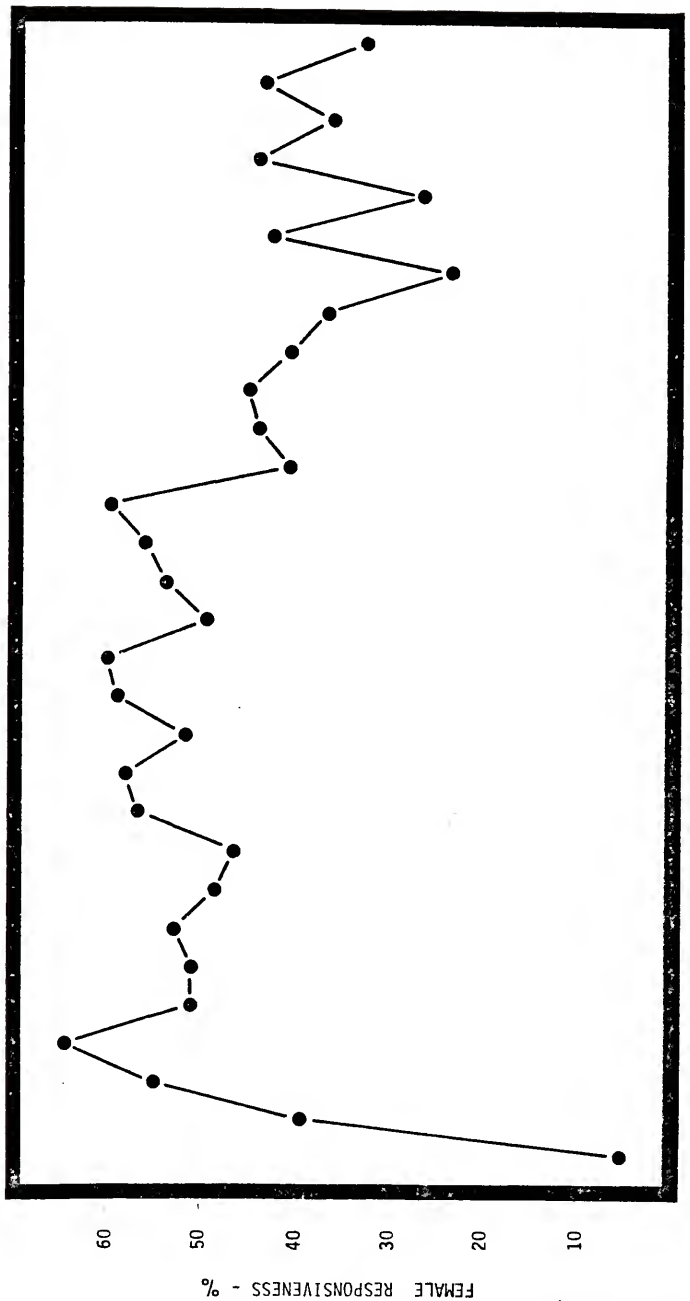

Fig. 1.10 Responsiveness of females at different ages to male flashes, percent responses out of 25 stimuli.

The number of responses received from the 11 females during each of the 5 test periods by the females at different ages is presented in Table 1.4 and Fig. 1.11. Female responsiveness was lower for 1- and 2-day old females than it was for older females observed earlier. The female responsiveness also decreased during the evening. The rate of decrease in female responsiveness for 3- to 8-day old females (Fig. 1.11) seemed to be decreasing as the females aged. To determine if this trend was significant the data from the 3- to 8-day old females were analyzed using 5 x 6 factorial analysis. The following conclusions were made:

1) There were no significant differences ($p=0.05$) in the responsiveness of females aged 3 - 8 days.

2) The decrease in responsiveness during the evening was significant ($p=0.01$).

3) Both the linear and quadratic response curves fit the responsiveness of females during the evening ($p=0.01$). The quadratic response curve indicates the rate of decrease in female responsiveness was highest early in the evening but stabilized later in the evening.

4) There was no significant change in the responsiveness of females during the evening as females aged, as suggested by inspection of the graph, since there was no significant interaction ($p=0.05$) between female age and responsiveness during the evening.

Lloyd (in press-b) suggests that a female's responsiveness to males may change as she ages and the likelihood that she will remain unmated increases. He notes that aging females of Lampyris noctiluca shine more brightly and change glowing stations more frequently than young females. Aging females would be expected to take more risks (from predators, etc.) in their efforts to attract a mate and would be more likely to accept a poorer quality mate (by whatever standards prevail) than younger females.

Table 1.4 Responses of 11 females to 5 male flashes during 5 consecutive 15 min periods (55 responses maximum).

Age of Females (days)	5 consecutive 15 min test periods					Total
	1	2	3	4	5	
1	4	2	2	1	2	11
2	27	19	11	13	11	81
3	47	22	21	23	21	134
4	47	38	25	27	27	164
5	42	29	28	18	22	139
6	42	26	26	18	21	133
7	39	32	24	21	28	144
8	33	28	32	21	27	141
Total	281	196	169	142	159	947

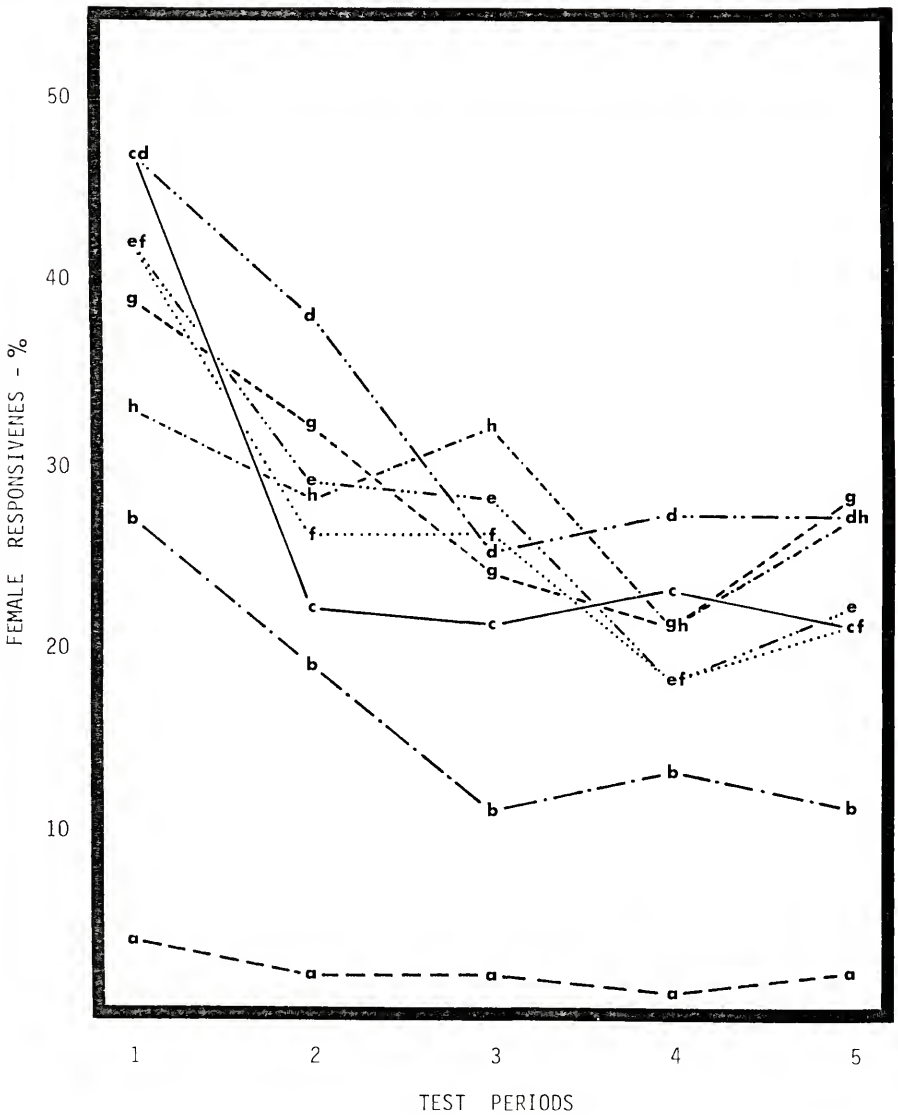

Fig. 1.11 Responses of 11 females to 5 male flashes during 5 consecutive 15 min periods by females at ages 1 through 8 days (55 responses maximum).

The responsiveness of P. lucifera females to male flashes increases over the first 3 days of their lives. These changes seem to be related to the reproductive maturity of the female (see below). The responsiveness of aging females (10 - 30 days old) seemed to decrease instead of increase and the responsiveness during the evening (3 - 8 days old) also did not seem to change with age. Sexual selection in this insect appears to be entirely passive, as explained by Lloyd (in press-b): the female accepts the first male to reach her.

Other Mating Behavior

In the field, the male locates the female by orienting to the female responses. He climbs up and down the vegetation until he reaches her. He immediately mounts and proceeds to copulate. There is no flash dialogue between a mating pair. In the laboratory I frequently induced copulations by causing the males to walk to females. They would hesitate only briefly, then mount; their antennae seemed to beat the female and they appeared to touch the female with their mouthparts. The response of the male to contact with the female seemed to be somewhat non-specific. Males also mount and attempt copulations with other males. When groups of males were kept in a jar, arrangements of up to 7 males one on top of the other were observed. This suggests that males can not distinguish between male and female, and they mount either sex indiscriminately. Such male-male mountings may be related, however, to competition among the males; e.g., the mounted male will not be able to fly to the female when she answers his flash.

When a male mounts a female, she immediately lowers her body, lifts her pronotum 30^{o} and shortens the egg-bloated abdomen. The position of the pronotum seems to aid the male in orientations since it interferes

with copulation attempts on the female's head. The position of the pronotum pushes the male down the female's back and the contraction of the abdomen brings the tip of the abdomen forward. Both actions put the male in position so he can reach the genital orifice of the female with his aedeagus. The male continues to probe with the aedeagus until it is inserted into the female genital orifice. Pairs in copulation usually do not easily disengage when they are disturbed; however, they can be forcefully pulled apart. When I dissected a pair that had been freeze-killed while in copulation, I found that the membraneous tip of the aedeagus was expanded within the female vagina (by hydrolic pressure?), and this action seemed to prevent accidental withdrawal of the aedeagus.

After the genitalia are engaged the female lowers the pronotum and the abdomen returns to its normal position (Fig. 1.12). The pair usually remains motionless but sometimes the female begins walking and performs side-to-side movements which suggest efforts to dislodge the male. The male remains on the back of the female throughout copulation. In many lampyrids, Pyropyga spp., Photinus spp. and Luciola spp., the male turns 180° and dismounts the female during copulation, and the pair face in opposite directions (J. E. Lloyd, personal communication). In Photuris spp. the male remains on the female back during copulation.

Mated pairs remained in copula for extended periods. In the laboratory, a male remained on a female's back almost continually even when the genitalia were not joined. Sometimes, pairs appeared to be in copula, but when touched with a probe they quickly disengaged. In the following observations I considered a pair to be in copula if they did not separate when touched with a probe. Pairs were observed

Fig. 1.12 Male and female in copula.

every 12 h to determine how long they would stay in copula. One group of 7 females, ages 3 - 42 days remained in copula 12 h (n=2), 24 h (n=1), 36 h (n=2), 48 h (n=1) and 60 h (n=1). Another group of 7 females, ages 3 - 4 days, remained in copula 12 h (n=3), 24 h (n=1), 48 h (n=2) and 72 hr (n=1). One mated pair was found in the field. This pair had apparently mated the previous evening about 18 h earlier. Prolonged copulations do not appear to be laboratory artifacts.

Female Reproductive Biology

Responsiveness of mated females to male flashes. The flash responses of mated females to flashlight or male flashes were recorded under the same conditions used for virgin females. Of 20 mated females tested, 15 did not answer flashlight or male flashes after they had mated (Table 1.5). These 15 females oviposited one or more batches of fertile eggs within 2 - 5 days of mating (more details later). Of the 20 mated females tested, 5 females began answering flashes at age 12 (#999), 14(#950, #915), 21 (#902) and 22 (#905) days. Four of these females (# 902, 905, 915 and 950) answered flashes only occasionally; each had oviposited at least one batch of eggs within 2 or 3 days of mating. The eggs of female #905 were infertile even after a second mating,and the eggs of #902 had a low hatch rate. The responsiveness of these 4 females was so low that it seems unlikely that they could have attracted another male in the field. Female #999 was unique in that she failed to oviposit within 2 - 5 days after mating as did the other females. She mated on day 2,and her responsiveness to male flashes was suppressed for 10 days. At age 12 days she began answering flashes fairly consistently and continued to do so for some 30 days. In the field she probably could have attracted another male.

Table 1.5 Flash responsiveness of mated females at different ages to male flashes (percent responses out of 25 stimuli) or responses to flashlight flashes (+ response, - no response).

Female number	Response of mated females to male flashes																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
999	-	-	m-	-	-	-	-	-	-	-	-	+		-	-	+	+	+	28	36	24	
957	-	-	m-	-	-	e-	-	-	-	e-	-	-		-	-e	-	-	-	0	0	0	X
902	-		m-	-e	-	-	-	-	-	e	-	-	-	-e	0	0	0e		0	0	20	4
943	-	-	m-	-	-	e-	-	-	-	-	-		-	-e	-	-	-	0	0	0		0e
986	-	+	m-	-e	-	-	-e	-	-	-	-e		-	-	-	-	-	0	0	0		0
1001	-	-	m-	-	-e	-	-	-	-	-	-	e	-	-	-	-	-	0	0e	0		0
948	-	-	m-	-e	-	-	-	-		-e	-	-	-	-	0	0	0e		0	0	0e	0
951	-	+	m-	-	-	-	-e	-	-		-	-e	-	-	-	-	-		X			
905			-	+	+	+m	-	e	-	-	-m	-	0	0e	0		0	0	0	0e	0	25
915	-	-	+	+	+	+m	-	-	-e	-	-	-	-	+		-	-	-	-	-	-	-
963	-	-	+	+	+	+m	-	-	-e	-	-	-	-		-	-	-	-	-	0	0e	0
1019	-	+	+	+	+	+m	-	e	-	-	-	-	-	-	-		-	-e	-	-	0	0
913		+	+	-	+	+m	+	-	e	-	-	-	-	0	0e	0		0	0	0	0	0
908			+	+	+	+m	-	e	-	-	-	-	0	0e	0		0	0	0	0	0	0
1099					+	+m	-	0e	0	0		0	0	X								
950	-	-	+	-	-	+m	-	e	-	-	-e	-	-	+	-e		+	-	+	+	0	56
1024	-	+	+	+	+	+m	-	e	-	-	-	-	-	-	-		-e	-	-	-	0	0
917					+	+m	-	0	0	0e		0	0	0	0e	0	0		0	0	0	0
1026						+m	-	-e	0	0	0		0e	0	0e	0	0	0	X			
937	-	-	+	+	+	+m	-	-e		-	-	-	-e	-	-escaped							

m=mated
e=eggs laid
X=female died

Table 1.5 - extended

23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
28	33	16e20		12	42		28	24	32	36	56	16	28	32	56	46	20	16	40	12	24	0	0	X
0	0e		12	4	0	0	0	0	0	X														
0	0	0	0	0		0e	0	0	0	0	0	0	0	0	0	0	0	0	0	X				
0	X																							
0	0	0	0	0	X																			
0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	X							
	0	0	0	0	0	0	0e	0	X															
	-	-	-	-	0	0	0		0	0	0	0	4	58		36	0	0	0	0	X			
	0	0	0	X																				
0		0	0	0		0	0	0	0	0	0	X												
X																								
	0	0	0	0	0	0	0	0e	0	0	0	0	0	0	0	0	0	0	0	0	escaped			
12		0e	0	0	0	0	0		0	0	0	X												
0		0	0	0	0e	0	0		0	0	0	0	0	0	0	0	0	X						
0	0	0	0	0	0	X																		

This female oviposited a small glob of infertile eggs on day 26. (Virgin females frequently began ovipositing small groups of infertile eggs when they were more than 20 days old.) Since females probably do not live more than 10 - 20 days in the field, it seems unlikely that females become responsive and mate a second time in the field.

Relationship between flash responsiveness and reproductive development. The development of the female reproductive system was determined by dissecting virgin females at different ages and counting the number of eggs in the lateral oviducts. Eggs in the lateral oviducts were presumably ready to oviposit. The number of eggs in the oviducts increased steadily from 0 on day 1 to 71.25 on day 8 (Table 1.6).

The age at which females oviposited was determined by mating females at different ages and checking for ovipositions once each day. Females that mated on day 2 oviposited 4.0 days later (age 6.0 days), females mated on day 6 oviposited 3.1 days later (age 9.1 days) and females mated on days 9-16 oviposited 2.3 days after mating (Table 1.7). There seems to be a fixed interval of 2 - 4 days between the start of copulation and oviposition.

Females did not oviposit earlier than day 5 or 6 when they mated early (day 2), but oviposition was also delayed when they mated late and their eggs were presumably ready. This delay in oviposition may be related to the extended period of copulation observed in these insects , 12 - 72 h. Thornhill (1976) discussed the ecological significance of prolonged copulation in the lovebug, Plecia nearctica Hardy. He concluded that in the lovebug prolonged copulation was probably related to male-male competition: the male remained in copula with the female to prevent her from mating with other males. In

Table 1.6 Number of eggs accumulated in the lateral oviducts of virgin females dissected at different ages.

Females	Age of females in days				
	1	2	4	6	8
1	0	8	13	96	62
2	0	0	33	36	66
3	0	16	15	18	60
4	0	3	34	73	74
5		1		48	88
6		4		58	63
7				69	74
8					83
mean	0	5.33	23.75	56.9	71.25
s		5.922	11.295	25.71	10.29
n	4	6	4	7	8

Table 1.7 Number of days elapsed between beginning of copulation and oviposition when females were mated at different ages.

Female	Age at mating		
	day 2	day 6	days 9-16
1	3	2	1
2	3	2	3
3	3	2	3
4	4	2	2
5	4	3	3
6	5	3	3
7	6	3	3
8		4	2
9		5	2
10		5	2
mean	4.0	3.1	2.33
s	1.633	1.792	3.277
n	7	10	9

P. lucifera I frequently observed females begin to oviposit soon after copulation terminated. It may be that the male prevents oviposition by remaining in copula. It appears that the delay between mating and oviposition (or prolonged copulation if that is the cause) has caused the female to shift her flash responsiveness forward in time. On the average, females are ready to oviposit on day 5 - 6 (dissection and oviposition data). Any delay in oviposition past day 5 - 6 unnecessarily subjects the female to natural hazards (e. g. predators) that could kill her before she oviposits her eggs. If there is going 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 the eggs are ready to oviposit. This apparently explains why the female becomes fully responsive by day 3 when her eggs are not ready for oviposition until day 5 - 6. Thus, if the female is successful in attracting a mate on day 3 she will be able to oviposit 2 - 4 days later at ages 5 - 7 days when her eggs are ready.

Female oviposition behavior. Females oviposit 1 - 5 times over a 20 - 30 day period. Ovipositions occur at intervals of 3 - 8 days. The eggs from each oviposition are laid in one spot, forming an egg mass in which many of the eggs touch each other. All eggs are placed on the substrate and each egg is covered with a transparent secretion which seems to fasten the egg to the substrate. In the laboratory, females seem to lay their eggs on a glass jar as often as on filter paper. Often the female crawls between 2 layers of filter paper to oviposit. In the field, 2 egg masses were found on aquatic vegetation, 0 - 15 cm above the water.

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, Schwalb 1960, Kiichiro 1961). Only Lamprigera tenebrosus oviposits its eggs in a group, but these eggs are laid in a chamber in the soil; the female broods the eggs (Bess 1956).

Fecundity and fertility of females. The number of eggs oviposited by 32 females and their fertility are summarized in Table 1.8. Of these 32 females, 25 laid 2 egg masses, 12 laid 3 egg masses, 7 laid 4 egg masses and 4 laid 5 egg masses. The hatch rate of the eggs averaged 95.6% and did not seem to decrease in succeeding ovipositions even though the females mated only once. Only 2 females had substantially lower hatch rates of 74% and 65% (Female #902 was a laboratory reared female that also answered male flashes, Table 1.8). The average number of eggs laid by the females was 101.8 (s=41.4, r=39 - 194, n=29). The number of eggs laid by the females was related to the weight of the female pupa. Larger females oviposited nearly twice as many eggs as small ones (Fig. 1.13). The number of eggs laid by several other lampyrids is thought to be less than 100 (Hess 1920, McLean et al. 1972, Bess 1956, Kaufmann 1965), but most of these estimates were based on dissections. Schwalb (1960) reported 41 - 198 eggs for Lampryis noctiluca and 57 - 147 eggs for Lamprohiza splendidula. Kiichiro (1960) reported 300 - 500 eggs for Luciola cruciata and 70 - 100 eggs for Luciola lateralis. Lloyd (1973b) found 321 eggs in a female Luciola sp.

Of 46 females that were mated in the laboratory during these experiments, 42 laid some fertile eggs, while 4 failed to lay fertile eggs. One fertile female laid only 5 eggs after the first mating and

Table 1. 8 Number of eggs, number of egg masses and hatchability of eggs laid by 32 fertile females.

Female number	Weight pupa-mg	Number of eggs hatched/number of eggs in consecutive oviposition 1	2	3	4	5	percent of eggs hatching	Total eggs
223	-	49/49					100%	49
224	-	67/68					99%	68
225	-	2/5	100/100				97%	105
227	-	64/66	7/13				90%	79
228	-	83/85	14/14				98%	99
230	-	43/48					90%	48
238	-	58/62	27/27	2/2	1/1		96%	92
239	-	-/77	-/16	-/6	-/4		-	103
240	-	112/114	-/4				98%	118
241	-	101/101					100%	101
243	-	75/75	4/8				95%	83
902	112/6	48/59	32/46	33/37		23/41	74%	183
904	107.7	-/101		-/29			-	101
908	106.0	103/105	48/48				99%	182
913	46.9	90/91	21/21				99%	112
915	52.0	71/73					97%	73
917	50.7	76/77	33/33				99%	110
937	57.7	62/63	24/24	escaped			99%	

Table 1.8 - continued

Female number	Weight pupa-mg	Number of eggs hatched/number of eggs in consecutive oviposition 1	2	3	4	5	percent of	Total
943	68.0	44/45	53/53	27/72	29/29	4/4	99%	158
946	85.4	95/96	-				99%	-
948	87.6	54/56	40/44	50/50	33/40	-/4	93%	194
950	66.8	74/74	44/44	26/27	20/22	-/9	99%	176
951	59.6	85/86	20/20				99%	106
957	45.3	45/45	4/4				100%	49
963	-	-	5/5				100%	-
986	37.2	35/36	26/26	11/11			99%	73
995	40.2	39/39					100%	39
1001	59.0	41/43	23/29	7/8			89%	80
1019	44.1	75/75	13/13				100%	88
1024	48.1	56/56	25/28	24/24			97%	108
1026	45.5	-	13/20	-/15			65%	-
1033	48.2		35/37	-/50			95%	87
Average percent of eggs hatching		97%	93%	99%	90%	-	95.6%	
Average number of eggs		66.9	27.8	18.9	19.2	14.5		101.8

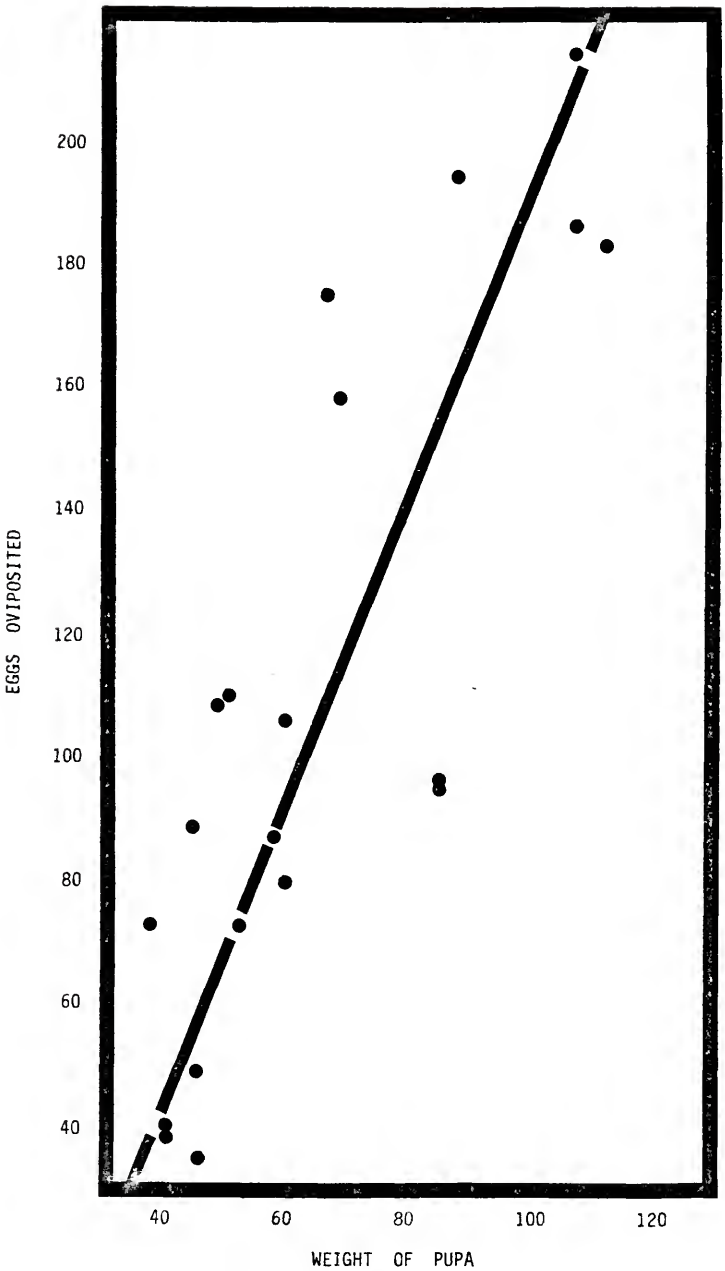

Fig. 1.13 The relationship between the number of eggs oviposited and the weight of the female pupa.

only 2 hatched. This female mated a second time and oviposited 100 eggs, all of which hatched. Three of the non-fertile females failed to oviposit eggs normally but expelled a small mass of infertile eggs at death. The fourth female laid a record 214 eggs, but they did not hatch. This female mated with 2 males and oviposited her eggs in 5 egg masses which appeared to be normal but did not hatch.

Female life span. In the laboratory, females lived up to 53 days, but it is doubtful if they live anywhere near that long in the field. Most females had laid most of their eggs by day 20, and no eggs were laid after day 31. Mated egg-laying females lived an average 31.5 days (s=9.9, n=19). Unmated, non-egg-laying females lived an average of 32.1 days (s=12.4, n=12).

Male Reproductive Biology

Multiple copulations by males. Male fireflies are capable of multiple copulations. In the laboratory, males often mated with more than one female. One male mated 4 females and they oviposited 178, 154, 84 and 134 eggs which hatched normally. In the field, multiple matings by males would be more limited since each copulation apparently takes 24 h or more. In addition, it may take several days of patrolling to locate a female. Lloyd (in press-b) found that male Photinus collustrans LeConte located females after an average 7.2 evenings of patrolling.

Male life span. The life span of male fireflies in the laboratory averaged 20.4 days (x=3.5, n=16) but this is undoubtedly much longer than the life span in the field. To measure the life span in the field, 2 mark-recapture experiments were conducted. The flight period of male P. lucifera is so short that only a few fireflies could be collected, marked and released in the standard procedure (Southwood 1966).

Therefore, a modified procedure was adopted. During the flight period fireflies were collected from the board-walk over the aquatic vegetation on Lake Alice. They were taken to the laboratory and marked with dots of airplane dope. In the first experiment, fireflies were given a code to identify the date captured. In the second experiment, fireflies received individually coded spots (to identify both the individual and the date of capture). The length and weight of each firefly were recorded so measurements of recaptured individuals could be compared with the original measurements and with the rest of the population. Since the fireflies could not be released during the flight period in which they were captured, I released them the following flight period. Males lived in laboratory conditions for several weeks, so holding them for 24 h should not have greatly affected their physical condition. To avoid collecting the males as they emerged from the release point, I made collections ca. 100 m from the point of release. The number of days between release and recapture does not include the 24 h holding period. Since these fireflies were at least 1 day old (0 - 24 h) on the day of capture, the age of recaptured individuals was at least 1 day (not counting the 24 h holding period) more than the days between release and recapture. In Aug. 1971 only 6 fireflies were recaptured, ca. 6% of the marked-released population (Table 1.9). In May and June 1972, 24 fireflies were recaptured, ca. 12% of the marked-released population (Table 1.10). This was a good recapture rate considering that I was able to collect only from a very restricted part of the habitat along the cat-walk. Since the longest recorded interval between release and recapture was 10 days (Table 1.10), it appears that the maximum life span of these males is about 11 or 12 days. This is almost twice as long as the life

Table 1.9 Number of males captured, marked-released, and recaptured at Lake Alice, Aug. 1971.

Date Collected	Number captured	Number marked-released	Number of males recaptured and number of days from release to recapture			
			1	2	3	4
Aug. 17	39	-				
Aug. 18	7	36				
Aug. 19	37	-	6			
Aug. 20	21	33				
Aug. 21	30	21				
Aug. 22	22	-				
Totals	156	90	6 recaptures			

Table 1.10 Number of males captured, marked-released, and recaptured at Lake Alice, May-June, 1972.

Date Collected	Number captured	Number marked-released	Number of males recaptured and number of days from release to recapture											
			1	2	3	4	5	6	7	8	9	10	11	12
May 23	13													
May 24	22	13												
May 25	-	-												
May 26	7	20												
May 27	-	-												
May 28	-	-												
May 29	31	7					2							
May 30	26	30	1											
May 31	12	22	4											
June 1	10	10	1	1										
June 2	11	9		1					1					
June 3	16	10			1							1		
June 4	12	16	1				1							
June 5	30	12	1		1		2							
June 6	21	29		1										
June 7	9	20	2		1									
June 8	3	-	1											
Totals	223	198	11	3	3	-	5	-	1	-	-	1		

number of recaptures = 24 (12%)

span recorded for Photinus tanytoxus Lloyd which appeared to have a life span of 6 or 7 days (Buschman, in press).

Feeding by male adult fireflies. Adult male fireflies are not known to feed except to drink dew or possibly flower nectar; they apparently depend primarily on energy reserves accumulated during the larval stage. Males held in the laboratory on moist filter paper but without other nourishment gradually lost weight. Newly emerged males weighed about 70% of the pupal weight but their weight decreased to about 50% of the pupal weight by day 15 (Fig. 1.14). To determine if fireflies in the field also lost weight as they aged, I compared the weight of recaptured fireflies with their weights when they were originally captured (Table 1.11). The weight of 12 fireflies decreased, but 10 others increased in weight; thus the weight loss was not demonstrated. This effort probably failed because the conditions for holding the fireflies until they were weighed were not standardized sufficiently. It would have been better to weigh the males immediately after they were collected, but that was not possible at the time.

Males emerging from large pupae were larger than males emerging from small pupae (Fig. 1.15). Since males do not feed but seem to depend on energy reserves accumulated during the larval stage, it would seem that, within limits, large pupae would transmit larger energy reserves to the adult than small pupae. Adult dimensions would be proportioned to utilize this energy maximally. Males with large energy reserves would probably live longer, patrol larger areas and thus have greater probabilities of finding females. Large males may also gain survival advantages (e.g. escaping predators) and may have competitive advantages (e.g. in shoving contests near females) over small males. The 2 males recaptured after 7 and 10 days (Table 1.11) weighed 10.5 and 16.3 mg and measured 9.0

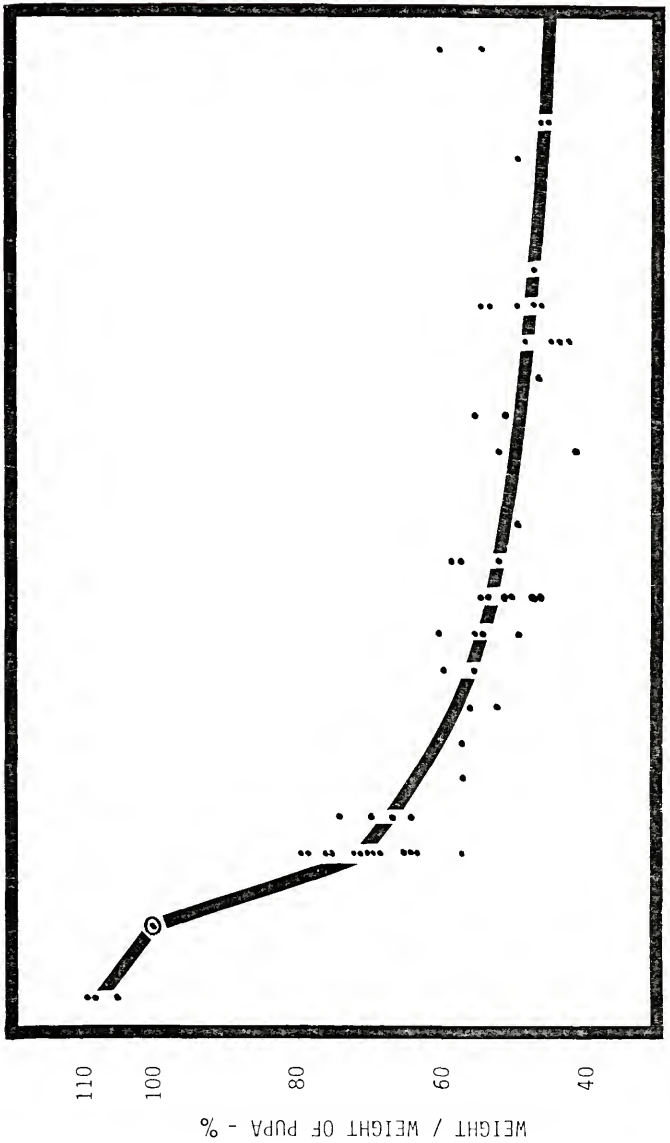

Fig. 1.14 Weight loss of males held in the laboratory on moist filter paper but without other nourishment.

Table 1.11 Weight and length measurements of the 24 males recaptured during the mark-recapture experiment, May-June, 1972.

Date Recaptured	Days from release to recapture	Original weight-mg	Recaptured weight-mg	Weight difference	Body length-mm
May 29	5	10.2	9.4	-0.8	-
	5	16.3	15.7	-0.6	-
May 30	1	10.5	10.0	-0.5	9.0
May 31	1	10.7	10.3	-0.5	9.0
	1	7.9	7.7	-0.2	8.0
	1	15.0	12.8	-2.2	9.5
	1	9.9	8.9	-1.0	8.5
June 1	1	14.0	13.2	-0.8	9.5
	2	8.1	7.0	-1.1	7.5
June 2	7	10.5	8.5	-2.0	9.0
	2	12.0	13.4	+1.4	9.5
June 3	10	16.3	14.6	-1.7	9.5
	3	12.7	13.3	+0.6	9.5
June 4	5	7.9	7.9	0.0	-
	1	10.2	10.7	+0.5	8.0
June 5	5	14.0	14.7	+0.7	9.5
	5	8.3	8.7	+0.4	8.0
	3	10.7	14.2	+3.5	9.0
	1	9.4	9.6	+0.2	8.5
June 6	2	11.5	11.6	+0.1	9.0
June 7	3	17.0	16.6	-0.4	10.0
	1	9.6	11.2	+1.3	8.0
	1	7.8	8.6	+0.8	8.0
June 8	1	10.3	-	-	9.0
				10 gain 12 loss	
	mean	11.28	11.24		8.83
	n	24	23		21
	s	2.811	2.803		0.695

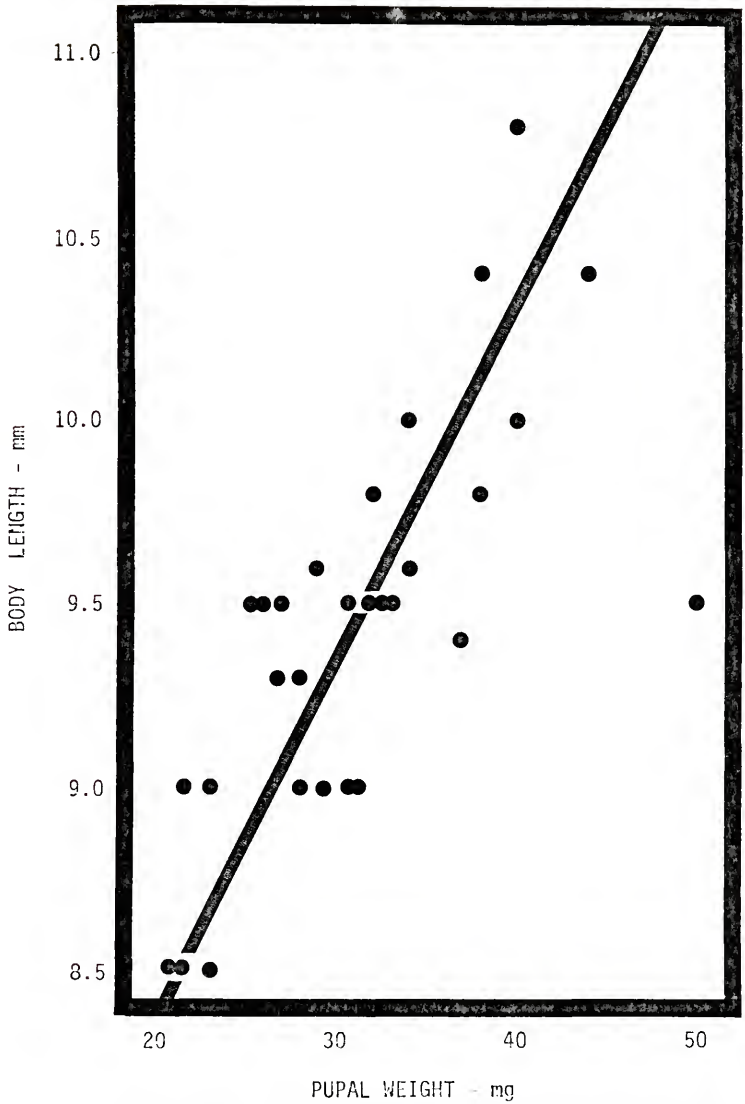

Fig. 1.15 The relationship between pupal weight and the length of the male emerging from the pupa.

and 9.5 mm long. These males were among the larger males captured during the experiment (Tables 1.12 and 1.13).

Biology of Eggs

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 the water. Gravid females are often found between leaves at the base of cattail and hyacinth plants and they probably oviposit in these areas also. The eggs of 2 females measured 0.80 x 0.91 mm (n=6) and 0.75 x 0.83 mm (n=6). Eggs are yellowish in color and the developing embryo is clearly visible through the egg shell. The eggs became luminescent 2 or 3 days after they were oviposited and remained luminescent until they hatched. The luminescence was faint; it took 15 - 20 min to dark-adapt my eyes sufficiently to see it (Fig. 1.16). Eggs oviposited by unmated females were not luminescent. The eggs required 14.8 days to hatch at room temperatures and 14 - 21 days under field conditions (Chapter 2).

Biology of Larvae

General Observations

Larvae of P. lucifera were consistently found on the aquatic vegetation on Lake Alice. They seemed to be particularly abundant in and around cattail stands, but larvae were also found throughout the extensive mats of water hyacinths that covered large areas of the lake. They seemed to spend most of their time near the water, but when the vegetation was wet after a rain or when dew was present they could be found on vegetation 1 - 2 m over the water. During the day, larvae were found in crevasses between the leaves of the hyacinths and cattails. At night the larvae were active and found climbing over the vegetation. Larvae

Table 1.12 Weight distribution of males collected May 23 to June 7, 1972

Date	Weight categories - mg																Totals
	6.0-6.9	7.0-7.9	8.0-8.9	9.0-9.9	10.0-10.9	11.0-11.9	12.0-12.9	13.0-13.9	14.0-14.9	15.0-15.9	16.0-16.9	17.0-17.9	18.0-18.9	19.0-19.9	20.0-20.9	21.0-21.9	
May 23				1	2	2	3	1	2		1					1	13
May 24			1	7	6	2	3	2	1								22
May 26				2		2				2	1						7
May 29		4	5	4	5	5	4	1		2	1						31
May 30			6	2	6	4	2	3	1	1	1						26
May 31		2	1	2	2	2	2		1								12
June 1		1	2		1	2	1	3									10
June 2			2	1	3	2		1		1	1						11
June 3		2		3	1	1	5	1	1			2					16
June 4		2	3	2	2	1		2									12
June 5		1	4	7	4	4	5	1	4								30
June 6	1		2	5	5	4	1	1	1			1					21
June 7	1		1		1	2	1				2				1		9
Total	2	12	27	34	40	31	29	16	10	6	7	3	0	0	1	1	

Table 1.13 Body length distribution of males collected May 30 to June 7, 1972.

Date	Length categories - nearest 0.5 mm						
	7.5	8.0	8.5	9.0	9.5	10.0	10.5
May 30		4	6	11	3	2	
May 31		2	2	4	2	2	
June 1	1		1	4	3	1	
June 2		2	3	3	2		1
June 3	1		4	6	3	1	1
June 4		3	4	2	2		
June 5		3	10	10	5		
June 6	1	3	7	8	1	1	
June 7	1	2	2	1	1	2	
Total	4	20	39	49	22	9	2

Fig. 1.16 Luminescence of eggs nearly ready to hatch in which the embryonic light organs are visible. Exposure was 24 h on Kodak recording film, developed at ASA 4000.

could be collected by searching for their glows. Glowing by these larvae was observed most frequently when they were crawling. Glows typically lasted several seconds and were repeated at somewhat irregular intervals.

One of the characteristic features of lampyrid larvae is the caudal grasping organ which consists of many eversible filaments which the larva is able to extend from the tip of the abdomen. The filaments are covered with minute hooks and are extended by hydraulic pressure (Balduf 1935). In P. lucifera the caudal grasping organ is used both in locomotion and in grooming. During locomotion on a flat surface the larva walks with the rather short thoracic legs, the tip of the abdomen is rhythmically brought forward and placed on the substrate but the filaments are not extended. When climbing on vegetation, the filaments are extended. The body is pushed forward and the substrate is grasped by the thoracic legs. When the thoracic legs have a firm grip, the caudal filaments are withdrawn and the tip of the abdomen is brought forward (Fig. 1.17). When the substrate is too smooth for the thoracic legs to grip it (such as on a glass surface) the body is lowered onto the substrate. The larva apparently is held on the substrate by the surface tension provided by moisture on the surface. The larva moves by anchoring the caudal filaments and pushing the body forward one segment at a time. In laboratory jars small larvae sometimes got caught in the surface moisture and were unable to escape.

Aquatic Behavior

On many occasions larvae of P. lucifera were observed climbing underwater on aquatic vegetation. No other North American lampyrid is known to be aquatic. Several Asian and one Jamaican lampyrid are

Fig. 1.17 Larva climbing with thoracic legs and with caudal filaments.

known to be aquatic (McDermott 1953, Annandale 1900, Blair 1927, Okada 1928). The larvae of P. lucifera were observed to crawl in and out of the water both in the field and in the laboratory. They captured snail prey underwater (Fig. 1.18) and dragged it above the water surface to feed (Fig. 1.19). Their behavior under water differed little from that above water but they seemed to move faster and often glowed continuously, not periodically, as they did above water. They were unable to climb on glass surfaces under water.

The larvae were able to survive indefinitely under water. In one experiment 4 groups of 7 medium-sized larvae were placed in vials with screened ends. Two vials were submerged in each of 2 beakers of water. Bottled nitrogen was bubbled through the water in one beaker to remove the oxygen from the water. Bottled air was bubbled through the other beaker to aerate the water. The vials were arranged so the water circulated through them continuously but the larvae were not exposed to the bubbles. After 20 h all the larvae were alive and clinging to the surfaces of the vials. The flow of gas was then increased and 4 h later all the larvae in the nitrogen beaker had released their grip on the substrate and were lying on their backs, apparently dead. The presumed-dead larvae were placed in a petri dish of water exposed to the air. Twelve of the 14 presumed-dead larvae revived. The larvae exposed to the bubbling air were still alive and clinging to the vial surfaces after being submerged 26 hrs.

In a second experiment, the following lampyrid larvae were held for 31 days under water: 5 large and 5 small P. lucifera larvae, 4 large and 4 small Photuris sp. (non-red) larvae, 2 large Photuris sp. (red)

Fig. 1.18 Larva capturing snail under water.

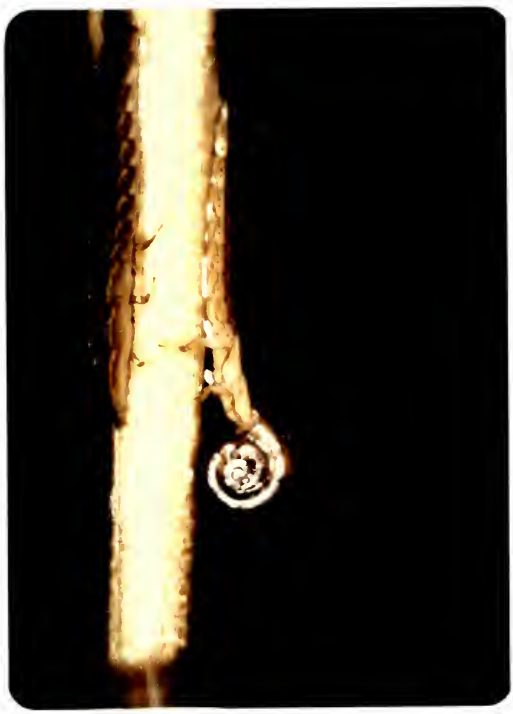

Fig. 1.19 Larva with captured snail pulled above water to feed on it.

larvae, 1 Pyractomena limbicollis larva, and 5 days later a Photinus consimilis larva was added. Snails were offered to the larvae but only the P. lucifera fed on them while under water. On the 3rd day of the experiment one Photuris sp. (red) larvae was dead and on day 12 one small Photuris sp. (non-red) larva was dead. All other larvae survived until the experiment was terminated 31 days later (the Photinus larva was in the experiment 26 days). One small P. lucifera and 1 large Photuris sp. (non-red) died soon after the larvae were removed from the water. All larvae except P. lucifera were rather sluggish when removed from the water, but they recovered completely in a day. Lampryids can survive extended periods under water and can apparently absorb oxygen through the membraneous cuticle or through the caudal filaments. None of these larvae have special aquatic adaptations such as gills which have been observed on other aquatic lampyrid larvae (Blair 1927, Okada 1928). Photinus larvae seem to have hydrophobic setae which cause them to float when they are dropped on water. When they are submerged they have silvery patches on their dorsal sclerites. However, these patches disappear after several hours under water. Pyractomena and Photuris larvae fall through the water surface much more readily. Photuris and Photinus larvae are sometimes found on aquatic vegetation and on mud flats along the shore of Lake Alice. When the lake flooded, these larvae were found clinging to floating debris. Photinus sp (red) larvae and P. limbicollis were found in much drier areas. The latter seemed to be arborial.

Predatory behavior

Larvae of P. lucifera captured snail prey both above and below water. In the field they probably capture most of their prey at the water surface or under water. Snails, their major prey, are frequently observed

crawling upside-down on the surface film and under water on aquatic plants. Only occasionally are snails observed crawling above water on emergent vegetation. Larvae seem to spend a lot of time patrolling the water edge. Sometimes larvae stick their heads into the water apparently testing for the presence of prey. Schwalb (1960) demonstrated that Lampyris noctiluca could follow snail trails and did not respond to the odor of snails. Larvae of P. lucifera did not orient to snail trails in petri dishes. On the other hand, when snails are placed near larvae, they become active after several minutes and begin extending and swinging their heads while they crawl straight to the snail. Larvae usually attack snails by climbing onto the shell and reaching under it to bite and chew at the snail body. At other times larvae begin biting and chewing at the snail body without climbing onto the shell. Schwalb (1960) reported that L. noctiluca larvae bit snails in the head region, injected a toxin and retreated; they did not begin feeding until the snail was immobilized by the toxin. There is no such hesitation in the attack of P. lucifera larvae; they follow the snail into the shell biting and chewing continuously. There does not seem to be a preference for any specific part of the snail body. After several minutes of biting and presumably ingesting, larvae often pull snails out of the water by crawling in reverse, reaching upward and backward with the caudal grasping organ and pulling the snail backwards. Snails are usually pulled several inches above the water before the larvae become motionless again. They continue biting and presumably ingesting throughout this process. I once observed a larva pulling a snail over a mat of decaying vegetation; there were no objects on which to climb, and it finally climbed onto a bullfrog that was sitting on the mat. Dragging behavior may reduce competition from other snail scavengers

that are attracted by snail blood released when snails are attacked under water. P. lucifera larvae do not release their prey as do other terrestrial lampyrids (Schwalb 1960, Chapters 3 - 5) during the attack, dragging or feeding stages. Snails that are released would fall away and be impossible for the larvae to retrieve.

Larval prey records for P. lucifera were as follows: 38 snails (Pulmonata), 5 freshwater limpets (Ancylidae), 1 small jumping spider (Salticidae), 1 damselfly nymph (Anomalagrion hastatum (Say)) and a leech (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). There are only 2 previous records of prey of Pyractomena sp. larvae. Farnworth (1973) found Pyractomena gamma larvae feeding on snails and Lloyd (1973a) photographed Pyractomena limbicollis larva feeding on a snail.

I found 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 often feed on the same prey, even when other prey is available. They are apparently attracted by chemicals released when the first larva injures the prey.

Biology of Pupae

When mature larvae approach pupation they become increasingly sedentary and eventually secrete an adhesive that fastens the abdominal segments to the substrate. Larvae usually orient head-down but sometimes in the laboratory they squeeze into the horizontal groove at the top of rearing jars. The pupa is cryptically pigmented and has a series of

sharp spines on the abdominal tergites which are not found in other life stages. The pupa of Pyractomena differ from other lampyrid pupa in several ways: 1) the larvae pupate on vegetation in exposed situations instead of in the soil, 2) the pupa becomes cryptically pigmented instead of milky white and 3) the pupa does not glow as do other pupa when disturbed or handled roughly. The pupal stage lasts 6 or 7 days at room temperature and is slightly longer for male than for female pupae (Chapter 2). In the field, pupae and prepupae were found 2 - 45 cm above the water on emergent vegetation. After a heavy rain that flooded Lake Alice, 2 pupae were found submerged under about 2 cm of water. These pupae were viable and adults emerged in the laboratory.

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. In the laboratory larvae are cannibalistic when severely starved. They usually attack dead larvae, prepupae and pupae. Small larvae attack unscleritized newly hatched larvae. No insect parasites were recovered from the hundreds of field-collected larvae reared during these studies. One dead larva developed a fungus growth: Penicillium sp.and Aspergillis flavus. In the laboratory, mites were found with eggs. They may have been feeding on the eggs or on the secretions around the eggs. A tree frog (Hyla sp.) captured a flying male. Another male was found in a spider web, Acanthepeira sp. A wolf spider (Lycosidae) was observed biting the female of a pair of copulating fireflies. Surprisingly, I have no records of P. lucifera falling prey to aggressive mimic Photuris females which were common in the vicinity.

Lloyd (1973e) compiled available records of firefly natural enemies and concluded that lampyrids are parasitized by phorid and tachinid flies, mites and nematodes. Predators that seem to specialize on fireflies include certain birds, spiders, anoles, frogs and aggressive mimic fireflies. Records of firefly natural enemies are extremely fragmentary.

CHAPTER 2
LIFE CYCLE OF THE FIREFLY
PYRACTOMENA LUCIFERA

Information on life cycles of American fireflies is limited. Williams (1917) and Hess (1920) suggested 2-year life cycles for several lampyrids occurring in northeastern United States, because they found half-grown larvae in spring and concluded they could not mature until the following year. Only 2 American firefly specimens have been reared from egg to adult: Lloyd (1969) reported that he and D. Minnick obtained an adult Photuris sp.in September from eggs oviposited in April in northcentral Florida,and McLean et al. (1972) obtained a female Photuris lucicrescens Barber after rearing the larva for 14 months in Maryland. Lampyrids appear to have 2-year life cycles in the northern states; however, life cycles may be less than 1 year in Florida. Extrapolation of laboratory developmental rates to field populations is questionable since there are many factors that influence development of field populations. There is generally little information available on development of field populations. The duration of the life cycle of various Old World lampyrids, based on development of laboratory populations, has been reported as follows: Subfamily Lampyrinae--Lampyris noctiluca L. 1, 2 and 3 years in southern and northern Europe (summarized in Schwalb 1960, Naisse 1966; see also Wootten 1976, Balduf 1935); Lamprohiza splendidula L. 1 year in southern Europe (Balduf 1935) and 3 years in northern Europe (Schwalb 1960); Lamprohiza delarouzei Jacq.-DuV. 1 year in southern Europe (Balduf 1935); Phosphaenus

hemipterus (Fourcroy) 1 year in southern Europe (Balduf 1935): Lamprigera tenebrosus (Walker) 1 year in India (Bess 1956); Subfamily Luciolinae--Luciola lusitanica Charp. 1 year in southern Europe (Balduf 1935); Luciola discicollis Laporte 1 year in West Africa (Kaufmann 1965); Luciola cruciata Motsch. 1 year in Japan (Kiichiro 1961); and Luciola lateralis Motsch. 1 year in Japan (Kiichiro 1961). Naisse (1966) suggested that the life cycle of Lampyris noctiluca was variable and changed from 1 year in southern Europe to 2 or 3 years in northern Europe.

Few North American fireflies have been reared successfully, and little is known about their life cycles. Therefore, I conducted the following rearing and life cycle studies on the firefly Pyractomena lucifera Melscheimer. This firefly was chosen for study because it was a common, local firefly and the larvae responded readily to laboratory rearing. This firefly was successfully reared from egg to adult. The role of light-dark cycles in controlling larval development was examined in laboratory-rearing experiments. The development of larvae under field conditions was determined in field-rearing experiments, and the development of field populations was monitored by repeated sampling.

Laboratory Rearing Experiments

Methods

In the laboratory all stages of the firefly P. lucifera were reared and maintained in 6 oz babyfood jars with metal lids (jars with plastic lids tended to "sweat" and the small larvae became trapped in the droplets). Each jar was fitted with 112 mm filterpaper, folded and rolled into a cone to stand in the jar. The filterpaper was kept saturated with

water and was changed when it became moldy. Initial rearing under natural photoperiod suggested that development was photoperiodically controlled. Subsequently, larvae were reared in "light boxes" under controlled photoperiods. The light boxes measured 0.9 x 0.9 x 1.2 m and were equipped with two 15-watt fluorescent lights controlled by a timer. The lights were mounted in the top of the box and separated from the floor by 2 glass plates that provided insulation from the heat generated by the lights. A fan was used to circulate room air into each box. During the year, the room temperature varied between 18 - 36°C but was usually between 21 - 27°C; temperatures in the 2 boxes remained within 0.5 - 1.0°C of each other. In the first 2 rearing experiments frozen chicken liver was chopped into small pieces, placed on small (1 cm^2) paper squares and then added to the rearing jars twice each week. The paper with leftover food was removed after 24 h to avoid putrification and growth of mold. In the 3rd rearing experiment 1 or 2 snails, about the size of the larvae, were added to the jars twice each week and the remains removed 24 h later.

Initial Rearing

Larvae that hatched in May 1970 (from eggs oviposited by several females which had been reared from spring field-collected larvae) were reared singly and in groups under natural light conditions and fed chicken liver. These larvae developed rapidly and 2 larvae pupated in Oct. of that year. The remainder of the larvae continued to grow but did not pupate. Since the larvae were exposed to natural photoperiod, I suspected that the winter photoperiod might be suppressing pupation. Therefore, in Dec., after they had been reared for 212 days, 20 larvae originally from one egg mass (same parents) were transferred to light

boxes: 10 larvae in 5 babyfood jars were reared under long photoperiod (15:9 h light-dark cycle) and another 10 larvae in 5 jars were reared under short photoperiod (11:13 h light-dark cycle). Of the larvae reared under long photoperiod, males pupated after 49 days (n=4, r=44-56), and females pupated after 108 days (n=4, r=89-117). None of the larvae exposed to short photoperiod had pupated after 182 days. These larvae were then transferred to long photoperiod and they pupated 31 days later (n=6, r=22-38).

Second Rearing Experiment

In the 2nd rearing experiment 60 first instar larvae from one egg mass (same parent) were reared individually in babyfood jars. The larvae were fed chicken liver twice each week. (Snails were not available in dependable quantities.) The larvae were divided into 4 treatment groups, A, B, C and D. In treatment A, 30 larvae were reared under a long photoperiod (15:9 h light-dark cycle) to see how fast the larvae would develop and how many times they molted. In treatments B, C and D, groups of 10 larvae were shifted between the long photoperiod and short photoperiod (11:13 h light-dark cycle) to determine which life stage was sensitive to photoperiod and controlled pupation. In treatment B, larvae were reared under short photoperiod but transferred to long photoperiod as each individual reached the 6th instar. In treatment C larvae were reared under short photoperiod but transferred to long photoperiod as each individual reached the 7th instar. In treatment D larvae were reared under long photoperiod but transferred to short photoperiod as each larvae reached the 6th instar.

The larvae in treatment A developed rapidly (Table 2.1): males pupated in 205.5 days, females in 224.8 days; male pupae weighed 26.5 mg and females 40.2 mg; male larvae had 4 - 7 instars and females 5 - 7 instars. Larvae in treatments B and C did not pupate until they were transferred to long photoperiod: larvae in treatment B had 6 and 7 instars and larvae in treatment C had 7 instars (Table 2.1). Three of the males in treatment D pupated as 5th instars and were, therefore, not transferred to the short photoperiod. Larvae that were transferred to the short photoperiod continued to grow and molt but did not pupate for about 270 days when the timer malfunctioned and exposed the larvae to 23:1 h light-dark cycle. This experiment suggests that it is the mature larva that is sensitive to photoperiod: larvae that developed under short photoperiod were not delayed in their development but pupated soon after they were placed in the long photoperiod (treatments B and C). Larvae that developed in long day photoperiod also did not pupate when the mature larvae were exposed to the short day photoperiod (treatment D).

Third Rearing Experiment

In the 3rd rearing experiment the larvae were reared on snails rather than on chicken liver. The snails, Helisoma trivolvis (Say), were reared in the laboratory so the supply was limited;only a small number of larvae could be maintained. Nineteen 1st instars hatching from one egg mass (same parents) were reared individually in jars. One or 2 snails about the size of the larvae were provided each larva twice each week. Ten larvae were reared under long photoperiod (16:8 h light-dark cycle), and 9 larvae were reared under short photoperiod (11:13 h light-dark cycle).

Table 2.1 The number of instars, average time of development and weight of pupae from larvae reared under various light conditions and fed chicken liver: 2nd rearing experiment.

Treatment	Light-dark cycle	Sex	Number of instars	Time for Development (days)	Weight of pupae (mg)
A	reared 15:9 h	males	4 (n=1) 5 (n=4) 6 (n=9) 7 (n=2)	a 205.5 (n=16) (s=50.3, r=124-306)	a 26.5 (n=15) (s=4.34, 4=21.2-34.8)
		females	5 (n=1) 6 (n=9) 7 (n=1)	a 224.8 (n=11) (s = 39.6, r=154-298)	b 40.2 (n=10) (s=7.47, r=30.0-56.3)
B	reared 11:13 h transferred to 15:9 h after 5 molts	males	6 (n=2)	189.5 (n=2) (r=180-199)	31.5 (n=2) (r=27.4 - 35.5)
		females	6 (n=1) 7 (n=1)	199.9 (n=2) (r=188-210)	42.7 (n=2) (r=39.1 - 50.2)
C	reared 11:13 h transferred to 15:9 h after 6 molts	males	7 (n=1)	208.0 (n=1)	31.0 (n=1)
		females	7 (n=4)	193.3 (n=4) (r=190-207)	48.8 (n=3) (r=39.4 - 54.3)
D	reared 15:9 h transferred to 11:13 h after 5 molts	males*	5 (n=3)	135.0 (n=3) (r=133-138)	21.9 (n=3) (r=19.6 - 23.4)
		males**	7 (n=1)	294 (n=1)	--
		females**	8 (n=1) 9 (n=1)	296.0 (n=2) (r=194-198)	--

*Three males pupated as 5th instar larvae before being transferred to the 11:13 h light-dark cycle.
**The timer on the 11:13 h light box malfunctioned after 270 days exposing these larvae to 23:1 h cycle.
The superscript letters indicate the result of "t tests" (p=0.05): different letters indicate differences are statistically significant.

The larvae were weighed once each week and the larval exuviae and the shells of consumed snails were preserved for subsequent measurements.

Larvae in Experiment # 3 developed much more rapidly on the snail diet than did larvae reared on chicken liver in previous experiments. Under long photoperiod the time for larval development averaged 65 days for males and 80 days for females (Table 2.2). This compares with 205 days and 224 days for males and females reared on chicken liver (Table 2.1). The weight of pupae was also greater, 39.7 mg for males and 71.0 mg for females reared on snails (Table 2.2); this compares with 26.5 mg and 40.2 mg for males and females reared on chicken liver (Table 2.1). The chicken liver diet seemed to be inferior to the more natural snail diet.

The time for larval development in the 3rd rearing experiment was significantly longer ($p=0.05$) under short photoperiod than under long photoperiod (Table 2.2). Larvae exposed to short photoperiod continued to feed and grow. They consumed significantly more snails ($p=0.05$) and produced pupae that were heavier (Table 2.2). (The difference in weight between male pupae reared in the 2 light conditions just missed being significant, $p=0.05$).

Analysis of Rearing Experiments

Photoperiodic control of development. The effect of photoperiod on development was dramatic. Pupation by larvae developing under short-day conditons was delayed while development by similar larvae under long-day conditions continued without delay (1st and 3rd rearing experiment). Since the delay in larval development was controlled by an environmental cue (photoperiod) and not by adverse conditions directly and the delay was not obligatory, this developmental delay can

Table 2.2 The number of instars, average time of development, weight of pupae and number of snails consumed when larvae were reared under 2 light conditions and fed snails: 3rd rearing experiment.

Light-dark cycle	Sex	Number of instars	Time for development (days)	Weight of pupa (mg)	Number of snails eaten
16:8 h	males	4 (n=3) 5 (n=3)	a 65 (s=8.5, n=6)	a 39.7 (s=10.3,n=6)	a 15.3 (s=2.07,n=6)
	females	5 (n=3) 6 (n=1)	b 80 (s=3.0,n=4)	b 71.0 (s=6.62,n=4)	b 20.0 (s=0.82,n=4)
11:13 h	males	5 (n=1) 6 (n=2)	c 177 (s=23.5,n=3)	abc 56.0 (s=14.6,n=2)	c 25 (s=2.65,n=3)
	females	6 (n=5)	c 175 (s=12.3,n=5)	d 108.0 (s=10.4,n=5)	d 33.2 (s=1.10,n=5)

Superscript letters indicate the result of "t tests" (p=0.05): different letters indicate differences are statistically significant.

be called a facultative diapause (Lees 1956). P. lucifera larvae continue to feed and grow when the light-dark cycle prevents pupation and in spring these large larvae produce heavy pupae (Tables 2.1, 2.2) which in turn produce large adults (Chapter 1). Since large females oviposit more eggs than small females and large males have a longer life expectancy than small males (Chapter 1), diapausing larvae seem to increase their reproductive fitness by continuing to feed and grow during the winter as conditions allow. In Florida larvae were active on warm evenings throughout the year.

Photoperiodic control of larval development has also been observed in Photuris spp. larvae. K. Smalley (personal communication) and McLean et al. (1972) observed that several Photuris spp. larvae can be induced to pupate during their winter diapause by exposing them to long-day photoperiods. However, the diapause of some Photuris spp. larvae has not yet been successfully terminated artificially (Chapter 4). Naisse (1966) was able to rear 2 generations of Lampyris noctiluca in a year. He reported that larvae reared during the winter had an additional molt, and that larval development in the winter was much longer: 7 months vs. 4 months during the summer. He did not report the photoperiodic conditions of his rearing, but based on my experience with P. lucifera the larvae were probably exposed to natural photoperiods. Schwalb (1960) observed that the development of L. noctiluca proceeded normally at room temperatures during the winter, but the development of Lamprohiza splendidula did not resume at room temperatures during the winter. Chippendale (1977) listed 45 other insects that diapause during various larval instars. Corbet (1957) observed a diapause in the development of Anax imperator Leach (Odonata: Aeschnidae) that was

similar to that of P. lucifera. Dragonfly nymphs continued to grow and develop into mature nymphs during the winter. In the spring mature nymphs became adults en masse when the light and temperature conditions were right.

Diapause in P. lucifera was terminated by long-day photoperiods in the 1st and 2nd rearing experiments. Larvae in the 3rd rearing experiment eventually pupated while exposed to short-day photoperiods. Larvae in experiments 1 and 2 were on the artificial diet, so this may have acted as a stress factor which intensified the effects of the short-day photoperiod. Larvae in the 3rd rearing experiment had a more natural snail diet, so they were not stressed in the same way. They must have responded to some other cue. These larvae began pupating in late February, which was only 10 - 20 days earlier than when field populations apparently began pupating. The larvae may have been responding to warmer room temperatures which fluctuated seasonally.

The mature larvae of P. lucifera seem to be the life stage that is sensitive to short-day photoperiods. In the 2nd rearing experiment, larvae that were reared under long-day photoperiod but transferred to short days after reaching the 6th instar (treatment D) were induced to delay pupation, whereas larvae that were reared under short days until they reached the 6th or 7th instars and then transferred to long days (treatments B & C) were not delayed and pupated together with larvae reared continuously under long days (treatment A).

Snails Consumed by the Larvae. During their development, larvae consumed 12 - 35 snails. Female larvae consumed significantly ($p=0.05$) more snails than male larvae under both photoperiodic conditions.

(Tables 2.2, 2.3). Larvae of both sexes consumed significantly ($p=0.05$) more snails under short-day conditions than under long-day conditions (Tables 2.2, 2.3). Male larvae reared under long-day conditions consumed an average of 15.3 snails while female larvae reared under short-day conditions consumed an average of 33.2 snails (Tables 2.2,2.3). Snails consumed by larvae in these 2 groups are illustrated in Figs. 2.1 and 2.2. Hutson and Austin reported that male larvae of Lamprigera tenebrosus consumed 20 - 40 snails, and female larvae consumed 40 - 60 snails (Balduf 1935). Larvae of L. tenebrosus measured up to 7.5 cm (Bess 1956) and attacked snails measuring 20 - 40 mm (Peterson 1957).

Since snails of all sizes were utilized in larval rearing, the snail count may not give an accurate picture of food consumed. Many of the additional snails consumed by larvae under short-day conditions were large snails. Two measurements of the diameter of snails (width and height) were made and averaged. The distribution, in 8 size categories, of snails consumed by each larva in the 3rd rearing experiment is presented in Table 2.3. The biomass of a snail is probably correlated with the volume of the snail shell. Therefore, the volume of snails consumed by each larva was calculated using the midpoint of each size category as the radius of a sphere (the sphere seemed to be a reasonable approximation of snail volume). Larvae consumed 425.3 - 2352.7 mm^3 of snail (Table 2.3). The average volume of snail consumed by male and female larvae and by larvae in the 2 light conditions were each significantly different ($p=0.05$). The relationship between the estimated volume of snail consumed and weight of pupa produced by each larvae is presented in Fig. 2.3.

Table 2.3 Size distribution and estimated volume of snails eaten by larvae reared in the 3rd rearing experiment compared with the weight of the pupae produced by each larva.

Size category	1	2	3	4	5
Average diameter - mm	0.0-0.99	1.0-1.99	2.0-2.99	3.0-3.99	4.0-4.99
Estimated volume - mm^3	0.065	1.76	8.18	22.5	47.7
long-day					
males #					
888	0	4	4	3	0
889	0	2	5	3	4
891	0	3	3	5	1
894	0	2	4	2	5
895	0	2	3	3	1
896	0	1	5	4	3
mean		2.3	4.0	3.3	2.3
females #					
887	0	2	6	3	5
890	0	5	4	2	5
892	0	4	4	2	4
893	0	4	3	6	0
mean		3.8	4.3	3.3	3.5
short-day					
males #					
898	0	6	4	3	7
900	1	3	4	6	5
903	0	3	4	4	6
mean	0.3	4.0	4.0	4.3	6.0
females #					
897	0	3	5	4	8
901	0	2	4	6	6
902	0	2	7	4	7
904	0	3	7	2	11
905	1	3	4	4	8
mean	0.2	2.6	5.4	4.0	8.0

Table 2.3 - extended.

6 5.0-5.99 87.1	7 6.0-6.99 143.8	8 7.0- 220.9	Total snails	Total volume-mm^3	Weight of pupae-mg
2	1	0	14	425.3	29.6
0	2	0	16	590.3	31.8
2	1	1	16	728.9	45.3
2	2	1	18	1002.4	56.6
2	1	0	12	461.3	32.9
1	1	1	16	727.7	41.7
1.5	1.3	0.5	15.3[a]	777.2[a]	39.7[a]
2	2	0	20	820.4	67.8
1	1	3	21	1218.6	71.2
3	2	1	20	1045.4	80.9
3	2	1	19	792.6	66.2
2.3	1.8	1.5	20.0[b]	1167.4[b]	71.0[b]
3	4	0	27	1281.2	66.3
2	4	1	26	1381.9	--
4	0	1	22	983.5	45.7
3.0	2.7	0.7	25.0[c]	1543.4[c]	56.0[abc]
9	5	0	34	2020.7	92.4
9	4	1	32	2033.8	121.0
8	2	4	34	2352.7	112.5
4	4	1	32	1773.9	107.7
8	4	2	35	2223.5	106.6
7.6	3.8	1.6	33.2[d]	2080.9[d]	108.0[d]

Superscript letters indicate the result of "t tests" (p=0.05): different letters indicate differences are statistically significant.

Fig. 2.1 Seventeen snails eaten by a male larva under long photoperiod.

Fig. 2.2 Thirty-four snails eaten by a female larva under short photoperiod.

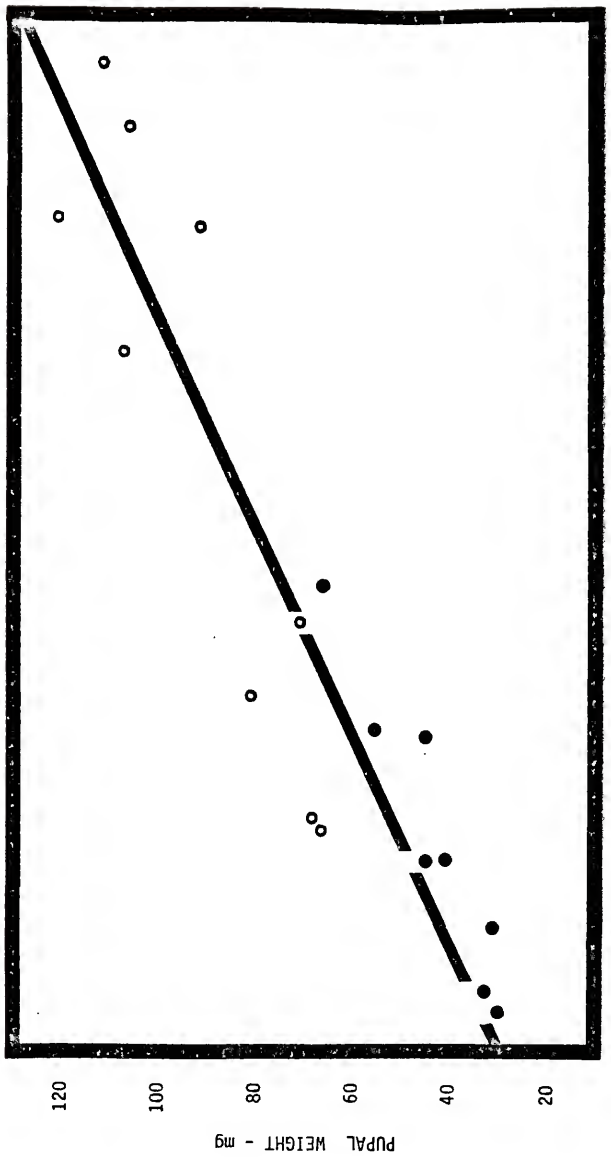

Fig. 2.3 The relationship between estimated volume of snails consumed and weight of pupa produced by each larva in the 3rd rearing experiment (solid circle = male, open circle = female).

Number of larval instars. The number of larval instars in experiments 2 and 3 was quite variable (Tables 2.1 and 2.2). Larvae in experiment 2 seemed to have more molts than larvae in experiment 3: 4 - 9 vs. 4 - 6. In both experiments there seemed to be a tendency (not statistically significant) for female larvae and larvae under short photoperiod to have more molts than male larvae and larvae under long photoperiod (Tables 2.1, 2.2). The additional molts may be related to possible stresses experienced by the larvae on the artificial diet and exposed to short photoperiods. Naisse (1966) observed that female larvae had 6 instars,while male larvae had 5 instars when reared during the summer; however, larvae reared during the winter had additional molts (6 instars for males and 7 instars for females). The number of larval instars among lampyrids seems to be variable and it seems to depend to some extent on growing conditions.

Measurements of larvae. Larvae in the 3rd rearing experiment were weighed once each week. The weight measurements during each instar, when plotted on semi-log graph paper, resulted in a straight line across instars (Fig. 2.4). Based on the slope of this line, the weight of each instar increased by a factor of 3.04. This compares with a factor of 2 associated with "Prizibram's factor" (Wigglesworth 1966). There was considerable overlap in the weight distribution of consecutive instars, particularly between the 4th and 5th instars. It also appears larvae were not weighed during the early stages of instars 3 and 4 as a result of the feeding and weighing schedule.

The following measurements were made on exuviae of larvae in the 3rd rearing experiment: length of pronotum, width of pronotum, length of head capsule and length of mesothoracic tibia. These measurements

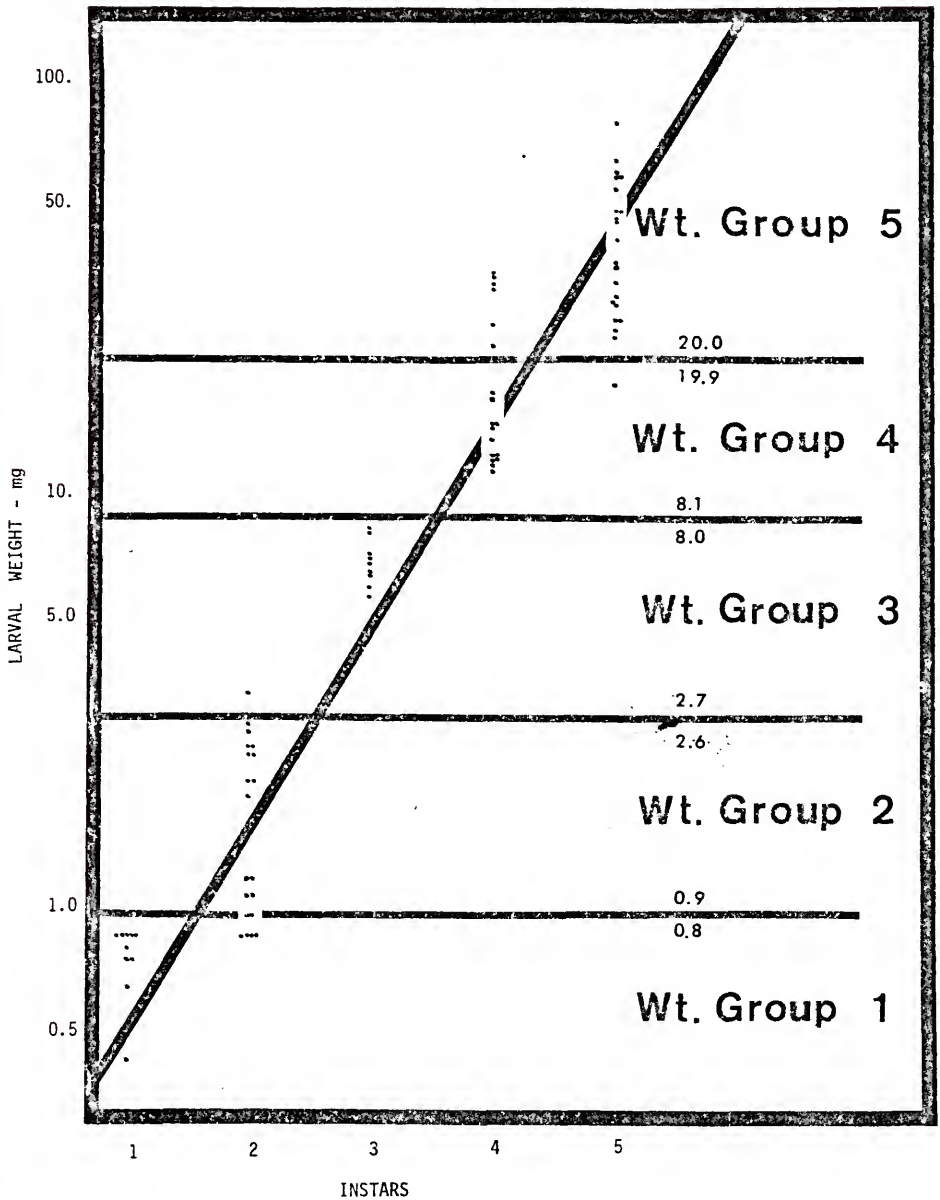

Fig. 2.4 Weight of 10 larvae weighed once each week, instars 1 - 5. The larvae were reared under long photoperiod (experiment #3). Five weight groups were assigned to correspond to the weight of larvae in the respective instars.

are presented in Table 2.4. There was virtually no overlap in these 4 dimensions among the 6 instars. Any of these measurements can, therefore, be used to determine the instar of a larva. Since the length of the pronotum was the most convenient measurement, it was used in subsequent work. The growth ratio between larval instars (as in Dyar's Law) averaged 1.34 and 1.35 for the length of the pronotum but averaged ca. 1.3 for other measurements (Table 2.5). Growth ratios for pronotum and head capsule tended to decrease steadily as the larvae grew, but the growth ratios for tibia were highest between instars 3 and 4 (Table 2.4). These growth ratios are slightly lower than the 1.4 proposed in Dyar's Law (Wigglesworth 1966).

Effect of sex on larvae. The duration of larval development was slightly different for males and females in all 3 rearing experiments but the difference was statistically significant ($p=0.05$) only for larvae in treatment A of Experiment #2. Female larvae produced pupae that were significantly heavier ($p=0.05$) than male pupae (Tables 2.1, 2.2). Since the female larvae grew larger they also consumed significantly more snails ($p=0.05$) (Tables 2.2, 2.3) than did male larvae. The number of instars was variable, and differences between the sexes were not pronounced. Male and female larvae seemed identical in most respects, but most of the larger larvae produced females.

Use of Weight Groups to Describe Larval Development

In the following discussions I chose to describe the development of various groups of larvae by assigning larvae to one of 5 weight groups as follows: 0.0 - 0.89 mg = weight group 1, 0.9 - 2.69 mg = weight group 2, 2.70 - 8.09 mg = weight group 3, 8.10 - 19.9 mg = weight group 4

Table 2.4 Five measurements of larvae in instars 1 - 6: live weight, length of pronotum, width of pronotum, length of head capsule and length of mesothoracic tibia. Larvae were reared on snails under long and short photoperiods: 3rd rearing experiment. Dimensions taken from exuvia.

Instar		Weight		Pronotum length	
		long	short	long	short
1	mean	*	*	0.619	0.618
	s=	*	*	0.0183	0.0279
	r=	0.35-0.8	0.35-1.0	0.59-0.65	0.57-0.64
	n=	10	8	9	6
2	mean	*	*	0.904	0.913
	s=	*	*	0.270	0.0256
	r=	0.8-3.1	0.8-3.3	0.87-0.95	0.87-0.94
	n=	10	8	8	7
3	mean	*	*	1.277	1.331
	s=	*	*	0.0463	0.0809
	r=	5.3-7.7	4.4-9.2	1.15-1.39	1.22-1.43
	n=	9	8	8	7
4	mean	*	*	1.779	1.804
	s=	*	*	0.06034	0.1028
	r=	10.8-32.4	8.4-33.0	1.65-1.89	1.70-1.88
	n=	10	8	8	7
5	mean	*	*	2.297	2.282
	s=	*	*	0.0918	0.1217
	r=	17.3-75.0	14.3-66.7	2.19-2.44	2.08-2.39
	n=	7	8	4	6
6	mean	*	*	2.69	2.663
	s=	*	*	-	0.1284
	r=	35.7-74.8	39.4-112.5	-	2.56-2.81
	n=	1	7	1	4

*arithmetic means were not calculated, see Fig. 2.3 for a graphic presentation.

Table 2.4 - extended

Pronotum width		Head length		Tibia length	
long	short	long	short	long	short
0.660	0.663	0.307	0.304	0.318	0.314
0.0206	0.0281	0.00577	0.0195	0.00447	0.0241
0.64-0.70	0.61-0.69	0.30-0.31	0.28-0.33	0.31-0.32	0.28-0.34
9	6	3	5	5	5
0.896	0.930	0.425	0.422	0.401	0.390
0.0316	0.0316	0.0181	0.0172	0.0288	0.0237
0.86-0.96	0.89-0.98	0.41-0.46	0.40-0.45	0.35-0.43	0.36-0.41
8	7	7	6	7	6
1.234	1.286	0.555	0.589	0.553	0.51
0.0342	0.0707	0.0428	0.0389	0.0134	0.0455
1.08-1.31	1.21-1.37	0.50-0.63	0.53-0.64	0.49-0.58	0.45-0.56
8	7	8	7	8	7
1.675	1.69	0.757	0.775	0.777	0.741
0.0739	0.963	0.0365	0.0509	0.0350	0.0615
1.53-1.78	1.61-1.75	0.70-0.83	0.72-0.89	0.73-0.83	0.62-0.83
8	7	7	6	8	7
2.074	2.108	0.960	0.927	0.959	0.975
0.1081	0.1839	0.0436	0.0905	0.0258	0.0657
1.96-2.24	1.94-2.45	0.91-1.03	0.82-1.09	0.87-1.01	0.91-1.08
4	6	4	6	4	6
2.49	2.435	1.10	1.048	1.13	1.107
-	0.1526	-	0.0574	-	0.075
-	2.25-2.55	-	1.00-1.13	-	1.03-1.18
1	4	1	4	1	3

Table 2.5 Growth ratios between instars 1 - 6 for larvae reared on snails under long and short photoperiods: based on data in Table 2.

Instars	Measurement:	Pronotum length		Pronotum width		Head length		Tibia length	
	Day length:	long	short	long	short	long	short	long	short
2:1		1.46	1.48	1.36	1.40	1.38	1.39	1.26	1.24
3:2		1.41	1.46	1.38	1.38	1.31	1.40	1.39	1.31
4:3		1.39	1.36	1.36	1.31	1.36	1.32	1.41	1.45
5:4		1.29	1.27	1.24	1.25	1.27	1.20	1.23	1.32
6:5		1.17	1.17	1.20	1.16	1.15	1.13	1.18	1.14
mean		1.34	1.35	1.31	1.30	1.29	1.29	1.29	1.29

and 20.0 mg or greater = weight group 5. The weight groups were delineated to follow the weight distribution of larvae in the first 5 instars in the 3rd experiment (Fig. 2.4). Since there was considerable overlap between the instars, the dividing lines were rather arbitrary. The lower limit of the 5th weight group was set at 20 mg so that all larvae that pupated did so from the 5th weight group (the smallest larvae to pupate weighed about 20 mg).

The instar of a larva can be estimated by making one of the measurements listed in Table 2.4 and referring to the measurements in the table. The most convenient measurement was the length of pronotum, so this measurement was used in the following experiment.

To compare the use of weight groups based on live weight and instar estimates based on length of pronotum, I used both methods to describe a group of 110 larvae collected Nov. 5, 1972. The live weights of the larvae were recorded and assigned to the 5 weight groups. The percent of larvae in each group is presented in Table 2.6. The larvae were preserved, and later the pronotum length of each larva was measured. The distribution of pronotum lengths was then plotted (Fig. 2.5). This distribution was rather continuous but with distinct peaks associated with measurements for instars 1 - 6. The number of larvae belonging to each instar was estimated from Fig. 2.5. The percent of larvae in each instar is presented in Table 2.6 together with the percent of larvae in the different weight groups. In the Nov. 5 sample of larvae the percent of larvae that fell into the first 3 categories was about the same for each estimate, but the percent falling into the 4th and 5th categories was quite different (Table 2.6). Apparently many of the 5th instar larvae fell into weight group 4. This was probably due to 5th instar larvae losing weight when they were unsuccessful in

Table 2.6 Distribution of 110 larvae collected Nov. 5, 1972 in the weight groups and 6 instars. The weight groups were based on live weight and the instars were based on the length of the pronotum.

Weight group/instar categories	Percent of larvae in each weight group	Percent of larvae in each instar
1	5	2
2	20	17
3	20	18
4	45	26
5	10	36
6		1

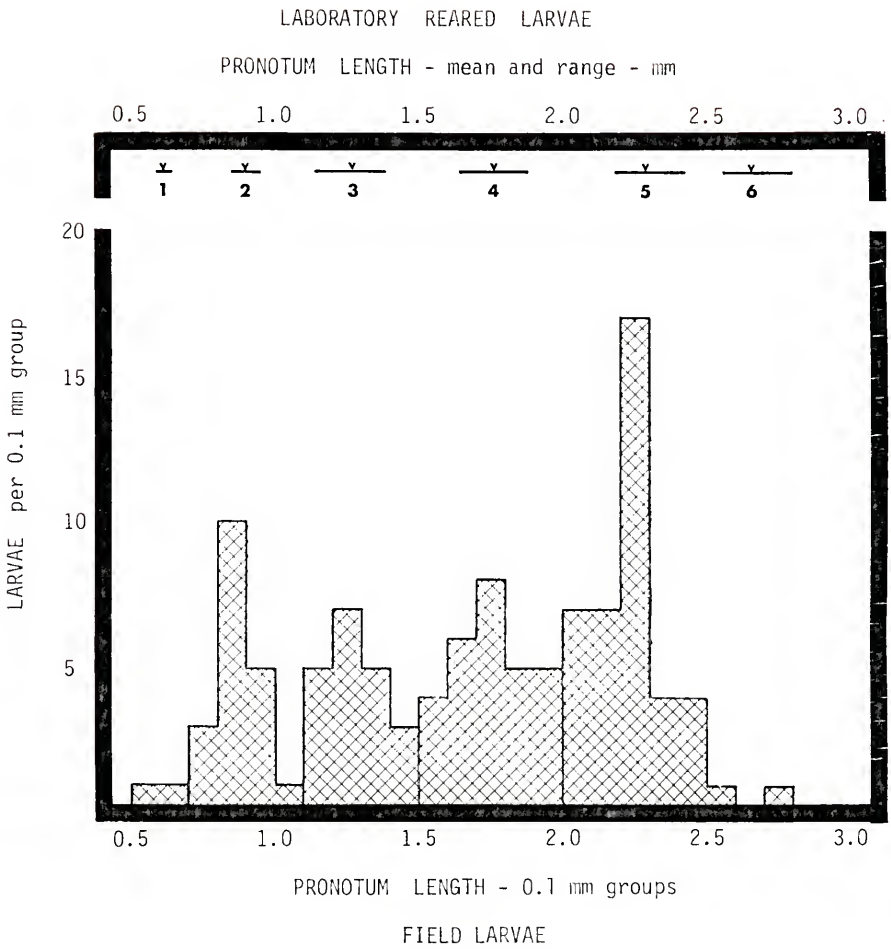

Fig. 2.5 Distribution of pronotum lengths of larvae collected Nov. 5, 1972. The arrows indicate mean pronotum lengths for laboratory reared larvae, instars 1 - 6 (Table 2.3).

finding prey. These underweight larvae probably must regain this weight before they can molt or pupate. These larvae were,therefore, more like 4th than 5th instars in terms of readiness to complete development.

In the following experiments I used live weight to follow larval development because it was the most convenient measurement to make on live larvae and because it seemed to give the best index of how close larvae were to completing development.

Development of Laboratory-reared Larvae

The development of the larvae in laboratory rearing experiments 2 and 3 was analyzed by using the weight group categories just described. The larvae reared in experiment 2 hatched from eggs laid in the spring when adult populations emerged, and larvae began pupating in October (Table 2.7). This was about the time field populations were disappearing. It was, therefore, not clear whether these insects could undergo 2 generations each year. In the 3rd rearing experiment larvae were fed snails instead of chicken liver and development was much more rapid. Larvae reared under long photoperiod represented larvae hatching from eggs laid in spring. These larvae developed rapidly and began pupating 9 weeks later (Table 2.8). At this rate larvae could easily complete a generation by August. The larvae reared under short photoperiod represented larvae hatching from eggs laid in fall. They did not pupate immediately when the larvae reached maturity, but continued to feed and grow during the simulated winter (Table 2.9).

These laboratory rearing experiments suggested that P. lucifera is capable of completing 2 generations each year: the spring generation gives rise to a fall generation which in turn gives rise to the next spring generation. The following experiments and observations were

Table 2.7 Development of larvae reared under long photoperiod and fed chicken liver: 2nd laboratory rearing experiment-long photoperiod.

Date	Larval weight groups - number of larvae					Pupae-number
	1	2	3	4	5	
June 22	30					
July 6	8	22				
Aug. 3		8	22			
Aug. 31		1	18	11		
Sept. 28			10	17	2	
Oct. 26			5	10	13	1
Nov. 2			5	18	2	3
Dec. 7			1	8	12	4
Jan. 4			1	6	6	8
Feb. 1				5	4	4
March 7				2	2	5
March 20					1	1
April 13						1

Table 2.8 Development of larvae reared under long photoperiod and fed snails: 3rd laboratory rearing experiment - long photoperiod.

Date	Larval weight groups - number of larvae					Pupae-number
	1	2	3	4	5	
Sept. 13	10					
Sept. 20	10					
Sept. 27	1	9				
Oct. 5		10				
Oct. 11		1	9			
Oct. 25			1	9		
Nov. 2			1	3	6	
Nov. 9				4	6	
Nov. 16				2	6	2
Nov. 24					5	3
Dec. 1					4	1
Dec. 8						4

Table 2.9 Development larvae reared under short photoperiod and fed snails: 3rd laboratory rearing experiment - short photoperiod

Date	Larval weight groups - number of larvae					Pupae-number
	1	2	3	4	5	
Sept. 13	9					
Sept. 20	6	3				
Sept. 26	4	4				
Oct. 5		5	3			
Oct. 11		2	6			
Oct. 25			1	7		
Nov. 2				4	4	
Nov. 9				2	6	
Nov. 16					8	
Nov. 24					8	
Dec.1					8	
Dec. 8					8	
Dec. 23					8	
Jan. 6					8	
Jan. 20					8	
Feb. 18					7	1
March 2					5	2
March 20					3	2
April 10						3

conducted to obtain field confirmation of this hypothesis.

Field Rearing Experiments

Development of larvae under field conditions was examined in a series of field rearing experiments. Groups of 5 - 10 larvae were maintained in babyfood jars. The jars were filled 1 cm deep with water to keep the snails alive. A filterpaper cone was placed in the jar to give the larvae substrate on which to climb. The lids of the jars had 0.5 cm openings covered with fine mesh screen. The babyfood jars were placed in a screen cage which floated in the aquatic vegetation on Lake Alice (Fig. 2.6).

In the first experiment a group of 30 first instars that hatched from a single egg mass (same parents) in May 1972 was divided equally among 4 babyfood jars; 2 jars were maintained in the laboratory under long photoperiod (16:8 h light-dark cycle), and the other 2 jars were maintained in the floating field cage. The development of larvae maintained in the laboratory was similar to the laboratory-reared larvae in experiment #3; they pupated in August (Table 2.10). Unfortunately, the larvae maintained in the field did not survive the first week. Since additional 1st instars were not available, field-collected larvae were used in subsequent field rearing experiments.

Six groups of field collected larvae were reared in the floating field cage. The following groups of larvae were reared in the field and their development in subsequent weeks is presented in the Tables as indicated:

1) 25 larvae weighing less than 2 mg collected June 1 (Table 2.11);
2) 25 larvae weighing less than 2 mg collected July 2 and 4 (Table 2.12);
3) 33 larvae weighing less than 2 mg collected July 29 (Table 2.13);

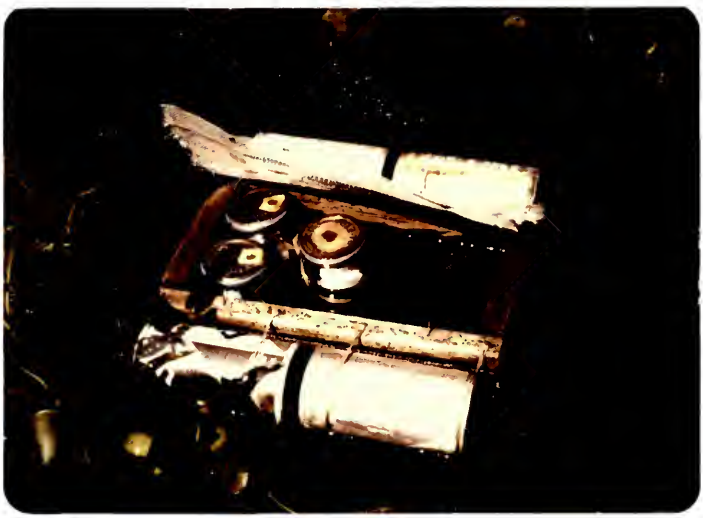

Fig. 2.6 Floating field-rearing cage containing 3 jars with larvae.

4) 25 larvae in 5 wt groups collected Sept. 3 (Table 2.14);

5) 18 larvae in wt groups 3, 4 and 5 collected March 4 (Table 2.15);

6) 27 larvae in wt groups 3 and 4 collected March 20 (Table 2.16).

The larvae weighing less than 2 mg were not collected during the previous winter. Since these small larvae appeared several weeks after adults appeared in the spring, I concluded that they had hatched from eggs oviposited in the spring. Most of the larvae collected June 1 and July 2 and 4 pupated by September (Tables 2.11, 2.12). This demonstrates that under field conditions, larvae that hatch in the spring can produce adult populations in fall. Only one of the small larvae collected on July 29 and the 5th wt group larva collected on Sept. 3 pupated in fall; the other larvae continued to feed and grow into 5th wt group but did not pupate (Tables 2.13, 2.14). Sept. 18 was the last day any of the field-reared larvae pupated (Tables 2.12, 2.13, 2.14). This indicates that the photoperiodic signal that suppresses pupation must have occurred shortly before this date. Adults were observed flying in the field as late as Oct. 30 and Nov. 3. In Nov. the experiment was terminated when vandals disturbed the float, killing the larvae. I had intended to rear them until spring. In spring, 2 new groups of larvae collected March 4 and 20 were reared in the field cage. These larvae began pupating April 20 and most of them had pupated by June when the experiment was terminated (Tables 2.15 and 2.16). Adults were observed flying in the field March 31 but a cold snap postponed most adult emergence until late April.

Development of Larvae in the Field

Development of larvae in the field populations was examined by making periodic larval collections and weighing the larvae to determine

Table 2.10 Development of larvae reared under long photoperiod and fed snails: control for field rearing experiments.

Date 1972	Larval weight groups - number of larvae					Pupae-number
	1	2	3	4	5	
May 26	15					
June 2	4	9				
June 10		7	2	3	1	
June 18		1	2	8	2	
June 24			1	6	5	
July 2				5	7	
July 9				3	9	
July 16				1	11	
July 23					11	1
Aug. 6					9	2
Aug. 13					4	5
Aug. 20					2	2
Aug. 27					1	1
Sept. 1					1	

Table 2.11 Development of larvae collected June 1 when reared in the field and fed snails.

Date 1972	Larval weight groups - number of larvae					Pupae-number
	1	2	3	4	5	
June 1	16	9				
June 10	2	13	6			
June 18		1	15	3		
June 23		1	9	8	1	
July 2			8	10	1	
July 9			5	11	3	
July 16			2	8	9	
July 23			1	6	10	2
Aug. 6				4	11	1
Aug. 13				3	9	3
Aug. 20					9	3
Aug. 27					4	1
Sept. 3					1	2

Table 2.12 Development of larvae collected July 2 and 4 reared in the field and fed snails.

Date	Larval weight groups - number of larvae					Pupae-number
	1	2	3	4	5	
July 2 & 4	13	12				
July 16	1	12				
July 23	1	5	7			
Aug. 6		2	7	2		
Aug. 13			6	5		
Aug. 20			2	5	4	
Aug. 27*				2		
Sept. 3					2	
Sept. 10					1	1
Sept. 18						1

* many larvae killed by an accident.

Table 2.13 Development of larvae collected July 29 reared in the field and fed snails.

Date	Larval weight groups - number of larvae					Pupae-number
	1	2	3	4	5	
July 30	10	23				
Aug. 6	2	11				
Aug. 13		9	3			
Aug. 20		2	8			
Aug. 27*			6			
Sept. 3			4	2		
Sept. 10			1	4	1	
Sept. 18				5		1
Sept. 24				2	3	
Sept. 30				2	3	
Oct. 7					5	
Oct. 13					5	
Oct. 27					5	
Nov. 4					5	
Nov. 12					5	
Nov. 19					5	
Nov. 28*					5	

*many larvae killed by an accident.

Table 2.14 Development of larvae collected Sept. 3 reared in the field and fed snails.

Date	Larval weight groups - number of larvae					Pupae - number
	1	2	3	4	5	
Sept. 3	2	6	9	7	1	
Sept. 10		5	8	6	4	
Sept. 18		3	5	10	3	1
Sept. 24		1	4	9	7	
Sept. 30			3	7	11	
Oct. 7			1	10	10	
Oct. 13			1	5	15	
Oct. 27*			1	4	11	
Nov. 4				2	14	
Nov. 12				1	15	
Nov. 19				1	14	
Nov. 28*				1	14	

* many larvae killed by an accident

Table 2.15 Development of larvae collected March 4 reared in the field and fed snails.

Date	Larval weight groups - number of larvae					Pupae - number
	1	2	3	4	5	
March 4			6	6	6	
April 6			4	2	11	
April 20			3	2	11	1
May 3				5	8	3
May 23				4	2	6
June 1					5	

Table 2.16 Development of larvae collected March 20 reared in the field and fed snails.

Date	Larval weight groups - number of larvae					Pupae-number
	1	2	3	4	5	
March 20			15	12		
April 6			9	13	5	
April 20			4	14	9	
May 3			1	7	15	4
May 23				6	8	5
June 1				1	9	2
June 15				1	3	4
June 30					2	

the weight distribution of larvae at different times of the year. Collections were made about once a month when conditions were favorable: larvae were collected most successfully on moonless nights after a rain. Larvae were collected while wading along a standard route through water hyacinths and cattails along the shore of Lake Alice (Fig. 0.1B). The larvae were located and collected by searching for their glows. Larvae of all sizes were collected by this method.

The weight distribution of larvae collected July 1971 - Sept. 1973 is presented in Table 2.17. In spring when small larvae reappeared there were still large numbers of overwintering 3rd, 4th, and 5th wt group larvae. The spring generation of larvae soon merged with the overwintering generation. Most of the overwintering larvae probably completed development during the summer but there could have been a few stragglers that overwintered a second year. The spring generation grew quickly and many larvae grew into the 2nd and 3rd wt group by late June and July. At that rate of growth some of the larvae probably completed development by fall. However, most of the larvae were probably forced to overwinter. The field populations did not seem to develop quite as rapidly as did the laboratory- and field-reared larvae. The field populations were probably limited by the availability of prey since food availability seemed to be the major factor affecting growth rate that differed between field-reared larvae and field populations.

Response of Field-Collected Larvae to Photoperiod

On several occasions field-collected larvae of the 5th wt group were held in the laboratory under controlled photoperiods. Larvae collected in Oct., Dec., and Jan. did not pupate readily when reared under short

Table 2.17 Weight distribution of field-collected larvae July 1971 - Sept. 1973: percent of each sample in respective weight groups.

Date	Larval weight groups - percent					Sample size
	1	2	3	4	5	
1971						
July 19 & 20	0	20	21	27	32	56
Aug. 14,17,18	4	12	44	28	12	25
Dec. 6	2	18	30	43	7	67
1972						
Jan. 11	0	16	43	30	10	67
Feb. 12	0	12	26	41	21	87
March 14	0	9	31	35	26	159
April 14	0	2	31	37	31	82
May 1 & 3	0	1	37	52	10	126
May 18	4	0	20	56	20	25
June 1 & 2	22	12	9	51	5	74
July 2 & 4	17	17	28	30	8	76
July 29	10	27	34	24	6	98
Sept. 3	4	24	35	15	2	53
Oct. 3	7	8	37	48	0	76
Nov. 5	5	20	20	45	10	114
Dec. 31	0	3	15	36	46	59
1973						
Jan. 27	0	0	0	46	54	35
March 4	0	4	18	25	53	135
March 20	0	1	16	44	39	94

Table 2.17 - continued

Date	Larval weight groups - percent					Sample size
	1	2	3	4	5	
1973						
April 27	0	0	16	48	36	50
May 5	0	0	22	63	14	49
May 24	7	24	24	28	31	29
June 22	9	29	50	29	12	34
July 31	12	40	31	17	4	84
Aug. 28	1	23	59	15	1	86
Sept. 23	3	7	40	47	2	97
					Total . . .	2079

photoperiods but pupated within about 20 days when placed in long photoperiods (Table 2.18). Larvae collected in March pupated within about 20 days under all photoperiod conditions (Table 2.18). This indicates that the natural photoperiods in Oct., Dec. and Jan. suppressed pupation, whereas the natural photoperiod in March no longer suppressed pupation. In March the final development of larvae had been triggered, and the return of these larvae to short photoperiods did not stop it.

Development of Eggs

Eggs hatched in an average of 14.8 days (s=0.92, n=31) when reared in the laboratory at temperatures of 22 - 28°C. One group of eggs reared in the floating field cage hatched between 16 and 21 days at temperatures of 7.5 - 33°C. A second group of eggs reared in the field cage hatched after 14 or 15 days at temperatures of 26 - 37°C.

Development of Pupae

When the larvae approached pupation they became increasingly sedentary and soon fastened the ventral surface of the abdomen to the substrate. This was the prepupal stage which lasted for 3 - 5 days. The pupal stage lasted 6.8 days (s=0.77, n=63) in the male and 6.4 days (s=0,70, n=35) in the female when reared at room temperature (22-28°C). The pupal stage was significantly longer in males than in females (t-test, p=0.05).

Adult Populations

Adults were observed as early in the season as March 31 and as late as Nov. 3 (Table 2.19). Large populations (thousands of flying males) typically occurred in spring, April or May, and again later in summer, July and August. The large populations in the summer and fall seemed to follow periods of heavy rainfall. The populations tended to be smaller (hundreds of flying males) during extended dry periods.

Table 2.18 Pupation of 5th weight group larvae collected in Oct. and Dec. 1972 and Jan. and March 1973, reared under long or short photoperiods.

Date collected	Photoperiod light-dark cycle	Days to first pupa	Days to 50% pupation	Number pupating
Oct. 3, 1972	16:8	21	25	5/5
	11:13	129	141	5/5
Dec. 31, 1972	16:8	5	19	13/14
	11:13	83	83	1/6
Jan. 27, 1973	16:8	12	17.5	11/13
	11:13	54	55	3/6
March 4, 1973	16:8	5	11	47/60
	11:13	6	12.5	22/30
March 20, 1973	16:8	5	9	15/21
	11:13	7	12.5	10/22
	field	16	22	13/22

Table 2.19 Observations on male populations on Lake Alice 1970-73.

Year	Earliest date	Large populations	Small populations	Latest date
1970	April 17	April 17, 18 June 19 July 14, 18	May 7, 19, 22 June 18 July 8 Oct. 5, 20, 30	Oct. 30
1971	April 16	May 7, 15, 16, 27 July 19, 20, 23 Aug. 2, 6, 8, 17 18, 19, 20, 21 22	April 16, 17, 18 June 15 July 2, 10 Sept. 11, 26 Oct. 24 Nov. 3	Nov. 3
1972	April 14	May 3, 14, 15, 18 23, 24, 25, 26 29, 30, 31 June 1, 2, 3 Aug. 28 Sept. 4, 11, 13, 25	April 14, 25 July 27, 29	Sept. 25
1973	March 31			

Conclusions on Life Cycle

The life cycle of P. lucifera in northcentral Florida is heterovoltine; larvae in the same brood mature at different times. Adults appear in spring (April and May) and are present continuously until fall (Sept. and Oct.). The largest adult populations generally occur in spring and periodically in summer or fall during wet weather conditions. Females oviposit several days after emerging,and eggs hatch after incubating 14 - 20 days depending upon temperature. In laboratory and field rearing experiments, larvae that hatched from eggs oviposited in spring, completed development by August,and thus produced a second generation. However, the weight distribution of field collected larvae indicated that the overwintering larvae overlapped the spring generation of larvae. This suggests that development of larvae in the field is not as rapid as in the rearing experiments. Some of the larvae that hatch in spring probably mature in fall,but most of them overwinter and mature the next year. A few larvae may overwinter a second year. The life cycle of P. lucifera is illustrated in Fig. 2.7.

In the fall, pupation by the larvae was inhibited by the short photoperiods. This response to photoperiod was demonstrated in laboratory and field rearing experiments. Larvae did not pupate after Sept. 18 in the field rearing experiments,and pupation by larvae collected in Oct. had already been inhibited. When the larvae approached pupation they entered a quiescent,inactive,prepupal stage lasting 3 - 5 days. The pupal stage lasted 6 or 7 days.

The life cycle of P. lucifera is extremely flexible. Larvae can mature in 2 months when food is abundant,but they can take 1 or 2 years to complete development when food is not readily available. This flexibility

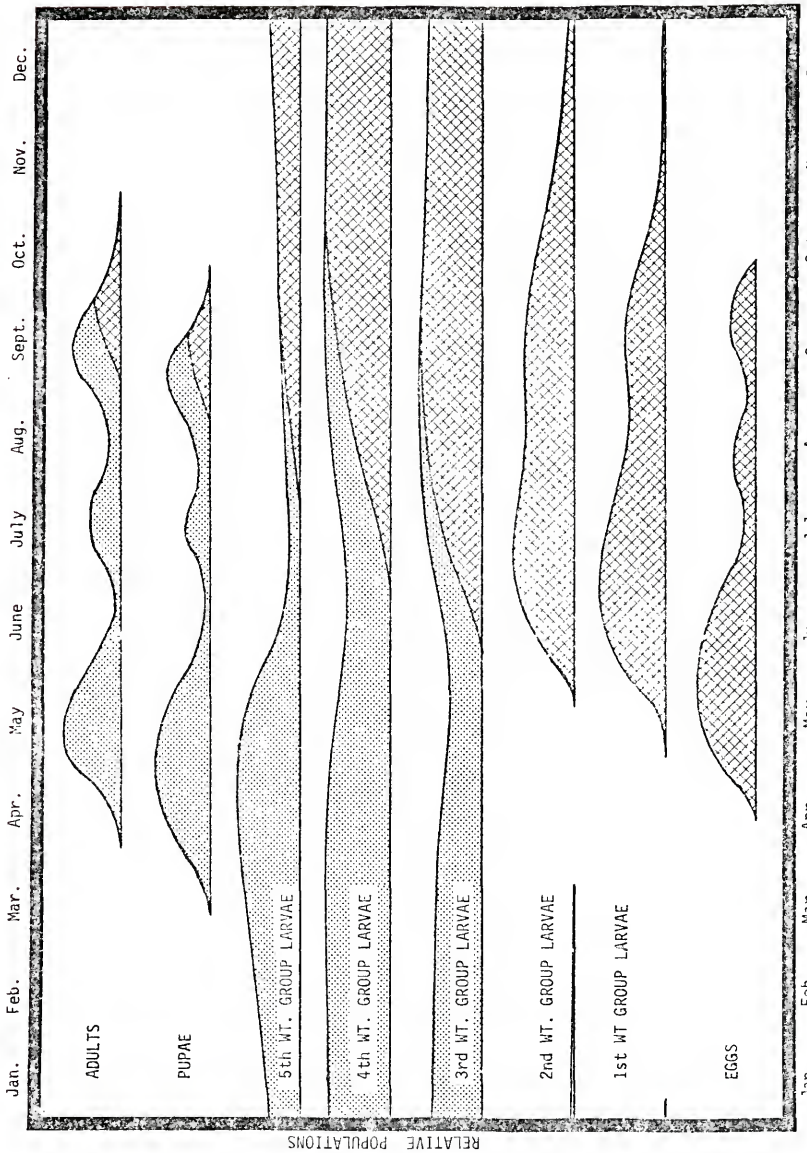

Fig. 2.7 Life cycle of Pyractomena lucifera, overwintering generation stippled, summer generation hatched.

is perhaps one factor contributing to the wide geographic distribution of this insect. In northern climates the life cycle is probably extended to 2 or 3 years.

CHAPTER 3
NOTES ON THE BIOLOGY AND FLASH BEHAVIOR OF FIREFLIES IN THE PHOTINUS CONSIMILIS COMPLEX

Photinus fireflies are among the most common fireflies in eastern United States. The biology and ecology of adult Photinus fireflies have been studied extensively (McDermott 1958, Lloyd 1966a, 1971), but information on the immature stages is considerably more difficult to obtain and is largely limited to observations of Williams (1917) and Hess (1920). No prey records have been recorded, but larvae feed on earthworms, cut-up flies and snails in the laboratory. Williams (1917) and Hess (1920) suggested Photinus fireflies had 2 year life cycles in New England because they found larvae of 2 sizes. McDermott (1958) suggested a 1 year life cycle for a Photinus in Maryland. No Photinus fireflies have yet been reared from egg to adult.

Greene (1956) described the firefly Photinus consimilis in his revision of the genus. Lloyd (1966a) observed populations of P. consimilis producing 2 different flash signals and called them "fast pulse" and "slow pulse". Since he had not visited the type locality of the species he could not tell which was the new species and thus deferred describing a new species. Later Lloyd reported observing "fast pulse" P. consimilis at the type locality but also reported observing "intermediate flashers" at several localities in Florida, so the situation remained unresolved (1969b).

The following observations on the biology and flash behavior of fireflies in the Photinus consimilis complex were accumulated while

studying another firefly, Pyractomena lucifera, which occurs in the aquatic vegetation on Lake Alice, Gainesville, Florida. At this location I observed 3 populations of fireflies in the Photinus consimilis complex which I will be referring to as "slow pulse", "slow-fast" and "fast-fast".

Biological Notes

Fireflies in the P. consimilis complex are almost always found in marsh situations. Males fly over aquatic vegetation as they emit their advertising flash patterns. They seem to stay fairly close to the aquatic vegetation during dry weather but sometimes drift over the shore vegetation when it is wet after a rain. P. consimilis are occasionally collected at lights during rainy periods. On July 15, 1975, after several days of heavy rain, 9 females and 2 males were found in a blacklight trap located ca. 1 km from the nearest marsh. One of these females was responsive to male flashes; the others were not, indicating they had already mated. These fireflies were probably engaged in dispersal flight to new habitats.

The larvae of P. consimilis spp. were frequently encountered while collecting luminescent larvae on the aquatic vegetation in Lake Alice. Photinus larvae were most frequently collected on old mats of decaying vegetation covered with fine organic silt and on organic mud flats along the shore. Photinus larvae seemed to avoid water and after heavy rains had flooded the lake they were found clinging to floating debris, tree stumps and trunks. These larvae seem to have a hydrophobic cuticle. They floated when they were dislodged from the vegetation and when forcibly submerged, there were silvery trapped-air patches on the tergites.

The largest numbers of Photinus larvae were collected in March, but small numbers were also collected during the rest of the year (Table 3.1). The large numbers collected in March were collected after heavy rains flooded the lake. Since these larvae do not generally climb up onto the vegetation they were difficult to collect at other times. In March the aquatic vegetation had been killed back by the winter freeze, so glowing larvae were easier to collect.

I have recorded only 2 prey records for Photinus larvae during 4 years of observations. One larva was found pulling a small leech (Hirudinea: Annelida) across a mud flat, and another larva was found pulling a small earthworm (Oligochaeta: Annelida) out of a mat of decaying vegetation. Large numbers of small earthworms were found in these mats so they probably are the major food of these larvae. In the laboratory these larvae did not feed on snails, leeches, or cut-up insects but fed readily on cut-up sections of earthworms. One group of larvae hatching from eggs oviposited by P. consimilis "slow pulse" fed on chicken liver and snails. They were reared to the 4th instar before they died when their culture dried up accidentally. Other larvae did not accept chicken liver or snails, and attempts to rear them were unsuccessful. Attempts to rear Photinus larvae on earthworms have not been made.

Several field-collected larvae held in the laboratory chewed up the filter paper and formed cells in which they molted to the next instar or pupated. Two larvae spent 7 and 17 days in the cell before molting and another larva spent about 10 days in the cell before pupating. The pupal stage lasted ca. 8 days (n=2). When the pupa is mechanically stimulated the larval light organ glows. The entire pupa also glows faintly when

Table 3.1 Number of *Photinus* larvae collected at Lake Alice, Gainesville, Florida.

Months	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Collections	0	8	13	0	9	0	0	0	5	0	0	0
	1		1	4	4	5	3	1	0		3	0
			40	6	4	1	1	5				
			27		5		3	1				
					2		1	2				
							0					
							2					
Totals	1	8	81	10	24	6	10	9	5	0	3	0

the larval light organs are not glowing. The luminescence of pupae is faint and disappears as the pupa matures.

Female P. consimilis oviposited eggs singly or in small groups in cracks and crevasses in moist folded filter paper. The eggs from 2 females measured 0.78 x 0.77 mm (n=6) and 0.74 x 0.69 (n=9) and the period of incubation was 18 and 25 days (n=2). The eggs were very faintly luminescent during the first 10 days or so and seemed to lose this luminescence gradually (eggs were not examined just prior to hatching and may have regained luminescence at that time).

The only natural enemies recorded for Photinus larvae were the fungi: Fusarium sp., Cladosporium sp., Metarrhizium sp., and Verticillium sp. Photinus larvae seemed more susceptible to the fungi than other lampyrid larvae. In the spring of 1976 about half of the Photinus larvae I was rearing were overcome by these fungi. This was the only "epidemic" I encountered during my lampyrid rearing studies.

Flash Behavior

Intervals between male flashes were measured by timing 5 or 6 flashes with a stopwatch in the field and dividing by the number of intervals involved. The interval between flash patterns was measured with a stopwatch in the field, or flashes were voice-recorded with a tape recorder and the intervals were later measured with a stopwatch. Flash dialogue between males and females were voice-recorded on tape and measured later with a stopwatch.

Photinus consimilis, slow pulse

P. consimilis, slow pulse, was observed at 4 localities in Alachua Co., Florida. At Lake Alice they were first observed in March

(as early as March 1) and were present in large numbers in late March and early April 1970 and 1976 (Table 3.2). They were present in small numbers the rest of the year until November. Males flew slowly 1 - 5 m over aquatic vegetation emitting 1 - 4 flashes, but patterns of 3 flashes were most common (Table 3.3). The interval between flashes was 1.0 - 1.9 sec depending on the temperature (Fig. 3.1), and the flash pattern was repeated at intervals of 10.0 - 20.5 sec depending on temperature (Fig. 3.2).

Several responsive females were found on mounds of decaying water hyacinth that had been cleared from the lake. The females had apparently emerged from larvae that were on the plants when they were piled on shore. The response delay from the first male flash to the first female response flash ranged from 4.9 - 10.0 sec or ca. 2.4 - 7.0 sec from the last male flash, ca. 18°C (Table 3.4). The females responded with 1 - 5 flashes but usually 2 flashes (Table 3.4). The intervals between female flashes averaged 1.5 sec, ca.18°C (n=5). A female reared from a field-collected larva answered flashlight flashes 0.9 - 1.3 sec apart with 1 (n=9) or 2 (n=3) flashes, and the response interval averaged 7.8 sec from the first flash or 5.7 sec from the last flash at 18°C (Table 3.5). This female answered a flying slow pulse male but did not attract him. She did not answer males of another species.

Males were decoyed with a flashlight from 7 - 10 m to within 1 m and occasionally they landed. My data agree with that reported by Lloyd (1966a) for P. consimilis "slow pulse" (Fig. 3.1, 3.2).

A slow pulsing P. consimilis was observed flying over a cattail marsh near Wilson, North Carolina. The interval between flash patterns was 10.5 sec at 23°C.

Table 3.2 Seasonal occurance of Photinus consimilis fireflies on Lake Alice, Gainesville, Florida: estimated numbers present * = 1 - 9, ** = 10 - 99, *** = 100+ .

Months	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
P. consimilis slow pulse												
1970				***	**	*	*		*	*	-	
1971			*	*	*		*	*	*	*	*	
1972			*	*								
1973			*	*								
1976			***	***	**			*	*	*	*	
P. consimilis slow-fast												
1970					**	**	**	**	**	*	-	
1971				*			**	***	**	*	*	
1974					***							
1976				***	***			***	***	**	**	
P. consimilis fast-fast												
1970					*	*	*		*	*	-	
1971					*		*	*	*	*	-	
1974					**							
1976				**	**			**	-	-	-	

Table 3.3 Number of flashes per flash pattern emitted by flying males of the 3 populations of *Photinus consimilis* on Lake Alice, Gainesville, Florida.

Number of flashes per flash pattern	1	2	3	4	5	6	7	8	9	10	11	12	Total observed flash patterns
P. consimilis slow pulse	2	23	89	9									123
P. consimilis slow-fast				1	1	6	18	10	3	0	1		40
P. consimilis fast-fast			2	0	12	9	11	2	2				38

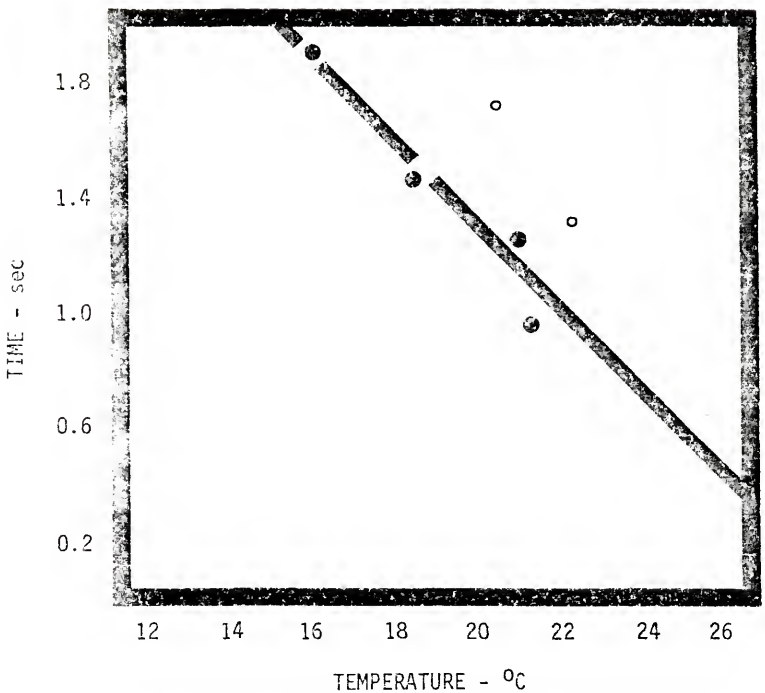

Fig. 3.1 P. consimilis slow pulse: relationship between ambient temperature and the interval between pulses in a male flash pattern (open circles = data from Lloyd 1966a).

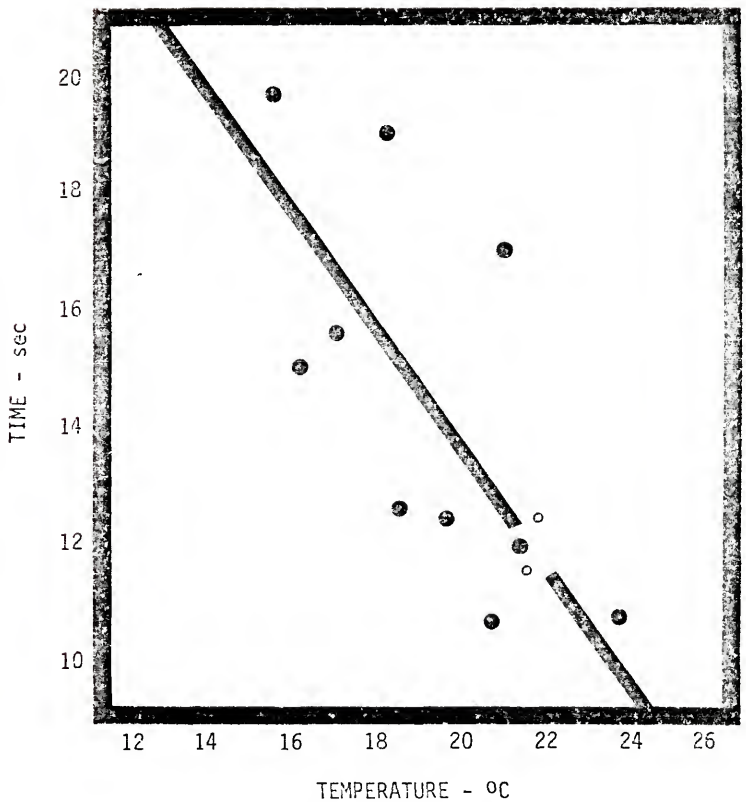

Fig. 3.2 P. consimilis slow pulse: relationship between ambient temperature and the interval between male flash patterns (open circles = data from Lloyd 1966a).

Table 3.4 Photinus consimilis female responses to male flashes.

Female	Date	Temp. °C	Female response delay: First male flash Mean sec	s=	n=	Last male flash Mean sec	s=	n=	Number of female flashes
slow-pulse									
#1	13 Apr.	ca. 18	9.7	0.86	6	5.9	0.53	5	2 (n=6)
#1	14 Apr.	ca. 18	10.0	0.58	3	-	-	-	2 (n=3)
#2	18 June	ca. 24	4.9	-	1	-	-	-	2 (n = 1), 5 (n=1)
#3	30 June	ca. 22	6.4	-	2	-	-	-	1 (n=1)
fast-slow									
#1	15 July	24	10.6	1.45	11	-	-	-	-
#2	18 Apr.	18	12.0	1.60	11	7.5	1.07	11	5 (n=3), 6(n=2) 7 (n=3), 8(n=2)
#2	25 Apr.	22	13.0	1.73	3	9.4	0.53	3	4 (n=1), 5 (n=1) 6 (n=1)
#3	6 May	23	8.9	1.41	4	5.9	0.74	4	2 (n=1), 3 (n=2) 5 (n=1)
#4	17 May	21	11.8	1.10	8	8.0	0.97	8	5 (n=1), 6 (n=4) 7 (n=3)

Table 3.5 *Photinus consimilis* female responses to flashlight flashes

Female	Date	Temp.	Flashlight signals	No response	Female response delay: First male flash mean -sec	s=	n=	Last male flash mean -sec	s=	n=	Number of female flashes
P. consimilis slow-pulse											
#4	20 May	21	3 long flashes 0.9 -1.3 sec intervals	7/8	8.0	0.61	7	5.9	0.57	7	1 (n=6) 2 (n=1)
			3 short fl. 0.9 - 1.2 sec intervals	4/4	7.4	0.3	4	5.4	0.54	4	1 (n=1) 2 (n=2)
			10 flashes at 0.28-0.44 sec intervals	1/5	8.0	-	1	5.9	-	1	1 (n=1)
P. consimilis slow-fast											
#3	6 May	23	6, 8 or 10 fl. at 0.31-0.4 sec intervals	7/7	11.3	0.65	7	8.7	0.52	7	1 (n=1) 2 (n=3) 3 (n=3)
			10 flashes at 0.5 - 0.54 sec intervals	1/3	13.0	-	1	8.8	-	1	1 (n=1)
			4 or 5 fl. at 0.3-0.33 sec intervals	1/3	11.1	-	-	10.1	-	-	2 (n=1)
#4	17 May	21	10 flashes at 0.31-0.41 sec intervals	5/5	12.1	0.52	5	8.8	0.61	5	1 (n=1) 4 (n=2) 5 (n=2)
			10 flashes at 0.52-0.53 sec intervals	2/2	12.6	-	-	7.9	-	-	5 (n=2)

Photinus consimils, slow-fast

P. consimilis (slow flash pattern rate-fast pulse rate = slow-fast) was observed in 4 localities in Alachua Co., Florida. At Lake Alice they were first observed in late March and were most common in late April and May (Table 3.2). They were present in large numbers (hundreds) until November. Males hovered among the cattails and out over the mats of water hyacinths as they emitted advertising flash patterns and continued to hover over the area for several seconds after flashing. Direction of flight between flash patterns was erratic and difficult to follow. Male flash patterns included 4 - 11 flashes, but patterns with 6 - 8 flashes were most common (Table 3.3). Flashes in male patterns were emitted at intervals of 0.4 - 0.6 sec depending on temperature (Fig. 3.3), and flash patterns were repeated at intervals of 14.2 - 25.2 sec depending on temperature (Fig. 3.4). Males that were in dialogue with caged females emitted flash patterns of 5 - 13 flashes (11 of 18 patterns had 9 - 11 flashes).

Four responsive females were obtained. One was found in a blacklight trap, 3 were reared from field-collected larvae. The delay between the last male flash and the first female flash averaged 5.9 - 9.4 sec, and the female flashed 1 - 8 times (Table 3.4). The female flashes were emitted at intervals 0.8 - 1.0 sec, 23 and 18^{o}C. The rhythm of female flashes was not as smooth as that of male flashes; they appeared to leave out flashes. Females also responded to flashlight flashes (Table 3.5). In the field they did not answer slow pulse or fast-fast males. The response interval seemed to increase during an evening even though the temperature remained fairly stable, and the number of pulses in the response decreased concurrently.

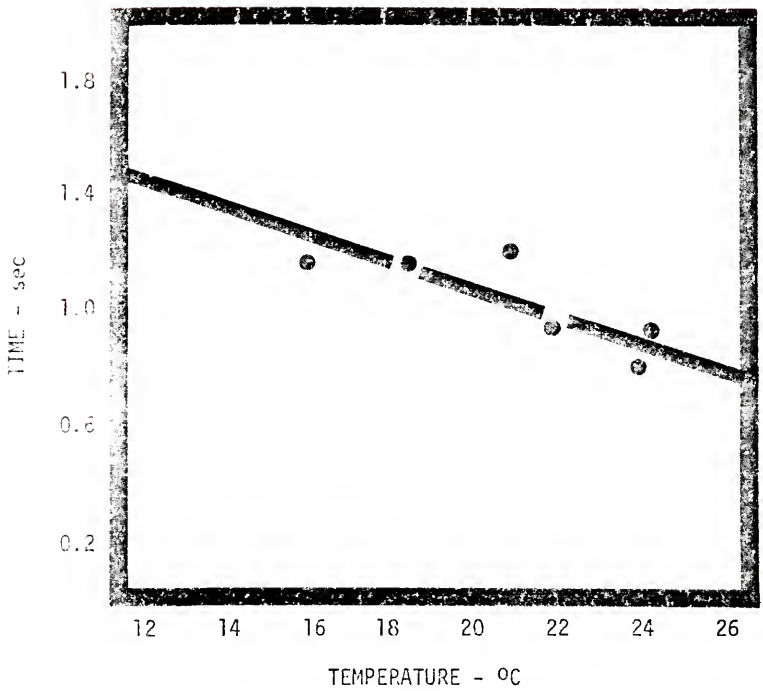

Fig. 3.3 P. consimilis slow-fast: relationship between ambient temperature and the interval between pulses in a male flash pattern.

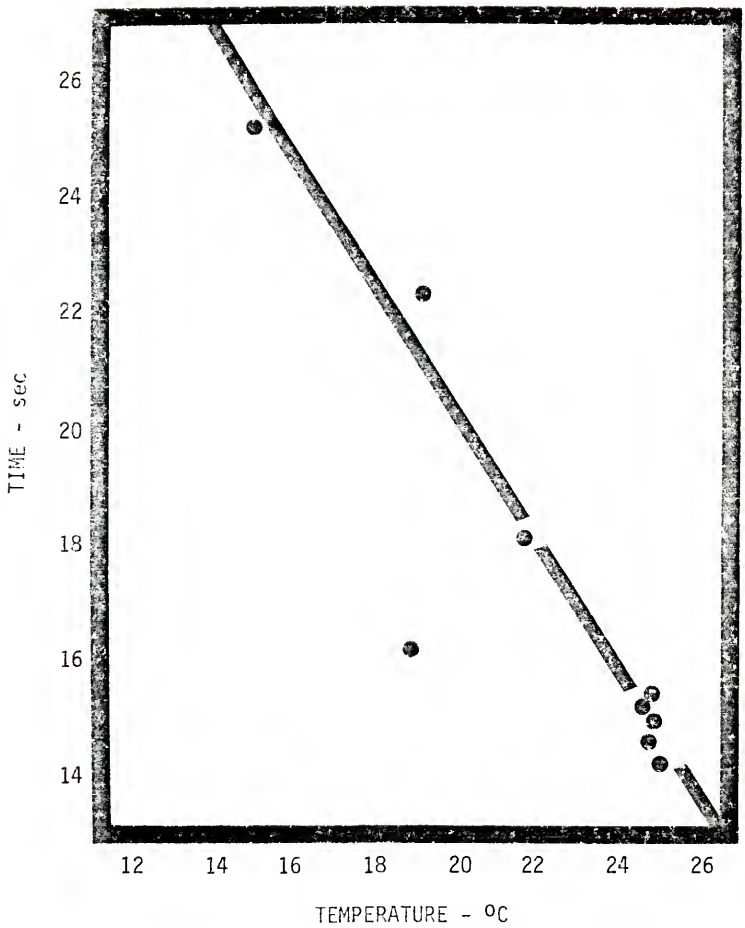

Fig. 3.4 P. consimilis slow-fast: relationship between ambient temperatures and the interval between male flash patterns.

Much of the observed variation in female response delay was probably due to differences in the ages of females: female #2, Table 3.4, had a response delay of 7.5 sec on April 18 and 9.4 sec on April 25,although the temperature was 4°C warmer on the second day.

Photinus consimilis, fast-fast

P. consimilis (fast flash pattern rate-fast pulse rate = fast-fast) was observed in 2 localities in Alachua Co., Florida. At Lake Alice they were first observed in early April and were common in April and May (Table 3.2). They were present in smaller numbers the rest of the season until October. Males hovered among the cattails or 1 - 2 m above them while they emitted advertising flash patterns. These patterns included 3 - 9 flashes,but patterns of 5 - 7 flashes were most common(Table 3.3). Male flashes were spaced 0.3 - 0.44 sec apart (Fig. 3.5),and the male flash pattern was repeated at 7.1 - 12 sec intervals depending on the temperature (Fig. 3.6).

I did not observe the flash dialogue between male and female P. consimilis, fast-fast, and I was not able to decoy males. Occasionally a male seemed to approach flashlight flashes presented 2 - 3 sec after his flashes,but he did not land.

A population of P. consimilis fast-fast was observed flying over a cattail marsh near Charleston, South Carolina. Males were flashed 3 - 4 fast pulses,and the flash patterns were repeated at 8.8 sec (n=5) intervals, 22.5°C.

These observations on P. consimilis fast-fast seem to agree with observations reported by Lloyd (1966a) for P. consimilis fast pulse (Fig. 3.5, 3.6). I observed a fast-fast at one of the sites where Lloyd observed a "fast pulse". He reported that the female response delay was

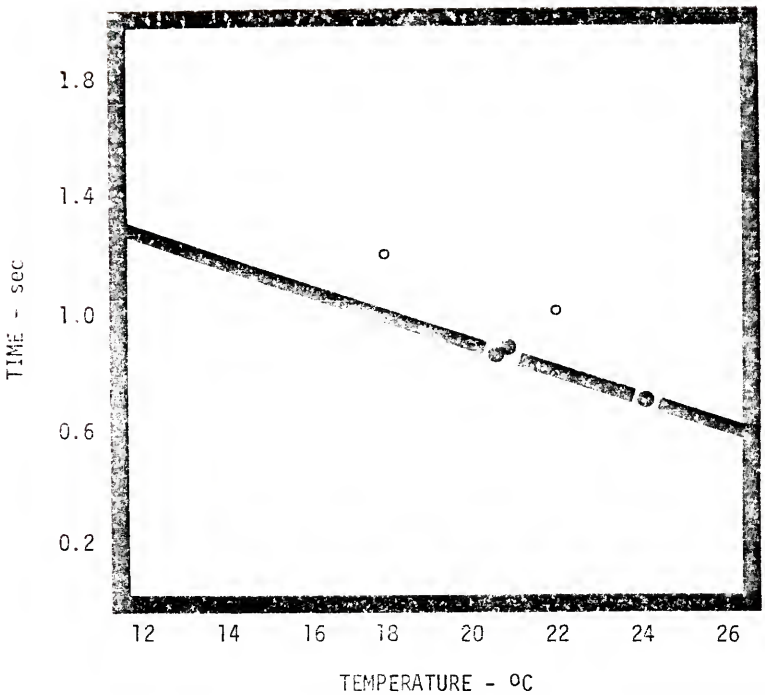

Fig. 3.5 P. consimilis fast-fast: relationship between ambient temperatures and the interval between pulses in a male flash pattern (open circles = data from Lloyd 1966a).

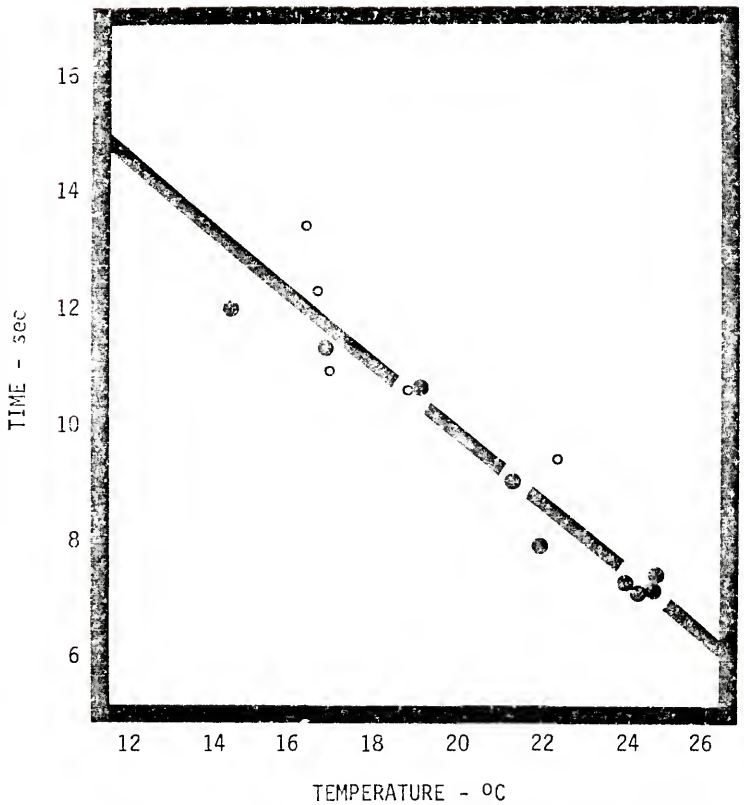

Fig. 3.6 P. consimilis fast-fast: relationship between ambient temperature and the interval between male flash patterns (open circles = data from Lloyd 1966a).

3.2 sec at 21°C and that the female response contained doubled pulses repeated 2 - 3 times. He found this firefly easy to decoy with doubled flashes presented 1 - 3 sec after the male flash pattern.

Concluding Observations

In the field it was difficult to distinguish P. consimilis fast-fast from slow-fast on the basis of a single flash pattern. Since the flash pattern interval for P. consimilis slow-fast was about twice as long as that of fast-fast at each temperature (Fig. 3.7) the 2 species can be separated by measuring the interval between flash patterns.

Lloyd (1969b) reported observing the "fast-pulsed" flash pattern at Roaring River State Park, Missouri, the type locality for P. consimilis. The interval between flashes was 0.35 sec, 20°C (Lloyd, personal communication). This value fits the data for P. consimilis fast-fast. Therefore, the fast-fast population appears to be the population described by Green (1956) as Photinus consimilis. P. consimilis slow pulse appears to be a valid new species. The firefly P. consimilis slow fast may be a new species but its relationship with P. carolinus and the "intermediate flashers" is still confused. There may be additional species in the complex.

The "intermediate flashers" observed by Lloyd (1969b) appear to be the slow-fast described here, since he stated that they had an intermediate pulse rate,and the flash pattern was 4 - 5 flashes. I have not observed slow-fast populations producing predominantly 4 - 5 pulsed flash patterns,but there was considerable variation in the number of pulses (Table 3.3). I observed a fast-fast population emitting 3 - 4 pulsed flash patterns in South Carolina,while Lake Alice fast-fast produced mostly 5 - 7 pulsed flash patterns.

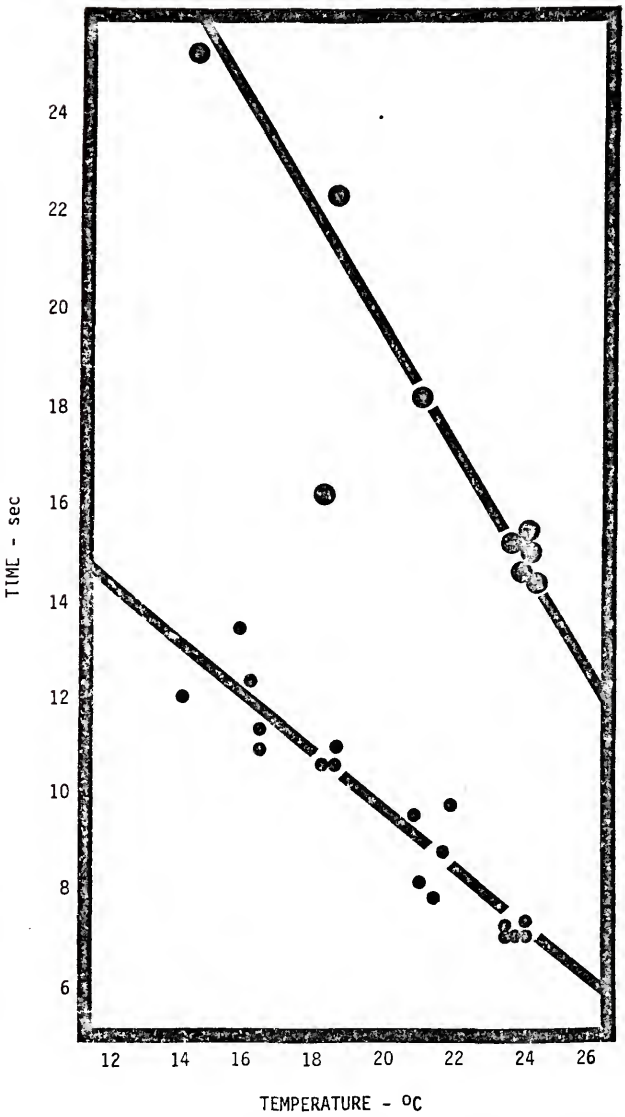

Fig. 3.7 P. consimilis fast-fast and slow-fast: a comparison of the flash pattern intervals of the 2 fireflies (small circles = fast-fast, large circles = slow-fast).

Flash characteristics of the closely related species P. carolinus Green are similar but do not agree with those of P. consimilis slow-fast (Lloyd 1966a). The female response delay is ca. 6 sec for both species, but in P.carolinus the female response is a double flash repeated at 1 sec intervals; in slow-fast it is 1 - 8 single pulses at 0.7 - 1.0 sec intervals. The interval between male flash patterns is also shorter in P. carolinus than in slow-fast, 13 sec vs. 22 sec at ca. 17°C.

CHAPTER 4
NOTES ON THE BIOLOGY AND ECOLOGY OF *PHOTURIS* SPP. LARVAE

The biology of *Photuris* spp. larvae was first described by Williams (1917) and subsequent observations by Hess (1920), McDermott (1958), Keiper and Solomen (1972) and McLean *et al*. (1972) have contributed to our knowledge of these fireflies. In northcentral Florida there are 10 - 20 species of *Photuris* (J. E. Lloyd, personal communication). There must be ecological differences among these species. As Barber (1951) pointed out,"feeding habits must differ between marsh-inhabiting species and other field or upland species." To analyze some of the differences that might occur between larvae of different species, large numbers of *Photuris* larvae were collected throughout the year and in a variety of habitats in the vicinity of Gainesville, Florida. Efforts were made to collect larvae in the act of feeding and a list of prey items was compiled. The larvae were reared in 6 oz babyfood jars containing moist, sifted sand 10 - 15 mm deep. They were fed chicken liver or cut-up insects at irregular intervals.

Seasonal and Ecological Distribution

Photuris spp. larvae were frequently found glowing periodically as they crawled in the leaf litter. They were common when leaf litter was wet, particularly after a rain that followed an extended dry spell. There was considerable variation in pigmentation among the larvae collected at different seasons and at different locations. Most *Photuris* larvae had

a gray or tan ground color (Figs. 4.3 - 4.6). One group of Photuris larvae had a pronounced reddish-brown or rufus ground color (Fig. 4.2). These 2 groups of larvae could be separated readily, and since they seemed to have different ecologies they will be discussed separately. I will be referring to the first group as "non-red" larvae and the second group as "red" larvae. Additional comments on pigmentation will be made later.

Non-red larvae were collected throughout the year but were most common in early spring and in fall; they were scarce during the summer (Table 4.1). They were collected at numerous sites but were usually found in areas that remained wet most of the year. However, some were collected in drier wooded areas (Table 4.1).

Red larvae were found in drier situations at the Medicinal Plant Garden and at Newnans Lake, usually in hardwood leaf litter. They were common only in Aug. and Sept. but were collected occasionally in Oct. and Nov. (Table 4.2). They were seldom found at other times of the year even when conditions seemed ideal.

The fireflies reared from field-collected larvae were identified using morphological characteristics furnished by J. E. Lloyd (personal communication). Most of the species of Photuris occurring in northcentral Florida are currently undescribed and are known by code names. Many of the species cannot be reliably identified by morphological characteristics at this time, so the following species or species groups are used here: Photuris congener LeConte is a single distinctive species; Photuris "A" is a single species currently known as Photuris "A"; Photuris "B + D" is a combination of 2 species currently known as Photuris "B" and Photuris "D"; Photuris "W" is a combination of 2 species currently known as

Table 4.1 The seasonal occurrence of "non-red" Photuris larvae at several locations in Alachua Co., Florida

Site larvae collected at	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Medicinal Plant Garden wet area	1	13	56	26	0	0	12	23	0	6	69	29	230
Medicinal Plant Garden woods	0	0	42	6	0	0	1	6	5	0	3	0	63
Lake Alice, shore	0	1	8	2	5	3	1	17	0	1	0	6	44
Gun Club, roadside	-	-	-	-	1	-	-	-	-	10	-	-	11
Archery Club roadside	-	-	-	-	-	-	-	10	-	-	-	-	10
Newnans Lake roadside	30	-	-	-	-	-	-	25	-	-	-	-	55
Newnans Lake woods	14	1	14	-	-	-	-	0	-	-	-	-	29
Other sites in Alachua Co.	-	-	2	-	-	4	1	-	-	-	-	-	7
Total Larvae	45	15	122	34	6	7	15	81	5	17	72	30	449
Number of collections at													
Medicinal Plant Garden and Lake Alice	1	6	7	9	3	2	3	7	2	1	1	1	43
Other sites	3	2	4	-	1	1	-	3	1	3	-	-	18

Table 4.2 Seasonal occurrence of "red" Photuris larvae at several locations in Alachua Co., Florida.

Site larva collected at	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Medicinal Plant Garden dry area	0	2	0	0	0	0	0	36	20	0	3	0	61
Gun Club roadside	-	-	-	-	0	-	-	-	-	1	-	-	1
Newnans Lake woods	0	0	0	-	-	0	0	18	-	-	-	-	18
Total larvae	0	2	0	0	0	0	0	54	20	1	3	0	80
Number of collections at													
Medicinal Plant Garden and Lake Alice	1	6	7	9	3	2	3	7	2	1	1	1	43
Other sites	3	2	4	-	1	1	-	3	1	3	-	-	18

Photuris "WD" and Photuris "WM"; Photuris "V" is a combination of at least 3 species currently known as Photuris "BR", Photuris "GR" and Photuris "J-3-4" (versicolor).

Photuris congener fireflies were reared from red Photuris larvae collected in Oct. and Feb. (Table 4.3) in the dry areas of the Medicinal Plant Garden and along the roadside at the Gun Club (Table 4.4). Although large numbers of red larvae were collected and maintained (Table 4.2) only 2 completed development (Table 4.3).

Photuris A fireflies were reared from larvae collected throughout the year (Table 4.3) and most frequently from larvae collected in the wet areas at the Medicinal Plant Garden and from the aquatic vegetation and shore of Lake Alice (Table 4.4). They seemed to be most common in areas where the soil was wet year round and flooded occasionally.

Photuris B + D fireflies were reared from larvae collected in early spring (Feb. - April) and in the fall (Aug. - Dec.) (Table 4.3). They were reared most frequently from larvae collected in the wooded area and the wet area at the Medicinal Plant Garden (Table 4.4). Most larvae collected in the woods in March produced Photuris B + D fireflies.

Photuris W fireflies were reared from larvae collected in Jan. and March (Table 4.3). They were reared from larvae collected from 2 different logs in the woods near Newnans Lake and from a larva collected in a log by a friend. Larvae of Photuris W may occur only in rotten logs.

Photuris V fireflies were reared from larvae collected throughout the year (Table 4.3) and were reared most frequently from the Medicinal Plant Garden (wet area), Gun Club (roadside) and Newnans Lake (roadside) (Table 4.4). Most of the larvae collected on the roadside at the Gun Club and at Newnans Lake produced Photuris V adults, whereas, only a small

Table 4.3 The number of Photuris fireflies of different species reared from larvae collected during the different months of the year.

Species	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Photuris congener (adults)	0	1	0	0	0	0	0	0	0	1	0	0	2
Photuris A (adults)	0	4	2	8	0	2	5	17	2	1	38	22	111
Photuris B + D (adults)	0	2	38	2	0	0	0	3	1	2	8	1	57
Photuris W (adults)	11	0	4	0	0	0	0	0	0	0	0	0	15
Photuris V (adults)	0	3	1	0	1	0	3	9	0	9	2	1	29
Total adults	11	10	55	10	1	2	8	29	3	12	48	24	214

Table 4.4 Number of Photuris fireflies of different species reared from larvae collected at different sites.

Species	Medicinal Plant Garden (wet area)	Medicinal Plant Garden (dry area)	Medicinal Plant Garden (woods)	Lake Alice (shore)	Gun Club (road-side)	Archery Club (road-side)	Newnans Lake (road-side)	Newnans Lake (woods)	Other sites in Alachua Co. (road-side)	Totals
Photuris congener	0	1	0	0	1	0	0	0	0	2
Photuris A	82	0	8	20	0	0	1	0	0	111
Photuris B + D	24	0	28	2	0	3	0	0	0	57
Photuris W	0	0	0	0	0	0	0	14	1	15
Photuris V	10	0	0	0	9	1	8	0	1	29

proportion of the larvae collected in the Medicinal Plant Garden produced Photuris V adults.

Effect of Cold Treatments and Light Cycles on Pupation

K. Smalley (personal communication) was able to induce larvae of P. divisa LeConte and Photuris "FF" in Kansas to pupate by exposing the larvae to a 16:8 h light-dark cycle. McLean et al. (1972) reported that they were able to induce larvae of P. versicolor and P. lucicrescens in Maryland to pupate by exposing the larvae to 6 - 8 weeks of cold treatment or by exposing them to a 16:8 h light-dark cycle. The following experiments were conducted to determine the response of Florida larvae to cold treatments and light-dark cycles.

A total of 44 red larvae collected in Aug., Sept., and Nov. and 93 non-red larvae collected in Nov. and Dec. was divided into 4 treatment groups as outlined in Table 4.5. On Dec. 16 groups 1 and 2 were placed in a refrigerator and reared for 36 days at 2 - 14^{o}C and 10:14 h light-dark cycle. After the cold treatment the larvae were transferred to light boxes where they were maintained at room temperature: group 1 was exposed to 15:9 h light-dark cycle and group 2 was exposed to 10:14 h light-dark cycle. Groups 3 and 4 were placed in light boxes on Dec. 16 and maintained at room temperature: group 3 was exposed to 15:9 h light-dark cycle and group 4 was exposed to 10:14 h light-dark cycle.

None of the red larvae in this experiment pupated,although they were reared well into the summer, long after the field populations had emerged. The factors controlling pupation in these larvae remain a mystery. It seems unlikely that they would require a longer cold treatment,since the field populations in Florida are not exposed to very severe winters. Adult emergence of P. congener is remarkably

Table 4.5 Number of red and non-red *Photuris* larvae collected between Aug. and Dec. and divided into each of the 4 treatment groups.

Larvae	Date collected	Previous treatment	Number of larvae in the 4 treatment groups Group #1 36 days at 2-14°C then 15:9 h L/D	Group #2 36 days at 2-14°C then 10:14 h L/D	Group #3 room temperature 15:9 h L/D	Group #4 room temperature 10:14 h L/D	Total
red larvae	Aug. 17, 18, 21	room temp. 120 days 1/2 15:9 h L/D 1/2 10:14 h L/D	4	6	8	4	22
	Sept. 11, 25	room temp. 38 & 54 days 15:9 h L/D 42 days 10:14 h L/D	4	5	5	5	19
	Nov. 4	room temp. 42 days 10:14 h L/D	2	1	0	0	3
	Total red larvae		10	12	13	9	44
non-red larvae	Nov. 4	room temp. 42 days 10:14 h L/D	16	16	18	16	66
	Dec. 6	room temp. 10 days 10:14 h L/D	8	7	7	5	27
	Total non-red larvae		24	23	25	21	93

synchronized; they appear by the thousands in early spring and are present for only 2 - 3 weeks. Whatever the cue that controls pupation by these larvae, it probably functions to synchronize the adult emergence. K. Smalley (personal communication) was able to induce Photuris divisa (closely related to P. congener) to pupate using a 16:8 h light-dark cycle. She was unable to induce larvae of P. missouriensis McDermott to pupate even when exposed to various cold and light treatments.

Of the 93 non-red larvae reared in this experiment,76 adults emerged (Table 4.6). Most of the mortality occurred among the Nov. 4 larvae in the cold treatments. Of larvae maintained at room temperatures, 33 of 34 produced adults. Cold treatments seemed to have a detrimental effect on these larvae. The 2 light-dark cycles had no apparent effect on larvae reared at room temperature,but adult emergence was significantly retarded for larvae in group 2 exposed to cold treatment and short-day photoperiod when returned to room temperature (Table 4.6). Apparently the 2 factors acting together can delay pupation.

The intervals between the date larvae were collected and the date adults emerged were compiled for larvae collected during each month and for larvae of the various species groups. Most of the larvae collected between Jan. and Sept. pupated and adults emerged within 25 - 70 days (Table 4.7). However, larvae collected in Oct., Nov. and Dec. pupated and produced adults after longer intervals of 60-140 days (Table 4.7). The natural cool temperatures and short-day photoperiods in the fall had apparently induced fall-collected larvae to delay pupation. Light-dark cycles did not seem to change this delay in pupation, although cold treatments followed by short photoperiods seemed to delay

Table 4.6 The number of days elapsing between date of collection and emergence of adults when the Photuris larvae were exposed to 4 different rearing regiments.

	Treatment #1 cold-short day warm-long day	Treatment #2 cold-short day warm-short day	Treatment #3 warm-long day	Treatment #4 warm-short day
Larvae collected on November 4				
-days to adult emergence	128.3^{ab}	142.6^{a}	$121.8^{\textcircled{a}\,b}$	114.4^{b}
-s =	13.23	28.60	17.85	13.19
-number of adults emerging	4	11	18	16
-larvae in treatment	16	16	18	16
-adults emerging				
A	2	6	16	14
B + D	1	4	2	1
V	-	1	-	1
Larvae collected on December 6				
-days to adult emergence	81.7^{b}	111.2^{a}	82.9^{b}	81.2^{b}
-s =	16.67	8.11	7.27	18.19
-number of adults emerging	7	7	7	6
-larvae in treatment	8	7	7	7
-adults emerging				
A	6	7	7	4
B + D	-	-	-	1
V	1	-	-	-

Same superscript letters indicate no statistically significant differences (t test, p = 0.05).
Circled letter indicates no significant difference at p = 0.05 but it is significantly different at p = 10.0.

Table 4.7 Time from date of collection to emergence of adults of several Photuris spp. for larvae reared on soil and at room temperatures. (Since the light cycle did not seem to affect pupation of larvae reared at room temperature these data have been pooled; however, most larvae were reared under long day light-dark cycle.)

Species	Measurement	Month larvae were collected				
		Jan.	Feb.	Mar.	Apr.	May
Photuris A	mean	--	65	33.4	72.4	--
	s	--	--	10.38	50.69	--
	r	--	--	23-52	17-154	--
	n	--	1	12	5	--
Photuris B + D	mean	--	47	31.3	56	--
	s	--	--	15.38	--	--
	r	--	--	18-80	--	--
	n	--	1	31	2	--
Photuris V	mean	--	--	--	--	24
	s	--	--	--	--	--
	r	--	--	--	--	--
	n	--	--	--	--	--
Photuris W	mean	35	--	35	--	--
	s	0.8	--	--	--	--
	r	34-36	--	--	--	--
	n	4	--	1	--	--
Photuris congener	mean	--	42	--	--	--
	s	--	--	--	--	--
	r	--	--	--	--	--
	n	--	1	--	--	--

Table 4.7 - Extended

Month larvae were collected						
June	July	Aug.	Sept.	Oct.	Nov.	Dec
48.5	51	25.8	58	63	120.0	82.9
--	--	12.67	--	--	31.38	13.14
29-68	51	15-56	--	--	43-168	76-97
2	3	13	1	1	29	10
--	--	38	--	134.5	123.7	--
--	--	--	--	--	--	--
--	--	25-54	--	115-154	115-137	--
--	--	3	--	2	3	--
--	59	32.2	--	98.8	75	--
--	--	15.14	--	13.61	--	--
--	51-67	11-51	--	64-107	--	--
--	2	9	--	9	1	--
--	--	--	--	--	--	--
--	--	--	--	--	--	--
--	--	--	--	--	--	--
--	--	--	--	--	--	--
--	--	--	--	141	--	--
--	--	--	--	--	--	--
--	--	--	--	--	--	--
--	--	--	--	1	--	--

this development further (group 2, Table 4.6). Pupation by Pyractomena lucifera larvae collected in the fall was also delayed when they were reared in short-day photoperiods but not when reared under long-day photoperiods (Chapter 2). The cold treatment (group 1) did not significantly delay adult emergence when adults were subsequently reared at room temperature in long day photoperiods (group 2). McLean et al. (1972) found that emergence of adults from their larvae was delayed by cold treatments, but their larvae responded readily to photoperiod treatments.

Both adults of Photuris congener emerged in March even though one larva was collected in Oct. and the other in Feb.

Soil Excavations: Molting and Pupation

Several authors have reported that Photuris larvae molt and pupate in earthen cells or "igloos" (Williams 1917, Hess 1920, McLean et al. 1972). Hess (1920) described and illustrated how the larva ingested soil and regurgitated it around and above itself until a dome was formed over the larva. The larva continued this process until the ceiling was 3 - 12 mm thick.

I observed several variations in construction of igloos. Cells in which larvae molted had ceilings that were 1.5 - 3 mm thick (Fig. 4.1 A,B). Cells in which larvae pupated had thicker ceilings, usually 10 - 15 mm (Fig. 4.1 C, D, E, F, G). Larvae often built shallow cells in which they remained inactive for extended periods. They later resumed digging and formed a deep cell in which they pupated. Larvae of Photuris A and B+D usually formed igloos with a rounded dome not much wider than the pupal chamber (Fig. 4.1 C,D). These igloos measured 10-19 mm across and were raised 2 - 6 mm above the surroundings. Larvae of Photuris V

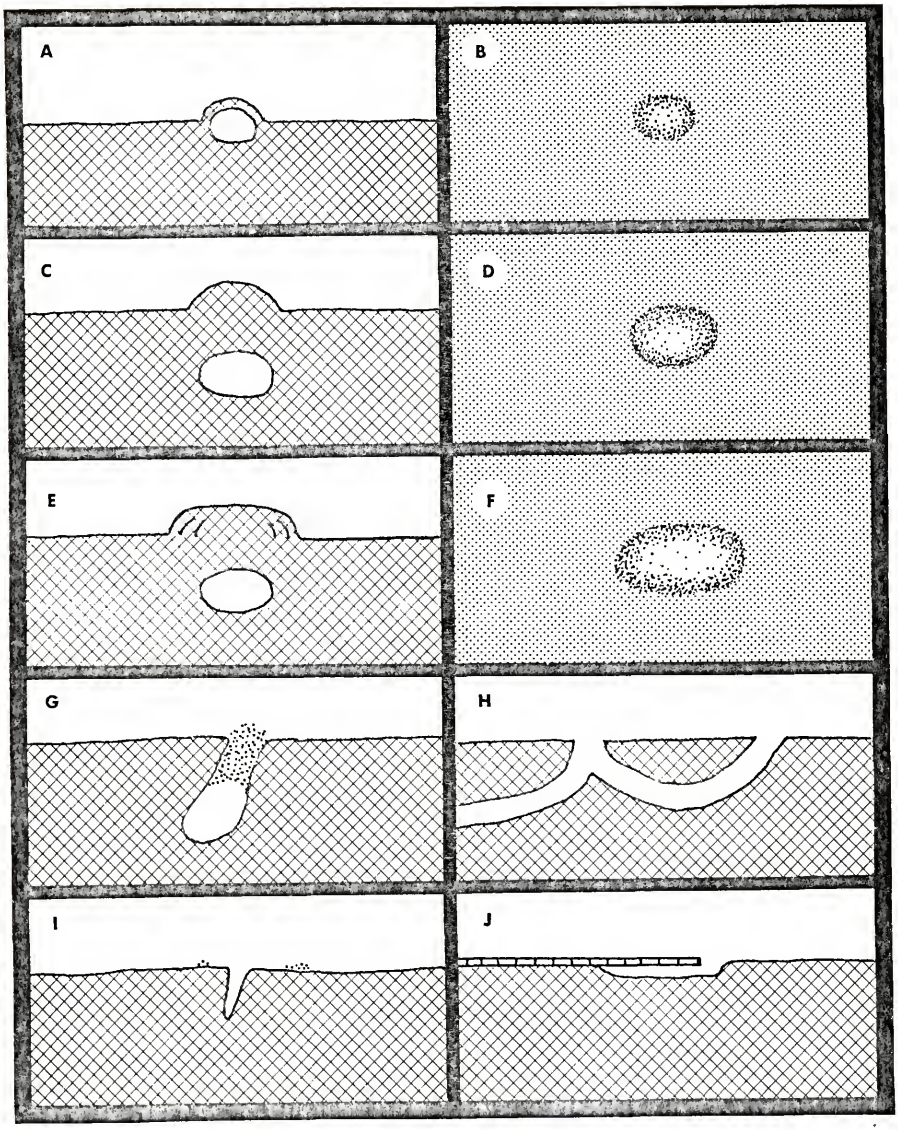

Fig. 4.1 Soil excavations by Photuris larvae: a molting igloo, A. cut away view, B. surface appearance; a pupal igloo formed by a Photuris "A" larva, C. cut away view, D. surface appearance; a pupal igloo formed by a Photuris "V" larva, E. cut away view, F. surface appearance; a pupal cell formed by a red Photuris larva, G.; burrows dug by a red Photuris larva, H.; a wedge hole, I., and a burrow under paper, J. in which larvae spend the day.

Fig. 4.7 Time exposure of a Photuris pupa in its "igloo". The whole body (except the eyes) was luminescent and the light organs on the abdomen illuminated the inside walls of the cell. Additional lighting was used to illuminate the soil.

usually formed igloos that were wider than the pupal chamber and were often flattened on top (Fig. 4.1 E,F). These igloos measured 14 - 22 mm across and were also raised 2 - 6 mm above the surroundings. Larvae of Photuris "W" formed small igloos similar to Fig. 4.1C and D, but the ceiling was only 3 - 5 mm thick. Red Photuris larvae built both shallow and deep igloos as already described (Fig. 41. A - D), but one larva formed a pupal chamber by burrowing into the soil and plugging up the opening with a mass of sand, without forming a true igloo (Fig. 4.1G). Larvae sometimes emerged from thin-topped igloos to feed but not from deep ones.

Photuris larvae also made other excavations in the soil. When non-red larvae were placed in dishes with sand and filter paper, some squeezed and burrowed under the paper to form a small chamber in which they stayed during the day (Fig. 4.1 J). Other non-red larvae would dig a small wedge-shaped hole in which they remained during the day (Fig. 4.1 I). Red larvae sometimes dug a networm of burrows in which they remained during the day (Fig. 4.1 H).

Larvae took 1 - 3 days to build an igloo. When molting, larvae remained in the chamber for ca. 5 days before shedding the exuviae; the larvae emerged a day or so later. When pupating, larvae remained upright in their chambers for variable periods of time, 2 - 4 weeks. During this period they closed the chamber if it was opened or built a new igloo if the old one was destroyed. When pupation approached the larva turned over on its back and remained in this position 3 - 5 days. At pupation the cuticle split around the lateral margin of the pronotum and the pupa wiggled free of the exuviae. The pupa was milky white and glowed brightly when disturbed (Fig. 4.7). The pupal stage lasted 7 or 8 days at room temperatures during which time the eyes and wings became black. After the adult eclosed from the pupal exuviae it remained in the earthen

chamber 2 - 4 days. During this period the adult light organs gradually became functional and larval light organs gradually stopped functioning. Both organs were functional for a day or two.

Life Cycle

The life cycle of Photuris larvae in the field is puzzling. Lloyd (1969a) reported that he and D. Minnick obtained adult Photuris V in Sept. from eggs oviposited in April. He suggested that if larvae developed continuously there could be 2 generations each year as observed in Pyractomena lucifera (Chapter 2). In the field, however, the Photuris larvae can be found only in certain restricted seasons. At Newnans Lake (roadside) where Photuris V larvae seemed to predominate, larvae were observed only in Aug. and Sept. and again in Jan. and Feb.; they could not be found at other times of the year even when conditions were ideal. Similar seasonal occurrence was observed at other sites. The red larvae could be found in large numbers only in Aug. and Sept. If the larvae are active only in these restricted periods and inactive at other times it could take several years to complete development. On the other hand, very few small larvae were observed, so it is possible small larvae are active deep in the leaf litter during other seasons. It is also possible that larvae are only luminescent during certain seasons. In any case, careful field-rearing experiments and more extensive field observations will be required to determine the life cycle of Photuris fireflies in Florida.

Predatory Behavior

Information on the natural food of Photuris larvae is rather limited. Williams (1917) found 3 Photuris larvae feeding on a limp earthworm (which they had apparently killed). Hess (1920) found Photuris larvae feeding on snails on 2 occasions. McLean et al. (1972) reported they had "almost

never seen them (Photuris larvae) feeding in the field." The list of items that Photuris larvae will eat in captivity is extensive (Williams 1917, Hess 1920, McDermott 1958, Keiper and Solomen 1972, and McLean et al. 1972). They will kill and eat snails, slugs, earthworms, potatoe-beetle larvae, cutworm larvae and young squash-bug nymphs. They will also eat non-living food items such as cut-up insects, Tubiflex worms, raw or cooked beef, pork or chicken liver, creamed cheese, boiled egg yolk, grapes, some vegetables and gelatin. I fed Photuris larvae various cut-up insects, cut-up earthworms and chicken liver.

I accumulated 21 prey records for Photuris larvae, 17 for red larvae and 4 for non-red larvae. These records can be summarized as follows: of the 17 records for red larvae, 5 were snails (Philonycus carolinianus (Rafinesque)) and slugs (Zonitoides arboreus (Say)), 11 were insects of varous kinds and 1 was a berry; of the 4 records for non-red larvae, 1 was an earthworm (Oligochaeta) and 3 were berries. The larvae were observed feeding on elderberries (Sambucus sp.) and wild grapes (Vitis sp.) after they had fallen to the ground. Of the insects recorded as prey items 4 caterpillars (Datana integerrima (Grote & Robinson): Notodontidae), 1 membracid (Platycotis vittata (F): Membracidae) and 1 cerabycid beetle (Oncideres cingulata (Say):Cerabycidae) were discolored from decay indicating the Photuris larvae were probably scavenging. However, Photuris larvae were also found attacking live insects on 5 other occasions. 3 lovebug larvae (Plecia sp. Bibionidae), a mycetophilid larva (Mycetophilidae) and a 4 cm caterpillar (Noctuidae: Herminiiae).

Photuris larvae apparently prey on a variety of small soft-bodied organisms. However, they are also scavengers, feeding on a variety of non-living food items, particularly dead insects and ripe berries. It is interesting that most of my prey records involved red Photuris larvae

and that most of their prey items were insects. Non-red larvae were collected much more frequently than red larvae but were not observed feeding as often nor were they found feeding on insects.

Photuris larvae attack their prey in 2 ways: larvae moved slowly with head extended as they approached and began biting and feeding when they made contact; on other occasions they approached slowly and then quickly climbed onto the prey and began biting into it while holding it with thoracic legs and caudal grasping organ. The second method of attack was probably specialized for subduing insect prey. I observed several larvae trying to bite a live active caterpillar but the mandibles did not penetrate the cuticle. Finally, a larva climbed onto the caterpillar and was able to bite into it while wrapping itself around the caterpillar. The caterpillar was subdued after a few minutes. In the field I observed 2 larvae holding insect prey with their legs: a live and thrashing lovebug larva and a live and thrashing caterpillar. Another larva reached deep into the leaf litter and captured a lovebug larva using only its mouthparts. Schwalb (1960) also observed 2 methods of attack: when Lampyris noctiluca attacked snails it climbed onto the shell and attacked the snail when it emerged. This larva attacked slugs from beside the prey. Lamprohiza splendidula did not mount the snail shell but attacked both snails and slugs from beside the prey (Schwalb 1960).

Photuris larvae appeared to be very sensitive to the oder of injured caterpillars and other food items. In the laboratory, larvae were frequently observed walking directly to food items placed in their containers. They held their head high and waved it from side to side as they approached the food. When a healthy caterpillar was added to a group of larvae they paid little attention to it but when it was injured

by one of the larvae or with a forceps many larvae soon converged on the kill. When I placed injured caterpillars near active larvae in the field they were usually attracted (4 of 6 larvae) and 2 larvae whose presence was previously unknown to me were also attracted. To see if injured caterpillars were more attractive than non-injured ones, a group of 10 freeze-killed and 10 injured (with a forceps) caterpillars were placed in the leaf litter in a red Photuris habitat. Two Photuris larvae were attracted to the wounded caterpillars, and none were attracted to the freeze-killed ones.

After a Photuris larva had located and captured a prey item it continued chewing (and feeding?) for several minutes. When the prey was subdued the larva left it for 1 - 2 min and crawled several cm away. It then returned to the prey and dragged it to the location it had just visited and continued to feed (n=5).

The predatory behavior of Photuris larvae differed only slightly from that of Pyractomena lucifera (Chapter 1). Photuris larvae left their prey unguarded while they searched for a feeding site, whereas, P. lucifera were not observed to leave their prey. One Photuris larva was observed to lose its prey to an ant when it retreated from its prey. Schwalb (1960) reported that Lampyris noctiluca also left its prey while it searched for a feeding site but Lamprohiza splendidula seldom left its prey. He also noted that L. noctiluca followed slime trails, attacked the anterior end of snails and slugs in preference to the posterior, and retreated after each bite until the snail was paralyzed. These behavior patterns were not observed in Photuris larvae. Photuris larvae did not respond to snail slime trails when presented in petri dishes. They did not retreat or release their prey during attack, only after the prey was no longer active.

Natural Enemies

Only a few natural enemies were observed. One fly parasite (Tachinid?) emerged from a medium-sized Photuris larvae but escaped before it could be examined. Seven large nematodes (mermithid?) emerged from a large Photuris larva collected by T. J. Walker in West Virginia. There was considerable mortality among larvae and pupae in the earthen cells but the causes were unknown.

Identification of Larvae

If Photuris larvae could be determined to species without rearing them to the adult stage it would be much easier to study the field ecology and behavior of the different species. During these studies I was able to separate red from non-red larvae. The red larvae appeared to be larvae of Photuris congener. The dorsal pigmentation of the red larvae was reddish-brown or rufus with some black pigmentation (Fig. 4.2). The non-red larvae produced all the other Photuris species. The dorsal pigmentation of these larvae was usually black with some gray or tan areas. The larvae collected in rotten logs producing Photuris W adults had large unpigmented areas on their tergites (Fig. 4.3). These larvae could be separated from the other non-red larvae both by pigmentation pattern and site of collection. The remainder of the non-red larvae could not be separated reliably. It was noted that most of the largest and most robust larvae produced Photuris V and many of the larvae that had almost completely black tergites and dark sternites produced Photuris B+D but observations on these forms were too limited to be conclusive. Larvae from each of these groups are illustrated in Figs. 4.3 - 4.6.

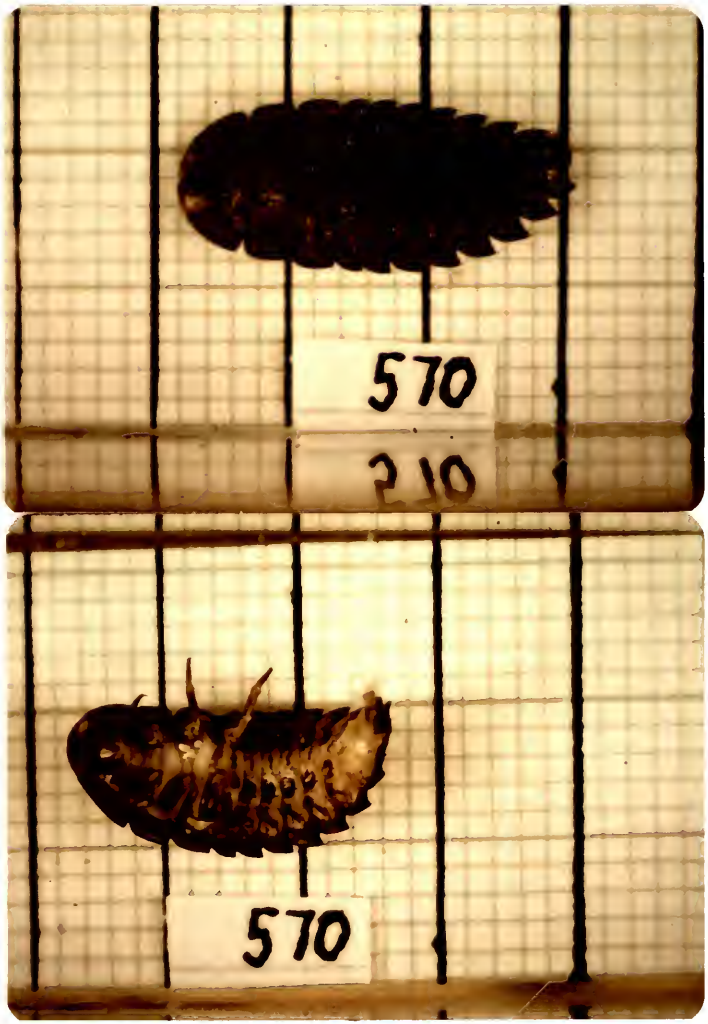

Fig. 4.2 Red Photuris larva, dorsal view (above) and ventral view (below).

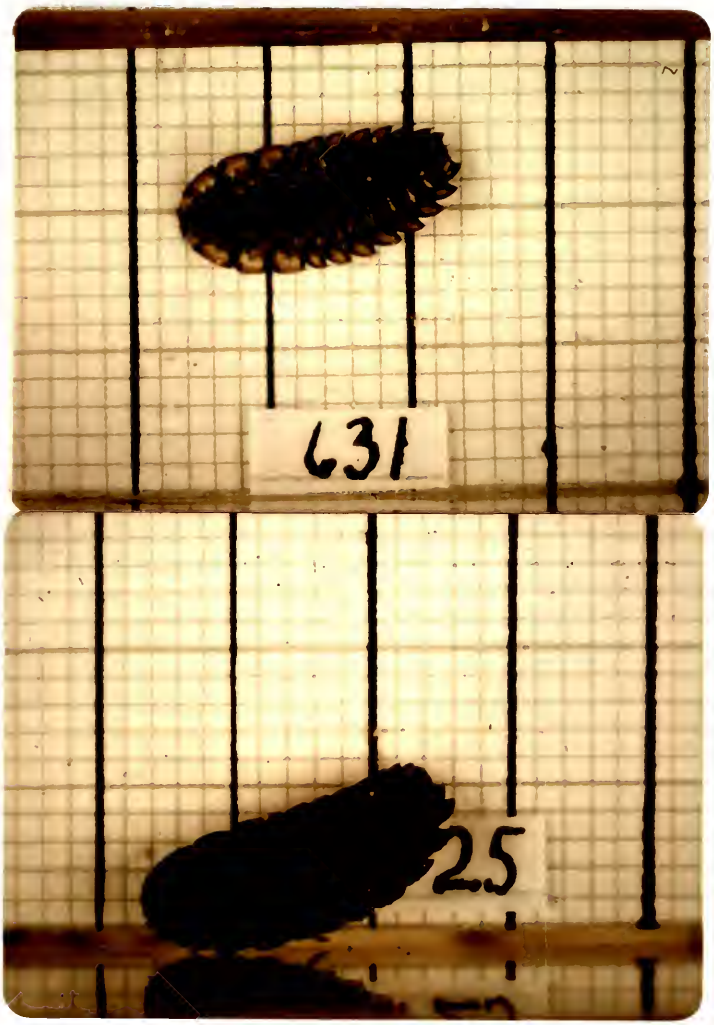

Fig. 4.3 Non-red Photuris larvae: above, larva of Photuris W collected in a rotten log; below, larva with unusually dark and uniform dorsal pigmentation collected at the Medicinal Plant Garden; this larva died.

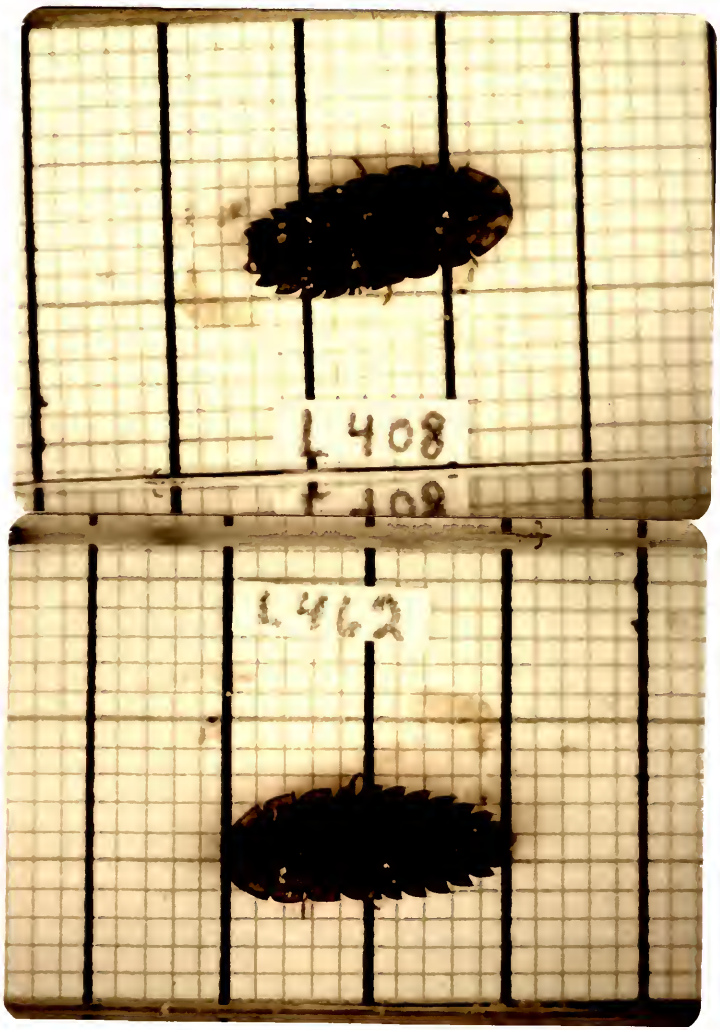

Fig. 4.4 Non-red Photuris larvae: above, larva of Photuris A: below, another "typical" non-red larva that generally produced Photuris A or B+D; this larva died.

Fig. 4.5 Non-red Photuris larvae: thse 2 larvae produced Photuris B+D fireflies.

Fig. 4.6 Non-red Photuris larvae: these 2 larvae produced Photuris V fireflies.

Since larvae of some species seem to predominate at certain collection sites and at certain seasons it is probably safest to study larvae at different locations and seasons (Tables 4.3 and 4.4)for comparative purposes until the morphological characteristics are better understood. It will probably require rearing larvae from adults of known identity to find morphological characters that could be used to identify larvae of additional Photuris species.

LITERATURE CITED

Annandale, N. 1900. Observations on the habitats and natural surroundings of insects made on the "Skeat Expedition" to the Malay Peninsula 1899-1900. Insect luminosity (An Aquatic lampyrid larvae). Proc. Zool. Soc. London. 862-865.

Balduf, W. V. 1935. The bionomics of entomophagous coleoptera. John S. Swift Co., Inc. 87-103.

Barber, H. S. 1951. North American fireflies of the genus Photuris. Smithsonian Misc. Coll. 117:58 pp.

Blair, K. G. 1927. An aquatic lampyrid larva from S. Celebes. Trans. Entomol. Soc. London--Part I. 43- 45.

Bess, H. A. 1956. Ecological notes on Lamprophorus tenebrosus (Walker) (Coleoptera: Lampyridae), an enemy of the giant African snail. Proc. Hawaiian Entomol. Soc. 16:24-29.

Buck, J. B. 1948. The anatomy and physiology of the light organ in fireflies. In E. N. Harvey. Bioluminescence. Ann. N. Y. Acad. Sci. 49:327-482.

Buck, J. B. and E. M. Buck. 1966. Biology of synchronous flashing of fireflies. Nature. 211:562-64.

Buck, J. B. and E. M. Buck. 1976. Synchronous fireflies. Sci. Amer. 234:74-85.

Buschman, L. L. 1972. Flash communication in the firefly Photuris divisa. (Coleoptera: Lampyridae). Entomol. News. 83:159-164.

Buschman, L. L. 1974. Flash behavior of a Nova Scotian firefly, Photuris fairchildi Barber, during courtship and aggressive mimicry. (Coleoptera: Lampyridae). Coleop. Bull. 28:27-31.

Buschman, L. L. Life-span of two sibling Photinus fireflies. (in press)

Case, F. F. H. Hanson, I. Polunin and A. T. Barnes. 1972. Mechanisms and adaptive significance of aggregation and synchronous flashing fireflies. Amer. Zool. 12:683.

Cason, J. H. 1970. Lake Alice--A study of potential pollution of the Floridan Aquifer.Compass of Sigma Gamma Epsilon. 47:206-210.

Center, T. C. 1976. The potential of Arzama densa (Lepidoptera: Noctuidae) for the control of waterhyacinth with special reference to the ecology of waterhyacinth (Eichhornia crassipes (Mart.) Solms). Ph. D. dissertation. Univ. of Florida. Gainesville, Fla.

Chippendale, G. M. 1977. Hormonal regulation of larval diapause. Ann. Rev. Entomol. 22:121-38.

Corbet, P.S. 1957. The life-history of the emperor dragonfly, Anax imperator Leach. (Odonata: Aeschnidae). J. Animal Ecol. 26:1-69.

Farnworth, E. G. 1973. Flashing behavior, ecology and systematics of Jamaican lampyrid fireflies. Ph. D. dissertation. Univ. of Florida. Gainesville, Fla. 278 p.

Green, J. W. 1956. Revision of the Nearctic species of Photinus (Lampyridae: Coleoptera). Proc. Calif. Acad. Sci. 28:561-613.

Green, J. W. 1957. Revision of the Nearctic species of Pyractomena (Coleoptera: Lampyridae). Wasmann J.Biol. 15:237-284.

Harvey, E. N. 1952. Bioluminescence. Academic Press. N. Y. 649 p.

Harvey, E. N. 1957. A history of luminescence. Amer. Phil. Soc. Philadelphia. 44:669p.

Hess, W. N. 1920. Notes on the biology of some common Lampyridae. Biol. Bull. 38:39-76.

Kaufmann, R. 1965. Ecological and biological studies on the west African firefly, Luciola discollis (Coleoptera: Lampyridae). Ann. Ent. Soc. Amer. 58:414-426.

Kiichiro, M. 1961. A study of fireflies. Published by the author, in Japanese. (U. S. Army translation no. 1-9415 (1966). I. D. no. 2204017766, 0371).

Keiper, R. R. and L. M. Solomen. 1972. Ecology and yearly cycle of the firefly Photuris pennsylvanica (Coleoptera: Lampyridae). N. Y. Entomol. Soc. 80:43-47.

Lees, A. D. 1956. The physiology and biochemistry of diapause. Ann. Rev. Entomol. 1:1-16.

Lloyd, J. E. 1964. Notes on flash communication in the firefly Pyractomena dispersa. Ann. Entomol. Soc. Amer. 57:260-61.

Lloyd, J. E. 1965a. Aggressive mimicry in Photuris: firefly femmes fatales. Science. 149:653-654.

Lloyd, J. E. 1965b. Observations on the biology of three luminescent beetles (Coleoptera: Lampyridae, Elateridae). Ann. Entomol. Soc. Amer. 58:588-591.

Lloyd, J. E. 1966a. Studies on the flash communication system in Photinus fireflies. Misc. Pub. Mus. Zool. Univ. Mich. No. 130:1-95.

Lloyd, J. E. 1966b. Signals and mating behavior in several fireflies (Coleoptera: Lampyridae). Coleopt. Bull. 20:84-90.

Lloyd, J. E. 1968. Illumination, another function of firefly flashes? Entomol. News. 79:265-268.

Lloyd, J. E. 1969a. Flashes of Photuris fireflies: their value and use in recognizing species. Fla. Entomol. 52:29-35.

Lloyd, J. E. 1969b. Flashes, behavior and additional species of nearctic Photinus fireflies (Coleoptera: Lampyridae). Coleopt. Bull. 23:29-40.

Lloyd, J. E. 1969c. Flashes and behavior of some American fireflies. N. Y. S. Conservationist. 23:8-12.

Lloyd, J. E. 1971. Bioluminescent communication in insects. Ann. Rev. Entomol. 16:97-122.

Lloyd, J. E. 1972a. Chemical communication in fireflies. Environ. Entomol. 1:265-266.

Lloyd, J. E. 1972b. Mating behavior of a New Guinea Luciola firefly: a new communicative protocol (Coleoptera: Lampyridae). Coleopt. Bull. 26:155-163.

Lloyd, J. E. 1973a. Fireflies--commonplace beetles and larvae by day, but tiny flashing lanterns on summer evenings. Animals. May: 220-225.

Lloyd, J. E. 1973b. A firefly inhabitant of coastal reefs in New Guinea (Coleoptera: Lampyridae). Biotropica. 5:168-174.

Lloyd, J. E. 1973c. Model for the mating protocol of synchronously flashing fireflies. Nature. 245:269-270.

Lloyd, J. E. 1973d. Fireflies of Melanesia: bioluminescence, mating behavior, and synchronous flashing (Coleoptera: Lampyridae). Environ. Entomol. 2:991-1008.

Lloyd, J. E. 1973e. Firefly parasites and predators. Coleopt. Bull. 27:91-106.

Lloyd, J. E. 1975. Aggressive mimicry in Photuris fireflies: signal repertoirs by fammes fatales. Science. 187:452-453.

Lloyd, J. E. Bioluminescence and communication. In Thomas A. Sebeok, ed. How animals communicate. Indiand Univ. Press. Bloomington, Indiana. (in press-a)

Lloyd, J. E. On sexual selection in luminescent beetles. In D. Otte, ed. Sexual selection in insects. Academic Press. (in press-b)

McDermott, F. A. 1911. Some further observations on the light-emission of American lampyridae: the photogenic function as a mating adaptation in the Photonini. Can. Entomol. 43:399-406.

McDermott, F. A. 1953. Glow-worms in a marine littoral habitat in Jamaica (Coleoptera: Lampyridae). Coleopt. Bull. 9:49-52.

McDermott, F. A. 1958. The fireflies of Delaware. 2nd ed. Soc. of Nat. Hist. of Delaware. Wilmington. 36 p.

McDermott, F. A. 1967. The North American fireflies of the genus Photuris DeJean. A modification of Barber's key (Coleoptera: Lampyridae). Coleopt. Bull. 21:106-115.

McElroy, W. D. and Marlene DeLuca. 1973. Chemical and enzymatic mechanisms of firefly luminescenc e. In M. J. Cormier, D. M. Hercules, and J. Lee eds. Chemiluminescence and bioluminescence. Plenum Press. N. Y. 285-308.

McElroy, W. D. and H. H. Seliger. 1966. Firefly Bioluminescence. In F. H. Johnson and Yata Haneda, eds. Bioluminescence in Progress. Princeton Univ. Press. Princeton, New Jersey. 427-458.

McLean, M., J. Buck and F. E. Hanson. 1972. Culture and larval behavior of Photurid fireflies. Amer. Midland Natur. 87:133-145.

Newport, G. 1857. On the natural history of the glowworm Lampyris noctiluca. J. Proc. Linn. Soc. Zool. London. 1:40-71.

Naisse. J. 1966. Controle endocrinien de la differenciation sexuelle chez l'Insecte Lampryis noctiluca (Coleoptera Malacoderme Lampyridae) I. - Role androgene des testicules. Arch. de Biol. (Liege). 77:139-201.

Okada, Y. K. 1928. Two Japanese aquatic glowworms. Trans. Entomol. Soc. London--Part I. 101-107.

Paiva, C. A. 1919. Notes on the Indian glowworm Lamprophorus tenebrosus (Walker). Rec. Ind. Mus. Calcutta. 16:19-28.

Peterson, C. D. 1957. Lamprophorus tenebrosus introduced into Guam to combat giant African snail. J. Econ. Entomol. 50:114.

Schwalb, H. H. 1960. Beiträge zur Biologie der einheimischen Lampyriden Lampryis noctiluca Geoffr. und Phausis splendidula Lec. und experimentelle Analyse ihres Beutefang--und Sexualverhaltens. Zool. Jahrb. Syst. 88:399-550.

Southwood, T. R. E. 1966. Ecological methods. Methuen & Co., Ltd., London. 391 p.

Thornhill, R. 1976. Reproductive behavior of the lovebug, Plecia nearctica (Diptera: Bibionidae). Ann. Entomol. Soc. Amer. 69:843-847.

Vogel, R. 1915. Beitrage zur kenntniss des baues und der lebensweiss der larve von Lampyris noctiluca.

Wenzel. H. W. 1896. Notes on Lampyridae, with the description of a female and larva. Entomol. News. 294-297.

Wigglesworth, V. B. 1966. Insect physiology. Methuen & Co., Ltd. London. 134 p.

Williams, F. X. 1917. Notes on the life-history of some North American lampyridae. J. N. Y. Entomol. Soc. 25:11-33.

Wootten, A. 1976. Rearing the glow-worm Lampyris noctiluca L. (Coleoptera: Lampyridae). Entomol. Record. 88:64-76.

Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behavior. Hafner Publ. Co. N. Y. 653 p.

BIOGRAPHICAL SKETCH

Lawrent Lee Buschman was born 29 May 1941 in Dudley, Kansas. His parents, Frank and Clara Buschman, were teachers and missionaries in the Belgian Congo (now Zaire) 1946-58. Since that time they have taught in Hutchinson, Kansas. He married Rose Adeline Friesen in 1965. They have one son, David Allen, born in 1969.

He graduated from Hillsboro High School, Hillsboro, Kansas in 1960. He attended Tabor College, Hillsboro, Kansas and received the A.B. degree in 1964. He received a National Science Foundation Academic Year Institute Fellowship for high school biology teachers to attend Kansas State Teachers College, Emporia, and received the M.S. degree in 1968.

His teaching experience includes teaching high school science at Minneapolis High School, Minneapolis, Kansas; teaching junior high school science at Center Consolidated School, Lunenburg Co., Nova Scotia, Canada; and teaching entomology (lab and lecture) at the University of Florida, Gainesville, Fla.

His research experience includes working as a technologist on the Florida lovebug project and as Interim Associate Entomologist working on soybean pests and their predators and parasites.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Dr. J. E. Lloyd, Chairman
Professor of Entomology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Dr. P. S. Callahan
Professor of Entomology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Dr. S. H. Kerr
Professor of Entomology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Dr. J. Reiskind
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Dr. T. J. Walker
Professor of Entomology

This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

March, 1977

Jack L. Fry
Dean, College of Agriculture

Dean, Graduate School